Various Drivers of Female-Limited Diversity

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Summary

Many ecologists and evolutionary biologists are motivated by a fascination for the immense diversity of the natural world. Here, I focus on one aspect of that diversity: individuals of the same species often differ from one another in important ways. In species with separate sexes, it is common for males and females to have very different phenotypes, but there are also cases in which distinct phenotypes exist among individuals of the same sex. Here, I discuss various systems in which males all look alike, while females come in two or more distinct morphs.

In the general introduction (chapter 1), I first introduce some important concepts and highlight common pitfalls in research on distinct morphs. In particular, I highlight the importance of negative frequency dependent selection for understanding genetic polymorphism, and explain why trade-offs alone are insufficient explanations for polymorphism maintenance. I then introduce three examples of female-limited color polymorphism that occur in some butterflies, some damselflies, and some hummingbirds, respectively. In each case, I discuss the drivers behind negative frequency dependent selection, and highlight important similarities and differences between the systems.

Chapter 2, titled "Fast or Fancy: Modeling a trade-off between female attractiveness and development time", aims to discover the mechanism by which the Alba polymorphism in *Colias* butterflies is maintained. In these butterflies, females come in two distinct color morphs, the white Alba morph and a colorful morph (orange or yellow), while males are all colorful. Female morph is determined genetically, and is characterized by several trade-offs. We propose a possible evolutionary driver that takes into account that Alba females have faster development but are less attractive to males compared to colorful females. Because males emerge earlier than females do, the faster development of Alba females allows them to emerge at a time when many males are still unmated and courtship is intense. The more attractive colorful females emerge later when a larger proportion of males have already mated and intense courtship is less prevalent.

Chapter 3, titled "Ecological Sexual Dimorphism and Population Consequences when One Sex Uses a Superior Resource", is concerned with the evolution of ecological sexual dimorphism. While differences between sexes usually result from sexual selection or other intrinsic differences between the sexes, it is also possible for sexual dimorphism to be driven by competition for some resource or niche. Males and females sometimes specialize on different resources, resulting in reduced competition. We identify a constraint that limits the effectiveness of ecological sexual dimorphism: if one resource is more abundant than the other (which is very often the case), then resource use would

be most efficient if more than half the population specialized on the more abundant resource. However, sex ratios are strongly constrained by the rarer-sex effect, and therefore each sex tends to make up half of the population. If morph is determined by a single locus, a sex-limited polymorphism can solve this problem, with one sex specializing on the more abundant resource, while the other sex is polymorphic for niche use. However, the efficiency of polymorphism is reduced when resource use is affected by multiple loci. In that case, we show that sexual dimorphism can evolve even if it results in suboptimal resource use.

Chapter 4, titled "Sex ratio theory for facultative parthenogens: from fortuitously optimal stick insects to the origin of haplodiploidy in Hymenoptera", shifts the topic away from female-limited diversity and instead investigates how asexual reproduction (parthenogenesis) affects whether it is better to produce male or female offspring. We first show that, if females can reproduce both sexually and parthenogenetically, this favors the evolution of female-biased sex ratios. We then investigate how the evolution of parthenogenesis is affected by constraints on the sex of parthenogenetically produced offspring. In many animals, details of the sex determination system (e.g. sex chromosomes) constrain the sex of parthenogenetically produced offspring, such that parthenogenesis produces either only daughters or only sons. We show that under stable rates of parthenogenesis, the female-producing parthenogenesis of stick insects and mayflies can achieve optimal sex allocation as if it were not affected by a constraint. Furthermore, we investigate scenarios in which parthenogenetically produced offspring are all male. This includes birds and also haplodiploids (a system where parthenogenesis produces only sons, and sexual reproduction produces only daughters). Finally, we highlight an old paper by J. J. Bull from 1981 on the origins of haplodiploidy in Hymenoptera (bees, wasps, and ants).

The general discussion (chapter 5) contains three short essays that are loosely connected to chapters 2-4. First, I focus on the Alba polymorphism and review hypotheses that have been suggested (and often rejected) concerning the maintenance of this polymorphism. Second, I discuss what our model on ecological sexual dimorphism can teach us about the female-limited color polymorphisms introduced in the general introduction. Third, I discuss why in some eusocial animals, such as Hymenoptera, workers are always female. In the general discussion, I also write about the role of theory in biology. I end on some thoughts on how theory can help bridge gaps between fields and discover general principles in evolution, while also highlighting the value of more taxon-specific research.

Zusammenfassung

Bewunderung für die enorme Vielfalt der Natur und die Faszination damit diese verstehen zu wollen, sind wohl einige der wichtigsten Beweggründe in der ökologischen und evolutionsbiologischen Forschung. Hier konzentriere ich mich auf einen Aspekt dieser Vielfalt: Männchen und Weibchen einer Art unterscheiden sich oft stark voneinander, aber es gibt auch viele Beispiele in denen Individuen desselben Geschlechts unterschiedliche Phänotypen aufweisen. Hier bespreche ich verschiedene Tierarten bei denen Männchen einander ähneln, während Weibchen in zwei oder mehr unterschiedlichen Morphen vorkommen.

In der allgemeinen Einführung (Kapitel 1) erläutere ich zunächst einige wichtige Konzepte und bespreche häufige Denkfehler bei der Erforschung von Polymorphismen. Insbesondere hebe ich die Bedeutung negativ frequenzabhängiger Selektion für das Verständnis genetischer Polymorphismen hervor und erkläre, warum das Aufzeigen von Vor- und Nachteilen beider Morphe unzureichend ist, um zu erklären, warum diese koexistieren. Anschließend gebe ich drei Beispiele auf Weibchen beschränkter Farbpolymorphismen, die bei einigen Schmetterlingen, Libellen und Kolibris vorkommen. In jedem Fall bespreche ich, wie es zu negativ frequenzabhängiger Selektion kommt, und gehe auf wichtige Gemeinsamkeiten und Unterschiede ein.

Kapitel 2 hat den Titel "Fast or Fancy: Modeling a trade-off between female attractiveness and development time" ("Schnell oder Schick: mathematische Modellierung eines Trade-Offs zwischen weiblicher Attraktivität und Entwicklungsdauer"). Das Kapitel modelliert den Alba-Polymorphismus bei *Colias*-Schmetterlingen mit dem Ziel herauszufinden wie es zu negativ frequenzabhängiger Selektion kommt. Bei diesen Schmetterlingen sind alle Männchen bunt (orange oder gelb), während Weibchen in zwei unterschiedlichen Farbmorphen vorkommen, der weißen Alba-Morphe und einer bunten Morphe. Ob Weibchen weiß oder bunt sind, ist genetisch bestimmt und der Polymorphismus ist durch mehrere Trade-Offs gekennzeichnet. Wir stellen eine Hypothese auf, die berücksichtigt, dass Alba-Weibchen schneller erwachsen werden, aber für Männchen weniger attraktiv sind als bunte Weibchen. Da Männchen früher schlüpfen als Weibchen, können Alba-Weibchen zu einem Zeitpunkt schlüpfen, zu dem viele Männchen sich noch nicht gepaart haben und die Balz besonders intensiv ist. Die attraktiveren, bunten Weibchen schlüpfen später, wenn ein größerer Anteil der Männchen sich bereits gepaart hat.

Kapitel 3 hat den Titel "Ecological Sexual Dimorphism and Population Consequences when One Sex Uses a Superior Resource" ("ökologischer Sexualdimorphismus und wie sich die Populationsgröße verändert wenn sich ein Geschlecht auf eine ertragreicherer Nahrung spezialisiert"). Das Kapitel beschäftigt sich mit der Evolution ökologischer Ge-

schlechtsdimorphismen. Unterschiede zwischen den Geschlechtern sind normalerweise auf sexuelle Selektion oder andere inhärente Unterschiede zwischen den Geschlechtern zurückzuführen, aber es gibt auch Fälle bei denen Konkurrenz um eine Ressource oder Nische eine wichtige Rolle spielen. Manchmal spezialisieren Männchen und Weibchen sich auf unterschiedliche Ressourcen, was zu verringerter Konkurrenz führt. Wir identifizieren einen Grund warum ökologischen Geschlechtsdimorphismus nicht immer optimal ist: Wenn eine Ressource häufiger vorkommt als die andere (was sehr oft der Fall ist), müssten sich für eine optimale Ressourcennutzung mehr als die Hälfte der Population auf die häufiger vorkommende Ressource spezialisieren. Es gibt aber einen starken Selektionsdruck, der dafür sorgt, dass etwa gleich viele Männchen wie Weibchen in einer Population vorkommen. Wenn die Nischennutzung durch einen einzigen Lokus bestimmt wird, kann ein geschlechtsbeschränkter Polymorphismus dieses Problem lösen. Hierbei spezialisiert sich ein Geschlecht auf die ertragreichere Ressource, während das andere Geschlecht für Nischennutzung polymorph ist. Die Effizienz eines Polymorphismus wird jedoch reduziert, wenn Ressourcennutzung durch mehrere Loki beeinflusst wird. In diesem Fall kann sich ein Geschlechtsdimorphismus entwickeln, selbst wenn dies zu einer suboptimalen Ressourcennutzung führt.

Kapitel 4 hat den Titel "Sex ratio theory for facultative parthenogens: from fortuitously optimal stick insects to the origin of haplodiploidy in Hymenoptera" ("Geschlechterverteilung bei fakultativer Parthenogenese: warum Stabschrecken zufällig perfekt sind, und wie Hymenoptera haplodiploid geworden sind"). Dieses Kapitel weicht von dem Thema weiblicher Vielfalt ab und untersucht stattdessen, wie sich ungeschlechtliche Fortpflanzung (Parthenogenese) darauf auswirkt, ob es besser ist, männliche oder weibliche Nachkommen zu erzeugen. Wir zeigen zunächst, dass fakultative Parthenogenese begünstigt, dass mehr Töchter als Söhne produziert werden. Des weiteren, untersuchen wir, welche Auswirkungen es auf Evolution von Parthenogenese hat, wenn diese entweder nur Töchter oder nur Söhne produzieren kann. Dies ist bei vielen Tieren der Fall, und hängt mit Details des Geschlechtsbestimmungssystems zusammen (z.B. Gonosomen). Für den Fall wenn Parthenogenese in jeder Generation gleich häufig ist, zeigen wir dass die Töchter-produzierende Parthenogenese von Stabschrecken und Eintagsfliegen eine optimale Geschlechterverteilung erreicht. Darüber hinaus untersuchen wir Szenarien, in denen Perthenogenese nur Söhne produziert. Dies umfasst Vögel und auch haplodiploide Arthropoden (ein System, in dem Parthenogenese nur Söhne und sexuelle Fortpflanzung nur Töchter hervorbringt). Abschließend verweisen wir auf eine alte Arbeit von J. J. Bull aus dem Jahr 1981 über die Ursprünge der Haplodiploidie bei Hymenoptera (Bienen, Wespen und Ameisen).

Die allgemeine Diskussion (Kapitel 5) enthält drei kurze Aufsätze, die lose mit den Kapiteln 2-4 verbunden sind. Zuerst konzentriere ich mich auf den Alba-Polymorphismus und gehe Hypothesen durch, die zur Aufrechterhaltung dieses Polymorphismus vorgeschlagen (und oft abgelehnt) wurden. Zweitens diskutiere ich, was unser Modell zum ökologischen Sexualdimorphismus uns über die in der allgemeinen Einführung beschriebenen Farbpolymorphismen lehren kann. Drittens diskutiere ich, warum bei einigen eusozialen Tieren, wie etwa den Hymenoptera, die Arbeiterkaste nur aus Weibchen besteht. Ich ende mit einigen Gedanken darüber, wie theoretischer Forschung helfen kann, Lücken zwischen Fachgebieten zu überbrücken und allgemeine Prinzipien der Evolution zu entdecken, während ich gleichzeitig den Wert taxonspezifischer Forschung hervorhebe.

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1

General Introduction

1.1 premise

Biologists are often faced with a simple observation made in nature, but the factors that lead to the observed pattern are far from obvious. For example, an evolutionary ecologist might observe that the males in a population all look alike, while females come in two distinct morphs, and, furthermore, that one female morph, at least superficially, resembled males. This observation has been made in multiple species, ranging from damselflies to hummingbirds (Fincke et al. 2005, Diamant et al. 2021). It is tempting to assume that the ultimate and proximate drivers are similar in the different system, but this assumption would be premature. Large parts of this thesis aim to understand a female-limited polymorphism in *Colias* butterflies, where some females are white (Alba morph) and others are colorful (Yellow or Orange morph) and resemble males in color (Tunström et al. 2023). Beyond this, the thesis aims to highlight the diverse evolutionary drivers of female-limited polymorphism and polyphenism. For this purpose, I will discuss various examples of such female-limited diversity.

Intraspecific variation can come in different forms. When investigating the drivers of this variation, it helps to distinguish them according to several criteria. Firstly, the variation can be continuous or discrete. Secondly, it can be genetically predetermined or phenotypically plastic. Thirdly, diversity can occur predominantly within a population, or between populations. Lastly, diversity can be linked to sex, resulting either in sexual dimorphisms or sex-limited variation.

Polymorphism is defined by having discrete morphs that are genetically determined and occur within populations (with gene-flow being largely uninhibited between morphs). Polyphenism is also defined by discrete morphs that occur within populations, but, unlike polymorphism, morphs are phenotypically plastic, i.e. they are expressed based on some environmental cue. Polymorphism and polyphenism are called female-limited when only females exhibit multiple morphs, while males are monomorphic. In the case of a polymorphism, males do not express the phenotype, but often still carry the alleles responsible for the polymorphism (unless the polymorphism is W-linked). This thesis focuses predominantly on female-limited polymorphism, but related forms of intraspecific variation (polyphenism, continuous variation, meta-population dynamics, sexual dimorphism) are also discussed, in order to highlight important similarities and differences.

The frequent occurrence of polymorphism is puzzling because morphs often differ in traits that affect fitness. If one morph has even slightly higher net-fitness than the other, the fitter morph should out-compete the other, eventually leading to the fixation of a

single morph. In some cases, morph diversity can be maintained by a constant inflow of alleles for the less fit morph through immigration, introgression or de-novo mutations. In the case of immigration and introgression, it becomes necessary to investigate not only the population in which the two morphs are observed, but also consider species with which it hybridizes or the meta-population that this population is part of. While it is important to consider these possibilities when investigating a natural system, this thesis will focus on cases in which polymorphism is maintained by the selection regime itself.

Balancing selection refers to any selection regime that maintains multiple coexisting alleles in a closed population without the need of introducing new alleles into the population (i.e. in the absence of mutations, introgression, or immigration). At its core, balancing selection is always characterized by negative frequency dependent selection acting on alleles, where an increased frequency of one allele either reduces its own fitness or increases the fitness of other alleles at the same locus. Furthermore, negative frequency dependence can lead to mutual invadability, where alleles for either morph could invade if the other morph is predominant. This can lead to one or more stable equilibrium frequencies, at which neither morph is expected to become more common, or it can lead to cyclic patterns where morph frequencies change over time without going extinct (Takahashi et al. 2010). Negative frequency dependence can be caused by a multitude of different mechanisms, including host-parasite coevolution (Johnson et al. 2009), heterozygote advantage (Hedrick 2012), fluctuating selection (Bertram and Masel 2019), spatial sorting (Berggren et al. 2012, Gordon et al. 2015), and niche partitioning (Comeault et al. 2015). Importantly, when explaining the maintenance of a polymorphism, it is not sufficient to simply show that both morphs have some advantage over the other, but these advantages also need to be frequency-dependent. Without frequency dependence, one morph will still have higher fitness than the other, leading to extinction of the less fit morph.

Note, that many authors have a more narrow understanding of "frequency dependent selection" compared to how I use the phrase. To illustrate the difference, consider the example of heterozygote advantage which is a relatively common mechanism of balancing selection (Hedrick 2012), but often distinguished from frequency dependent selection. Consider a locus with two alleles, A and B, where AB individuals produce more offspring than either homozygote, and AA individuals produce more offspring than BB individuals. The number of offspring produced by AB, AA, and BB individuals is not dependent on frequencies of these morphs, but negative frequency dependence nevertheless acts on a different level. If allele B is very rare, it predominantly occurs in heterozygotes resulting in high fitness and consequently in the spread of allele B. This spread is only halted when BB individuals become common. Similarly, when the allele A becomes common, it predominantly occurs in AA homozygotes that produce fewer offspring than the AB heterozygotes they compete with. Negative frequency dependence also acts on the individual level when measuring fitness in terms of grand-offspring rather than offspring. If allele B is rare, then a BB individual predominantly mates with AA individuals resulting in the production of highly fecund heterozygote AB offspring, and hence in the production of many grand-offspring. In contrast, if allele B is more common, a BB individual mates more frequently with AB or BB individuals, resulting in a larger proportion of BB offspring, and hence the production of fewer grand-offspring. Hence, BB individuals produce more grand-offspring when allele

B is rare compared to when allele B is common. From an empirical viewpoint, it can make sense to distinguish between balancing selection in general, and negative frequency dependence acting on morphs directly. This is because, when measuring fitness in terms of offspring (rather than grand-offspring), the fitness of the morphs is not frequency dependent under heterozygote advantage. However, from a modeling perspective, I find it more useful to consider all mechanisms of balancing selection in a common conceptual framework by emphasizing that balancing selection only occurs when some form of negative frequency dependent selection acts on the alleles in a population, even if this negative frequency dependence might not be immediately apparent.

Particularly in older papers, the distinction between polymorphism and polyphenism is often not made, but instead they are jointly referred to as a polymorphism (e.g. Ford 1945, Harrison 1980, and see Simpson et al. 2011 for a brief history of the terms). While it can be difficult to determine whether morphs are determined genetically or conditionally (e.g. Cook 2021), this information is often essential when trying to understand the coexistence of multiple morphs (Engqvist and Taborsky 2016). For theoreticians, it is also important to realize that very different models might be required in order to explain the maintenance of a polymorphism vs. that of a polyphenism. To give an example where this distinction is important: males of various species exhibit alternative reproductive tactics where large dominant males coexist with much smaller sneaker males. In fishes, both genetically determined (e.g. Zimmerer and Kallman 1989, Wirtz Ocana et al. 2014) and conditional alternative reproductive tactics occur in different species (e.g. Leiser and Itzkowitz 2002). Importantly, a conditional strategy (polyphenism) can be maintained without the need for negative frequency dependence (Engqvist and Taborsky 2016). Even if one morph always has lower fitness than the other, it can be maintained if it is expressed only by low quality individuals as a 'best of a bad lot' strategy. A polymorphism, however, requires balancing selection and hence negative frequency dependent selection to be maintained.

1.2 various drivers of female-limited color polymorphism

Now that the basic concepts have been defined, I will go through several examples of female-limited color polymorphism in order to illustrate some different evolutionary drivers than can be responsible for their maintenance. Female-limited polymorphism has already been the subject of multiple reviews (e.g. Svensson et al. 2009, Mank 2023). Here, my focus lies on the mechanisms that cause negative frequency dependence in different systems.

Several species of butterflies have independently evolved a female-limited mimetic polymorphism, where female morphs mimic different species of toxic butterflies (relevant reviews: Kunte 2009, Allen et al. 2011). Furthermore, some of these species also have a non-mimetic female morph that resembles males. Batesian mimicry occurs when a poisonous or unpalatable species (the 'model') has evolved a warning signal and this warning signal is then copied by a harmless species (the 'mimic'). Batesian mimicry is inherently negative density dependent for the mimic. If the mimic becomes very common (in relation to the model), predators no longer learn to associate the warning signal with unpalatability, and as a result, both the mimic and model species

suffer from increased predation. Furthermore, warning signals are often conspicuous to predators and therefore increase predation pressure when mostly adopted by harmless individuals. Hence, species with a mimetic polymorphism experience negative frequency dependence to the extent that mimicry becomes ineffective when a mimicking morph becomes too common relative to the model species.

As Kunte (2009) points out, a mimetic polymorphism should follow multiple rules: If the mimicking species is relatively rare compared to the model, the mimicking morph always has higher fitness than the non-mimicking morph and should therefore reach fixation. If, however, the mimicking species is relatively common, the mimicking morph can reach an equilibrium frequency where its fitness equals that of the non-mimicking morph (e.g. Barrett 1976). (Note, that this matches the pattern described in the premise of this thesis because the non-mimetic female morph resembles males, while the other female morph is a mimic for a different species of butterfly.) If additional mimicking morphs appear (that mimic different models), these can also spread in the population, further reducing the frequency of the non-mimicking morph, possibly replacing it entirely. Male butterflies in these mimetic systems are often monomorphically non-mimetic, and this tends to be explained through two factors: firstly, females are heavier than males and might therefore be more vulnerable to predation, and secondly, color in males might be constrained by sexual selection (Kunte 2009).

The damselfly genus *Ischnura* has been studied extensively for its female-limited color polymorphism and it is now widely accepted that it is maintained by frequency-dependent male harassment. This insight is the result of fruitful collaborations between naturalist, computational, and mathematical approaches (Sherratt 2001, Fincke et al. 2005, Le Rouzic et al. 2015, Svensson et al. 2005, Ting et al. 2009, Gosden and Svensson 2009, Takahashi et al. 2010, Iserbyt et al. 2013). These damselflies exhibits two or three female morphs. One of these morphs ("androchrome" females) is brightly colored and resembles males, while the other morph or morphs are cryptic ("heterochrome" females). This type of female-limited color polymorphism is also common in other Odonata (Fincke et al. 2005). The color polymorphism is controlled by a single locus with female-limited expression (Abbott and Gosden 2009).

Negative frequency dependence emerges from frequency-dependent male harassment because males are able to adjust their courting behavior such that they approach each female morph more often when that morph is common compared to when it is rare. The simplest mechanism proposed is that males preferentially approach the more common morph because they have learned to recognize them as females, e.g. through a learned 'search-image' ('learned mate recognition' hypothesis, Ting et al. 2009). However, Sherratt (2001) pointed out that this simple explanation is likely unrealistic and instead proposed another mechanism why male harassment might depend on female morph frequency ('male mimicry' hypothesis, Ting et al. 2009). Sherratt (2001) proposes that androchromes are easier to spot than heterochromes due to their conspicuous coloration, but that approaching an androchrome comes with the risk of accidentally approaching males. When androchromes are rare, males should be particularly wary of approaching male-like individuals, because they are very likely to be male. However, when androchrome females are common, approaching a male-like individual is more likely to pay off. As a result, androchrome females can suffer stronger harassment when common. The model of Sherratt (2001) also predicted that harassment of heterochrome females should remain relatively constant with morph frequency because it is influenced

by males' ability to spot females rather than an active choice by the males. However, Ting et al. (2009) found evidence for a combination of both these hypotheses.

Irrespective of the exact details, it is important to note that male learning is an essential component in the maintenance of this female-limited polymorphism because it is the source of the frequency dependence. It is therefore useful to ask under which circumstances, male learning is likely to be adaptive. Dukas et al. (2006) modeled this and concluded that male learning can evolve best when there are many encounters between males and females and when females mate multiply.

Several species of hummingbirds have a female-limited polymorphism where one female morph carries the same ornamental plumage as males, while the other female morph has no such ornamental plumage (Diamant et al. 2021). Falk et al. (2022) investigated this polymorphism in white-necked jacobins and found that it was not driven by male harassment. Androchrome females do benefit from being mistaken for males, but for a different reason: In this species, males are more aggressive than females and this allows males to access more resources. Male-mimicking females are avoided by competitors, including conspecific females and other species of hummingbirds. Hence, in this system, negative frequency dependence occurs because competitors stop avoiding ornamented individuals when a larger proportion of them are non-aggressive females rather than aggressive males.

All examples above share the commonality that they are driven by learning. In a mimetic polymorphism, predator learning causes predation pressure on mimics to increase when the mimic is common. In damselflies, male learning causes common morphs to be harassed more. Finally in hummingbirds, learning by competitors causes them to stop avoiding androchrome females when these females are common.

1.3 chapter summaries

Chapter 2 aims to find plausible mechanisms for the maintenance of the Alba polymorphism in *Colias* butterflies. These butterflies exhibit two female morphs that are determined by a single locus. Some females are colorful and resemble males in color (either orange or yellow), while the other morph (called 'Alba') has white wings. The two morphs differ in attractiveness, but unlike the damselfly system described above, it is the colorful females who are approached more by males. Alba females develop faster and eclose with larger fat bodies (Graham et al. 1980), probably because they save resources by not investing into the pigments that colorful females have in their wings. The Alba polymorphism also has another important difference compared to the damselfly system described above: in *Colias*, male preference appears to be innate and males are unable to adjust their courtship preferences based on female morph frequency (Limeri 2017). In the general discussion, I will describe various proposed and rejected hypotheses on what might be driving balancing selection in this system. For now, I merely note that, so far, no mechanism for negative frequency dependence has been discovered in this system.

We propose the novel hypothesis that the Alba polymorphism might be maintained by a combination of protandry and differences in emergence time of the two female morphs. In each generation, males eclose earlier than females do, and Alba females eclose earlier than colorful females (Graham et al. 1980). As a result, the less attractive

Alba morph emerges at a time when male density is high, and most males are actively searching for females. Colorful females, on the other hand, emerge later when males are more likely to have already mated, and are therefore less persistent in their courtship (Rutowski 1979). According to this hypothesis, Alba and colorful females can be understood as alternative reproductive tactics where both morphs acquire resources from male spermatophores but use somewhat different tactics to do so. Alba emerges early and hence at a time when male courtship is highest, while colorful females invest into an attractive trait and hence more easily find mates later in the season. Using an individual-based model, we show that, at least in principle, this mechanism can maintain a polymorphism. We further discuss what empirical evidence is required to show or disprove whether this mechanism is responsible for the maintenance of the Alba polymorphism specifically.

Chapter 3 is concerned with the question of how within-population diversity can evolve when two niches are available in the same area and a species adapts to fill both niches. The model focuses on two possibilities: genetic polymorphism and sexual dimorphism for niche. Both of these are subject to constraints. A genetic polymorphism is easily broken up by recombination unless it is controlled by a single locus, while a sexual dimorphism for niche-use is constrained by the optimal sex ratio which is unlikely to match the optimal morph frequency. The topic of ecological sexual dimorphism (males and females using different niches) is interest in itself, but it also has interesting connections to sex-limited diversity. According to our model, a sex-limited polymorphism can evolve if one niche can sustain more individuals than the other (e.g. if a resource is more abundant or higher quality than another resource). In this case, one sex specializes on the larger niche while the other sex is polymorphic for niche use. In the general discussion, I will discuss how chapter 3 relates to the examples of female-limited polymorphisms described above.

Chapter 4 deviates from the focus on female-limited polymorphism and is instead concerned with sex ratio theory in facultative parthenogens. Nevertheless, there are two ways in which this topic is connected to main topic of this thesis. Firstly, facultative parthenogenesis is a form of female alternative reproductive tactic where females can either reproduce sexually or asexually, and often asexual and sexual females differ in various traits (e.g. Simon et al. 2002). This makes facultative parthenogenesis yet another form of female-limited diversity (although reproductive mode is typically not genetically determined). Secondly, sex ratio theory is strongly concerned with negative frequency dependent selection. In obligately sexual organisms, there is usually balancing selection that maintains sex ratios at 50/50. This is because every individual has a mother and a father, and hence the reproductive success of all males equals that of all females in a population. If one sex is rarer than the other, that reproductive success is divided between fewer individuals and hence the reproductive success of individuals increases when they belong to the rarer sex (Gardner 2023 and references therein). We show that the rarer sex effect also acts in facultative parthenogens, but that the optimal sex ratio becomes increasingly female-biased with increasing rates of parthenogenesis.

We then turn our attention to various taxa that differ in their sex determination system and the resulting constraints on sex ratios of parthenogenetically produced brood. In many animals, the sex determination system constrains the sex of parthenogenetically produced offspring to be either all male or all female. In contrast, some other animals (cyclic parthenogens) can freely adjust the sex ratios among their parthenogenetically

produced offspring allowing them to react to cyclic changes in the environment. We show that the presence or absence of constraints has import consequences for the evolution of parthenogenesis. Furthermore, we discuss some older (and partially neglected) modeling studies on different types of haplodiploidy and the sex determination systems from which they have likely evolved. In particular, we highlight an idea by Bull (1981) about the origin of haplodiploidy in Hymenoptera specifically. In the general discussion, I will return to the topic of female-limited diversity and discuss the question why the worker caste in Hymenoptera consists only of females.

2

Fast or Fancy: Modeling a trade-off between female attractiveness and development time

Authors: Kora Klein, Chris Wheat, and Hanna Kokko

Abstract

Many species of *Colias* butterflies have a female-limited polymorphism where white 'Alba' females coexist with colorful females (orange or yellow). This polymorphism is characterized by several trade-offs, including reduced attractiveness and faster development of Alba females compared to colorful females. Attractiveness is likely beneficial for females in this system because males transmit nutrient-rich spermatophores during mating. However, so far, no convincing mechanism has been identified that could drive balancing selection that maintains this polymorphism. Here, we build a model that shows that protandry and morph differences in emergence time can maintain the polymorphism. Alba females emerge early in a season when male courtship is most intense, while the more attractive colorful females emerge later. In our individual-based model, polymorphism maintenance is robust to large changes in population density, as long as males are able to regenerate resources for spermatophores after mating. Negative frequency dependence occurs because Alba females compete primarily for the spermatophores provided by virgin males, while colorful females compete for spermatophores provided by males later in the season. We additionally propose several avenues for empirical research that allow our hypothesis to be tested.

Keywords: balancing selection, alternative reproductive tactics, life history

2.1 Introduction

The drivers behind genetic polymorphism can be difficult to determine. While theory clearly predicts that some form of balancing selection (selection for rare alleles) plays a role (Hedrick 2007), it is often far from obvious what ecological, behavioral, or physiological mechanisms cause balancing selection in each case. Here, we model a female-limited polymorphism that occurs in many species of *Colias*. In these butterflies, two genetically determined female morphs coexist: a white morph called Alba, and a

colorful morph that resembles males. The continued coexistence of these two morphs in the same population indicates that balancing selection is acting in this system, but the drivers behind this balancing selection remain a mystery.

In several genera of Coliadinae butterflies (Limeri and Morehouse 2016), colorful and white (Alba) females co-occur in the same population. This polymorphism is best studied in the genus *Colias*. The Alba polymorphism is characterized by autosomal inheritance, the Alba allele is dominant, and the polymorphism is only expressed in females, while males are (almost) always colorful (but see Kratochwil 2020 for a single recorded example of an Alba male). In *Colias*, the Alba allele results from a transposable element insertion (Woronik et al. 2019) which causes the up-regulation of the transcription factor *BarH1* in the Alba morph. This causes a reduced number of pigment granules in the wing scales of Alba females and hence causes the white coloration of their wings (Watt 1973, Woronik et al. 2019).

The Alba polymorphism of *Colias* has originated once at the base of the genus and has since been maintained by a combination of balancing selection and introgression (Tunström et al. 2023). While repeated losses of either morph have resulted in monomorphism both for Alba and for colorful females (Limeri and Morehouse 2016), there are many populations in which the polymorphism remains stable over long time scales (Tunström et al. 2023). Furthermore, *Colias* is geographically widespread and the Alba polymorphism occurs in various different species across the northern hemisphere and South America (Limeri and Morehouse 2016, Kir'yanov 2021). Hence, it stands to reason that the mechanism of balancing selection behind this polymorphism must be generalizable across the various environments and across the different species of *Colias*.

The Alba phenotype is associated with various physiological benefits that likely arise because the reduction of pigment granules allows them to save resources (Graham et al. 1980, Woronik et al. 2018). Alba females have faster development, particularly under food stress and cold temperatures (Graham et al. 1980, Woronik et al. 2018). Alba females also have larger fat bodies at eclosion (Graham et al. 1980). The only benefit for colorful females appears to be that they are more attractive to males, and as a result, receive more courtship (Kemp and Macedonia 2007).

In species with conventional sex roles (the majority, Janicke et al. 2016), male reproductive success is limited by mating opportunties, and it is a reasonable expectation that males benefit from being attractive. In these species, it is not obvious what role attractiveness plays for females. Attractiveness can be detrimental to female fitness if attractive females suffer from increased harassment. In *Ischnura* damselflies, a female-limited polymorphism is maintained by harassment because males preferentially court (and harass) the more common female morph (Sherratt 2001, Fincke et al. 2005, Le Rouzic et al. 2015, Svensson et al. 2005, Ting et al. 2009, Gosden and Svensson 2009, Takahashi et al. 2010, Iserbyt et al. 2013). In *Colias*, harassment also occurs: When males court females that have already mated previously, females sometimes start so called ascending flights where they fly upwards until the male stops pursuing them (Rutowski 1978). However, there are several important differences between the Alba polymorphism and the *Ischnura* system that rule out frequency-dependent harassment as a mechanism of balancing selection in *Colias*. Most importantly, male *Colias* butterflies do not adjust their preferences according to female morph frequencies (Limeri 2017). The colorful morph is always more attractive to males than the Alba morph, and in addition to this, colorful females suffer physiological costs. Hence, if harassment

has significant costs for females, then colorful females suffer two types of cost without this hypothesis evoking any benefit for them, and it fails as an explanation behind a polymorphism.

There are also important ways in which female *Colias* benefit from male courtship. Firstly, being attractive increases the chances of mating at least once, although this is unlikely to play a significant role in *Colias* because females rarely fail to find a mate. Secondly, males provide nutrient rich spermatophores and therefore female *Colias* can benefit from multiple matings. Spermatophores have high protein content and, in some *Colias* species, represent 6-7% of male body mass (Marshall 1985). The high nitrogen content in spermatophores is particularly important in butterflies because their nectar-based diet does not allow them to consume much nitrogen as adults (Stjernholm et al. 2005).

Despite decades of research (reviewed in the general discussion of this thesis), no clear mechanism has been identified that could drive balancing selection in this system. One important contribution, Nielsen and Watt (2000), tested whether the Alba polymorphism might be maintained by fluctuating selection. Specifically, they found that Alba females suffer interspecific harassment from *Pieris* males (white butterflies). Using population densities of both *Colias* and *Pieris*, they calculated that the two *Colias* morphs are favored in different years, with Alba benefiting from low *Pieris* and high *Colias* densities. They conclude that this temporal variability is not sufficient to allow for polymorphism maintenance, but suggest that spatial heterogeneity could maintain the polymorphism.

Here, we propose a novel hypothesis, which highlights a mechanism for polymorphism maintenance without requiring any spacial structure. Our model focuses on three [Kora here you had four?] key aspects of *Colias* butterflies and the Alba polymorphism: First, males provide large, nutrient-rich spermatophores that are important for female fecundity. Second, colorful females are more attractive to males than Alba females. Third, sexes and morphs differ in their developmental timing, with males developing faster than females, and Alba females developing faster than colorful females. Fourth, population dynamics are characterized by clear fluctuations in densities (of adults) that result from multiple generations each year (Fig. 2.1, Colom et al. 2022).

Taken together, these four factors allow for the hypothesis that Alba and colorful females follow two different reproductive tactics: The differences in development time cause Alba females to emerge early during a generation (Graham et al. 1980). At this time, male densities are high, female densities are low, and many males are still unmated, while colorful females emerge later during a generation when male densities are lower, the adult sex ratio is more female-biased, and most males have already mated before. The distinction between virgin and mated males is important because this can affect the intensity of courtship as well as the size of spermatophores, e.g. In *Pieris protodice* both spermatophore size and courtship persistence are considerably reduced after the first mating (Rutowski 1979). In our model, we consider some specific aspects of *Colias* reproductive biology: It has been found that younger males produce larger spermatophores (Watanabe et al. 1997), and, in other butterflies, that spermatophore size of males increases with longer intervals between matings (Svärd and Wiklund 1986).

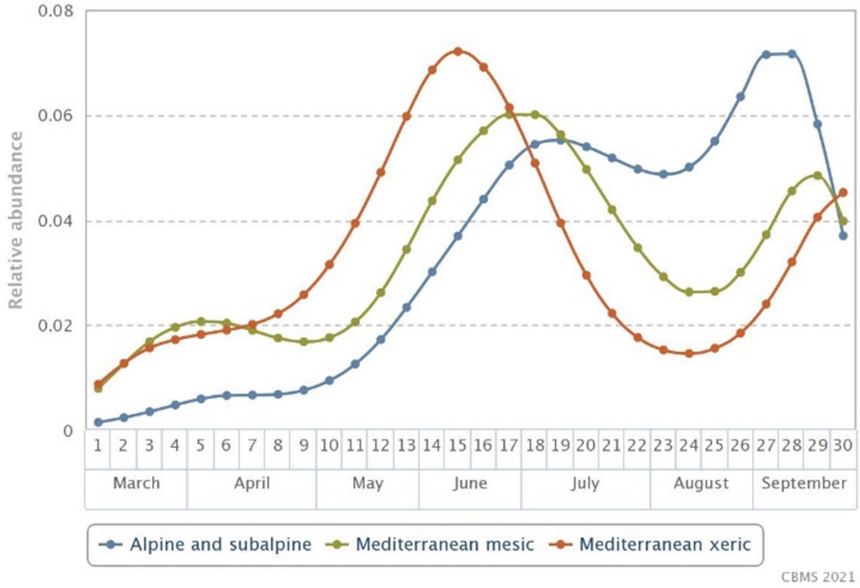

Figure 2.1: ***Population Densities of Colias croceus:*** *The graphs represent the population dynamics of Colias croceus in three different areas of Catalonia in Spain over the course of 30 sampling weeks. The figure is taken with permission from the supplementary material of Colom et al. (2022) and the data was gathered as part of the Catalan Butterfly Monitoring Scheme (CBMS, https://www.catalanbms.org/en/especies/pieccr/#mapes).*

2.2 Methods

basic premise

Each simulation considers a single generation with N female individuals and N male individuals. A fraction p of the females have the Alba phenotype, and a fraction $1-p$ of females have the colorful phenotype. The model runs in continuous time using a Gillespie algorithm (Gillespie 1977, Kokko 2024, in press) to model eclosion, encounters, and deaths. We also assign each individual a resource reserve (described in more detail below) that changes linearly over time.

Initially, all $2N$ individuals start as juveniles (larvae or pupae). Over the course of the simulation, all individuals eclose, many of them mate and lay eggs, and all finally die. Because we are interested only in the fitness of females (not males), the simulation ends when all females have died. Then, for each simulation, the mean reproductive success of alba females is compared to that of colorful females. For each set of parameters, simulations are run for 99 different Alba frequencies, p_a, ranging from 1% to 99% of the females having the Alba morph. The results of these 99 runs are then used to estimate frequency dependent selection and hence whether a polymorphism can be maintained.

Note that a central assumption of this model is that the generations are non-overlapping. This assumption is largely met in *Colias* butterflies (Fig. 2.1, supplementary material of Colom et al. 2022), where generations are either non-overlapping or only partially overlapping.

All code is written in R version 4.3.3 (2024-02-29 ucrt). For figures, the packages

ggplot2 version 3.5.0, and ggpattern version 1.0.1 are used.

simulation

In our model, population densities are governed by eclosion rates and death rates. The eclosion rates are e_m for males, e_a for alba females, and e_o for orange females, where $e_m >> e_a > e_o$. Furthermore, after eclosion, each individual has a death-rate d.

Our model captures the nutrient transfer through spermatophores, by assigning each individual a "reserve". All females start with a reserve of a_f at eclosion. The initial reserve of males differs between individuals to reflect that males can differ in quality and that higher quality males produce larger spermatophores. The initial reserves of individual males are drawn from a normal distribution with mean 30 and a standard deviation of 7.5, with negative values set to zero. In females, this reserve diminishes over time as they lay eggs (changing by $b_f = -1$ per unit time). In males, the reserve replenishes over time (by $b_m = 0.1$ per unit time, but we can also set this to be zero, to investigate the consequences for polymorphism). Note that the change in resource reserve does not follow the exponential wait times used by the Gillespie algorithm, instead the linear change in reserves creates a predicted time ('time stamp' in the terminology of Kokko (2024, in press) at which reserve depletion or accumulation results in a state change. During mating, a fraction $k = 0.5$ of the male's reserve is transferred to his mate.

For females, the reserve affects both egg laying and remating: In nature, *Colias* females lay only one egg per oviposition bout, and they can lay hundreds eggs in total over the course of their life. In our model, we capture this by having females continuously produce eggs as long as they have at least some reserve. Each egg is laid immediately upon production if the mother has mated at least once, while virgin females accumulate unfertilized eggs until their first mating (and then lay them immediately after mating). If a female's reserve is entirely depleted, she stops laying eggs. Females with high reserve (above $R_{f,max} = 10$) cannot remate, and therefore any encounter with a male results in harassment, rather than a mating. Note that a depleted reserve is intended to only indicate that the female has run out of resources to produce additional eggs, but it does not imply that they are sperm-limited. Spermatophores carry both sperm and nutrients, and females can run out of nutrients long before the sperm are depleted. At the same time, virgin females eclose with an initial reserve, but they are nevertheless sperm-limited if they fail to mate before dying (resulting in zero fitness if females die as virgins).

Reserve additionally affects courtship for both males and females. Males with low reserve (below a threshold, $R_{m,min} = 20$) do not attempt to court any females, while males with reserves above that threshold attempt to mate with any female they encounter. Females with a a reserve below $R_{f,max}$ mate with courting males, while females with reserve larger than $R_{f,max}$ reject courtship attempts, and hence these courtships are considered to be harassment. During mating, the male transfers a fraction k of his reserve to the female. We choose the thresholds, $R_{m,min}$ and $R_{f,max}$, to be such that a male only attempts to court females if his reserve is high enough to produce large enough spermatophores to prevent females from remating immediately afterwards ($R_{m,min} = R_{f,max}/k$).

An encounter describes a situation where a male that is ready to mate spots and courts

a female (who might or might not be willing to mate). The rate at which encounters happen is governed by the density of the population as well as the attractiveness of females. The population density, n, is a parameter that impacts encounter rates such that an increase in n results in a proportional increase in the likelihood that a given male encounters a given female. As already defined above, N describes the number of females included in the simulation, but this should be understood as the number of individuals sampled from a population rather than the number of individuals that are actually present in a population. Colorful females are encountered more frequently than Alba females, and this is captured by the parameters α_a and $\alpha_o = 1$. In order to ensure that N does not affect how many females a male encounters, we calculate the probability that a particular mate-searching male encounters a particular adult female as $\frac{n}{N}\alpha_a$ for Alba females and $\frac{n}{N}\alpha_o$ for colorful females. (Females are adult when they have eclosed and not died yet, while males are mate-searching if they have eclosed, not died yet, and their reserve is at least $R_{m,min}$.)

determining equilibrium frequencies

We investigate whether negative frequency dependence acts by running simulations for 99 different Alba frequencies, $0.01 \leq p \leq 0.99$, and noting the mean lifetime reproductive success for Alba females and orange females in each simulation. The aim is to find a morph frequency at which the two morphs of females have equal fitness, and furthermore show that if a morph becomes more common than this equilibrium, it results in reduced relative fitness of that morph compared to the other morph.

Let $w_{a,p}$ and $w_{y,p}$ denote the mean lifetime reproductive success of Alba and orange females derived from a simulation with an Alba frequency of p. We quantify the difference between Alba and orange fitness as $log(w_{a,p}) - log(w_{y,p})$. We then draw a linear regression to investigate how these fitness differences are affected by morph frequencies (Fig. 2.2). If the zero point of this regression is between 0 and 1, this constitutes an equilibrium frequency, but in order to be stable, it is also necessary that selection is negatively frequency dependent. This is the case when the slope of the regression is negative.

investigated parameter space

All simulation presented here share some parameter values. We set $e_m = 0.5$ and $e_a = 0.1$, while e_o functions as a parameter that varies between 0.01 and 0.1. Death rates are $d = 0.01$ for all individuals. The initial reserve of females is $a_f = 10$ and the initial reserves of males are drawn from a normal distribution with mean 30 and a standard deviation of 7.5. The attractiveness of orange females is $\alpha_o = 1$. We run simulations with $N = 1000$ females and equally many males. Females mate when their reserve is below $R_{f,max} = 10$, and males start searching for mates when their reserve is above $R_{m,min} = 20$. During mating, a fraction $k = 0.5$ of the male's reserve is transferred to the female. The reserve of females changes by $b_f = -1$ per unit time. Here, we only report the baseline case where harassment is not costly to males or females. Harassment is unlikely to be key to polymorphism maintenance, as explained in the introduction above.

There are also some parameters that vary between simulations: We report results on

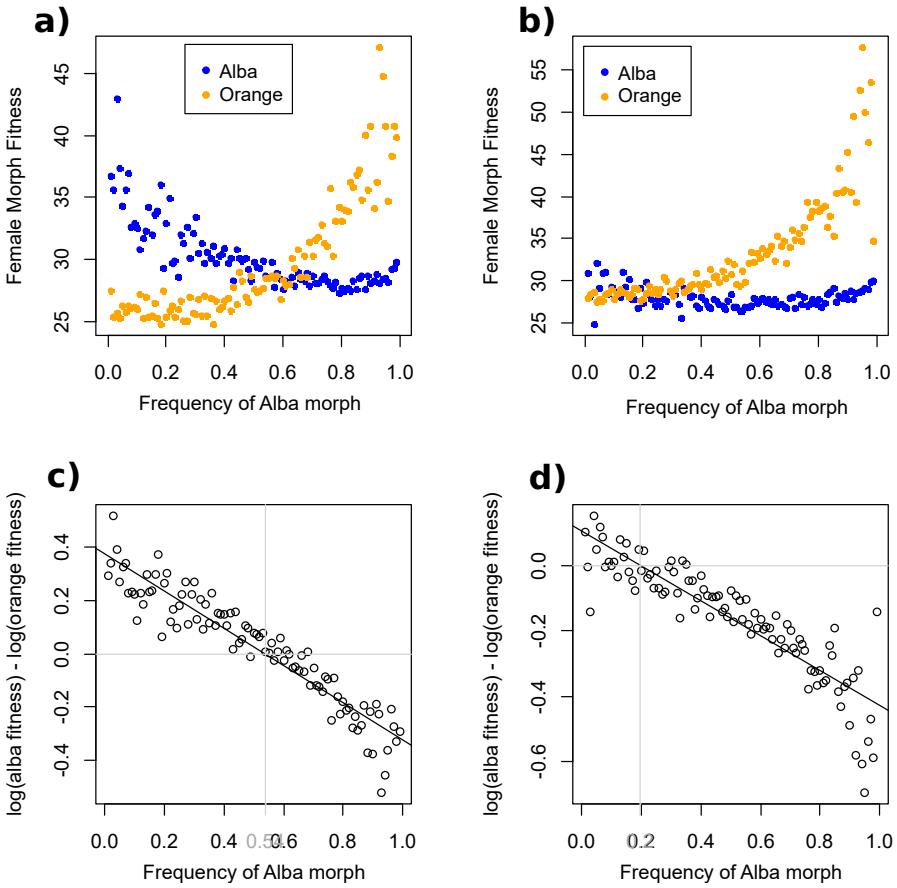

Figure 2.2: ***Equilibrium Morph Frequencies:*** *(a-b) The lifetime reproductive success of both morphs of female is depicted from 99 simulations that differ in the morph frequency in the population. (c-d) A linear regression is drawn to describe how* $log(albafitness) - log(orangefitness)$ *depends on the morph frequency of Alba. An Equilibrium Frequency is reached when this regression equals zero. In the depicted cases, the equilibrium Alba frequency is approximately (a,c) 54% Alba and 46% Orange, and (b,d) 20% Alba and 80% Orange*

various population densities $0.1 \leq n \leq 100$. We also vary the eclosion rates of orange females from $0.01 \leq e_o \leq 0.1$ (note that at at $e_o = 0.1$, Alba and orange do not differ in their eclosion rate). Furthermore, the attractiveness of Alba females is set either to $\alpha_a = 0.2$ (Fig. 2.3 and 2.4) or $\alpha_a = 0.5$ (Fig. 2.5). Males either increase their reserve by $b_m = 0.1$ per unit time (Fig. 2.4 and 2.5), or do not replenish their reserve, $b_m = 0$ (Fig. 2.3).

2.3 Results

limited prospects for polymorphism when males do not replenish their reserve over time

When males are unable to replenish their reserve as adults ($b_m = 0$), prospects for a protected polymorphism are poor. Although there is a narrow parameter range that allows for polymorphism (Fig. 2.3) under these conditions, even slight changes in population density are sufficient to disrupt this balance, with increasing population densities resulting in the fixation of the Alba morph, and decreasing population densities resulting in the fixation of the orange morph. We also increased the eclosion rate of orange females, e_o, while keeping that of Alba females, e_a, fixed. This increase in e_o favors the orange morph and hence a higher population density is required to allow for polymorphism or fixation of the Alba morph. In summary, when $b_m = 0$, there are some prospects for negative frequency dependent selection, but relatively minor changes in population density are sufficient to cause fixation of one morph.

when males replenish reserve, polymorphism is much more stable

When males can replenish their reserve over time ($b_m = 0.1$), polymorphism becomes possible over much larger parameter ranges (Fig. 2.4, and 2.5). Similarly to the results above, the orange morph is favored by low population densities and small differences in emergence time between the morphs (increasing e_o, with unchanged e_a). At low population densities, the orange morph can reach fixation, and higher population densities can favor the Alba morph by promoting polymorphism or allowing Alba to reach fixation (2.5). Unlike the scenario above (where b_m was zero), the polymorphism is far less sensitive to changes in population densities, and even a hundredfold change in density can, for some e_o, be insufficient to destabilize the polymorphism. In these cases, only the equilibrium frequency changes to be more Alba-biased under high population densities and more orange-biased under low population densities.

We also investigate how the attractiveness of females affects the prospects of polymorphism by setting $\alpha_a = 0.2$ or $\alpha_a = 0.5$ (while keeping $\alpha_o = 1$ constant). In both cases, there are some values for e_o that allow polymorphism for a large range of population densities. Lower differences in attractiveness between the two morphs ($\alpha_a = 0.5$), are associated with more fixation of the Alba morph, reduced parameter regions for polymorphism, and less fixation of the orange morph (Fig. 2.4, and 2.5).

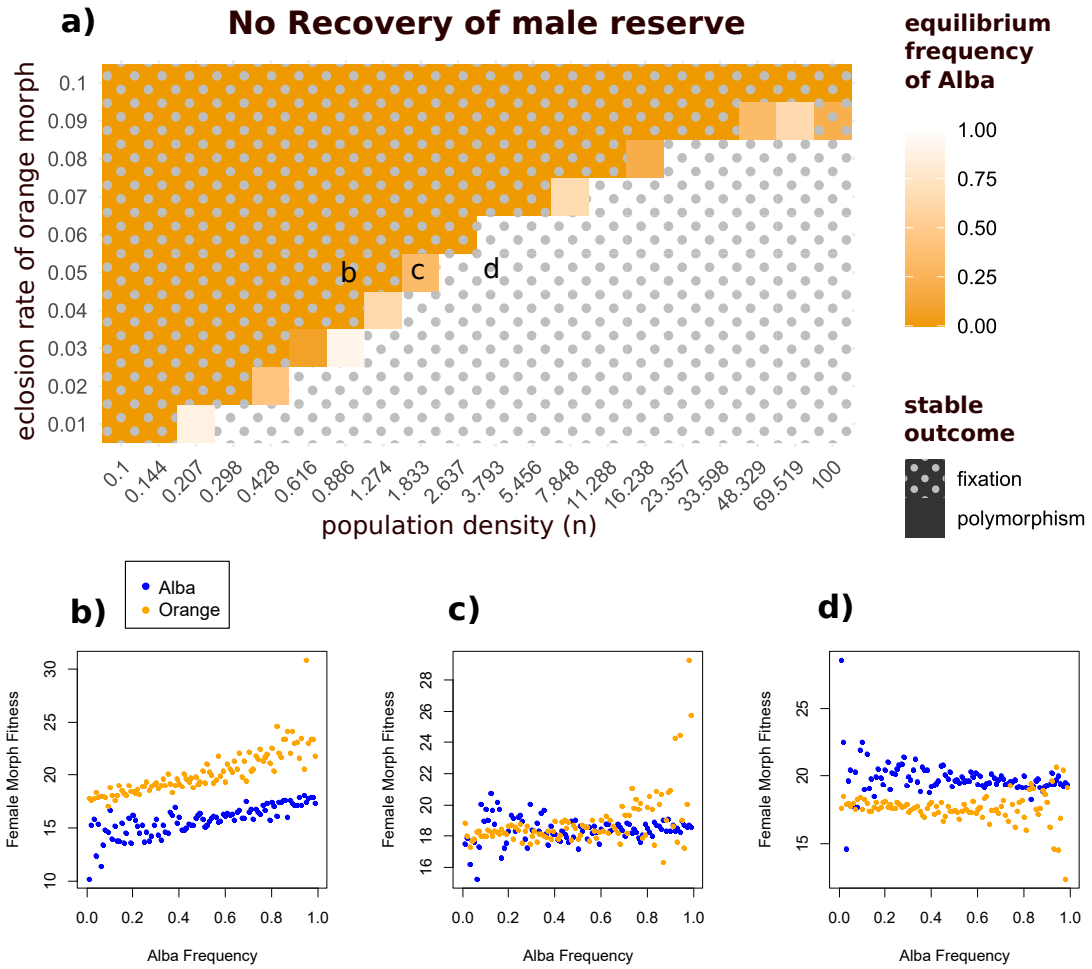

Figure 2.3: ***Restricted prospects for polymorphism when males do not restore their reserve:*** *(a) A heatmap showing how the equilibrium Alba frequencies depend on the population density, n (x-axis), and the eclosion rate of orange females, e_o (y-axis). Dots indicate that one morph reaches fixation, either because there is no intermediate equilibrium or because selection is positive frequency dependent. The eclosion rate of Alba is $e_a = 0.1$. Results are depicted for $\alpha_a = 0.2$ and $b_m = 0$. Other parameters are as described in the methods. The three marked squares correspond to the subplots b-d that show the mean lifetime reproductive success of Alba females and colorful females depend on the frequency of the Alba morph.*

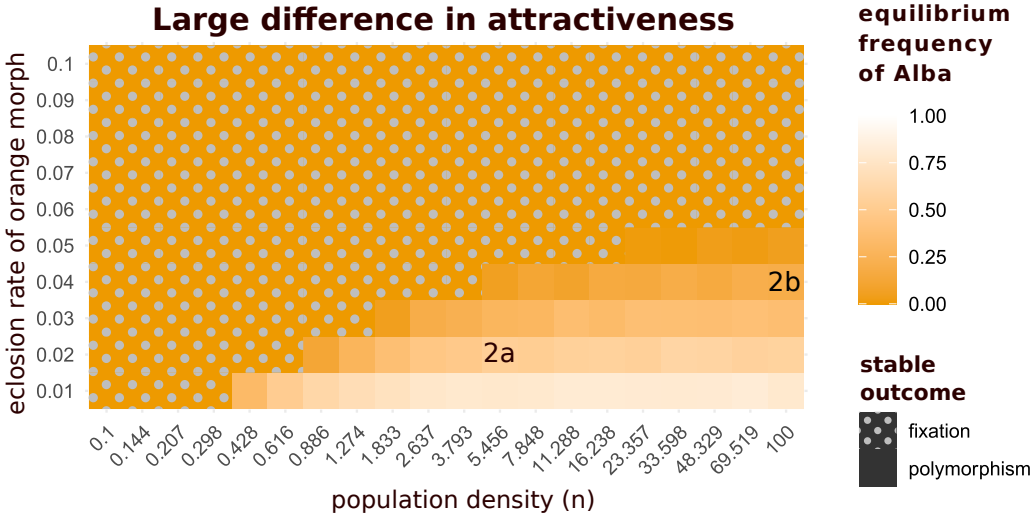

Figure 2.4: ***Results when males replenish their reserve and orange females are much more attractive than Alba females:*** *A heatmap showing how the equilibrium Alba frequencies depend on the population density, n (x-axis), and the eclosion rate of orange females, e_o (y-axis). The two marked squares correspond to the simulations depicted in Fig. 2.2a and 2.2b, respectively. The eclosion rate of Alba is $e_a = 0.1$. Results are depicted for $\alpha_a = 0.2$ and $b_m = 0.1$. Other parameters are as described in the methods.*

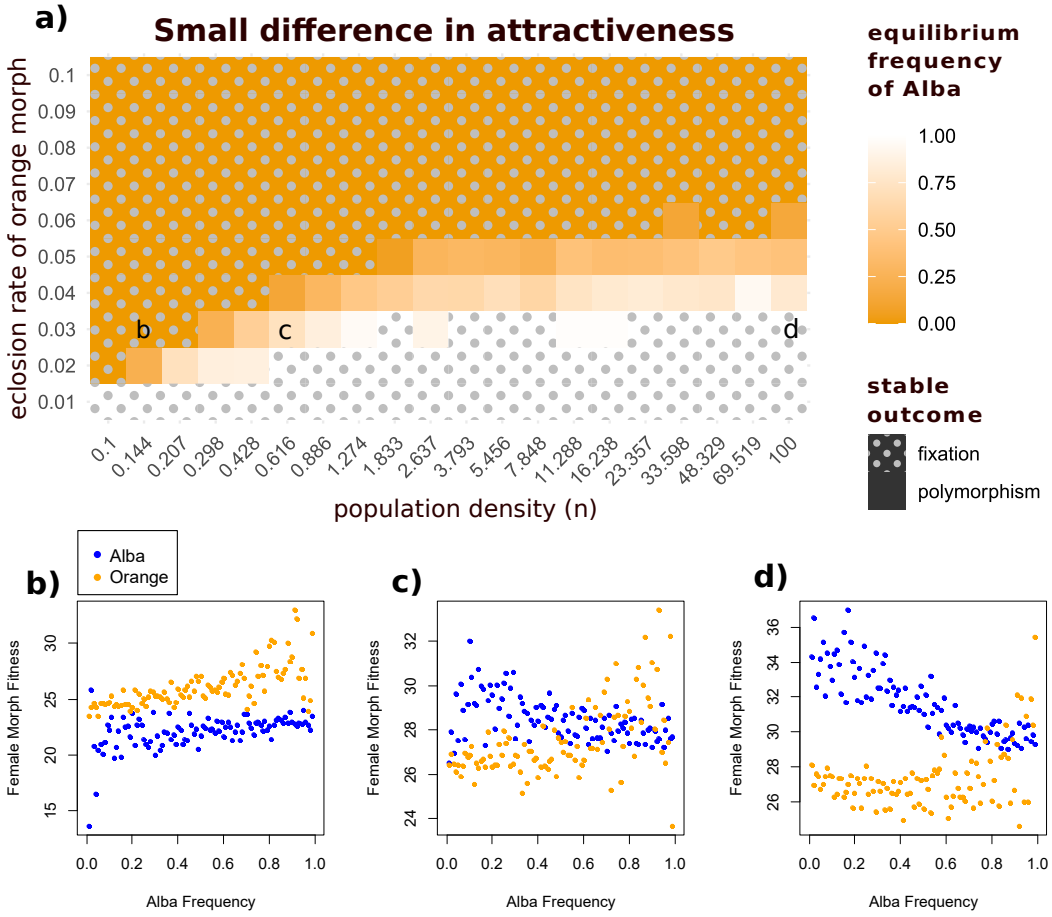

Figure 2.5: ***Results when males replenish their reserve and orange females are only twice as attractive as Alba females:*** *(a) A heatmap showing how the equilibrium Alba frequencies depend on the population density, n (x-axis), and the eclosion rate of orange females, e_o (y-axis). The eclosion rate of Alba is $e_a = 0.1$. Results are depicted for $\alpha_a = 0.5$ and $b_m = 0.1$. Other parameters are as described in the methods. The three marked squares correspond to the subplots b-d that show the mean lifetime reproductive success of Alba females and orange females depend on the frequency of the Alba morph.*

2.4 Discussion

Our model shows a possible mechanism that could be maintaining the Alba polymorphism in *Colias* butterflies, in which orange females coexist with white, Alba females. While the morphs differ in various traits in nature, we focus on only two differences, development time and attractiveness, and show that, under suitable parameter values, these are sufficient to maintain the polymorphism. As long as males regenerate spermatophore reserves after mating, we find that a polymorphism for emergence time and attractiveness can be stable and robust under various population densities.

In addition to being frequency dependent, we additionally show that the fitness of morphs is density dependent. Alba is favored by high densities and colorful females are favored by low densities. At high population densities, encounters between males and females are relatively common, while at low population densities, males have to spend more time searching for females and as a result courtship occurs less frequently. Therefore, attractiveness is more beneficial to females when densities are low, and this favors colorful females. This result matches that of Nielsen and Watt (2000) who constructed a model that takes harassment into account. In their model, densities also have different fitness effects on the two female morphs. At low densities, courtship is rare, and therefore being attractive is beneficial to females, which favors the colorful morph. At high densities, courtship is common, and therefore attractiveness leads to more harassment, hence selecting against the colorful morph.

Our finding that a trade-off between emergence time and attractiveness can result in a polymorphism is in line with the findings by Hendrickx et al. (2015) who studied a male alternative reproductive tactic in the dwarf spider, *Oedothorax gibbosus*. These spiders are characterized by two male morphs, one of which invests heavily in a sexually selected trait (a hump on the head), while the other morph lacks this trait. The ornamented morph develops much slower than the non-ornamented morph and this has important consequences for the maintenance of this polymorphism. Similarly to *Colias* butterflies, these spiders also have multiple generations per year that are only partially overlapping. Non-ornamented males develop into adults slightly earlier than females do, while ornamented males only develop into adults later than females do. As a result, non-ornamented males can mate with virgin females and these already lay some eggs before remating with ornamented males later in the season. Using an individual based model, Hendrickx et al. (2015) further show that this trade-off in development time and ornamentation can maintain this male-limited polymorphism.

A central assumption to both our model and the model of Hendrickx et al. (2015) is that generations are non-overlapping, at least concerning adult individuals: adults of one generation die before the next generation develops into adults. This assumption is largely met in natural populations of *Colias*. Some species of *Colias* only exhibit one generation per year and hence generations are entirely non-overlapping. In other species, multiple generations occur per year, and generations partially overlap (Fig. 2.1, Colom et al. 2022). Nevertheless, even in these species, there is a highly repeated pattern where population densities fluctuate in multiple distinct waves each year representing the multiple generations. The dwarf spider *O. gibbosus* shows a similar pattern of partially overlapping generations (Hendrickx et al. 2015).

While temporal fluctuations in the sense of seasonal emergence of males and females are essential for the validity of our hypothesis, it is important to note that our model

does not rely on fluctuating selection. Fluctuating selection occurs when the direction of selection changes between generations, e.g. in *Colias* fluctuating selection would imply that Alba is favored in some generations and colorful females in other generations (Nielsen and Watt 2000). In contrast, the density fluctuations in our model occur within a single generation.

Another central assumption of our model is that females generally benefit from increased male courtship, i.e., we did not consider costs of harassment. Future work could usefully study the effects of harassment in detail; here we simply note that intuition suggests it will depress the fitness, and consequently the equilibrium frequency, of the more attractive (pigmented) morph. Harassment also highlights an important difference between the male-limited polymorphism in dwarf spiders and the female-limited Alba polymorphism. In dwarf spiders, the increased attractiveness of investing males directly translates into higher mating rates with a clear positive impact on siring success. In contrast, whether female *Colias* benefit from increased male courtship is a much more complex assumption to consider. This is because increased courtship can be both beneficial and detrimental in this system. Harassment is common in *Colias*, causing females to perform elaborate ascending flights to escape courting males (Rutowski 1978), and this is likely associated with strong energetic costs while also taking time away from foraging or oviposition. On the other hand, females also receive large spermatophores from males that are important for reproductive success.

Yet another factor that might mitigate the costs of harassment is the possibility that long courtship or escape flights allow females to assess the quality of males. While we do not include assessment of quality in our model, it is instructive to speculate on the likely effects. Assessment could allow more attractive females to choose between a larger number of males and hence pick higher quality mating partners. Put differently, some observations of harassment in *Colias* might also be interpreted as female mate choice with females flying away from males as a way to test their quality. This possibility is important because it adds another reason why increased courtship from males could be a net positive for female if it allows females to pick higher quality mates.

While our model focuses on the maintenance of the Alba polymorphism, and hence on the fitness of females, it is also worth considering the role that spermatophores play for the fitness of males, as this can impact the optimal male behavior which in turn affects females. From the male perspective, the nutritious spermatophores are both a form of paternal investment and a post-mating sexually selected trait that increases siring success. A larger spermatophore has been found to prolong the time until a female remates (Sugawara 1979, Watanabe et al. 1997). This is important because female *Colias* lay eggs one at a time and these eggs are always fertilized by the female's last mate (Boggs and Watt 1981). Hence, a male's siring success is directly associated with the time that females take to remate. Lüpold et al. (2014) has shown that, in species in which males are unable to monopolize females, males are expected to follow roughly the same strategy when allocating resources into either post-mating or pre-mating traits. This has two interesting consequences for *Colias* butterflies in which monopolization of females is not possible: Firstly, it implies that pre-mating traits, such as courtship, correlate positively with post-mating traits, such as spermatophore size. There is some support for this positive correlation of spermatophore size and courtship persistence in a related butterfly (Rutowski 1979). Secondly, it implies that pre-mating traits correlate positively with the general quality of a male. Therefore, pre-mating traits, such as

courtship intensity and male wing color, might represent honest signals which enable females to choose males who are of better general quality and who provide more nutrients to her offspring.

Another question worth asking, is why *Colias* males preferentially court colourful females in the first place. An important possibility is that the preference for colorful females might not be adaptive, but rather based on sensory limitations that make it more difficult to spot Alba females. Limeri and Morehouse (2014) tested the visual contrast of the two morphs to background foliage and found that Alba females show a lower color contrast, but a higher brightness contrast to the background compared to colorful females. However, it is currently not known which of these contrasts have a stronger impact on *Colias* behaviour. Hence, the proximate mechanisms for male choice are currently not sufficiently understood to confirm or reject a non-adaptive hypothesis.

It is also worth considering in what scenarios male choice can be adaptive. If male and sperm availability is not limiting, the evolution of female attractiveness is an evolutionary puzzle. Females clearly need to signal in some systems, e.g. by emitting pheromones, to aid male mate-searching efforts (Harari and Steinitz 2013), but this does not yet explain why males should consistently favour one type of conspecific female (a strong signaller) over another (Fitzpatrick and Servedio 2018). Even in cases where some females offer better reproductive opportunities for the male than others, it is not automatically in the interest of the male to reject any one mating opportunity (Barry and Kokko 2010). If matings are brief and sperm is abundant, rejecting the poorer option does not improve male fitness; reluctance to mate with one female type only evolves if it improves another male fitness component, often modelled as the success with another (preferred) female type (Servedio and Lande 2006). If males cannot possibly make use of every opportunity, because recovering from each mating takes time, then prospects for male mate choice and, consequently, female ornamentation evolution improve (Jennions et al. 2014). Variation in female attractiveness is thus predicted to become important when males invest significantly in each mating, either by offering significant nuptial gifts (e.g., nutritious spermatophores, Hare and Simmons 2019) or by investing afterwards in parenting behaviours (Kokko and Johnstone 2002, Fargevieille et al. 2023). In butterflies, the former is clearly the significant route to potential variation in attractiveness.

Our model shows that the trade-off between development time and attractiveness can only maintain the Alba polymorphism if males are able to ”replenish their reserve”. This result requires some further explanation because it is not necessarily clear what the reserve even is biologically or what it means to replenish it. The reserve represents some resource that is limiting for female reproduction and that males transmit through their spermatophores. Hence, in order to test the assumption of reserve recovery empirically, it is first necessary to ask what essential resources are transmitted through spermatophores and to what extent these limit female reproduction. In butterflies, nitrogen is often limiting for reproduction (Stjernholm et al. 2005), and we have constructed our model with nitrogen in mind. This is because most butterflies feed on nectar as adults, and this is a very nitrogen-poor resource. Hence, the number of eggs that females can lay is limited by the amount of nitrogen that they took up as caterpillars. Furthermore, males transfer nitrogen in spermatophores. It is also possible that some other nutrients function in a similar way, i.e. that they are limiting for reproduction and transfered through spermatophores.

In our model, polymorphism maintenance is made possible because Alba females and colorful females avoid competition to some extent. Alba females predominantly mate early in the season while colorful females mate later. Male reserve recovery is of crucial importance for this argument because without it, spermatophore availability late in the season would limit the reproduction of pigmented females too much for a polymorphism to be maintained. Thus, when there is no male reserve recovery, Alba females and colorful females effectively compete for the same resources, limiting the prospects for polymorphism.

The most obvious mechanism of male reserve recovery is that males might be able to acquire resources through feeding and use these to build new spermatophores. However, this is not the only mechanism by which males can direct resources towards their spermatophores late in the season that were not available to females earlier during the season. In many butterflies (including *Pieris napi* which is in the same family as *Colias*), both males and female show a reduction in biomass as well as nitrogen-content with age (Stjernholm et al. 2005). This indicates that these butterflies use some of the resources (including nitrogen) stored in their own bodies and reallocate them towards reproduction. Resources can even be reallocated from the flight-muscles toward reproduction. This further matched with the observation that males of another *Pieris* species reduce their courtship after the first mating (Rutowski 1979).

2.5 Conclusion

We have proposed a novel hypothesis concerning the maintenance of the Alba polymorphism and shown that, at least in theory, the polymorphism can be maintained due to differences in emergence time of the two morphs. While this constitutes a significant step forward, it would be premature to conclude that this mechanism is the driving force behind balancing selection in this system. Additional empirical research is required to test the assumptions of our model. We suggest that three lines of empirical research would be particularly useful. Firstly, we suggest further investigation on sex- and morph-specific emergence times of males and females and how these differ between species and environments. Secondly, we encourage research on the possibility that attractive females might benefit from increased courtship from males, e.g. because it allows them to choose higher quality males or distinguish between virgin males and mated males. Lastly, our model shows that the polymorphism is only robust to density changes, if, after mating, males are able to allocate new nutrients towards the production of additional spermatophores. This could either be due to nutrient acquisition, or because males metabolize nutrients from other parts of their body. So far, we have only argued that these possibilities are plausible by citing research on other butterflies. Thus, *Colias*-specific research is required to show the validity of our hypothesis.

Alternative Conclusion

Some grow slow to be a delight,
while plain ones reach prime in a much shorter time.
Maybe they mate before colors take flight?

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Competing Interests

The authors declare no competing interests.

3

Ecological Sexual Dimorphism and Population Consequences when One Sex Uses a Superior Resource

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Abstract

Some species exhibit strong intraspecific variation that allows them to use multiple ecological niches (e.g. two resources). Intraspecific variation can come in different forms, including genetic polymorphism and sexual dimorphism, and these are subject to different constraints. A genetic polymorphism is easily broken up by recombination, while sexual dimorphism is constrained by a mismatch of sex ratios and optimal morph frequencies. We construct a mathematical model in which a consumer species is initially adapted to one ecological niche and then is allowed to evolve to (additionally) use a second niche. We find that a large variety of evolutionary outcomes are possible, and that these depend not only on ecology and genetic architecture, but also on the order in which mutations occur. If resource use is controlled by a single locus, either a sex-limited polymorphism or a sex-independent polymorphism evolve (depending on mutation order), while a sexual dimorphism only evolves in the unlikely scenario when both resources are of equal abundance and quality. If morph is determined by multiple loci with additive effects, sexual dimorphism also becomes possible when one resource can sustain more individuals that the other. In this case, mutation order determines which sex specializes on the superior resource with important consequences for population size: if females use the superior resource, this results in larger population sizes than if females use the inferior resource. Nevertheless, both of these outcomes are evolutionarily stable, and there is no a-priori prediction on which sex evolves to use which resource.

Keywords: sexual dimorphism, polymorphism, disruptive selection, ecological character displacement

3.1 Introduction

The availability of two ecological niches for the same population can lead to disruptive selection. Examples include disruptive selection for color, e.g. a situation where dark

and bright morphs are better camouflaged than individuals with intermediate color (Villoutreix et al. 2023). Another example involves optimal exploitation of two different resources when this requires somewhat different morphologies.

Disruptive selection, when acting on its own, selects for extreme phenotypes, but when it is coupled with negative frequency dependence, it can also help to maintain diversity within a population. The example where two different resources require different morphologies results in both disruptive selection -because intermediate morphologies are selected against- and negative frequency dependence -because very rare morphs can avoid competition by using a different resource from the rest of the population. Disruptive selection for resource use can therefore lead to the evolution of a polymorphism maintained by reduced intraspecific competition.

There are multiple proximate mechanism by which a population can be split into different morphs. Here, we focus on the contrast between two non-plastic mechanisms: First, a genetic polymorphism may create genetically determined morphs that specialize on using different resources. Alternatively, in species with distinct sexes, niche use dimorphism may become linked to sex, such that males and females occupy different niches (Hindell et al. 2021, Bravo et al. 2024). Well studied examples of such ecological sexual dimorphisms are relatively scarce (review: De Lisle 2019), but striking examples exist: bill morphology impacts flower use in hermit hummingbirds (Temeles et al. 2000, Temeles et al. 2010), with another spectacular example, the huia *Heteralocha acutirostris*, offering interesting phylogenetic evidence of the timing of sexually dimorphic bill evolution (Gibb and Shepherd 2022), but due to its extinction it is not available for further ecological study. Furthermore, experimental evolution can produce different diets in male and female *Drosophila melanogaster* in just a few generations (De Lisle 2023).

The two mechanisms, while not mutually exclusive (Cooper et al. 2011, Meiri et al. 2014, De Lisle and Rowe 2017, Li and Kokko 2021), each come with their own constraints. Genetic polymorphism maintenance is difficult if a large number of loci are involved, as recombination quickly breaks them up. Optimal resource exploitation involves a combination of morphology and physiological and behavioural traits, making it a complex trait affected by many loci. Optimizing each morph involved in the polymorphism thus requires evolving differences at many loci. However, in a panmictic population, the problem is that morph-specific combinations of alleles are quickly broken up by recombination, unless this is prevented by large non-recombining regions (e.g. inversions, Küpper et al. 2016, Funk et al. 2021, and indels, O'Connor et al. 2021) or large-effect alleles such as those in regulatory regions (Llaurens et al. 2017, Mérot et al. 2020). Y- and W-chromosomes are another example of large non-recombining regions that can control polymorphisms, albeit only sex-limited ones (Meisel 2022). In the absence of such polymorphism-promoting features of genetic architecture, it is difficult to avoid erosion of the polymorphism into more continuous variation, leading to a high prevalence of maladaptive intermediate phenotypes. It is not impossible to have a polygenic polymorphism, however (e.g. Kocher et al. 2018), as it may be maintained through continued correlated selection (Svensson 2017) or seasonality (Wittmann et al. 2017).

Ecological sexual dimorphism is subject to a different constraint which results from a likely mismatch between sex-ratio and resource availability. Sex-ratios are strongly affected by the rarer-sex effect (traditionally called Fisher's principle, but see Gardner

2023 for the contribution of others before R.A. Fisher) which tends to result in an even sex-ratio with equally many males as females. The optimal morph-ratios, however, are determined by the availability of the two resources. It most cases, one resource is more abundant and/or higher quality than the other, and therefore one consumer morph is selected to be more common than the other. Although the rarer-sex principle only applies to offspring production and does not prevent biased population-wide sex ratios to emerge via sex-specific mortality after offspring have reached independence (West 2009, Pirrie and Ashby 2021), this does not create an expectation of a match between the sex ratio among consumers and the optimal morph frequencies derived from the perspective of resource availability. Ecological sexual dimorphism therefore is prone to generating suboptimal morph frequencies.

Ecological sexual dimorphism has already been the subject of modeling work (Slatkin 1984, Bolnick and Doebeli 2003, Van Dooren et al. 2004, Li and Kokko 2021). While the verbal explanations of sexual dimorphism often describe the existence of multiple resources or niches, the mathematical models often assume a single resource peak with unimodal variation around the highest abundance of the resource. This makes it difficult to capture the likely effect that intermediate phenotypes might be unable to exploit any resource effectively. Slatkin (1984) and Li and Kokko (2021), however, modeled this effect, by considering two resources with varying distance between them in terms of the consumer trait value that is best adapted to exploiting the resource (if the distance is zero, the situation collapses to being equivalent to a single resource). Both studies stress that polygenic polymorphism is not an automatic outcome, with Slatkin (1984) emphasizing the ability of genetic correlations to destroy it, and Li and Kokko (2021) showing that even if correlations are absent, the problem of the intermediate phenotypes still applies. Even so, in Li and Kokko (2021), the polymorphism could, in some cases, be maintained (in both sexes separately), if the best-adapted individual in each site is much more fit than one that is almost as good at extracting the resource (e.g. due to strong sexual selection, such that one male monopolizes most matings). Alternatively, monogamy or near-monogamy could in their model lead to the two sexes using complementary resources on their shared territory, but this is easily broken down by too frequent multiple mating and/or the fact that not all sites have both types of resources present. Since Li and Kokko (2021) considered only ”presence” and ”absence” of each resource at each site, and assumed that resource types that are present are equally abundant, they did not comment on the question we phrase above: the abundance of resources does not automatically match the abundance of consumers. This could create a further constraint to the evolution of sex-linked polymorphism, in addition to the factors that they considered.

Here, we present a mathematical model to study the evolutionary response of populations to disruptive selection while being explicit about the traits of the two different resources and how this shapes disruptive selection in the consumer species. Specifically, we investigate how recombination and uneven resource availability lead to the evolution of polymorphism, ecological sexual dimorphism, or sex-limited polymorphism.

3.2 Methods

General premise

Our aim is to model evolution subject to two constraints: (1) recombination can cause high frequencies of intermediate phenotypes that are unable to use either resource effectively and (2) the sex-ratio is fixed to 1:1, thus ecological sexual dimorphism might not lead to an optimal exploitation of the resources when one resource can sustain many more individuals than the other (e.g. by being the more abundant resource). These two constraints are the focus of our study and therefore we constructed the model in a way, that some other constraints are removed.

We consider a single, randomly mating and panmictic consumer species with non-overlapping generations and 1:1 sex ratio. We assume it is ancestrally evolved to optimize use of resource A, and may acquire, via mutations, sex-specific trait values that enhance the ability to use resource B that also occurs in the environment. The two resources A and B differ in a trait, e.g. corolla length, so that optimal exploitation requires a corresponding trait value in the consumer, e.g. beak length. To simplify calculations (and without loss of generality), we use the same metric for both traits, i.e. a consumer with trait value of x is best at using a resource with trait value of x. Mutations are assumed to be rare, meaning that extant alleles evolve towards an equilibrium frequency before new mutations arise.

Resource distribution

Resources A and B both show a normal distribution of the trait with means of $+x_0$ and $-x_0$ respectively, and equal variance, V. Associating resource A with the mean $+x_0$ implies that the ancestral population matches the right (as opposed to left) resource peak in all of our figures. We define one unit of resource as the amount that can support one consumer individual that is adapted to this resource. Hence, we use N_0 to denote both the density of resource A and the initial population density of the consumer. Resource B can sustain either fewer or more individuals than A. We model this effect by the parameter β, such that resource B can sustain a consumer density of βN_0. For example, $\beta = 2$ indicates that resource B can support twice as many consumers as resource A. Note that β can increase either via higher abundance or higher quality (or both) of resource B, and thus we will refer to one resource as being superior and the other being inferior to indicate that one resource can sustain higher densities of adapted individuals.

The trait distributions of resource A and B are given by the functions:

$$R_A(x) = N_0 \, exp[-(x - x_0)^2/2V] \tag{3.1}$$

$$R_B(x) = \beta N_0 \, exp[-(x + x_0)^2/2V] \tag{3.2}$$

The total trait distribution of resources is

$$R(x) = R_A(x) + R_B(x) \tag{3.3}$$

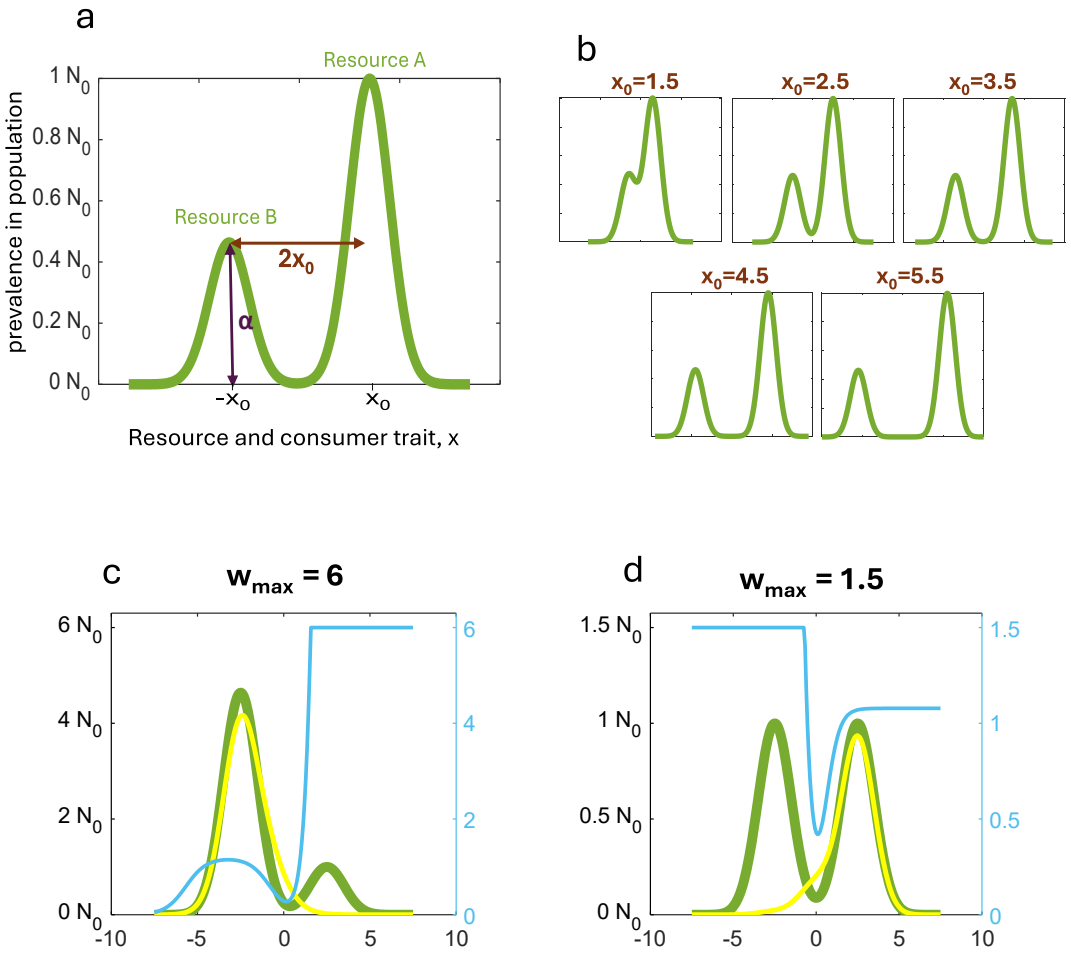

Figure 3.1: **Explanation of Model Parameters:** *The green line shows the distribution of resource traits ($R(x)$), with resource A on the right (positive values for x) and resource B on the left (negative x). The resource distribution is based on two parameters: x_0 determines how different the two resources are, and hence how large the fitness valley between them is; β determines how many consumers resource B can sustain compared to resource A (while resource A is fixed to having an amplitude of N_0). Subplot b gives multiple examples for x_0. Subplots c and d show the effect of the maximum fitness, w_{max}: the yellow line shows the population-wide resource-use distribution of the consumer ($C_{total}(t,x)$), and the blue line shows the fitness gained by consumers when using a resource with trait value, x ($W(t,x)$). Usually, fitness is derived by dividing the resource distribution by the consumer distribution. Hence, the fitness of a consumer increases when there are few individuals and many resources with the same trait value. However, fitness can not exceed w_{max} even if there are many more resources than consumers.*

The resource distribution (Fig. 3.1a) creates the conditions for disruptive selection, since consumers with intermediate phenotypes (e.g. trait value of 0) have access to fewer resources than consumers with phenotypes that match the resource means (trait values of $-x_0$ and $+x_0$). Without loss of generality, we assume that $V = 1$ (Generality is not lost because it is possible for any V and x_0 to set $V = 1$ and find another value for x_0 that gives the same result. This is due to two assumptions of our model: the variance in resource trait and the variance in consumer resource use are both equal to V, and the effect of mutations scales with x_0). The resource distribution stays constant throughout a simulation.

Genetic Architecture

Mutations introduce alleles that shift the consumer phenotype towards using resource B (below, these alleles are called B-alleles). Each individual of the consumer population is haploid, with a total of $3m$ loci: an equal number m of loci that are female-limited in their expression, male-limited in their expression, or expressed in both sexes. Each locus can carry either an A-allele or a B-allele. If an individual has A-alleles on all loci, it has a trait value of x_0 which allows for optimal exploitation of resource A. A single B-allele shifts the mean phenotype by $-2x_0/m$. This value is chosen such that an individual must express m B-alleles to fully shift the phenotype towards optimal exploitation of resource B. On a female-limited locus, B-alleles shift only the phenotype of females towards resource B. On male-limited loci, B-alleles only shift the phenotype of males. On loci that affect both sexes, B-alleles shift the phenotype of both sexes. Note that if an individual has B-alleles on all loci, it is not adapted for resource B, but has instead overshot the distance between resources A and B by 100%. We construct the model in this way to ensure that evolution can cover the distance in multiple different ways and hence allow different evolutionary outcomes.

In total an m-Loci Model (with m loci of each type) can exhibit up to 2^{3m} genotypes because it considers $3m$ loci. Each genotype is associated with two resource-use distributions: one for females and one for males. Let n_f denote the number of B-alleles that genotype g has on loci that affect females (female-limited loci and loci that affect both sexes), and let n_m denote the same for males. Genotype g has a phenotype for males, $x_{m,g}$, and a phenotype for females, $x_{f,g}$.

$$x_{m,g} = x_0 - n_f \frac{2x_0}{m} \tag{3.4}$$

$$x_{f,g} = x_0 - n_m \frac{2x_0}{m} \tag{3.5}$$

Individuals with a given phenotype are best at using resources with the same trait value, but can also use resources with similar trait values. The degree to which they use similar resources is governed by their resource-use distribution which has a variance of V. Hence, the resource-use distributions of genotype g is given by

$$c_{f,g}(x) = exp[-(x - x_{f,g})^2/2V] \tag{3.6}$$

and

$$c_{m,g}(x) = exp[-(x - x_{m,g})^2/2V] \tag{3.7}$$

for females and males, respectively.

Note that the model assumes that resource-use has the same variance as the resource distribution, V. This assumption is not intended to be realistic. Instead, this assumption is made to ease the interpretation of results by ensuring that evolution is always driven by both resources: If the variance in the resource trait were larger than the variance in the consumer trait, then multiple morphs could evolve even if only a single resource were present (Slatkin 1984,Ackermann and Doebeli 2004). In the opposite case, a single generalist genotype might be able to optimally exploit both resources simultaneously.

Competition and Fitness

Throughout our model, a fitness of 1 implies that an individual can replace itself; in a sexual population with 1:1 sex ratio, a fitness of 1 implies an expectation of having produced one female and one male offspring. More generally, for any sex ratio (fraction of females), s, an individual with fitness 1 produces one female offspring and $(1-s)/s$ male offspring.

Below, we differentiate between the fitnesses of genotypes and alleles, as well as the fitness gained by exploiting a resource with trait value x. This distinction is necessary because each allele might be present in multiple genotypes, and because each genotype is best exploiting the resources with matching trait value but also exerts competition on similar genotypes by using resources with trait values that slightly deviate from its optimum.

The fitness gained by a female consumer using a resource with trait value x, depends both on the availability of resources, $R(x)$, and on the number of competitors, $C_{total}(t,x)$. $C_{total}(t,x)$ describes how much the consumer uses resources with trait value x, at time t, and is given by the equation:

$$C_{total}(t,x) = \sum_{g=1}^{2^{3m}} N_g(t)(sc_{f,g}(x) + (1-s)c_{m,g}(x)) \tag{3.8}$$

where N_g denotes the number of individuals with genotype g. By making fitness dependent on the density of competitors, we include density dependence and competition into our model.

We assume that the fitness of female consumers increases linearly with the resource availability $R(x)$, divided by consumers adapted to use this resource, $C_{total}(t,x)$, up to a cap of maximum fitness w_{max}. Biologically, w_{max} should be interpreted as the degree to which a consumer benefits from unlimited resources, e.g. if $w_{max} = 6$ then an individual with unlimited resources has six times as many offspring as an individual that has just enough resources to replace itself. The fitness function, $W(t,x)$, assigns each trait value a fitness value between 0 and w_{max} (Fig. 3.1c and d):

$$W(t,x) = min\left(\frac{R(x)}{C_{total}(t,x)},\ w_{max}\right) \tag{3.9}$$

The fitness of a genotype depends on its performance in both female and male individuals. We assume that female fitness is solely responsible for population growth, i.e. that there is no sperm limitation or paternal care. The fitness of females with a genotype, g, depends on the fitness function, $W(t,x)$, and on the resource-use

distribution of females with that genotype. The fitness of females with genotype g is given by:

$$w_f(t,g) = \frac{\int W(t,x) \cdot c_{f,g}(x)\, dx}{\int c_{f,g}(x)\, dx} \tag{3.10}$$

Male fitness is calculated similarly (again, we assume linear increase with resources obtained), but additionally, we need to ensure that the total fitness of males is always equal to the total fitness of females. First, it is useful to give an uncorrected estimate of male fitness, $w_{m,uncorrected}(t,g)$, and then use this to calculate the actual fitness of males with a given genotype, $w_m(t,g)$.

$$w_{m,uncorrected}(t,g) = \frac{\int W(t,x) \cdot c_{m,g}(x)\, dx}{\int c_{m,g}(x)\, dx} \tag{3.11}$$

$$w_m(t,g) = w_{m,uncorrected}(t,g)\ \frac{s(\sum_{i=1}^{2^{3m}} N_i(t) w_f(t,i))}{(1-s)(\sum_{i=1}^{2^{3m}} N_i(t) w_{m,uncorrected}(t,i))} \tag{3.12}$$

(above, i denotes all possible genotypes)

Finally, the total fitness of a genotype is given by the equation:

$$w(t,g) = \frac{s w_f(t,g) + (1-s) w_m(t,g)}{2s} \tag{3.13}$$

The genotype fitnesses are then used to calculate the fitness of alleles. The fitness of an allele a is simply the weighted sum of all the genotype fitnesses of genotypes that carry this allele, with genotype frequencies as weights. The genotype frequency of a genotype is given by

$$q(t,g) = \frac{N_g(t)}{\sum_{i=1}^{2^{3m}} N_i(t)} \tag{3.14}$$

Because we assume haploidy, half of all genotypes contain the allele a. Let G_a be the set of all genotypes that contain a. Then the allele fitness of a is

$$f(t,a) = \sum_{g \in G_a} q(t,g)\ w(t,g) \tag{3.15}$$

Our model allows both changes in allele frequencies and changes in population size. The allele fitnesses described above can reflect either of these two processes. Changes in population size are reflected in the total fitness of females ($\sum_{g=1}^{2^{3m}} N_g(t) f_f(t,g)$). Let allele a have an allele frequency $p_a(t)$ at the start of generation t, and fitness $f_a(t)$, then

$$p_a(t+1) = \frac{p_a(t) f_a(t)}{\sum_{g=1}^{2^{3m}} N_g(t) f_f(t,g)} \tag{3.16}$$

With this, we have described how allele frequencies and population density changes from one generation to the next. Below, we will describe the evolutionary dynamics over longer time scales as well as how we model mutations.

Evolutionary Dynamics

At the beginning of each simulation, the consumer species is adapted to optimally use a single resource (resource A). Initially, the population has a density of N_0, where N_0 is defined as the density of consumers that can be sustained by resource A alone. Over the course of the simulation, the consumer evolves to use both resources, which also increases population size.

At the beginning of each simulation, only a single genotype is present in the consumer population. Each locus is fixed for an allele that allows the optimal exploitation of resource A (i.e. A-alleles). This initial genotype with A-alleles at each locus has a resource-use distribution, c_1, which is a normal distribution with mean x_0, variance V, and an amplitude of 1. Initially, there are N_0 individuals in the populations, leading to a total phenotype-distribution of

$$C_{total}(0,x) = N_0 c_1(x) = N_0 \; exp[\frac{-(x-x_0)^2}{2V}] \tag{3.17}$$

where $C_{total}(t,x)$ describes the resource use (x) at time t

We assume that mutations are rare. First, a stable state is calculated for the extant alleles (described below). After a stable state is reached, a mutation adds one B-allele to the population, either on a male-limited locus, or a female-limited locus, or on a locus that affects both sexes. A mutation is simulated by increasing the allele-frequency of a B-allele from 0% to 1%. The temporal order in which mutations happen can impact the final evolutionary outcome. Therefore different orders are used. When reporting the order in the results, F stands for mutations on female-limited loci, M stands for male-limited loci, and B stands for loci that affect both sexes. For example, in a one-locus model ($m = 1$), the order [F,M,B] indicates that the first mutation introduced a B-allele at the female-limited locus, the second mutation introduced a B-allele at the male-limited locus, and the third mutation introduced a B-allele at the locus that affects both sexes. More generally, for any m, [F,M,B] indicates that the first m mutations are on female-limited loci, the next m mutations at male-limited loci, and then there are another m mutations at loci that affect both sexes.

After the introduction of a mutation, equilibrium frequencies are calculated. Because the model is much too complex for analytical investigation, we use numerical approximations for all calculations. An equilibrium frequency is reached when no allele changes frequency by more than 0.00001 in a generation. Additionally, we define a parameter that impacts when alleles go extinct. If an allele reaches a frequency lower than $p_{min} = 0.0001$, it goes extinct (the allele frequency is set to 0), and if it reaches an allele frequency higher than $1 - p_{min} = 0.9999$, it reaches fixation (allele frequency is set to 1. If alleles did not go extinct (or fix), the number of coexisting genotypes would be very high and this would increase computation time immensely.

After these initial $3m$ mutations, we test whether any additional A-alleles or B-alleles can invade. There are six types of mutations to consider. In addition to the three B-allele introducing mutations, back-mutation can reintroduce an A-allele that has previously gone extinct by decreasing the allele frequency of a B-allele from 100% to 99%. If multiple alleles can invade, then preference is given according to the mutation order used in the initial simulation. If no alleles can invade, then the population has reached a final evolutionary state.

Quantification of Resource Specialization

We need a measure of the resource specialization of males and females in the population to be able to compare the evolutionary outcomes of the different simulations.

We use the cumulative frequency distributions (normalized to have a maximum of 1) of resource A, resource B, of male resource-use and of female resource-use (Fig. 3.2). Specialization is measured by investigating to what extend the consumer's cumulative frequencies matches that of the resource. A sex is said to specialize on a resource when its cumulative frequency distribution exactly (or almost) matches that of the resource.

As described above, $R_A(x)$ and $R_B(x)$ denote the distribution of resource A and B. We now define $C_m(x)$ and $C_f(x)$ as the distributions of males and females in the final population. The respective cumulative frequency functions are $F_{R_A} = P(R_A \leq x)$, $F_{R_B} = P(R_B \leq x)$, $F_{C_m} = P(C_m \leq x)$, and $F_{C_f} = P(C_f \leq x)$. Using these, the degree to which males use resource A is given by:

$$U_{m,A} = \frac{\int F_{R_B}(x) - F_{C_m}(x)\ dx}{\int F_{R_B}(x) - F_{R_A}(x)\ dx} \tag{3.18}$$

and the degree to which males use resource B is given by:

$$U_{m,B} = \frac{\int F_{C_m}(x) - F_{R_A}(x)\ dx}{\int F_{R_B}(x) - F_{R_A}(x)\ dx} \tag{3.19}$$

Note that this definition results in $U_{m,A} + U_{m,B} = 1$.

The resource use of females are defined in the same way (using C_f instead of C_m).

3.3 Results

Our model aims to investigate two constraints that affect the evolution of polymorphisms and sexual dimorphisms for resource use. Sexual dimorphisms become suboptimal when one resource can sustain more individuals than the other. This is captured by our parameter β. Polymorphisms (whether sex-limited or unrelated to sex) are constrained by recombination because intermediate phenotypes are selected against. Our model includes three parameters that impact how severely recombination hampers the evolution of a polymorphism (m, x_0, and w_{max}). m notates the number of B-alleles that are required to shift the phenotype from using resource A to using resource B. As m increases, genotypes with extreme phenotypes (that can optimally use either resource) become less common and intermediate phenotypes become predominant under random mating. x_0 denotes the difference (along the trait axis) between the two resources. If x_0 is large, intermediate phenotypes are strongly selected against because they can use neither resource. w_{max} denotes the fitness of an individual that experiences no competition for resources. A large value of w_{max} assigns very high fitness to extreme rare genotypes. Parents under such conditions benefit from producing one or more offspring with a rare, extreme genotype, counteracting and possibly overriding the cost of their other offspring having a more common intermediate genotype.

We will present the results based on which constraints apply: recombination constrains evolution when $m \geq 2$, but not when $m = 1$. When $\beta \neq 1$, there is a mismatch

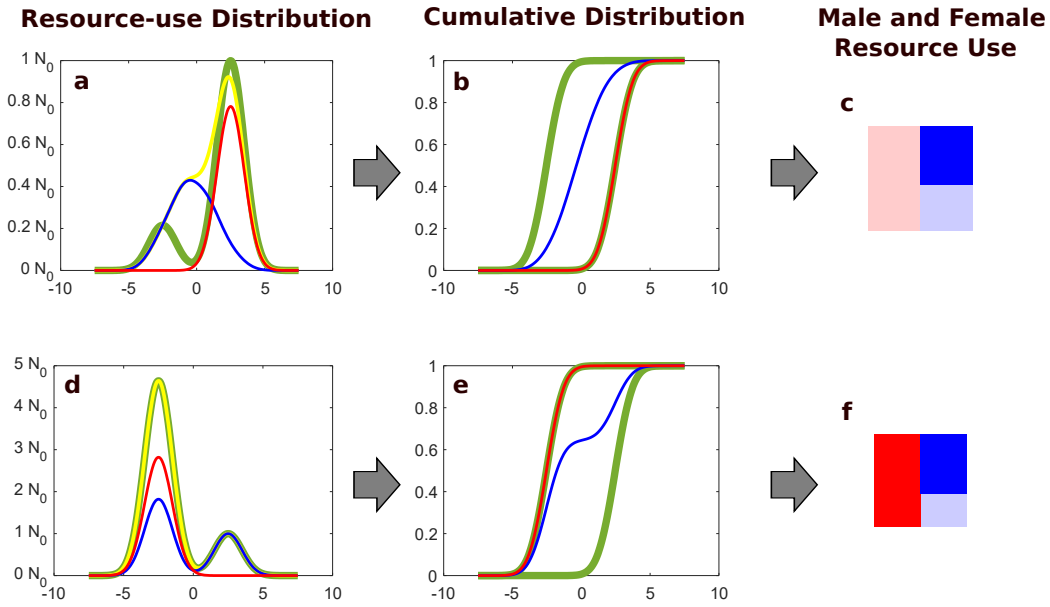

Figure 3.2: **Quantification of Resource Use:** *Two examples to illustrate how resource use is quantified and illustrated in figures 3.3 - 3.5. (a and d) The green line shows the distribution of resource traits, the red and blue lines show the resource-use of females and males, respectively, and the yellow line shows the total resource-use distribution of consumers (males plus females). (b and e) cumulative trait distributions of resources A and B in green (resource B is on the left, and resource A is on the right), and the cumulative distributions of resource use by males and females in blue and red, respectively. For each sex, the resource use is quantified by comparing the area between that sex's distribution and resource A's distribution with the area between that sex's distribution and resource B's distribution. This gives an indicator of how closely a sex's distribution matches the distribution of a resource. (c and f) summary of the resource use of males (right half of square, in blue) and females (left half of square, in red). Saturated colors indicate the use of resource B, while unsaturated colors indicate the use of resource A. The parameters are (for a-c)* $\beta = 0.22$, $x_0 = 2.5$, *3 loci, mutation order [B,M,F],* $w_{max} = 51$ *and (for d-f)* $\beta = 4.64$, $x_0 = 2.5$, *1 locus, mutation order [F,M,B], any* w_{max}

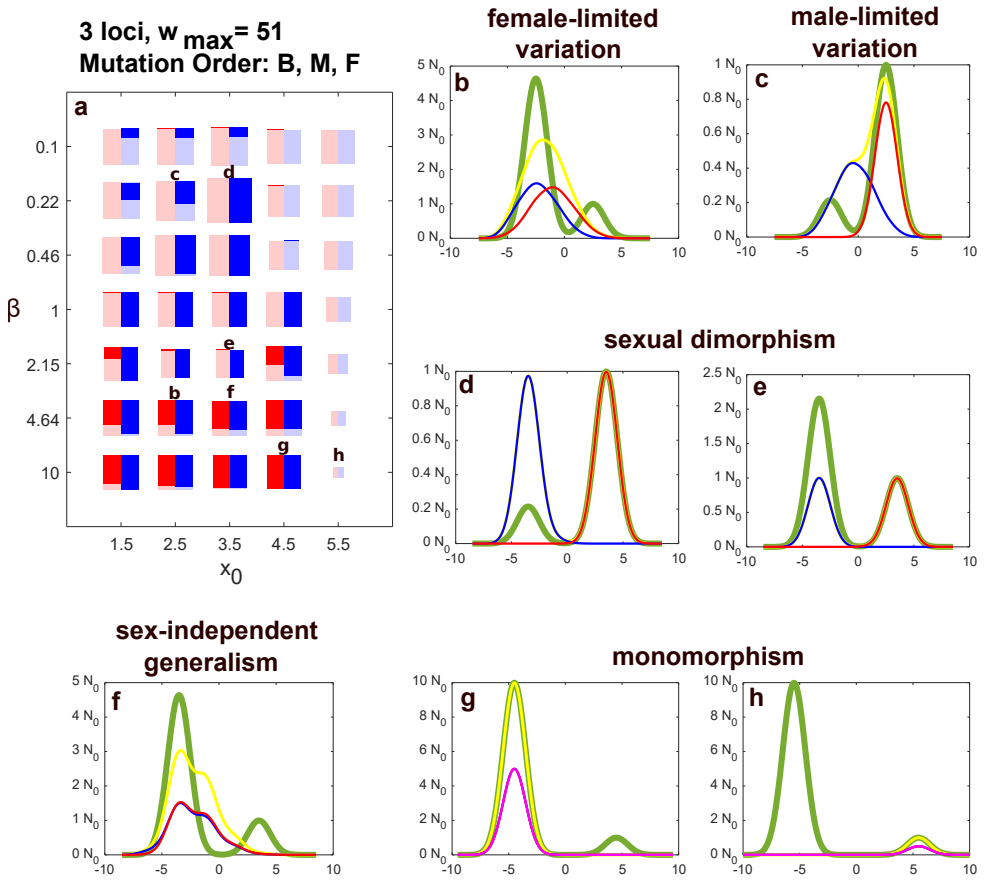

Figure 3.3: **Possible outcomes of three locus model:** *three B-alleles are required to switch from resource A to resource B, the maximum fitness is $w_{max} = 51$, and the order of mutations is [B,M,F]. (a) summary of results for different values of β and x_0. Square color indicates the resource use of males and females (see fig. 3.2), and square size indicates the population size (corrected to total resource abundance, $N_0 + \beta N_0$). Subplots b-h show selected outcomes in more detail, with the green line showing the distribution of resource traits, red and blue lines showing the trait distributions of females and males, respectively, and the yellow line showing the total trait distribution of consumers (males and females). When the male and female trait distributions overlap, they are shown in magenta instead. Possible results include (b) males exclusively use resource B and females use both resources, resulting in a relatively small population size because males specialize on the superior resource; (c) males use both resources, and females exclusively use resource A, resulting in relatively high population size because females specialize on the superior resource; (d) females use the superior resource, resulting in high population size; (e) females use the inferior resource, resulting in low population size; (f) both sexes use both resources, and the trait distributions of males and females almost overlap; (g) all individuals use resource B which is the superior resource; (h) the fitness valley between the two resources is so large (i.e. x_0 is very large) that the population is unable to adapt to using resource B. Therefore, all individuals use resource A even though it is inferior, resulting in a small population size.*

between sex ratio and optimal morph frequencies, but this constraint vanishes when $\beta = 1$.

Outcomes when $m = 1$: polymorphism, sex-limited polymorphism, and sexual dimorphism

First, we report on the results in the extreme case where a single B-allele is sufficient to shift the phenotype to optimal exploitation of resource B (i.e. $m = 1$). In such a setting, no intermediate genotypes are created and, hence, recombination does not constrain the evolution of a polymorphism. The evolutionary outcomes can be grouped into three categories: sexual dimorphism, sex-limited polymorphism, and polymorphism not linked to sex. The outcomes are affected by β and mutation order, but not by w_{max} or x_0. When recombination does not pose a constraint, all evolutionary outcomes lead to a perfect match between the trait distributions of consumers and that of resources (Fig. 3.4), and result in a final population size of $N_0 + \beta N_0$.

If the first B-allele to invade is an allele that affects both sexes (Mutation orders [B,F,M] or [B,M,F]), then a sex-independent polymorphism evolves (Fig. 3.4d). Here, both sexes exhibit two distinct morphs with morphs specializing on one of the two resources.

The evolutionary outcomes is different when a sex-limited B-allele invades first. In this case, a sex-limited polymorphism tends to evolve where one sex specializes on the superior resource and the other sex is polymorphic for resource use (Fig. 3.4b and c). A sexual dimorphism only evolves when both resources can sustain the same number of consumers ($\beta = 1$, Fig. 3.4). Mutation order is in this case the sole determiner for which sex uses which resource (and which sex is polymorphic for resource use). If male-limited B-alleles invade first, then the evolutionary outcome is that males use resource B more than females do (either because males are monomorphic for resource B or because females are monomorphic for resource A). Likewise, if female-limited B-alleles invade first, then females evolve to use resource B more than males do.

Outcomes when $m \geq 2$ and $\beta = 1$: sexual dimorphism or monomorphism for resource A

Next, we consider scenarios in which $m \geq 2$ and $\beta = 1$, i.e. the two resources can sustain equally many individuals (any squares with $\beta = 1$ in Fig. 3.5). In this case (assuming unbiased sex ratios $s = 0.5$) a sexual dimorphism allows for optimal exploitation of the two resources, while the efficacy of a polymorphism is compromised by recombination. There are three possible evolutionary outcomes: a sexual dimorphism with females using resource B, a sexual dimorphism with males using resource B, and a monomorphism in which all individuals use resource A. Note that, unlike the single-locus case, there is no evolution of generalism (or a polymorphism) that is unrelated to sex.

When a sexual dimorphism evolves, either sex can specialize on either resource. Which sex specializes on which resource is solely determined by the order in which mutations occur: Whichever sex evolves towards using resource B first, ends up using it in the final population.

The monomorphism for the ancestrally used resource A remains stable when the population is unable to cross the fitness valley to adapt towards using both resources.

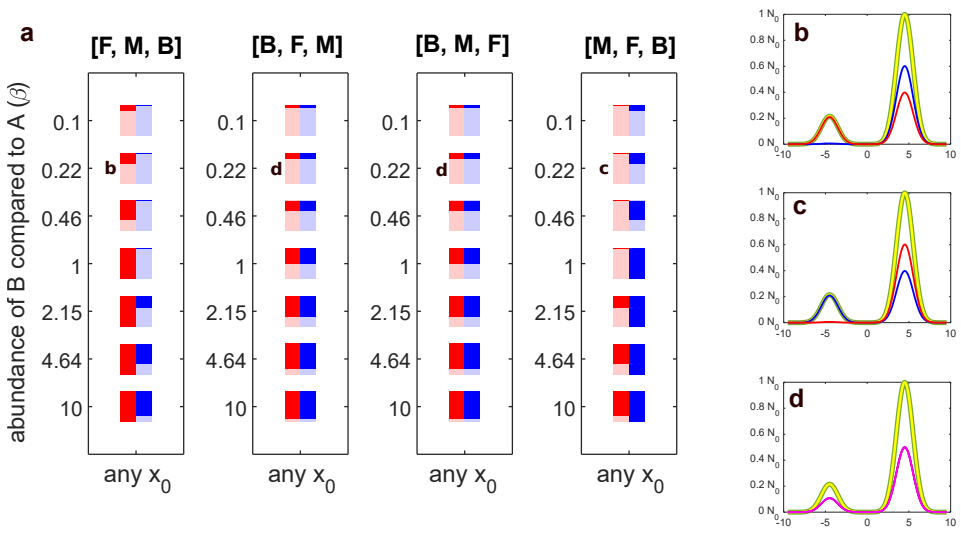

Figure 3.4: **Results for one-locus model ($m = 1$)** *(a) outcomes of the one-locus model depend solely on β and mutation order (see figures 3.2 and 3.3 for an explanation of the graphs). The temporal order of mutations is given in brackets; (b) if the female-limited locus mutates first, females end up using resource B more than males do and (c) the opposite happens when the male-limited locus mutates first. (d) If the first mutation occurs at a locus that affects both sexes, a sex-independent polymorphism evolves.*

This occurs when the costs of recombination are high, i.e. when m is large, x_0 is large, and/or w_{max} is small.

Various outcomes when $m \geq 2$ and $\beta \neq 1$

We now turn our attention to scenarios in which both constraints occur simultaneously: recombination limits the efficacy of polymorphism and unequal resource abundances limit the efficacy of ecological sexual dimorphism. In this case, we classify our results into four broad categories: sexual dimorphism, monomorphism (all individuals use the same resource), sex-limited variation (one sex specializes on the more abundant resource, and the other sex uses both), and generalism unrelated to sex (both sexes use both resources). The last two outcomes are analogous to the sex-limited polymorphism and sex-independent polymorphism in the one-locus model, respectively, but our different terminology here addresses the fact that intermediate phenotypes (which were absent in the one-locus model) are common in the multi-locus models. In the case of a sexual dimorphism, it is also important to take note of the sex that specializes on the superior resource, as this considerably impacts population size due to female demographic dominance.

In the multi-locus model ($m \geq 2$), sexual dimorphism can evolve even if one resource is superior than the other, particularly if x_0 is large. This outcome was not found in the one-locus model ($m = 1$). Similarly as above, the order of mutations determines the final evolutionary outcome. Resource B is used by whichever sex happened to evolve towards using resource B first. In the case where dimorphism evolves, the sex ratio,

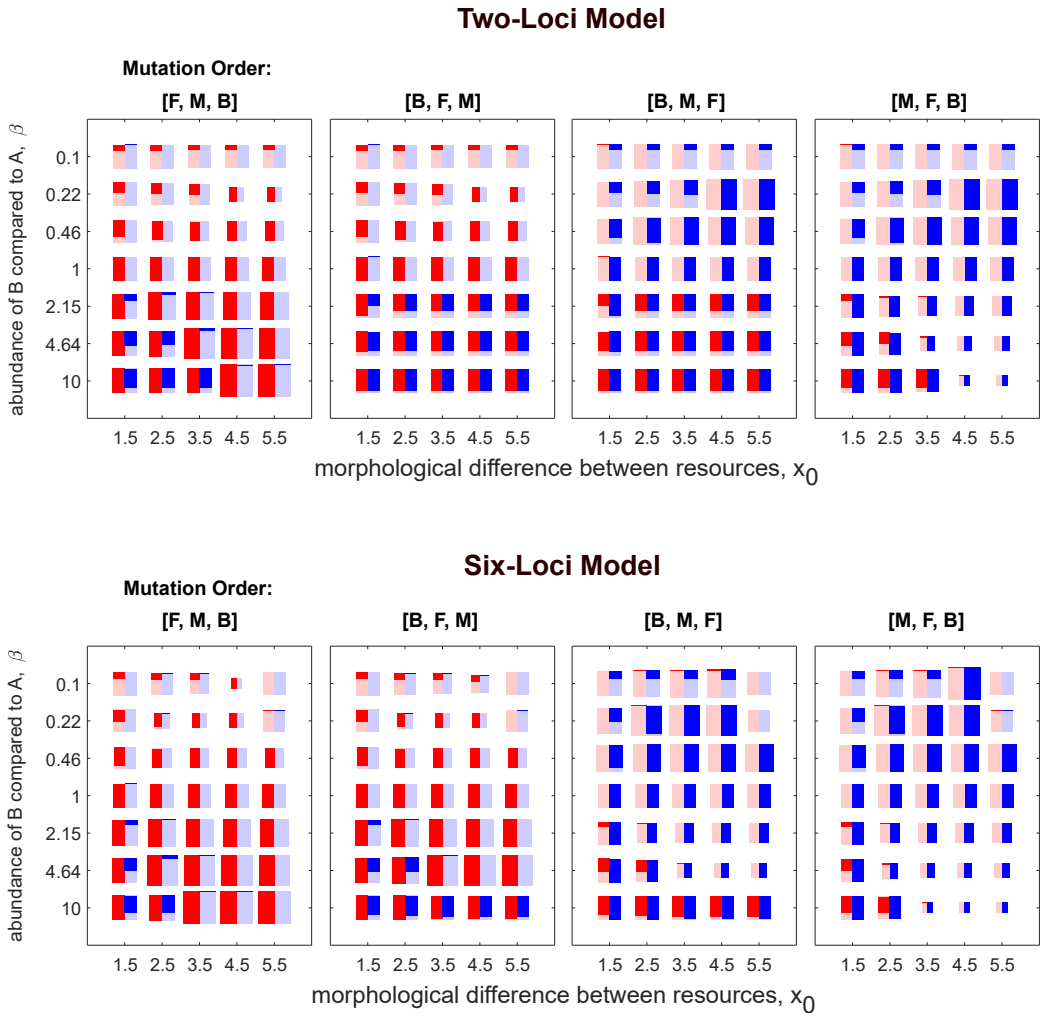

Figure 3.5: **Results for multi-locus models** *Results are shown for $m = 2$ and $m = 6$. In both cases the maximum fitness is very high ($w_{max} = 50001$). The temporal order of mutations is given in brackets. See figures 3.2 and 3.3 for an explanation of the graphs.*

$s = 0.5$, does not match the optimal morph frequencies. When one resource can sustain more individuals than the other, this has considerable impact on the population size. If females use the superior resource, population size equilibrates at a much higher value than in cases where the males use the superior resource. This is due to our assumption that population growth is determined exclusively by female reproduction (demographic dominance). Hence, mutation order alone can determine whether a population evolves towards a state with high population fitness where females use the superior resource without competition from males, or, alternatively, towards a state with much lower population fitness where males use the superior resources while females specialize on the inferior resource. Once one of these states evolves, it no longer switches towards

the other state even if new mutations occur.

There are two types of monomorphisms than can evolve: A population can fail to evolve towards resource B, resulting in the population remaining in the state of using only resource A. This predominantly happens when m is large, x_0 is large, and/or w_{max} is small. Additionally, it is possible for populations to evolve to use only resource B. The latter happens only under a few parameter combinations, specifically when resource B is much superior that resource A (high β) and x_0 neither too low nor too high: A low x_0 instead results in sex-limited variation or sex-independent generalism, while a high x_0 instead prohibits the population from evolving to use resource B at all.

Generalism that is not linked to sex occurs only under mutation orders where the first introduced B-alleles affect both sexes. When $m = 2$, generalism only occurs when $\beta > 1$ and when x_0 is sufficiently high. For larger values of m the evolution of sex-independent generalism is further impaired.

3.4 Discussion

We fill an important gap in the literature of potentially sexually dimorphic niche use (Bolnick and Doebeli 2003, Cooper et al. 2011, De Lisle 2019, Li and Kokko 2021, De Lisle et al. 2022), by considering two niches that do not necessarily sustain the same number of individuals. Unequal abundance or quality of the two niches creates a constraint for the evolution of sexually dimorphic niche use: unless sex ratios fortuitously match the resource, the sex using the inferior niche will effectively experience more crowding, and the consequent sex-specifically acting density dependence can hamper sexually dimorphic niche use. We have thus identified an additional constraint that deviates from those discussed in the literature previously, e.g. that sites might not always offer both resources (Li and Kokko 2021); our effect operates in the absence of any spatial heterogeneity of resources.

Despite the hampering effect that occurs when one resource can sustain more individuals than the other, a key result of our model is that ecological sexual dimorphism can evolve under these conditions, as long as niche use is impacted by more than one locus and intermediate genotypes are strongly selected against. The outcomes are often path-dependent, as they depend on which mutations arise first. Thus, the population may evolve towards polymorphism or, instead, solve the problem (even if somewhat inefficiently) via sexually dimorphic niche use. Highly interestingly, our model includes female demographic dominance (such that total reproductive output is dependent on female, rather than male, performance), but this does not predict that females are more likely to specialize to use the superior resource. If they do, the population as a whole does better in terms of its equilibrium size, but the evolutionary outcome is not dictated by this asymmetry, but instead by the temporal order of which sex evolves first.

Our finding that either of the two sexes can shift their traits first, which then weakens the selection on the other sex to do so, arises in other contexts too: for example, inbreeding avoidance can lead to either males or females dispersing, without females being necessarily selected to do so more strongly despite the reproductive roles being different (Perrin and Mazalov 2000, see Li and Kokko 2019 for a verbal explanation); likewise, parental care provided by one sex may weaken the selection on the other to contribute (McNamara and Wolf 2015). A similar argument has also been made for the

evolution of single-sex helping in some eusocial animals (Davies et al. 2016). These, together with ours, are all examples where the sexes are placed on widely divergent evolutionary trajectories based on small and initially random asymmetries (Lehtonen and Kokko 2012), but with potentially asymmetric consequences for population fitness.

Differences in population fitness may start playing a role if factors outside our current modeling effort are included: if a large (sub)population can produce more individuals that disperse and colonize other areas, while small ones are more extinction-prone, then female performance can form stronger weights when deriving results for selection as a whole (Harts et al. 2014). Our model shows that a population can sometimes evolve towards either polymorphic or sexually dimorphic resource use, and therefore, that the same resource distribution can result in different equilibrium population sizes. Population performance (which in our context can be measured as the equilibrium population density) is best when females use the superior resource with males specializing to feed on the inferior resource, followed by a general polymorphism where a suitably small (depending on β) proportion of individuals use the inferior resource, followed by the poorest option for population performance, where males use the superior resource and females the inferior one. Therefore, when taking meta-population dynamics and extinction risk into account, populations in nature might be more likely to have females using the superior resource, but this requires spatial effects to play a role.

Like any model, ours comes with limitations. For example, or model assumes that the consumer species is haploid. This has the important consequence that no intermediate phenotypes occur when a polymorphism is controlled by a single locus. For the same to be true in a diploid organism, it is not only necessary that the polymorphism is controlled by a single locus, but also that one allele is dominant over the other. However, if the locus has additive dominance (and hence heterozygotes have an intermediate phenotype), the polymorphism is subject to the same constraint as the multi-locus scenarios in our haploid model. Hence, when considering a polymorphism in a diploid organism, it is necessary to consider not only the number of loci involved, but also the dominance patterns at these loci.

We also do not consider that the resources might differ in more nuanced ways than just abundance and quality. We assumed that the two modeled resources are essentially interchangeable, as this creates a situation where either sexual dimorphism or a polymorphism that is unlinked to sex could in principle solve the problem of resource use. This does not take into account that sexes may differ in their nutritional demands for physiological reasons. For example, in mosquitoes, both sexes feed on nectar and other sugar sources, while females are the only sex that also take in blood meals (Barredo and DeGennaro 2020); since protein-rich meals aid egg production, a situation with both females and males being polymorphic for seeking vs not seeking blood meals is unlikely to arise. The mosquito example also highlights that we did not consider that utilizing the alternative resource might be more risky or require alternative physiological adaptations (rather than just a quantitative trait value).

The mosquito example is not an isolated one: Similarly, in many pollinators, females forage for pollen much more than males do (Smith et al. 2019). Whenever there are sex-specific nutritional needs, the situation is likely to shift to make sexually dimorphic niche use more likely. Our model can still give some insights here, because the sexual dimorphism still results in reduced intraspecific competition between opposite-sex

individuals. One could thus hypothesize male pollinators specializing on flowers with little pollen, that help them avoid competition by females that in turn seek pollen-containing flowers. The extent of specialization will, however, be impacted by the possibility that sites may not contain resources that cater for both sexes (Li and Kokko 2021); specialization remains advantageous if males and females do not need to forage close to each other, which may arise through multiple causal routes: physical proximity may only be required during mating (many ungulates, Ruckstuhl and Neuhaus 2006), a highly mobile species can feed its young biparentally while foraging in different parts of the habitat (albatrosses, Patrick and Weimerskirch 2014), or a large part of the season may be spent off the breeding grounds (migrating birds, Nebel 2005).

As a whole, our ecological explanation of sexual dimorphism should not be viewed as being incompatible with explanations based on sexual selection or brood care adaptations, but rather as an additional evolutionary process with the potential to shape sexual dimorphism. On the other side of the question - polymorphism without sexual dimorphism - the question has often been phrased as ecological sexual dimorphism being an alternative to polymorphisms that could even lead to speciation (Cooper et al. 2011, Pincheira-Donoso et al. 2018). Although ours is not a speciation model, our results are of some relevance in this context too, as we highlight how initial small asymmetries, such as the occurrence of one mutation ahead of another, can start moving the population towards either a polymorphism, which then could lead to assortative mating (which we did not consider), or to sexual dimorphism, the latter offering no direct route to reduced gene flow and speciation (Van Dooren et al. 2004).

3.5 Conclusion

We have investigated how a single consumer species can evolve to use two different niches. We show, that sex-limited or sex-independent polymorphism easily evolve when niche-use is governed by a single locus, but that the prospects for either type of polymorphism is impaired when multiple additive loci are involved, particularly if intermediate phenotypes have very low fitness (high x_0 in our model). In these scenarios, sexual dimorphism for niche-use can evolve even if optimal sex ratios do not match optimal morph ratios, i.e. if one niche can support more individuals than the other niche. Interestingly, our model shows that sexual dimorphism can be evolutionarily stable irrespective of which sex uses which niche, but that the population size is higher when females use the superior niche. Rather than merely asking which evolutionary outcome is favored, it becomes necessary to ask which evolutionary state can evolve more quickly. Hence, when males and females use different niches, it is important to consider not only the environment of that species, but also its evolutionary history, e.g. by considering which of the two niches is ancestral and hence whether males or females evolved to use the novel niche.

Acknowledgements

We want to thank Colin Olito, Angela Nava Bolaños, Benjamin Jarrett, and Xiang-Yi Li Richter for fruitful discussions.

Competing Interests

I really wanted to conclude
(with purely selfish motivation)
that girls should get the better food.

While this deduction has appeal,
to base it just on procreation
would contradict my core ideals.
So, I'll resist the sweet temptation

... and declare no competing interests.

4

Sex ratio theory for facultative parthenogens: from fortuitously optimal stick insects to the origin of haplodiploidy in Hymenoptera

Authors: Kora Klein and Hanna Kokko

Abstract

Sex ratio theory typically assumes obligate sex; rare exceptions with facultative sex typically consider species-specific cases of cyclic parthenogens. We show that facultative parthenogenesis selects for female-biased sex ratios by elevating the class reproductive value of females. The degree of this bias depends on the future rate of parthenogenesis, complicating calculations for cyclic parthenogens. In stable environments (with stable rates of parthenogenesis), however, the optimal sex ratio becomes easily achievable: unbiased sex ratios among sexually produced offspring and 100% female parthenogenetically produced offspring (example: stick insects and mayflies) yield optimality for any rate of parthenogenesis. Constraints posed by the sex determination system consequently impact the spread of parthenogenesis. In stick insects, all parthenogenetically produced offspring are female, which promotes parthenogenesis. In birds and haplodiploids, parthenogenesis produces males, hampering the spread of parthenogenesis. Even so, parthenogenesis can still invade and reach an equilibrium frequency, if the reproductive value of parthenogenetically produced brood is compromised by less than 50%. We argue that this condition is not met in birds due to inviability of WW offspring and homozygosity in ZZ offspring. For haplodiploids, on the other hand, our work resurrects a somewhat forgotten idea by Bull (1981) that haplodiploidy in Hymenoptera evolved from a diplodiploid ancestor with complementary sex determination.

Keywords: facultative parthenogenesis, evolutionary constraints, thelytoky, haplodiploidy, complementary sex determination, inbreeding

4.1 Introduction

In obligately sexual animals, Fisherian sex ratio theory typically predicts equal parental investment into sons and daughters (Gardner 2023 and references therein): Each

individual has a mother and a father, and as a result the total (class) reproductive value of males in a population is equal to that of females. If one sex is more common than the other, then the average individual of the rarer sex has more offspring than the average individual of the more common sex. Therefore, parents who produce more offspring of the rarer sex benefit by giving rise to more grand-offspring. This leads to negative frequency dependent selection favoring unbiased sex allocation.

Sex allocation has been the subject of substantial theoretical and empirical investigation, and a number of factors have been identified that can select for male-biased or female-biased sex allocation. Some prominent factors include local mate competition, local resource competition, and non-linear relationships between parental investment and offspring fitness (West 2009, Brunet 1992). However, most sex ratio theory has been derived for obligately sexual organisms, while facultatively parthenogenetic organisms have received less attention. Furthermore, models that do investigate facultative sex tend to be very taxon-specific and focus on fairly complicated systems. For example, many models are inspired by cyclic parthenogens, such as *Daphnia*, that live in unpredictable environments (Gerber, Booksmythe and Kokko 2018, Aparici et al. 1998). A much simpler point has received very little attention: Facultative parthenogenesis selects for female-biased sex ratios simply because some individuals (those that are produced asexually) only have a mother and no father.

Here, we focus on facultative parthenogens in stable environments (with stable rates of parthenogenesis) that differ in the sex ratio of asexually produced offspring. At the one extreme, stick insects can reproduce through thelytoky where asexually produced offspring are (almost) always female. At the other extreme, haplodiploidy (arrhenotoky) describes a system where asexually produced offspring are always male. Note that it is unconventional to view haplodiploids as facultative parthenogens. We believe that this is a useful and valid perspective, because some individuals (males) are produced parthenogenetically, while others (females) are produced sexually. As we show in this paper, including haplodiploids in a model of sex allocation under facultative sex leads to interesting insights about the evolutionary path towards haplodiploidy.

Our choice of stick insects and solitary haplodiploids to illustrate features of our model stems from their shared feature that the rate of parthenogenesis is relatively stable between consecutive generations - in contrast to cyclic parthenogens, where some generations can be entirely asexual, and other generations entirely sexual. We discuss stick insects to aid conceptual clarity, as it helps us to go through the entire argumentation in a specific biological setting. This choice is not meant to imply that the model only applies to stick insects. There are many other taxa in which parthenogenesis produces only females, including termites (Matsuura et al. 2004, Vargo 2019), a scorpion (Braga-Pereira and Santos 2021), lizards (Fujita et al. 2020), and mayflies (Funk et al. 2010, Liegeois et al. 2023). However, taxa differ from each other in their ecological details. We have therefore chosen one (stick insects) for illustrative purposes and discuss all other examples in the Discussion.

Gardner (2014b) investigated optimal sex allocation in haplodiploids (arrhenotoky without thelytoky; see Glossary) and concluded that females should invest equally into sons and daughters because two effects work simultaneously and cancel out exactly: (1) The class reproductive value of females is twice that of males. If this effect worked on its own, it would select for female-biased sex allocation. (2) Sons are twice as effective at transmitting their mother's genes to the next generation (because males

do not have a father). If this effect worked alone, it would select for male-biased sex allocation. We generalize Gardner's first argument by stating that any form of facultative parthenogenesis (not only haplodiploidy) increases the class reproductive value of females.

Furthermore, we show that the argument inherent in Gardner's 2nd factor also generalizes: asexually produced progeny are the ones that are more efficient at transmitting their mother's genes; in haplodiploids they happen to be male, while in stick insects they are female. Hence, in stick insects, the average daughter is more efficient at transmitting their mother's genes than the average son (because some daughters are asexually produced). As a result, the two effects do not cancel out in stick insects; instead, both effects select for female-biased sex allocation. We will show below that, as long as the rate of asexual reproduction is stable between consecutive generations, thelytoky automatically achieves an optimal degree of female-bias in sex allocation for any rate of asexual reproduction. In contrast, the asexual production of males generates suboptimal sex-ratios.

The sex of parthenogenetically produced offspring can be constrained by the sex determination system of a species (Engelstädter 2008). In ZW systems (ZW females and ZZ males), automixis produces WW and ZZ offspring, leading to the loss of half of all offspring (inviable WW), while the the other half develops as males. In XY systems (XX females and XY males) with automixis or apomixis, all asexually produced offspring are female because they can not receive a Y-chromosome from their mother (and the same is true under apomixis in a ZW system). Constraints caused by the sex determination mechanism thus distort the sex ratio either in a favorable (female-biased) or a detrimental (male-biased) direction. This leads to the insight that facultative sex is easier to establish in the former case (e.g. stick insects) than in the latter (e.g. birds, where unfertilized eggs sometimes hatch, but there are no species that do this regularly enough to be classified as facultatively sexual, Ramachandran and McDaniel 2018).

Our paper develops two models on sex ratios in facultative parthenogens. We first derive the optimal sex ratio rules for a given rate of parthenogenesis, thereafter we turn the question around and examine the spread of (facultative) parthenogenesis if the sex determination system creates a constraint for the sex that can be produced asexually. Finally, we discuss an importnat case of complementary sex determination (CSD) in a diploid organism (as recently demonstrated in a butterfly, van't Hof et al. 2024). CSD refers to a system where female development requires heterozygosity at the sex-determining locus. Bull (1981) argued that diplodiploid CSD presents a plausible origin of haplodiploidy in Hymenoptera. We expand on this idea by arguing that diploid CSD provides a mechanism to avoid the dead-end that otherwise awaits male-producing parthenogenesis: diplodiploid CSD avoids the inviable-WW cost that ZW systems suffer from, and it also avoids the inbreeding cost that is a problem for haplodiploid CSD (inbreeding producing inviable diploid males).

4.2 Methods and Results

We present two models. Our first model ('Prescient Optimality Model') derives what we call the prescient optimum, defined as the optimal sex ratio when organisms are perfectly informed of the next generation's rate of parthenogenesis and sex ratio. We

show a simple relationship between the prescient optimum and the rate of parthenogenesis. To keep the analysis simple, we assume discrete generations in a well-mixed population (no local mate competition or local resource competition between siblings), that sons and daughters are equally costly to produce, and that parental investment into offspring gives linear returns on investment. We further assume the adult sex ratio (the ratio among mature adults) is the same as the sex ratio at birth/hatching (the production of sons vs. daughters). Importantly, in the prescient optimality model, we consider a species where there is perfect information about the future environment and parents can plastically adjust the sex ratios of their offspring without constraints. With this setup in mind, we derive the prescient optimum for a population where a proportion $\overline{\alpha}$ of offspring are produced parthenogenetically. We then show that, if the rate of parthenogenesis is constant over time, a system where asexually produced offspring are always female (e.g. thelytoky of stick insects) achieves, without actually being prescient, a system of sex allocation that is optimal in the prescient sense. This happens without there being any selection to modify sex ratios of either sexuals (that thus can remain at 1:1 sex allocation) or asexuals (that likewise can remain at the sex ratio dictated by the sex determination system). This statement is true regardless of the value of $\overline{\alpha}$. It ceases to be true in cyclic environments, where the proportion of parthenogens varies over time, and where evolutionary knowledge of likely sex ratios in the near future impact current decisions.

While our prescient optimality model supports the intuition that female-biased sex ratios make it easier for parthenogenesis to spread, its assumption of a specific $\overline{\alpha}$ prevents it from examining this statement explicitly. We therefore proceed to our second model ('Invasion of Asexuality Model', or 'Invasion Model' for short). Here we reverse the question to ask: given a specific - not necessarily optimal - sex ratio among the asexually produced offspring, which may differ from the sex ratio among sexually produced ones, what are the prospects for asexuality to invade and/or to fix? This includes the possibility that the system equilibrates at a polymorphism with both sexual and asexual reproduction. In the invasion model, we are specifically interested in the role of constraints dictating the ease of evolving asexuality. Therefore, we focus on the case where the sex ratio among sexually produced broods remains unbiased, and that of the asexually produced broods is constrained by the sex determination system, such that asexuality produces either only males or only females.

While we do not model the mechanisms of sex determination explicitly, we consider, in the invasion model, the consequences of the following alternatives: (i) automixis in an XY system, where asexually produced offspring are always female (results also extending to apomixis in either an XY or ZW system), and (ii) a ZW system with automixis, where asexuality halves the number of surviving offspring and the survivors are always male. We then proceed to discussing the possibility of diplodiploid complementary sex determination (DD-CSD for short), arguing that it is a starting point from which haplodiploidy may have evolved.

4.2.1 Model 1: Prescient Optimality

Reproductive Value

Before describing the models, it is useful to briefly review the concepts of individual and class reproductive value. Class reproductive value refers to the total reproductive value of a group of individuals (Taylor 1990, Grafen 2006). For example, the class reproductive value of females refers to the percentage of gene copies of a future generation that descents from gene copies that are currently in a female. In obligately sexual organisms with autosomal inheritance, the class reproductive value of females is the same as the class reproductive value of males. This is because each individual inherits half their genes from their mother and the other half from their father.

The class reproductive value, in itself, does not depend on the sex ratio of the population. But since more individuals of the more numerous sex contribute to the class reproductive value of that sex, the individual reproductive value declines with the number of same-sex competitors (Fig. 4.2). This frequency dependence is captured by individual reproductive value, which is quantified it a similar fashion as class reproductive value above: when considering a gene copy in the distant future, the individual reproductive value describes the probability that this gene copy is descended from the focal individual. Due to negative frequency dependence, the average individual reproductive values of females and males do depend on the sex ratio.

Prescient Optimum

We use the term "prescient optimum" to describes the optimal sex ratio resulting from a situation when there is perfect information about the rate of parthenogenesis in the next generation and mothers are able to optimize the production of sons and daughters to maximize the reproductive value of the whole set of offspring. While perfect information may remain rare in reality, we use this as the ideal benchmark, to be later compared to the actual sex ratios achieved by organisms with known sex determination systems acting as constraints.

Practically, we derive the prescient optimum to result from the demand that marginal returns on investment must be equal between parthenogenetically produced females and parthenogenetically produced males, as well as between sexually produced females and sexually produced males (otherwise there would be selection on either asexual or sexual mothers to adjust the sex allocation). Hence, prescient optimality is achieved if the individual reproductive values of parthenogenetically produced females equals that of parthenogenetically produced males and the individual reproductive values of sexually produced females equals that of sexually produced males.

It is not necessary that all mothers use the same sex allocation. For example, while the familiar pattern of equal investment into sons and daughters in obligately sexual diploid organisms is usually achieved by fair meiosis, frequency dependence can also operate in a population with split sex allocation (also known as monogenic reproduction, Baird et al. 2023). Here individuals specialize in the production of daughters or sons (but see Verner 1965 for problems caused by local variability in sex ratios in finite populations, particularly if they are not panmictic).

General Model Formulation

Our goal is to estimate the optimal sex allocation of the parent generation, t, which requires us to estimate the class reproductive values of males and females of the offspring generation, $t+1$. The class reproductive values, in turn, are estimated by investigating the proportion of paternally vs. maternally inherited gene copies in the grand-offspring generation, $t+2$. This makes the class reproductive values of generation $t+1$ depend on the class reproductive values in generation $t+2$ which in turn depends on the class reproductive values in generation $t+3$ and so on ad infinitum. We will first formulate the equations in this general way and then make an additional simplifying assumption under which we only need to consider the three generations, t, $t+1$, and $t+2$. We also assume no age structure beyond the need to distinguish between eggs and hatchlings (Figure 1).

We use $\overline{\alpha}_t$ to denote the population-wide rate of parthenogenesis in generation t. To be precise, $\overline{\alpha}_t$ denotes the proportion of eggs laid by generation t are parthenogenetically (as opposed to sexually) produced. In stick insects, individual females specialize in either asexual or sexual reproduction, and therefore $\overline{\alpha}_t$ can be conceptualized as the proportion of females who reproduce parthenogenetically. In Hymenoptera, individual females usually reproduce both sexually and asexually, and for them, $\overline{\alpha}_t$ should be interpreted as the average proportion of unfertilized eggs. Our model is equally applicable to either case.

$z_{a,t}$ and $z_{s,t}$ denote the post-hatching sex ratios (percentage male) of eggs laid by generation t among asexually and sexually produced broods, respectively (Note that this is equivalent to the sex-ratio among hatchlings of generation $t+1$. We choose to denote it as t because sex ratios are under parental control). For example, $\overline{z}_{a,t} = 0.2$ indicates 20% of asexually produced hatchlings are male (and the other 80% of asexually produced offspring are female). Similarly, $\overline{z}_{s,t} = 0.2$ indicates 20% of sexually produced hatchlings are male. Below, we will calculate the post-hatching sex ratio of the population, which we denote $\overline{z}_t$. This variable includes the effects of an additional parameter δ, which denotes any disadvantage of asexual reproduction. In the supplementary material, we distinguish between two types of costs: hatching failures of parthenogenetically laid eggs (e.g. the death of WW embryos) and reduced fecundity of parthenogenetically produced adults (e.g. due to deleterious recessive alleles). Most results generalize to both types of costs and we therefore focus on the simpler case, where δ only captures hatching failures.

In order to derive the class reproductive values of generation $t+1$ it is useful to first derive the proportion of males that are asexually produced. We denote this proportion as $P_{t+1}(asex \| ♂)$; it is given by

$$P_{t+1}(asex \| ♂) = \frac{P_{t+1}(♂ \cap asex)}{P_{t+1}(♂)} \tag{4.1}$$

where $P_{t+1}(♂ \cap asex)$ denotes the proportion of hatched individuals that are male and asexually produced, while $P_{t+1}(♂)$ denotes the proportion of hatched individuals that are male. These are calculated as:

$$P_{t+1}(♂ \cap asex) = \frac{(1-\delta)\overline{\alpha}_t z_{a,t}}{1-\delta\overline{\alpha}_t} \tag{4.2}$$

and

$$\bar{z}_t := P_{t+1}(\male) = \frac{(1-\delta)\bar{\alpha}_t z_{a,t} + (1-\bar{\alpha}_t) z_{s,t}}{1-\delta\bar{\alpha}_t} \tag{4.3}$$

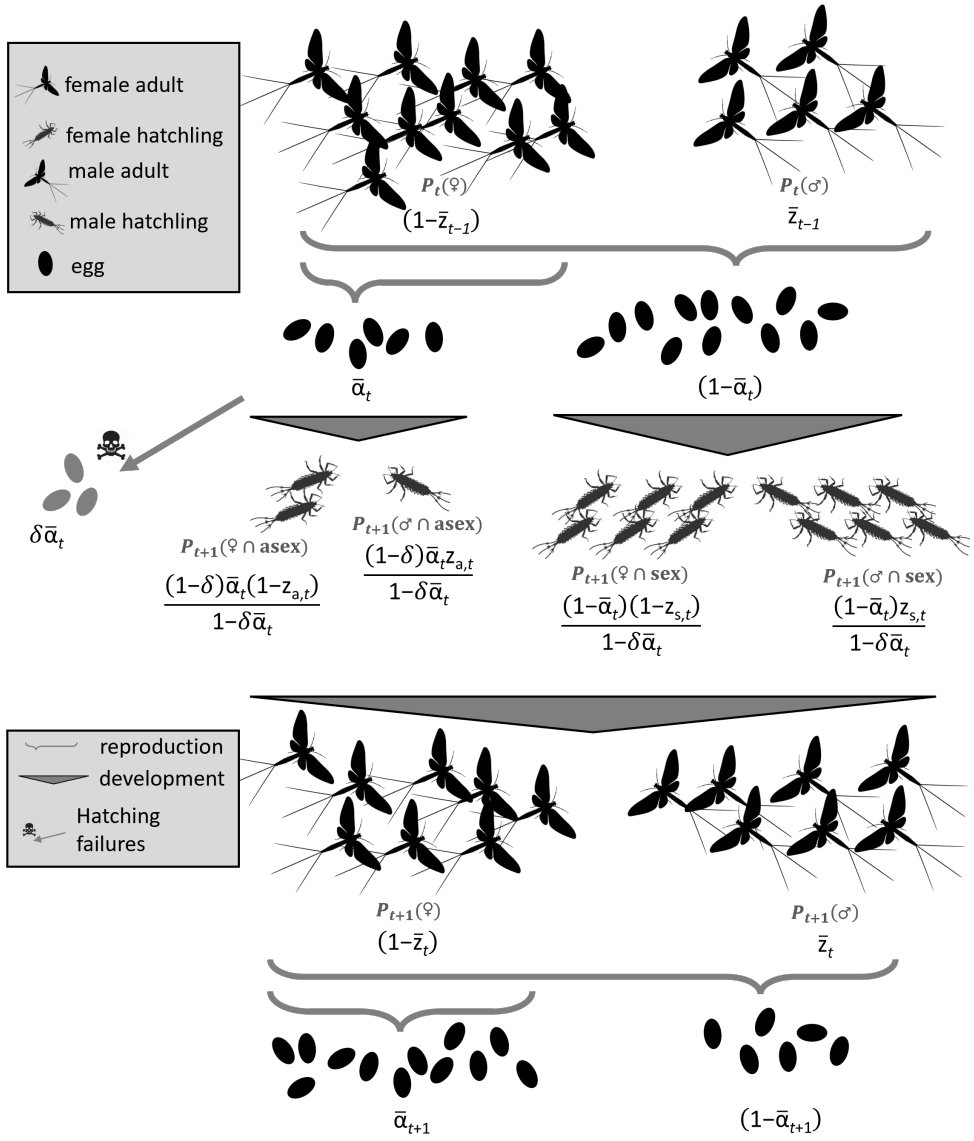

Figure 4.1: **Conceptual illustration of equations 4.1 to 4.5 of the Prescient Optimality Model:** *Individuals in generation $t+1$ are devided into four groups: parthenogenetically produced females, $P_{t+1}(\female \cap asex)$; parthenogenetically produced males, $P_{t+1}(\male \cap asex)$; sexually produced females, $P_{t+1}(\female \cap sex)$; and sexually produced males, $P_{t+1}(\male \cap sex)$. The parameters illustrated here are: the rate of parthenogenesis with $\bar{\alpha}_t = 1/3$ and $\bar{\alpha}_{t+1} = 2/3$; the cost of asexuality $\delta = 1/2$; the sex ratio among parthenogenetically produced offspring $z_{a,t} = 1/3$; and the sex ratio among sexually produced offspring $z_{s,t} = 1/2$. The mean sex allocation $\bar{z}_t$ is derived in equation S2.1.*

Our notational choice links generations t and $t+1$ in that $\bar{z}_t$ equals $P_{t+1}(\male)$: the sex allocation decisions of the parental generation, $z_{a,t}$ and $z_{s,t}$, cause an observed post-

hatching sex ratio $\bar{z}_t$ among hatched young, and this is measured as the population-wide sex ratio in the offspring generation $(t+1)$. Our choice is to measure this after hatching failures (a potential cost of asexuality) have taken place and are accounted for.

At this point, some readers familiar with sex allocation theory might worry about our focus on the post-hatching sex ratio, rather than the primary sex ratio at fertilization. To be clear, we consider $z_{a,t}$ and $z_{s,t}$ to be the sex allocation decisions by generation t. The results on selection, however, end up depending on $\bar{z}_t$, and we present many of our results using this variable. For example, in birds, $z_{a,t} = 1$ because all asexually produced hatchlings are male, and the hatching failure of WW embryos is captured in the cost of asexuality, $\delta = 0.5$. In this case, it would be odd to attempt to define a population-wide sex ratio at fertilization (WW individuals will not hatch as either females or males), somewhat akin to situations discussed by Kahn et al. 2015 where certain situations do not permit quantifying an 'equal allocation' in any meaningful way. Our variable of interest, $\bar{z}_t$, provides a meaningful way to summarize the consequences of sex allocation decisions made by generation t, $z_{a,t}$ and $z_{s,t}$, as well as the rate of parthenogenesis, $\bar{\alpha}_t$.

Inserting equations 4.2 and S2.1 into equation 4.1, we get:

$$P_{t+1}(asex\|♂) = \frac{(1-\delta)\bar{\alpha}_t z_{a,t}}{(1-\delta\bar{\alpha}_t)\bar{z}_t} = \frac{(1-\delta)\bar{\alpha}_t z_{a,t}}{(1-\delta)\bar{\alpha}_t z_{a,t} + (1-\bar{\alpha}_t)z_{s,t}} \tag{4.4}$$

Similarly, the proportion of females that are parthenogenetically produced is given by

$$P_{t+1}(asex\|♀) = \frac{(1-\delta)\bar{\alpha}_t(1-z_{a,t})}{(1-\delta\bar{\alpha}_t)(1-\bar{z}_t)} = \frac{(1-\delta)\bar{\alpha}_t(1-z_{a,t})}{(1-\delta)\bar{\alpha}_t(1-z_{a,t}) + (1-\bar{\alpha}_t)(1-z_{s,t})} \tag{4.5}$$

These proportions can now be used to calculate the class reproductive values of males and females of generation t.

$$V_t^m = \left(\frac{1-P_{t+1}(asex\|♀)}{2}\right)V_{t+1}^f + \left(\frac{1-P_{t+1}(asex\|♂)}{2}\right)V_{t+1}^m \tag{4.6}$$

$$V_t^f = \left(\frac{1-P_{t+1}(asex\|♀)}{2} + P_{t+1}(asex\|♀)\right)V_{t+1}^f + \left(\frac{1-P_{t+1}(asex\|♂)}{2} + P_{t+1}(asex\|♂)\right)V_{t+1}^m \tag{4.7}$$

Also note that $V_t^f = 1 - V_t^m$.

The difference in class reproductive value between the sexes of generation $t+1$ is the basis for calculating the optimal sex ratio produced by the previous generation (generation t). Since we assume that sons and daughters are equally costly to produce, the sex ratio is optimal when the average individual reproductive value of males equals that of females (Fig. 4.2). The average individual reproductive value of males, v^m, and females, v^f, respectively, are:

$$v_{t+1}^m = \frac{V_{t+1}^m}{\bar{z}_t N} \tag{4.8}$$

$$v_{t+1}^f = \frac{V_{t+1}^f}{(1-\bar{z}_t)N} \tag{4.9}$$

where N denotes the population size. From equations 4.8 and 4.9, it follows that $v^m_{t+1} = v^f_{t+1}$ exactly when $\bar{z}_t = V^m_{t+1}$, i.e. when male production by one generation equals the class reproductive value of males in the next generation. Hence, denoting the optimal post-hatching sex ratio as $\bar{z}^*_t$, we get

$$\bar{z}^*_t = V^m_{t+1} \tag{4.10}$$

Prescient Model Formulation

In the prescient optimality case, our aim is derive the optimal sex allocation strategy by generation t assuming the availability of a perfect cue of the next generation's environment, in particular the rate of parthenogenesis in the next generation. We also assume that the sex determination system does not prevent individual mothers from making the optimal decision. Since we are interested in perfect optimality in this section, generation t can operate under the assumption that generation $t+1$ will, too, achieve prescient optimality, as does generation $t+2$ and so on. Mathematically, this assumption means that $v^m_{t+2} = v^f_{t+2}$ which is true exactly when $\bar{z}_{t+1} = \bar{z}^*_{t+1} = V^m_{t+2}$. We then derive the prescient optimum of generation t by calculating the class reproductive value of males, V^m_{t+1} (because $\bar{z}^*_t = V^m_{t+1}$).

Using the above reasoning and equations S2.6 and 4.10, we get:

$$\bar{z}^*_t = V^m_{t+1} = \left(\frac{1 - P_{t+2}(asex \| ♀)}{2}\right)(1 - \bar{z}_{t+1}) + \left(\frac{1 - P_{t+2}(asex \| ♂)}{2}\right)\bar{z}_{t+1} \tag{4.11}$$

which simplifies to

$$\bar{z}^*_t = V^m_{t+1} = \frac{\frac{1}{2}(1 - \bar{\alpha}_{t+1})}{1 - \delta\bar{\alpha}_{t+1}} \tag{4.12}$$

Equation 4.12 recovers the classic result that obligate sex (here modeled as $\bar{\alpha} = 0$) predicts unbiased sex ratios. More generally, it shows that as soon as a proportion of offspring are produced asexually, the optimal sex allocation becomes female-biased (although the bias becomes less pronounced if the cost of parthenogenesis, δ, is high).

Above, we assume that the cost of asexuality, δ, takes the form of hatching failures or brood size reductions that do not allow reallocating investments into other fitness components. The result that parthenogenesis favors female biased sex ratios also holds if the cost of asexuality is due to reduced fecundity or increased mortality of parthenogenetically produced offspring (for details see supplementary material). However, the details are different, thus any quantitatively precise test of equation 4.12, requires differentiating between different types of costs in any system where parthenogenetically and sexually produced broods differ in their sex ratio, i.e. if $z_s \neq z_a$ (supplementary material).

A key insight from equation 4.12 is that the optimal decisions taken by one generation, summarized here via their consequences for the post-hatching sex ratio $\bar{z}^*_t$, depend on the prevalence of parthenogenesis in the next generation, $\bar{\alpha}_{t+1}$. This justifies the term 'prescient' optimum: optimality requires that parents can predict the prevalence of parthenogenesis in the next generation. This is a non-trivial task for cyclic parthenogens, and they require specific modeling efforts for each system (Gerber, Booksmythe and

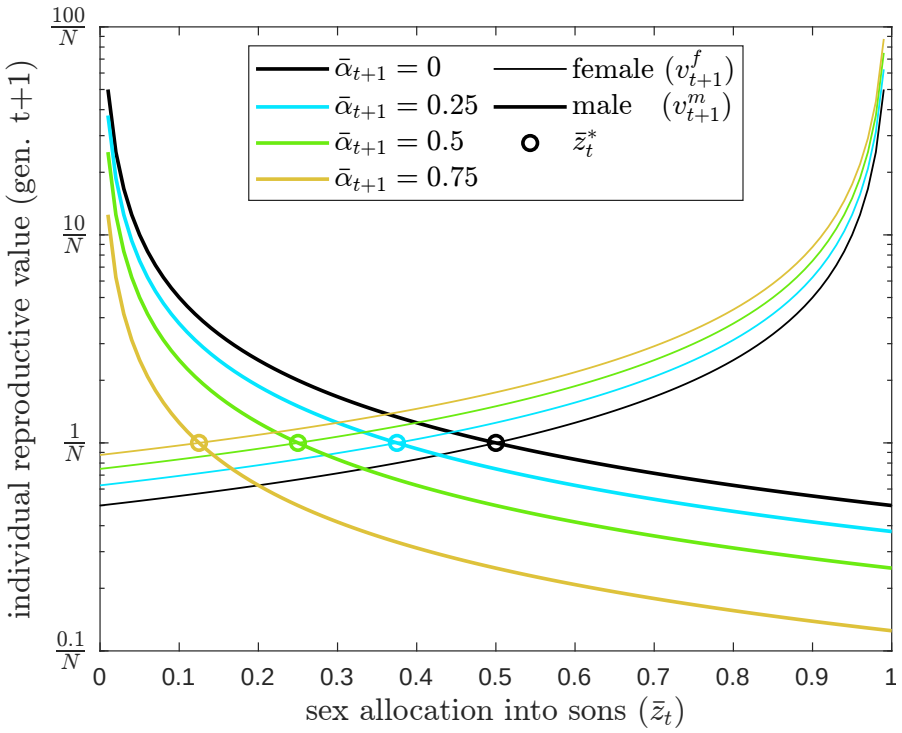

Figure 4.2: **individual reproductive values of males and females:** The average individual reproductive values of males and females (in generation $t+1$) are affected by the sex ratio ($\bar{z}_t$) and the rate of parthenogenesis ($\bar{\alpha}_{t+1}$). Circles: optimal sex ratio, defined as the sex ratio at which the individual reproductive values of males and females are equal. Higher rates of parthenogenesis select for more female-biased sex ratios. For this figure, it is assumed that there is no cost to asexuality (i.e. $\delta = 0$). The figure is based on equations 4.4 - 4.9.

Kokko 2018, Aparici et al. 1998). In stable environments, however, there is a possibility that an organism possesses, fortuitously, just the right sex determination mechanism to optimize the sex ratio for asexuals and sexuals simultaneously, as we show in the next section.

Thelytoky achieves sex ratios equivalent to prescient optimality

When $\bar{\alpha}_t = \bar{\alpha}_{t+1}$ (no temporal variation in the rate of parthenogenesis), equation 4.12 gives $\bar{z}^*_t = 0.5(1-\bar{\alpha}_t)/(1-\delta\bar{\alpha}_t)$. In principle, selection could work to make each mother produce offspring according to the optimal $\bar{z}^*_t$, after which there is no selection to bias the sex ratio further. However, there is another, fortuitous route to this ratio that requires no selection at all: a sex ratio that matches prescient optimality can arise directly via a pre-existing sex determination mechanism. This route only requires that sexually produced offspring have a 50:50 sex ratio,i.e. $z_s = 0.5$, and all asexually produced offspring are female, i.e. $z_a = 0$.

This can be seen for any $\bar{\alpha}_t$ (as long as $\bar{\alpha}_t = \bar{\alpha}_{t+1}$, for all t): Using the assumptions described above ($\bar{\alpha}_t = \bar{\alpha}_{t+1}$, $z_s = 0.5$ and $z_a = 0$), equations S2.1 and 4.12 show that the actual sex ratio among hatched young, $\bar{z}_t$, equals the prescient optimal sex ratio, $\bar{z}^*_t$:

$$\overline{z}_t = \frac{(1-\delta)\overline{\alpha}_t z_{a,t} + (1-\overline{\alpha}_t) z_{s,t}}{1-\delta\overline{\alpha}_t} = \frac{0.5(1-\overline{\alpha}_t)}{1-\delta\overline{\alpha}_t} = \frac{\frac{1}{2}(1-\overline{\alpha}_{t+1})}{1-\delta\overline{\alpha}_{t+1}} = \overline{z}_t^* \tag{4.13}$$

Note that the 0.5 and the 1/2 in different parts of equation 4.13 indicate different biological features: the former specifies that 50% of sexually produced offspring are male, while the latter denotes that sexually produced offspring inherit half of their genome from their father (this is required to account for the difference that parthenogenetically produced offspring inherit their entire genome from their mother).

Equation 4.13 shows that the starkly deviating sex allocation of sexual vs. asexual mothers (the latter producing only females) creates an automatic match between the prevalence of parthenogenesis and the consequent optimal sex ratio. This alignment is perfect for every proportion (between 0 and 1) of mothers opting to reproduce parthenogenetically. The only requirement is that the proportion of parthenogens should not increase (or decrease) so fast from one generation to the next that $\overline{\alpha}_t = \overline{\alpha}_{t+1}$ ceases to be a good approximation.

Stick insect biology matches these assumptions, as their thelytoky creates all-female progeny, and they live in stable environments (as opposed to the varying environments experienced by cyclic parthenogens). A developmental constraint that makes it difficult to produce males asexually removes any need for selection to act on either sexual or asexual mothers to create sex ratios perfectly equivalent to the presciently fine-tuned case where optimal sex ratios depend on perfect cues of the future.

4.2.2 Model 2: Invasion of Asexuality

Our second model takes a specific sex allocation rule of asexuals as its starting point, and investigates the consequent prospects that asexuality can spread. The motivation for this model stems from the prescient optimality model's conclusion (above) that a population of asexuals and sexuals may fortuitously achieve sex ratios equivalent to the prescient optimum, without selection on either type of mother. However, this is true for some sex determination mechanisms but not others. Different sex determination systems and different modes of asexual reproduction constrain the sex ratio of parthenogenetically produced offspring (Engelstädter 2008), with obvious potential for consequences for asexuality itself.

We assume, as the starting point, an obligately sexual organism with unbiased sex ratios. We assume an autosomal locus with two potential alleles a and A, where a causes sexual reproduction while A induces facultative asexuality. Specifically, individuals with the allele A produce a proportion of α_a of their offspring asexually. For simplicity, we assume that the organism is haploid, thus A is always expressed.

We assume that the sex determination system constrains sex ratio evolution: sexual reproduction never deviates from producing unbiased sex ratios (i.e. $z_s = 0.5$), while asexuality produces offspring with a sex ratio of z_a. Thus, the only way for the population-wide sex ratio to change is via a change in the frequency of the A allele. Like our prescient optimality model, this model also includes a parameter δ, which denotes any disadvantage of asexual reproduction. In the current model, however, it is not necessary to differentiate between costs incurred due to hatching failures and those incurred due to reduced fecundity of adults, because both costs have identical effects on the spread of asexuality. Parameter δ allows us to capture the effects of

inbreeding depression and/or the death of WW embryos (despite us not modeling these diploidy-related processes explicitly); any other potential inefficiency of asexual reproduction is also included in δ.

We construct a system of two difference equations that track the changes of allele frequencies in females and males. The variables p_f and p_m denote the frequency of allele A in females and males, respectively, in generation t. The allele associated with sexual reproduction at the same locus, a, has the complementary frequencies $q_f = 1 - p_f$ and $q_m = 1 - p_m$.

In generation $t+1$, individuals can be categorized into five groups depending on the genotype of their parents. Their relative frequencies (before normalizing) are $q_f q_m$ for offspring resulting from matings between two a-allele parents, $q_f p_m$ result from matings involving a father with the A-allele and a mother with the a-allele, $(1-\alpha_a)p_f q_m$ result from a mother with the A-allele mating with a father with the a-allele, $(1-\alpha_a)p_f p_m$ result from the mating of two A-allele individuals, and finally, $\alpha_a(1-\delta)p_f$ are produced asexually by a mother with an A-allele (and have no father). Assuming that sexual reproduction creates offspring with unbiased sex-ratios while the sex ratio of asexually produced offspring is given by z_a, we arrive at the difference equations

$$p_f(t+1) = \frac{\frac{1}{2}(1-z_s)q_f p_m + \frac{1}{2}(1-z_s)(1-\alpha_a)p_f q_m + (1-z_s)(1-\alpha_a)p_f p_m + \alpha_a(1-z_a)(1-\delta)p_f}{(1-z_s)q_f + (1-z_s)(1-\alpha_a)p_f + (1-z_a)\alpha_a(1-\delta)p_f} \tag{4.14}$$

$$p_m(t+1) = \frac{\frac{1}{2}z_s q_f p_m + \frac{1}{2}z_s(1-\alpha_a)p_f q_m + z_s(1-\alpha_a)p_f p_m + \alpha_a z_a(1-\delta)p_f}{z_s q_f + z_s(1-\alpha_a)p_f + z_a\alpha_a(1-\delta)p_f} \tag{4.15}$$

These equations allow us to investigate the invasion and fixation of the A-allele and look for stable equilibria. Following our focus on constraints, we assume that the sex ratio among sexually produced offspring remains at $z_s = 0.5$ (the prescient optimality model above suggests that this case can be very relevant) and derive explicit results for two biologically important cases: $z_a = 0$ (parthenogenesis produces only daughters) and $z_a = 1$ (parthenogenesis produces only sons).

Results when parthenogenesis produces only daughters

The results for $z_a = 0$ are simple. Allele A fails to invade when the cost of asexuality $\delta > 0.5$, and invades and fixes when $\delta < 0.5$ (4.3-A). There is never an intermediate equilibrium frequency.

This special case recovers a commonly discussed situation in the general literature on the two-fold cost of sex (Lehtonen et al. 2012). Asexuality that avoids male production altogether invades and fixes unless it leads to a dramatic (half or more) reduction in fecundity. In other words, the reproductive mode that results in a superior production of female offspring outcompetes the other.

The invasion and fixation prospects of the A-allele are independent of the rate of parthenogenesis, α_a, that it induces. This statement comes with a caveat, however: α_a has an impact on how quickly the allele spreads. Slow spread could harm the invasion prospects of a rare A allele in a stochastic setting that includes drift, which we do not consider (our model is deterministic).

The above results require $z_a = 0$, and thus apply to organisms with XX/XY chromosomes. Whether automictic or apomictic, XX/XY systems make parthenogenetically produced offspring always female because they cannot receive a Y-chromosome from their mother. The XX/X0 system of stick insects also causes parthenogenetically produced offspring to be female, although rare loses of an X-chromosome can very rarely result in the occurrence of parthenogenetically produced males.

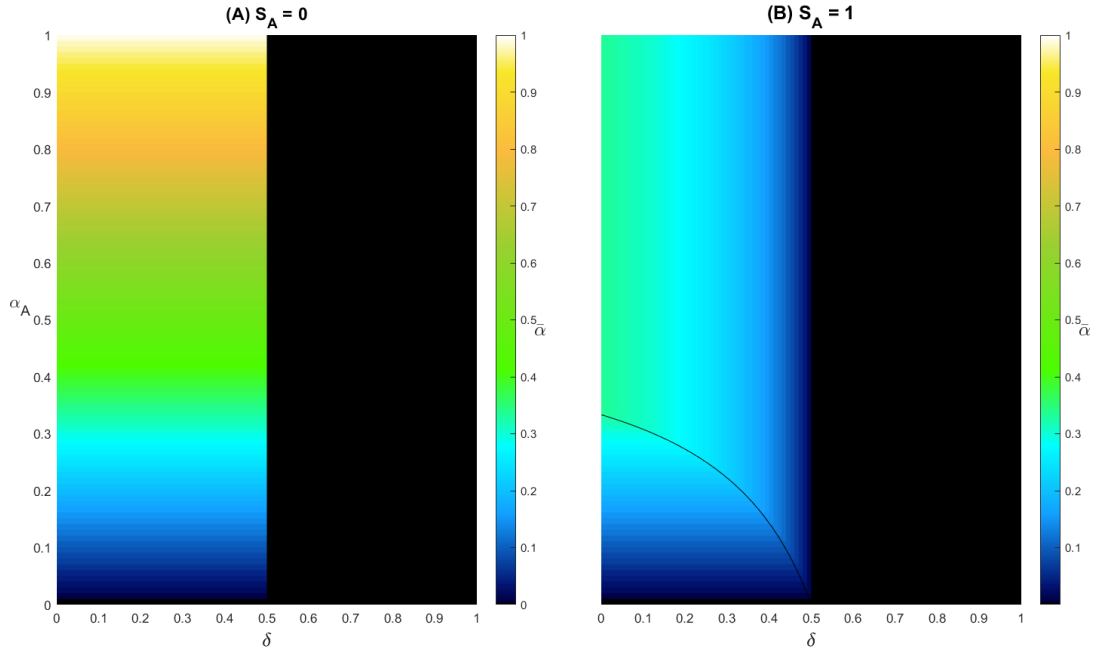

Figure 4.3: **Results from Invasion Model:** *The results of the invasion model if parthenogenesis produces (A) only daughters or (B) only sons. Colors indicate the evolutionarily stable population wide rate of parthenogenesis, $\overline{\alpha}$, after the invasion of an asexuality allele that causes females to produce a proportion α_a of their offspring asexually (Y-axis), for different costs of asexuality δ, (X-axis). The asexuality allele spreads to fixation below the black line in (B); above the line, there is a stable polymorphism where the equilibrium proportion of population-wide male production depends on δ but not α_a. No invasion is possible if $\delta > 0.5$ (dark blue).*

Birds and Bees: results when parthenogenesis produces only sons

We now turn our attention to the case where $z_a = 1$, i.e. when all parthenogenetically produced offspring are male. Again, we investigate the effects of α_a and δ on the spread of the A-allele.

For the initial invasion of the A-allele, the results are identical to the previous case where asexually produced offspring were female. Invasion occurs if $\delta < 0.5$; it fails if $\delta > 0.5$. The dynamics of the subsequent spread, however, differs from the previous section, now that asexually produced progeny develop as males.

Allele A reaches fixation if

$$\alpha_a < \frac{1-2\delta}{3-4\delta} \tag{4.16}$$

The proportion of asexually produced young is simply a function of α_a, the degree to which allele A induces parthenogenesis (horizontal stripes under the curve in Fig. 4.3-B).

At larger values of α_a, assuming $\delta < 0.5$ holds, A invades, but does not reach fixation. The intermediate equilibrium frequency is

$$p_f = \frac{1-2\delta}{\alpha_a(3-4\delta)} \tag{4.17}$$

This can also be written in the form of $p_f\alpha_a = (1-2\delta)/(3-4\delta)$, which gives the proportion of asexually produced young in the population as a whole. This proportion is a decreasing function of the cost δ (vertical stripes above the curve in Fig. 4.3-B).

There are several lessons one can learn from this result. First, if there is no disadvantage to asexuality in terms of fecundity or the viability of offspring ($\delta = 0$), then A can reach fixation if $\alpha_a < 1/3$, i.e. if it causes females to produce up to one third of their offspring asexually. If A causes higher rates of parthenogenesis, then a polymorphic equilibrium frequency is reached where the population of A and a females as a whole produce one third of their offspring parthenogenetically ($\overline{\alpha} = \alpha_a p_f = 1/3$). The exact reason behind the value $1/3$ is surprisingly complicated to derive; we direct interested readers to the supplementary text.

Second, the results for high values of δ are relevant for ZW systems. Here automixis causes half of all offspring (those that carry two W-chromosomes) to die. The surviving offspring are all male, but likely suffer additional costs due to high rates of homozygosity. In our model, this corresponds to $\delta > 0.5$, which confirms the intuition that in ZW systems parthenogenesis through automixis cannot reach a state of a protected polymorphism, let alone fixation.

Third, the result suggests an interesting dynamic whenever all parthenogenetically produced are male, but with $\delta < 0.5$. The situation of a hypothetical diploid species that follows complementary sex determination is likely to satisfy these values, and this possibility is discussed in more detail in a separate section below. For now, it is important to note that facultative asexuality can invade (and sometimes fix) when a single female can divide her effort into asexual and sexual reproduction, even if the former mode of reproduction yields only males.

As a whole, equations 4.16 and 4.17 yield the following summary: If there is no cost to asexuality ($\delta = 0$), the system evolves towards a population-wide rate of parthenogenesis $\alpha_a = 1/3$, unless the A allele is not capable of producing one third of offspring asexually. In that case ($\alpha_a < 1/3$) A reaches fixation, and the proportion of asexual reproduction in the population as a whole is limited by A's ability to cause asexuality ($\overline{\alpha} = \alpha_a$). When asexuality is costly (but not too costly: $0 < \delta < 0.5$), the equilibrium rate of asexuality is lower than $1/3$. Higher costs ($\delta > 0.5$) entirely prevent the invasion of asexuality.

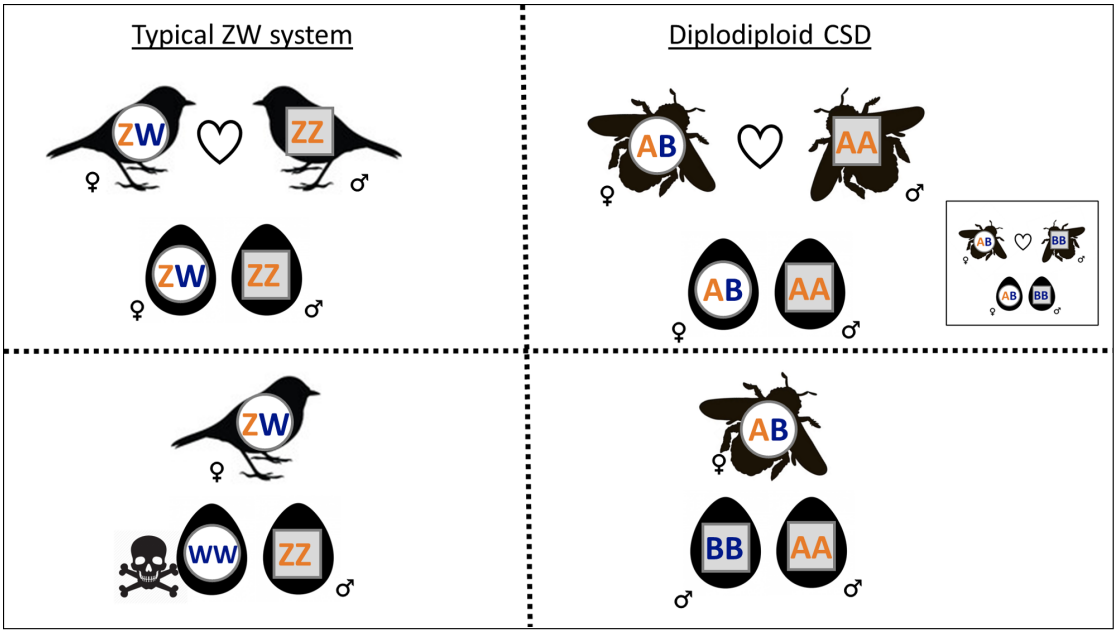

Figure 4.4: **Illustration of ZW sex chromosomes and diplodiploid complementary sex determination (DD-CSD):** *ZW systems are characterized by two sex chromosomes: females carry one Z and one W chromosome, while males carry two Z-chromosomes. Bull (1981) proposed a sex determining system that we call diplodiploid CSD. Here, a sex determining locus on the sex chromosomes makes heterozygous individuals develop into females, while homozygous individuals develop into males. In an obligately sexual organisms with diplodiploid CSD, a simple two-allele system is favored where females carry one A and one B allele and two types of males can occur, either carrying two A alleles or two B alleles. Drift can cause one of the two alleles to go extinct in males. In that case, DD-CSD appears identical to a ZW system. However, the consequences for parthenogenesis (through automixis) are different: in a ZW system, half of all offspring die and the surviving offspring are all males. In DD-CSD, all parthenogenetically produced offspring develop into viable males. Note that here parthenogenesis is depicted as automixis (producing diploid offspring), but that parthenogenesis could also function by producing haploid offspring.*

4.3 Implications for the origin of haplodiploidy

As described above, our Invasion of Asexuality Model shows that parthenogenesis can invade even if it produces only males, while the Prescient Optimality Model shows that parthenogenesis would favor a female-biased sex ratio in the absence of constraints. By making it explicit that the association between reproductive mode and sex ratios matters, our model invites reconsideration of the evolution of haplodiploidy, which is a clear case of such an association.

One aspect that requires explanation is how evolution proceeds from an ancestor that is likely to combine obligate sexual reproduction with unbiased sex allocation to a system where all parthenogenetic offspring are male, and all sexually produced offspring are female. This means that theories for the origin of haplodiploidy ought to

be explicitly linked to sex allocation. Classically, Hartl and Brown (1970) and Bull (1981) already showed that asexual production of haploid males can invade a diplodiploid population, proposing this as a possible origin of haplodiploidy. Here, we extend this idea by providing the explicit link to sex allocation theory, showing that it is very useful to conceptualize haplodiploids as facultative parthenogens.

Parthenogenesis that is at least half as effective as sexual reproduction can invade, even if it subject to a constraint that causes all parthenogenetically produced offspring to be male. This particular result of our invasion model is in line with earlier work (Hartl and Brown 1970, Bull 1981), but we additionally show that the resulting male-biased sex ratios, which arise if the sexuals do not shift their sex allocation from 1:1, are suboptimal. Therefore, male-producing parthenogenesis immediately creates selection for female-biased sex allocation. In principle, a female bias could be achieved either by the asexual production of females, or by the sexual part of the population evolving a female bias among their progeny. The latter is the route taken by existing haplodiploids.

Our model thus suggests that a diplodiploid ancestor can evolve towards haplodiploidy if it satisfies the following three conditions: (1) a genetic constraint causes all parthenogenetically produced offspring to be male; (2) parthenogenesis has a low enough cost (less than 50%); and (3) the sex ratio of sexually produced offspring can easily evolve to be female-biased (while (1) prevents parthenogens from evolving female-biased sex allocation).

Hartl and Brown (1970) and Bull (1981) propose two different sex determination systems - X0 and complementary sex determination (CSD) - that satisfy these three conditions. Interestingly, the idea of the X0 route has been kept alive in the literature much better than the CSD route. We argue that the two routes are relevant for different taxa; below we will discuss the X0 system first, before 'resurrecting' the ideas of Bull (1981) for Hymenoptera.

Hartl and Brown (1970) envisions an X0 (or XY) system in which parthenogenesis produces haploid offspring with only one X-chromosome (and only one set of autosomes and no Y-chromosome). These haploid individuals are assumed to be male - an assumption that is not always realistic, e.g. if the sex determining locus is on the Y-chromosome, or if the sex is determined by the relative dosage of X-linked and autosomal loci (e.g. *Drosophila*, Schüpbach 1985). Nevertheless, it is plausible that at least some taxa might have an X0 sex determination system where haploid individuals develop into males, fulfilling the 1st requirement above. This parthenogenesis can invade if haploid males are at least half as viable as diploid males (2nd requirement above).

While haploid males may suffer fitness costs (discussed in more detail below), these costs of parthenogenesis are probably not as stark as the ¿50% cost in ZW systems that combine inviability of WW with homozygosity problems of ZZ offspring. As a whole, the 2nd requirement above of sufficient viability is met. Assuming that parthenogenesis can invade, the 3rd requirement is also easily met by the proposed sex determination system: Haploid males transmit their entire haploid genome to their offspring, including their X-chromosome. These sexually produced offspring also receive another haploid genome (including an X-chromosome) from their mother. As a result, the offspring of haploid males are always diploid and carry two X-chromosomes, and hence develop into females. Therefore, the sex ratios of sexually produced offspring automatically become more female-biased as asexual reproduction (and hence haploidy

in males) becomes more common.

There are at least two reasons why the 2nd requirement ($\delta < 0.5$) might not always be met: haploid males express deleterious recessive alleles and they may not have optimized their gene dosage. The former issue can be mitigated if the population was already inbred before the invasion of haploid males, or if the X-chromosome makes up a large fraction of the genome (Blackmon et al. 2015). In both cases, many deleterious recessive alleles are already purged from the population. Another common hypothesis for the existence of haplodiploidy is that it allows females to reproduce in the absence of males. Low population densities or strongly female-biased sex ratios cause mate limitation for females, causing some eggs to be unfertilized. In principle, females benefit if some of these eggs develop into haploid males (even if those haploid males are barely viable), rather than foregoing reproduction entirely. If generations overlap, the female can then mate with her sons to produce female offspring as well. Bull (1979) considers coexistence of haploid and diploid males (plausible if mate limitation is common enough), stating that selection then favors increased fitness of haploid males, while ploidally antagonistic selection simultaneously reduces the fitness of diploid males. This diminishes the fitness differences between the two male types. Once the difference is less than twofold, the condition for the further spread and maintenance of haploid male production is fulfilled. In this scenario, mate-limitation sets the stage for haplodiploidy, leading to selection for highly viable haploid males, and then, even if mate limitation ceases to play a role, haplodiploidy is stabilized by the twofold cost of sex (because haploid males are twice as effective at transmitting their mother's genes compared to diploid males).

While the above route from X0 sex determination to haplodiploidy is plausible for some taxa, such as mites (Blackmon et al. 2015), it fails for Hymenoptera, where evidence points at complementary sex determination (CSD) being ancestral (Asplen et al. 2009), even though some present-day Hymenoptera have other sex determination systems as derived traits. CSD is characterized by one or more loci that cause female development when heterozygous, and male development when homo- or hemizygous. Under haplodiploid CSD inbreeding is costly beyond 'normal' homozygosity as it can bias the sex ratio in a maladaptive direction (we explain below in more detail why this is the case). Intriguingly, Bull (1981) published theory on CSD as the likely ancestor for Hymenoptera decades before new confirmatory evidence by Asplen et al. (2009) came to light. Here we use the term diplodiploid complementary sex determination (DD-CSD for short) to refer to the ancestral system proposed by Bull (1981), and that was recently discovered in a butterfly (van't Hof et al. 2024). This system satisfies all three requirements above, and it is not entirely clear why more recent work (e.g. Heimpel and De Boer 2008, Beukeboom and Perrin 2014, Blackmon et al. 2015, Ross et al. 2019) cites Hartl and Brown (1970) and Bull (1979) but not Bull (1981). This is particularly inexplicable because Bull (1981) was not failing to attract attention from the start; it is cited in an older review of sex determination in Hymenoptera (Cook 1993), but no longer in a later one (Heimpel and De Boer 2008), nor in other works where it would have been highly relevant (e.g. Asplen et al. 2009, Harpur et al. 2013, Beukeboom and Perrin 2014, Blackmon et al. 2015, Miura et al. 2015, Ross et al. 2019, van't Hof et al. 2024).

Below, we briefly summarize the main idea of Bull (1981), but we also encourage readers to read the original paper because his model is in some regards more detailed

than ours. CSD involves a single sex-determining locus which, if heterozygous, causes an individual to develop into a female; homozygosity leads to males, as does hemizygosity. This mechanism means that diploids can, in CSD systems, develop as males if inbreeding increases homozygosity or if genetic diversity as a whole is low (Collet et al. 2016). In haplodiploids with CSD, the sex-determining locus normally has a large diversity of alleles (Cook and Crozier 1995), thus most sexually produced offspring are heterozygous and, hence, female. Asexually produced offspring are haploid and, hence, hemizygous and male.

It is important to reflect on diploid males in CSD systems in the context of present-day production of diploid males (due to homozygosity at the sex-determining locus) in haplodiploid systems. Diploid males are usually much less viable than haploid males (reviewed in Harpur et al. 2013), but even if this cost was negligible, sexual production of males would be detrimental in the context of sex allocation. Our model's most robust prediction is that parthenogenetic production of males creates selection for female-biased sex allocation. Sexual mothers of a CSD species fail to achieve this if they mate with relatives. Given CSD in haplodiploids, inbreeding therefore has costs beyond the simple expectation that homozygosity is detrimental to individual fitness. A number of counteradaptations have evolved to mitigate this cost of haplodiploid CSD, including inbreeding avoidance, the removal of diploid male larvae or queens that produce diploid males (reviewed in Van Wilgenburg et al. 2006), and increased viability of diploid males (Cowan and Stahlhut 2004, Elias et al. 2009).

Now consider a DD-CSD species with obligate sexual reproduction (as a potential ancestor of extant Hymenoptera); diploidy and lack of parthenogenesis favor unbiased sex-allocation. Recall that heterozygosity at the sex-determining locus implies development as females, while homozygosity creates males. In this setting, unbiased sex allocation can be achieved if the sex-determining locus has precisely two alleles; higher diversity of alleles would cause females in excess, as homozygotes would be rare. Given two alleles and no selection for a female-biased sex ratio, inbreeding under DD-CSD lacks the extra cost of causing unfortunate sex ratios described above.

Next, assume that a mutation to parthenogenesis (via the production of haploid offspring, or through automixis, Fig. 4.4) happens in a species with a DD-CSD system. All parthenogenetically produced offspring are hemizygous (or homozygous) and, hence, male (1st requirement above). For the second argument above (that asexually produced males have at least half the fitness of sexually produced males), the argumentation proceeds along similar lines as discussed above for the X0 system. Let us therefore assume that the second requirement is met, and focus on the third requirement. Here, DD-CSD provides a simple mechanism by which sexually produced offspring evolve to be all female: if complementarity already exists as a mechanism, then additional alleles at the sex-determining locus are all that is needed for sex to begin producing a female-biased sex ratio.

Above, we were deliberately ambiguous about whether parthenogenesis produced haploid or diploid offspring. This is because the truth might be somewhere in between: parthenogenesis can result in mosaic embryos that are made up of a combination of diploid, haploid and/or triploid cells (Galis and van Alphen 2020, Sperling and Glover 2023). Hence, it is possible that full haploidy in males might have evolved secondarily to ensure more stable development. In figure 4.4 we illustrate parthenogenesis as producing diploid offspring, while Bull (1981) assumes that parthenogenesis produces

haploid offspring.

Bull (1981) argues that haplodiploidy under CSD would be unlikely to develop under inbreeding because the production of diploid males (a consequence of inbreeding) creates a strong cost of inbreeding. We disagree with this argument (at least partially); if evolution proceeds in several steps, this difficulty disappears. The proposed route from DD-CSD to haplodiploid CSD can be separated into two phases: The population starts out with only two alleles at the sex determining locus, resulting in unbiased sex ratios in an obligately sexual population. In the first phase, facultative parthenogenesis invades until an equilibrium frequency of parthenogenesis is reached. This creates a population with male-biased sex ratios, and results in strong selection for less male-biased sex ratios. In the second phase, the sex determining locus acquires a higher diversity of alleles causing high heterozygosity (and, hence, female-biased sex ratios) in sexually produced offspring. Inbreeding becomes detrimental for the sex allocation in the second phase of this transition, where it prevents the mothers of inbred offspring of achieving female-biased broods. During the first phase, however, CSD presents no additional costs of inbreeding, as sexually produced offspring will retain a 50/50 sex ratio even if inbred (analogy: in an XY system, sex ratios do not become biased just because a female might be mating with a male whose X chromosome is identical by descent to one of hers). Therefore, we argue that, even under CSD, inbreeding can be a pre-adaptation for the evolution of haplodiploidy because it purges deleterious recessive alleles. Note, however, that the X0 system proposed above does have a different advantage under inbreeding compared to DD-CSD: the X0 system easily allows for female-biased (rather than unbiased) sex ratios among sexually produced offspring (Ross et al. 2019).

Bull (1981) proposes DD-CSD as the the ancestral system to Hymenopterans, and this is essentially a ZW system (4.4). Ross et al. (2019) proposed another system, that they refer to as "X-linked CSD": In this proposed system, individuals are diploid for autosomes, but also have an X- and a Y-chromosome. It differs from DD-CSD because Ross et al. (2019) propose that the CSD locus is only located on the X-chromosome, but lacking on the Y-chromosome. As a result "X-linked CSD" selects for many alleles at the sex determining locus to prevent male-biased sex ratios (because homozygous XX-individuals would develop as males just as haplodiploid CSD can cause the production of diploid males), In contrast, in DD-CSD, the CSD locus is located on both sex chromosomes, and only two alleles are required to achieve unbiased sex ratios. The DD-CSD, as proposed by Bull (1981), is more parsimonious and has recently been found in nature (van't Hof et al. 2024).

4.4 Discussion

Our models produce three distinct insights. First, and in line with earlier work (Gardner 2014b), facultative parthenogenesis selects for female-biased sex allocation, as the paucity of sexual reproduction implies meager reproductive success for males. Note, however, that we assume that only females can reproduce asexually and, hence, that our models do not apply when males can do the same (as in vegetative reproduction of dioecious plants, Benevides et al. 2015). Second, pre-existing sex determination mechanisms can constrain systems to make the invasion of asexuals very easy (there

is no need for selection to fine-tune sex ratios either in the asexuals or in the sexuals, if asexuality produces females and the rate of parthenogenesis is stable over time), or it can hinder the spread of asexuality. The two extremes - from the fortuitous case to its opposite, i.e. the impossibility of asexual invasion - applies to stick insect thelytoky and to birds, respectively. These taxa of course do not represent an exhaustive list, and other taxa may also provide examples that fall in intermediate parameter regions. Third, the modeling allows us to reevaluate two routes to haplodiploidy, which we have explained in more detail above. In particular, we want to draw attention to the idea suggested by Bull (1981) that haplodiploidy in Hymenoptera developed from an ancestor with diplodiploid complementary sex determination. Below, we discuss the implications of these results in more detail.

Our simplest result is that facultative parthenogenesis selects for female-biased sex allocation. This result is similar to two classical result which are, that selfing in plants selects for higher investment into ovules opposed to pollen (Charlesworth and Charlesworth 1981), and that sib-mating selects for female-biased sex ratios (Taylor 1981). The similarity goes so far, that our equation 4.12 is equivalent to equations given in earlier papers: e.g. equation 3 in Charlesworth and Charlesworth (1981), or equation 1 in Taylor (1993) (although our model also allows the rate of parthenogenesis to change between generations). One difference compared to our results lies in the verbal reasoning that leads to these equations. For sib-mating and selfing, a number of different approaches have been used to explain why exactly they select for female-biased sex allocation (summarized in Chapter 4.2 of West 2009). For example, Taylor (1981) explains the female-biased sex allocation through two factors: Firstly, under sib-mating brothers compete with each other for matings, and as a result males reduce the fitness of their brothers. Secondly, females often mate with their brothers, and as a result the production of additional daughters also increases the fitness of sons. Here, we use a different argument to explain the female-biased optimal sex ratios under facultative parthenogenesis. We argue that, whenever some parthenogenesis happens, females have a higher class reproductive value than males, and that this selects for female-biased sex ratios. We believe that this line of thought is more useful in the context of parthenogenesis, but we also want to note that these are not necessarily different processes. As an illustration, consider a plant with some selfing rate, and ask yourself how much this plant should invest into female vs. male reproduction. There are two equally valid ways to conceptualize this system: One can conceptualize the plant as a facultatively asexual organism (i.e. by viewing the sporophyte as an individual and the pollen and ovules as gametes). Alternatively, the pollen and ovules can be interpreted as individuals who reproduce through some rate of sib-mating. Both conceptualizations lead to the same conclusions.

Another difference between our prescient optimality model and earlier models, is that we explicitly model multiple generations. Our prescient optimality model shows that the degree to which sex allocation should be female-biased is dependent on the rate of parthenogenesis in the next generation. This is easiest to see working backwards in time: The class reproductive value of females of a specific generation increases if many of them reproduce parthenogenetically. As a result, parents of the previous generation would have benefited from investing more into daughters than into sons. This means that cyclic parthenogens, where the prevalence of sex varies over time, are required to estimate the future success of sons using some cues that associate with

whether sex will occur when the currently produced offspring are mature.

While we phrased the requirement to predict the future in a discrete-generation setting, it also applies under iteroparity. For example, *Daphnia* females can switch back and forth between sexual and asexual reproduction, as well as producing male and female broods (asexually). The resulting sex allocation patterns need to take into account that individual males are available for longer than one breeding cycle of a female (Gerber, Booksmythe and Kokko 2018). Experiments show that females use both population density and the local sex ratio as cues to modulate their current sex ratio (Booksmythe et al. 2018); there is evidence that facultatively sexual rotifers (*Brachionus*) possess similar capabilities (Li et al. 2022). All these factors mean that cyclic parthenogens require tailor-made modeling. For *Daphnia* as well as rotifers (Serra et al. 2008, Li et al. 2022) it is additionally relevant to know that sexually produced offspring enter diapause while asexually produced males and females develop directly, which means that sex becomes the favorable option when immediate population growth is ecologically difficult (Gerber, Kokko, Ebert and Booksmythe 2018). Sex in such settings also becomes a form of bet-hedging whenever the season length is uncertain, since all asexual progeny die at the end of the season, and an entire lineage can fail unless it has initiated sex by then (Gerber, Booksmythe and Kokko 2018). While cyclic parthenogens share similarities, they also differ from each other: rotifers differ starkly from *Daphnia* due to their unusual combination of haplodiploidy and ontogeny: females can be fertilized when young, but they no longer offer this opportunity later. Modeling rotifers therefore requires explicitly accounting for female age (Aparici et al. 1998). Furthermore, cyclic parthenogens can differ in the timing at which the reproductive tactic is determined: For example, in aphids it is under maternal control whether an individual develops as a sexual female or a parthenogenetic female (or as a male, Simon et al. 2002), but in Daphnia a female can switch between parthenogenetic and sexual reproduction within her lifetime. All these differences between taxa need to be taken into account when modeling cyclic parthenogens.

The above complications disappear if the environment is stable and if parthenogenesis produces female offspring. The example that we use to illustrate this case is stick insects. Their ability to fortuitously match the optimal sex ratio for every current rate of parthenogenesis remains true as long as this rate is stable over time (or changes slowly enough that the differences from one generation to the next represents a negligible change for the currently optimal sex ratio). Considering thelytokous animals more generally, we want to point out one scenario in which this result of ours is likely to be important: In some species, low population densities cause some females to remain unmated in each generation and in this situation females benefit from parthenogenesis even if parthenogenetically produced eggs are much less viable than sexually produced eggs. Our model shows that this selects for female-biased sex ratios. Furthermore, as long as mate-limitation stays constant between generations, optimal sex allocation can be achieved simply by having parthenogenesis produce only female offspring. As an example, this argument might apply to mayflies (Funk et al. 2010, Liegeois et al. 2023).

At the same time, the extreme female bias of asexual progeny represents a constraint for adapting to settings where environmental fluctuations require large switches in the rate of sex over time. Examples of such requirements are cases where sexual reproduction associates with 'survival structures' such as dormant eggs (review: Gerber and Kokko 2018). Parthenogenesis that only yields females also makes it impossible to

evolve life cycles where sex is completely absent in some generations, such as aphids, which go through a number of asexual, all-female generations during a year, and then produce a single sexual generation at the end of the year (with unbiased sex ratios, Wilson et al. 1997). Sex determination mechanisms that retain the ability to produce males parthenogenetically are thus a key adaptation to living in cyclic environments, as it allows sex ratios to be adjusted to changes in the environment.

The contrast between aphids and stick insects is intriguing, as their sex determination also shares some features. Both taxa have an XX/X0 system (no Y chromosomes), where females are XX and males are hemizygous for X (Wilson et al. 1997, Schwander and Crespi 2009). The difference is that aphids have evolved the ability for mothers to transmit only one X chromosome during parthenogenesis, and hence produce males parthenogenetically. Hence, in aphids, the sex ratio of parthenogenetically produced offspring is under maternal control and can be adjusted according to the season. In stick insects, this route appears possible, but parthenogenetically produced males remain very rare: less than 1% of parthenogenetically produced offspring are male, and these are not always fertile (Morgan-Richards et al. 2010, Schwander et al. 2013). Parthenogenetically produced male stick insects differ from aphids in that the former most likely represent the result of developmental accidents where an entire X-chromosome is lost during meiosis. Hence, for stick insects it can be argued that the parthenogenetic production of males is not under maternal control.

It is worth commenting on another common scenario where the stick insect system (asexuality producing female-only broods) may fail to reach optimality: sex ratios may be so strongly female-biased that it results in mate-limited females, who then are forced to reproduce asexually (Castel et al. 2014, Gardner 2014a, Gerber and Kokko 2018, Burke and Bonduriansky 2019, Liegeois et al. 2023). There are two possible causes for mate-limitation: encounters between males and females can be rare either because of low population densities, or because of highly female-biased sex ratios. In the former case our model still applies (and this might be relevant for mayflies, Funk et al. 2010, Liegeois et al. 2023), but in the latter case, there is a causal dependence from the sex ratio to the rate of parthenogenesis that we did not include in our model. In the most extreme case, male absence in one generation forces females to be parthenogenetic ever after, even if females were still, in principle, able to offer eggs for fertilization. The introduction of a single male would, in such a case, reintroduce sexual reproduction. In practice, when evaluating our model predictions, it is important to keep in mind that the current rate of parthenogenesis might be constrained by the availability of males. If sperm limitation is a temporally fluctuating problem (for any ecological reason, e.g. local problems of male availability only being lifted through immigration which itself may fluctuate), this further erodes the perfection of the fortuitous optimality that we have shown.

Regardless of these limitation in fluctuating environments and in female-only populations, the excellent ability of stick insects to match the optimal sex ratio in stable environments prompts the question why the combination of facultative sex with asexuals specializing in female production is not more common in nature. While our modeling does not give a straightforward answer to this question, our Invasion Model highlights that asexuality can spread to fixation in a stable environment, unless there is some disadvantage associated with asexual reproduction. If a species has taken this route (i.e. if there is no significant problem that reduces the fitness of parthenogens), it

becomes a classic case of an all-female parthenogen, where sex allocation questions no longer arise.

The stability of facultative sex therefore requires understanding what might hamper the reproductive success of parthenogens. In cyclic parthenogens, sexual and asexual progeny often show very different ecological adaptations (Burt 2000, Gerber and Kokko 2018), but stick insects lack clear ecological differences of this kind. The maintenance of facultative parthenogenesis in stick insects is therefore a currently unresolved question (Larose et al. 2023). In *Timema* stick insects it has been suggested to be a transient state or maintained through immigration from sexual and asexual populations (Larose et al. 2023).

More generally, heterozygote advantage might be a possible mechanism maintaining sexual reproduction in stick insects. Thelytokous parthenogenesis has evolved repeatedly in stick insects, and the exact mode of parthenogenesis differs between species, resulting in different degrees of homozygosity (Alavi et al. 2016, Jaron et al. 2022). Intuitively, the fact that heterozygotes are more viable than homozygotes (Burke and Bonduriansky 2022) can contribute to maintaining sexual reproduction; however, in natural populations the picture is further complicated by maternal effects (Burke and Bonduriansky 2022). Heterozygosity could also act via improved immunocompetence. Although understudied in stick insects, such an effect would make the reasons for sex similar to environmentally fluctuating cases after all: parasites play a role in many situations where the rate of sex varies over time (Morran et al. 2011, Vergara et al. 2014), but importantly, similar effects also occur in less variable situations (Ashby 2020). Alavi et al. (2016) made the interesting observation that obligately parthenogenetic species of stick insects tend to reproduce by apomixis, while facultatively parthenogenetic species tend to reproduce through automixis. This pattern, if robust, would emphasize the role of heterozygosity in stabilizing facultative parthenogenesis. However, a recent study (using more advanced genomic methods) has shown that at least some *Timema* stick insects that were thought to have apomictic parthenogenesis (Schwander and Crespi 2009) are actually more likely to be automictic (Jaron et al. 2022). Hence, it is currently an not known to what extent parthenogenesis in stick insects results in homozygosity and what effect it has on the spread of parthenogenesis.

We also investigate how parthenogenesis spreads when it only produces sons. In this case, the necessary condition for asexuality to invade at all is that it should be at least half as efficient as sexual reproduction in yielding viable progeny (mirroring the result if offspring are female). We argue that this is not easily the case for ZW systems such as birds, where ZZ males can be produced, but their viability or fertility are likely to be compromised, and half of their siblings are inviable WW embryos (Ramachandran and McDaniel 2018). The exact value of costs of asexual attempts in a bird depends on whether investment into doomed WW offspring can be 'recycled' with ease to benefit the production of viable offspring. Possible routes include reabsorbing a WW egg before laying; or if the egg was laid and fails to hatch, those that hatched may receive better parental care in a reduced brood. A recent summary of hatching failures does not comment on sex chromosomes of inviable eggs (Marshall et al. 2023), making it difficult to judge the frequency with which these factors apply. There are other cases (outside ZW sex determination) where viability costs are probably much smaller, and for such cases, we predict a stable rate of parthenogenesis can evolve, where parthenogenesis and sexual reproduction coexist.

In haplodiploids, unfertilized eggs develop into males, and therefore this can also be viewed as male-producing parthenogenesis. Hence, our models are relevant for the evolution of haplodiploidy. Today, the origin of haplodiploidy is usually discussed with a focus on maternal-paternal genetic conflict (Bull 1979, Blackmon et al. 2015) or the ability of mate-limited females to reproduce (Hamilton 1967, Jordal et al. 2001). Here, we want to draw attention to the idea by Bull (1981) that haplodiploidy in Hymenoptera specifically could have evolved from a diplo-diploid ancestor with obligate sexual reproduction that already used complementary sex determination (CSD).

Since 1981, several new empirical insights have emerged that make the route from diplodiploid CSD (DD-CSD) to haplodiploid CSD, as envisaged by Bull (1981), more plausible. A key finding is that haplodiploid CSD is ancestral in Hymenoptera (Asplen et al. 2009), even though some present-day Hymenoptera have other sex determination systems as derived traits. Additionally, it is now known that diploid males can evolve to become viable in haplodiploid Hymenoptera (Cowan and Stahlhut 2004, Elias et al. 2009), indicating that changes in male ploidy are not too difficult over evolutionary time. Furthermore, a diplodiploid form of CSD has now been discovered in a Lepidopteran (van't Hof et al. 2024), showing that such a system is possible. A multi-locus version of DD-CSD has also been proposed for the rice frog (Miura et al. 2015), but molecular proof is still lacking.

It is possible that DD-CSD is more common in nature, but that its discovery has been delayed until now, both because scientists were unaware of its importance, and because the molecular techniques have only been developed recently. For single-locus DD-CSD, it is important to note that at first sight it appears identical to a ZW system with undifferentiated sex chromosomes where both sex chromosomes are of equal size. Both DD-CSD and ZW have female heterozygosity and male homozygosity at the sex-determining locus, and the sex determining locus has two alleles (unlike the diversity of alleles in haplodiploid CSD). This makes it very difficult to discover DD-CSD (see Fig. 4.4 for a key difference: if a parthenogenetic mutant arrives, the offspring viabilities are dramatically different). In the absence of parthenogens and/or mutations that increase allelic diversity at the sex-determining locus, DD-CSD is easily overlooked. It also is not easily possible to scan species for molecular pathways that control CSD in Hymenoptera. This is because molecular mechanisms for CSD in Hymenoptera are currently being discovered (Koch et al. 2014, Miyakawa and Miyakawa 2023, Otte et al. 2023), and, to complicate things further, even within Hymenoptera, CSD can be controlled by different genes and proteins in one species compared to another species (Koch et al. 2014).

4.5 Conclusion

Our study links sex-allocation theory with genetic constraints in facultative parthenogens. We have shown that facultative asexuality selects for female-biased sex allocation, and that the degree of this female-bias is directly related to the rate of parthenogenesis in the next generation. This has interesting consequences for cyclic parthenogens because they require intricate adaptations to predict the population composition in the next generation (or, in iteroparous organisms, in the next breeding bout). In stable environments, optimal sex allocation can be achieved much more easily. Some systems,

specifically stick insects, achieve perfectly optimal sex allocation automatically, thanks to fortuitous features of their sex allocation mechanism. At the other extreme, some sex determination systems result in all parthenogenetically produced offspring developing as males. This creates a severe constraint on e.g. avian asexuality, but there are other situations where male-producing asexuality can predispose a species to a transition towards haplodiploidy. We particularly encourage studies on the possibility that a diplodiploid complementary sex determination system may have been an ancestral state leading to haplodiploidy in Hymenoptera.

Alternative Conclusion

When reproducing without sex
sticks have daughters, birds have sons.
This makes sticks the clever ones!

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Competing Interests

The authors declare no competing interests.

5

General Discussion

In this thesis, and during my PhD, I have worked on a broad range of topics and taxa. In addition, I have tried to work on various levels of abstraction and generality. I believe that the an important advantage of theoretical biology (over empirical biology) is that it allows work on a very broad range of topics and does not require the same degree of specialization as empirical biology. This is because similar mathematical methods are applicable across taxa and topics. Furthermore, theoreticians can contribute to the scientific community by providing an overview of large fields of study and by finding connections between otherwise separate fields.

While chapter 2 focused on a specific polymorphic trait in one genus of butterflies, chapter 3 had the much more general and somewhat abstract topic of ecological sexual dimorphism. Finally, chapter 4 focused on a broad range of taxa that share the commonality that females can reproduce both sexually and asexually. The taxonomic breadth of this project ranges from animals where parthenogenesis produces only daughters (e.g. stick insects, mayflies, and many others), to cyclic parthenogens where the sex ratio of parthenogenetic offspring is under maternal control (e.g. aphids and *Daphnia*), to birds where the combination of a ZW sex chromosomes and automixis has the unfortunate consequence that half of parthenogenetically produced eggs have a WW genotype and fail to hatch while the remaining eggs develop as males. We additionally highlight haplodiploidy as another form of facultative parthenogenesis in which parthenogenesis produces only males. Finally, we distinguish between different forms of haplodiploidy, such as complementary sex determination and dosage dependent sex determination, and discuss how these differences have important consequences for the evolution of haplodiploidy.

I have also tried to learn and apply different modeling methods during my work. Chapter 2 uses an individual-based model, while chapter 3 uses a mathematical model with numerical approximations, and chapter 4 uses a mathematical model that focuses on reproductive value as well as a simple analytical model that investigates the spread of parthenogenesis. These different types of models offer different versatilities and the best choice of model therefore depends on the research question. Hence, and theoretician benefits from learning a full toolbox of modeling approaches.

Below, I give three short essays that discuss female-limited diversity, with each essay focusing on one of the projects presented in this thesis. First, I will review earlier hypotheses about the maintenance of the Alba polymorphism in *Colias* butterflies. Secondly, I will focus on a minor result of chapter 3, specifically that a sex-limited polymorphism can evolve as a way for one species to occupy two niches, and what insights this can give us for the female-limited color-polymorphisms discussed in the

general introduction. Third, I will focus on the female-limited polyphenism in eusocial Hymenoptera and discuss why workers in Hymenoptera are always female. Finally, I will end with a discussion on the usefulness of research that aims to find general principles in biology, as well as the usefulness of more taxon-specific research.

5.1 Many proposed drivers behind the Alba polymorphism in Colias butterflies

Colias butterflies present an intriguing example of a female-limited color polymorphism. In these butterflies, one female morph resembles males in color (either yellow or orange), while the other female morph (called 'Alba') is white. Males preferentially court colorful females over white females (Graham et al. 1980). Alba females have faster development, larger fat bodies at eclosion, and sometimes faster maturation of eggs compared to colorful females, probably due to a simple metabolic advantage because Alba females do not produce the costly pigments that colorful females do (Graham et al. 1980). The polymorphism is controlled by a single autosomal locus, and the white morph is dominant over the colorful morph (Gerould 1911, Woronik et al. 2019) Males are always colorful even if they carry the Alba allele. In Chapter 2, I have presented this polymorphism in more detail and discussed two models that I have constructed in order to investigate its maintenance. Here, I will give an overview of different hypotheses that have been proposed by other authors about the maintenance of the Alba polymorphism, as well as the reasons why many of these hypotheses have been rejected.

It has been suggested that the Alba morph could be a mimic of white *Pieris* and *Pontia* butterflies (jointly referred to as white pierines below). This idea has been tested and rejected (Ley and Watt 1989, Watt et al. 1989) for two reasons. Firstly, it has been found that *Pieris* and *Pontia* butterflies are neither toxic nor unpalatable and that birds will readily eat them (Ley and Watt 1989), clearly ruling out that Alba females can avoid predation by mimicking them. An alternative hypothesis would be that Alba has a different reason to mimic white pierines: rather than avoiding predation from birds, Alba might be mimicking other white butterflies in order to avoid harassment from conspecific males. The argument being that when white pierines occur in high densities, *Colias* males might learn to avoid courting white butterflies because of the high risk of courting heterospecific individuals. Hence, Alba might be approached less when white pierines are common, and this effect should be most pronounced when Alba is rare (because male *Colias* have the least to gain from approaching white butterflies, when very few conspecific females are white). If harassment poses a strong cost on *Colias* females, Alba females could therefore benefit from cooccuring with white pierines. However, this hypothesis can be ruled out as well: the co-occurence patterns between Alba and other white butterflies do not match what would be expected under mimicry (Watt et al. 1989). If Alba females were mimicking other white butterflies (due to predation or harassment), then there should be a positive correlation between the population densities of white pierines and Alba frequencies. However, Watt et al. (1989) found a negative correlation instead. Hence, it can be firmly ruled out that Alba females benefit from being mistaken for white pierines.

The negative correlation between Alba frequencies and white pierine densities opens

up a range of new hypotheses: rather than benefiting, Alba females might suffer from the resemblance for at least two reasons (Watt et al. 1989): Firstly, as described in the previous paragraph, Alba females might receive less courtship from conspecific males when there are many heterospecific white butterflies in the same area. If attention from conspecific males is more beneficial than detrimental to *Colias* females (e.g. if the costs from harassment are less severe than the benefits from receiving more spermatophores), then Alba females would suffer a cost when cooccuring with white pierines. Secondly, *Pieris* males have been observed harassing Alba females of *Colias eurytheme*. Both of these factors -reduced mating attempts from conspecific males and harassment from heterospecific males- offer a plausible explanation for the negative relationship between the occurrence of the Alba morph and white pierines.

Nielsen and Watt (2000) investigated whether this interference competition might also play a role in maintaining the Alba polymorphism. Through a combination of modeling and field observations, they show that the fitness of a the Alba and orange morph are affected by population densities of both *Colias* and white pierines. Furthermore, they found that these densities fluctuate over time, and that the Alba morph is favored in some years while the orange morph is favored in other years. While their temporal model does not predict polymorphism maintenance, they propose that spacial structure with varying densities in different areas might play a role. I will discuss this possibility in more detail below. For now, however, I want to focus on the fact that their model finds no mechanism that would generate negative frequency dependence within a single generation in a single population. This is simple enough to explain verbally: Even if we assume that the males of *Colias* and *Pieris* are capable of learning and can adjust their courtship behavior based on Alba frequencies, such learning would not lead to negative frequency dependence in either case. *Colias* males would benefit from increasing courtship of white butterflies when Alba is common, and reducing courtship when Alba is rare. Hence, Alba females would suffer particularly strongly from reduced matings when the Alba morph is already rare, resulting in positive frequency dependence which hampers the maintenance of the polymorphism (assuming that females tend to benefit from being courted). *Pieris* males, on the other hand, have more opportunities to learn to avoid *Colias* Alba females when the Alba morph is common. This also leads to positive frequency dependence because Alba females would suffer from increased harassment from *Pieris* males when the Alba morph is already rare. To my knowledge, no studies have shown that such male learning actually happens in *Colias* or *Pieris* butterflies (and there is even evidence to the contrary in *Colias philodice*, Limeri 2017). Therefore it is not clear whether the proposed positive frequency dependence actually acts or not. Nevertheless, it is clear that even if such male learning does happens in *Pieris* butterflies, it would not promote, but instead hinder the maintenance of the Alba polymorphism. In the case of learning by *Colias* males, it is less clear whether one should expect this to promote or prohibit the maintenance of the polymorphism, as this depends on whether females tend to benefit from male attention (due to spermatophores) or suffer costs from it (due to harassment).

Limeri (2017) investigated whether male *Colias philodice* are capable of learning, and hence of adjusting their courtship preferences based on Alba frequencies and pierine densities. Using both field experiments on natural populations and lab experiments on captively reared butterflies, she found that *Colias philodice* males always prefer colorful

females over Alba females, and that, while the degree of this preference can vary in natural populations, it does not correlate with morph frequencies. Hence, males appear to be unable to adjust their mating preferences based on morph frequencies. This has important consequences for the maintenance of the Alba polymorphism. In the *Ischnura* damselflies system described above, a female-limited polymorphism is maintained because males of these damselflies can adjust their mating preference based on female morph frequencies. As a result, rare female morphs of these damselflies suffer reduced harassment and this is the driving force behind the balancing selection that promotes the polymorphism. In the absence of male learning, this explanation fails for *Colias* butterflies.

Yet another rejected hypothesis centers around thermal preferences of the two morphs. It had been suggested that Alba and colorful females might fly at different times of the day, the idea being that the pigments play a role in heat absorption. However, it has been shown that the two morphs do differ neither in their flight times nor in thermoregulatory behaviors (Leigh and Smith 1959, Watt 1973).

Gilchrist and Rutowski (1986) made another intriguing observation: In high density population of *Colias eurytheme*, colorful females show higher rates of dispersal compared to Alba females. This difference is mainly due to colorful females leaving high density sites. The authors suggest that this might be the incidental result of harassment from males. When a female is harassed, she often starts an ascending flight where she flies upwards to escape the male and later lands somewhere farther away. Because colorful females are more attractive to males, they more frequently get harassed, and hence do ascending flights more often, resulting in higher dispersal, particularly from high density sites. While we did not model this, it is intriguing to consider whether such a difference in dispersal might help to maintain the Alba polymorphism, even though it is only an incidental consequence of harassment. At the very least, it seems to imply that colorful females can avoid high-density areas in which they suffer strong harassment, giving more credibility to the possibility that spacial structure might play a role (as suggested by Nielsen and Watt 2000). To my knowledge, this hypothesis has not been investigated further. However, as Gilchrist and Rutowski (1986) mention themselves, this difference in dispersal only becomes apparent in high density populations that occur in agricultural landscapes (on alfalfa fields). Hence, the argument most likely does not work for lower density populations that are also polymorphic at the Alba locus. Nevertheless, the possibility that differences in dispersal maintain the polymorphism in meta-populations, is likely worth further consideration, particularly if high- and low-density fields occur in close spacial proximity as might be the case in many agricultural areas.

In chapter 2C, we have modeled a novel hypothesis, which focuses on the differences in development time in the two female morphs. Like most butterflies, *Colias* are protandrous, meaning that males eclose earlier than females do. Because Alba females have faster development than colorful females (Graham et al. 1980), they eclose at an earlier time during the season and therefore encounter more virgin males than colorful females do. Using a simulation model, we have shown that this mechanism could - at least in principle - maintain the polymorphism in this system, as long as three conditions are met. These conditions are that courtship has a net positive effect on female fitness, that seasonality causes the occurrence of separate generations that are either non-overlapping or only partially overlapping, and that male spermatophores

late in the season are derived from some nutrients that were not available for females earlier in the season. All three of these conditions have some empirical support either in *Colias* or in related butterflies (Rutowski 1979, Svärd and Wiklund 1986, Watanabe et al. 1997, Stjernholm et al. 2005, Colom et al. 2022). While more empirical research is needed to test whether differences in emergence time are truly the driver behind the Alba polymorphism, our model makes a valuable contribution to solving this riddle by highlighting a plausible mechanism and pinpointing what aspects of the system require further study in order to test this novel hypothesis.

5.2 Sex-limited polymorphism for ecological niches and ecological sexual dimorphism

Chapter 3 touched on another evolutionary mechanism that can result in a sex-limited polymorphism. The chapter focuses on the evolution of ecological sexual dimorphism where males and females differ in their resource use or another ecological niche.

One result of chapter 3 is that a sex-limited polymorphism can evolve when one resource is more abundant and/or better quality than the other. In such a case, one sex can evolve to be monomorphic for using the superior resource, while the other sex displays two distinct morphs (one for each resource). Interestingly, our model shows that under the same ecological conditions both a sex-limited polymorphism and a sex-independent polymorphism can be stable. Which of these evolves, depends only on the temporal order in which mutations occur. Furthermore, if a sex-limited polymorphism evolves, there is no a-priori prediction on which sex is monomorphic vs. dimorphic because this also depends on the order in which mutations happen to occur.

Black-browed albatrosses provide one example where females use a broader niche than males. Here, females show a higher variance in foraging distances compared to males (Patrick and Weimerskirch 2014). While the differences between females are continuous (and, hence, do not constitute a polymorphism), they nevertheless show yet another scenario where a trait is more diverse in females compared to males, and some females have a phenotype that resembles that of males.

While we phrase chapter 3 in terms of the exploitation of two resources, it also applies to other ecological niches, as long as these combine disruptive selection with negative frequency dependent selection. Batesian mimicry is another example for such an ecological niche As described in the general introduction, several species of Lepidoptera have evolved a female-limited mimetic polymorphism, where different morphs are Batesian mimics for different toxic species, and one morph is non-mimetic (Walbauer and Sternburg 1975, Kunte 2009, Allen et al. 2011). In these systems, the optimal morph frequencies depend on the density of the different toxic model species (as well as on densities of other mimics in the same mimicry ring).

To see how our model ties in with these mimetic systems, consider a scenario in which a harmless, palatable species evolves a morph that mimics a toxic species, and, further, that the optimal morph frequencies are such that more than half the population should be non-mimetic. In this case optimal morph frequencies can be achieved with a sex-limited polymorphism, where one sex is entirely non-mimetic, while the other sex is polymorphic. Our model makes no prediction about whether such a polymorphism should evolve to be male-limited or female-limited. However, our model does indicate

that when one of these evolves, it becomes uninvadable by the alternative. In reality, pre-existing differences between the sexes are likely to shift the outcome into one direction or the other.

In butterflies, female-limited mimicry has evolved repeatedly (Walbauer and Sternburg 1975, Kunte 2009, Allen et al. 2011), but there are no known examples of male-limited mimicry. The monomorphism in males is usually explained either by females being more vulnerable to predation, or by males being more influences by sexual selection (Kunte 2009). However, our model also suggests that if female mimics are already common enough to fill the mimetic niche, males no longer benefit from mimicry. Interestingly, male-limited mimicry has been found in a moth (Walbauer and Sternburg 1975). In this species, females only fly at night, while males fly during the day. As a result, females in this species do not benefit from mimicry, and this might have left the niche open for males to evolve mimicry instead. This possibility is further supported by the fact that two butterfly species (where both sexes are diurnal) have evolved female-limited mimicry in the same area (Walbauer and Sternburg 1975).

Sex-limited polymorphism for niche can also occur in a system where females are already polymorphic for other reasons. As described in the general introduction, *Ischnura* damselflies often have multiple female morphs that are maintained by frequency-dependent male harassment. In *Ischnura senegalensis*, these morphs also differ in oviposition sites and egg morphologies (Takahashi and Kawata 2013). The brown gynomorph almost exclusively lays eggs on brown decaying plants, while the blue-green andromorph frequently lays its eggs on fresh, green plants. This difference in oviposition behavior is accompanied with a difference in egg shape: andromorphs produce more elongated eggs making it easier to lay them into fresh plants (Takahashi and Kawata 2013). Hence, the difference in oviposition sites between the two morphs might be a by-product of the preexisting color polymorphism. Females seek out oviposition sites in which they are well camouflaged, and this eventually leads to selection for different egg shapes. Nevertheless, it is intriguing to consider that this niche partitioning might also reduce intraspecific competition, and thereby strengthen balancing selection on this color polymorphism.

5.3 Why are workers in Hymenoptera always female

Chapter 4 focused on sex ratio theory in facultative parthenogens, including haplodiploids, and also contained an extensive section about Hymenoptera specifically. Here, I will continue this focus on Hymenoptera in order to discuss a female-limited polyphenism that has independently evolved several times, specifically the repeated evolution of eusociality with an all-female worker caste in Hymenoptera (da Silva 2021). In eusocial Hymenoptera, some females develop as reproductive queens while other females develop as workers that are either entirely sterile or only occasionally lay unfertilized eggs. Males all develop into reproductives and are usually monomorphic. Here, I will not discuss why eusociality has evolved repeatedly in Hymenoptera (but see Boomsma 2009), but instead I will only focus on the question of why this polyphenism is female-limited. In other words: Why are there no male workers in Hymenoptera?

Importantly, the absence of male workers is not universal across eusocial animals. Many eusocial animals have both male and female helpers, although female-only

helping has also evolved several times (Ross et al. 2013): Female and male workers occur in several eusocial groups, such as the eusocial shrimp *Synalpheus elizabethae* (Chak et al. 2015), mole-rats (Lutermann et al. 2014), thrips (Chapman et al. 2008), and termites (Korb and Hartfelder 2008). Female-only helping occurs in Hymenoptera (da Silva 2021), ambrosia beetles Kent and Simpson 1992, and eusocial spiders (Vollrath 1986).

The evolution of female-only helping in Hymenoptera has some interesting connections to the projects that I presented in chapters 3 and 4. Firstly, I will argue that the evolutionary drivers behind female-only workers has an important similarity to my result in chapter 3: in both cases the final evolutionary outcome is strongly influenced by the initial ancestral state. Secondly, due to their haplodiploidy, female-only helping has interesting consequences for sex ratio theory in eusocial Hymenoptera. In addition, many of the arguments below build on the conceptual frameworks that were introduced throughout this thesis.

According to the 'preadaptation hypothesis' (Starr and by Robert W. Matthews 1985a, Ross et al. 2013, Davies et al. 2016), females are often pre-adapted in some way that makes them better at helping. In this context, it is important to distinguish between "worker-first" eusociality, where helping predominantly involves brood care, and "soldier-first" eusociality, where helping predominantly involved colony defense (Tian and Zhou 2014, Ross et al. 2013). Ross et al. (2013) showed that female-only helping evolves only in worker-first eusociality, and only if the ancestor was characterized by maternal care only (and lacked paternal care). In these species, females were pre-adapted to take care of brood, and female-only alloparental care evolved as a result of this initial difference. In contrast, the sterile caste of soldier-first eusociality consists of both sexes, and the same is true for worker-first eusociality in which the ancestor had biparental care (Ross et al. 2013). In Hymenoptera, eusociality evolved for brood care, but interestingly female Hymenoptera can also be argued to be preadapted for colony defense. Eusocial Hymenoptera belong to the subclade Aculeata which are characterized by having a stinger (Starr and by Robert W. Matthews 1985a) which clearly helps with colony defense. This stinger has evolved from the ovipositor, and as a result it is a female-limited trait.

Davies et al. (2016) modeled the joint evolution of sex-specific helping and sex allocation. Interestingly, their model predicts that, if sex ratios can evolve easily, helping always evolves to be done by a single sex (either males or females). This is because any initial difference in helping ability causes a positive feedback loop. If one sex is more efficient at helping than the other sex, then mothers benefit from producing more offspring of the more helpful sex. This causes the sex ratios to be biased towards the more helpful sex. Due to the rarer-sex effect, the more common sex then benefits less from seeking out mating opportunities, making helping a more favored strategy. This in turn selects for the more common sex (which is also the more helpful sex) to become even more proficient at helping. This positive feedback loop ultimately causes the evolution of single-sex helping even if the initial differences in helping ability were minor. While the strict association between labile sex ratios and single-sex helping does not always always hold empirically, the model highlights that additional factors must be at play for helping by both sexes to evolve.

Positive feedback loops in evolution make it necessary to closely consider the evolutionary history of a species, rather than just the adaptiveness of traits. When initially

small differences are amplified over time, it becomes essential to consider the ancestral state from which a species has evolved. This is similar to our result in chapter 3 of this thesis where the order of mutations had a major impact on the final evolutionary outcome. Similar evolutionary feedback loops have also been found in other context (Spencer et al. 1995, Perrin and Mazalov 2000, Lehtonen and Kokko 2012, McNamara and Wolf 2015, Li and Kokko 2019). In these systems, it is essential to consider the evolutionary history of a species. More generally, the role of history might be underappreciated in ecology and evolution in general (see Spencer 2020 for an interesting philosophical discussion on this).

Sex-limited polymorphism for niche shares another similarity with single-sex helping. The rarer-sex effect plays an important role in both cases, albeit in very different ways. The rarer-sex effect describes the effect that individuals of the rarer sex have higher reproductive value because they face reduced competition for reproduction. It typically favors the evolution of unbiased sex-ratios, and this is essential for the evolution of a sex-limited polymorphism for niche. The unbiased sex-ratios cause a mismatch between optimal morph frequencies and optimal sex ratios, making it impossible for a sexual dimorphism to optimally use the niche space. A sex-limited polymorphism, however, allows for optimal morph frequencies even if the sex-ratio remains fixed. The rarer-sex effect plays a very different role for female-only helping. During the evolution of eusociality, queens benefit from biasing sex allocation towards the more helpful sex. The rarer-sex effect then causes a positive feedback loop because the more common sex benefits less from seeking out matings, and hence evolves to do even more helpful. Ironically, the rarer-sex effect can therefore favor the evolution of highly biased sex ratios during the evolution of eusociality.

The absence of male workers in Hymenoptera has historically been connected to haplodiploidy (arrhenotoky) and the resulting asymmetries in relatedness. Under haplodiploidy, fertilized eggs develop into diploid females, while unfertilized eggs develop into males. This results in asymmetrical relatedness where females have a relatedness of 0.75 to their sisters, and a relatedness of 0.25 to their brothers (as opposed to the 0.5 relatedness that diplodiploid animals have to siblings of either sex). Hamilton (1972) argued that the high relatedness of females to their sisters might explain why eusociality has repeatedly evolved in Hymenoptera, and why workers are all female. However, this 'haplodiploidy hypothesis' has largely been rejected on both theoretical and empirical grounds. Empirically, it has been shown that there is no clear association between haplodiploidy and eusociality (Ross et al. 2013). On theoretical grounds, it has been pointed out that the reduced relatedness of females to their brothers exactly cancels the effect of increased relatedness to sisters. Hence, relatedness asymmetries caused by haplodiploidy neither promote nor hinder the evolution of eusociality. Relatedness asymmetries are an even poorer explanation for the absence of male workers in Hymenoptera because some models even predict that they should favor the evolution of male helping over female helping (Starr 1985b, Davies et al. 2016). Note, however, that haplodiploidy might promote female-only helping through a mechanism unrelated to relatedness asymmetries: it provides a simply mechanism to adjust sex ratios to be more female biased (Gardner and Ross 2013, De La Filia et al. 2015).

Even if relatedness asymmetries have no meaningful impact on the initial evolution of eusociality, they nevertheless have important consequences for conflicts in euso-

cial societies. There are two reasons why the combination of haplodiploidy and a female worker caste results in within-colony conflict: Firstly, due to the relatedness asymmetry, female workers gain more inclusive fitness from raising their sisters to be reproductive individuals compared to doing the same with their brothers. Hence, under haplodiploidy, female workers benefit from female-biased sex ratios. Secondly, haplodiploidy (arrhenotoky) allows female workers to lay unfertilized eggs that develop into males. Additionally, female workers are more closely related to both their sons (0.5 relatedness) and their nephews (0.375 relatedness) compared to their brothers (0.25 relatedness). Hence, female workers have no inclusive fitness benefit from raising the male offspring of their mother when they could be raising their own sons or their nephews instead, causing within-colony conflict over who produces male offspring (Starr 1985b).

5.4 Some thoughts on general principles and taxon-specific research

I want to use this opportunity to share some opinions about the role of theory in biology. This is not intended to be a thorough philosophical essay on the topic, but I hope it encourages some useful discussions.

I believe that theoretical research has two great strengths. Firstly, theory aims to be particularly thorough when explaining concepts, and it can highlight common reasoning errors. This is especially the case, when mathematical models are used. Secondly, theory can foster communication between different fields. Theoreticians can highlight important connection between fields, or apply conceptual frameworks to new contexts.

One general concept that I have used in this thesis is the rarer-sex effect, which describes the fact that the reproductive value of individuals is increased when they belong to the rarer sex. The rarer-sex effect was initially proposed in order to explain why most animals have roughly equally many males and females. This is also the context in which I cite it in chapter 3 of this thesis. In chapter 4, I also cite the rarer-sex effect, but here I show that the argument inherent to it can be extended to facultative parthenogens and that sex-ratios are selected to be more female-biased with increasing rates of parthenogenesis. Finally, in my short essay above, I highlighted that the rarer-sex effect has also been used to explain strongly female-biased sex ratios in some eusocial animals (Davies et al. 2016). Clearly, this conceptual framework has aided understanding beyond the context for which it was initially devised. This shows the strength of research approaches that search for general principles.

However, attempts to derive general principles come with their own risks. One difficulty is that concepts and results are not always easily applicable to other systems. For example, if the rarer-sex effect were applied to facultative parthenogens and to Hymenoptera eusociality in a naive way, e.g. by reducing it to the result that unbiased sex-ratios are favored by evolution, then this would fail to aid understanding. Similarly, if someone is already familiar with male-mimicking females in damselflies, and then observes hummingbird females with male ornamental plumage, they might prematurely assume that this male-mimicry has also evolved to avoid harassment from males. The first example highlights the importance of thoroughly testing your reasoning when

applying concepts to new contexts. The second example highlights that theory alone cannot answer whether a mechanism shown to work in one taxon also works in another taxon, but that empirical results are required in each taxon separately in order to differentiate between different hypotheses on a taxon-by-taxon basis.

In evolutionary biology, "taxon-specific" or "species-specific" are often used as derogatory terms to indicate that someone's research lacks conceptual depth. There is some truth to this: Often, researchers have specific taxa in mind when formulating their ideas, and this can cause an unintentional bias even if they attempt to formulate general principles. For example, research on eusociality has often focused on Hymenoptera, and this has sometimes led to premature conclusions about eusociality in general, e.g. the proposed association between haplodiploidy and female-only worker castes seems plausible when considering only Hymenoptera, but fails when other taxa are considered, some of which combine haplodiploidy with a sterile caste that consists of both sexes (Ross et al. 2013). I would argue, however, that it is not the focus on a specific taxon that is the issue, but rather the lack of awareness about this taxon-specific focus.

My section of the origin of haplodiploidy in chapter 4, provides an example where it is both useful to highlight general mechanisms that promote the evolution of haplodiploidy, but it is also important to consider taxon-specific peculiarities. I highlighted that haplodiploidy is particularly likely to evolve from sex determination systems that share the three key features, that parthenogenesis produces only sons, that parthenogenesis is at least half as effective at producing offspring as sexual reproduction, and that sexual reproduction can easily evolve to only produce daughters. Bull (1979) and Bull (1981) focus on two different sex determination systems that combine these features. Initially, the two papers were cited together, but today, Bull (1979) is usually cited alone, usually to reference the general principle that haplodiploidy is favored because the parthenogenetic production of sons allows mothers to transmit a larger fraction of their alleles to the grand-offspring generation. The important difference between the dosage-dependent sex determination and complementary sex determination has unfortunately been largely forgotten. (As a side note, the two papers also raise the more pragmatic question of whether it is better to put similar results into one long paper than into two short papers.)

I would like to end on some opinionated, philosophical musings on the topic of general principles and taxon-specific research. Some fields of science (particularly physics) appear to have a strong underlying belief that nature can be explained from a few or a single universal principle. Hence, a search for universal principles is seen as synonymous to a search for an underlying truth. However, I see no compelling reason to make the a-priori assumption that nature is necessarily governed by only one or a few universal laws, and this is particularly the case in biology where organisms differ in many interesting ways that often have considerable impact on their evolution. This is not to say that I discourage the search for general principles, indeed much of my own work aims to unify different fields in a common conceptual framework. I merely want to highlight that taxon-specific research, that fosters a deep understanding of only one peculiar system, is just as important in our quest to understand nature, as research that aims to find general mechanisms that shape many taxa. The aim of scientific inquiry should not be to find universal principles, but rather to understand the world as it is. Whether universal principles are more truthful than taxon-specific peculiarities

depends not on our approach to science, but rather on the natural world itself.

6

General Conclusion

I started this thesis with the narrative of an evolutionary ecologist observing a system in which females come in multiple distinct morphs while males all look the same. I have given various examples of evolutionary drivers that can cause this pattern and argued that there is no single explanation that fits all systems. In the general introduction, I discussed three systems of mimicry: Bayesian mimicry in some female butterflies, and male-mimicking females in damselflies and hummingbirds. While all three polymorphisms are maintained by learning, they differ in who is learning: predators, males, and competitors, respectively. I then discussed the Alba polymorphism in *Colias* butterflies in which the mechanism for balancing selection is currently not clear. In chapter 2, I proposed a novel hypothesis that this polymorphism might be maintained by a trade-off between emergence time and attractiveness. Chapter 3 highlights yet another mechanism by which sex-limited diversity can evolve. If two niches (e.g. two resources) are available to a species, and one of these niches is larger than the other, a sex-limited polymorphism for niche use can evolve. Which sex evolves to be polymorphic depends only on the order in which differences between the sexes initially evolve.

While my focus was on genetic polymorphism, I also worked on two female-limited polyphenisms: facultative parthenogenesis and female-only worker castes in some eusocial animals. A female-only worker caste also matches the pattern of having two female morphs and one of these resembling males. This is because reproductives of both sexes require different morphological adaptations than workers do, e.g. in ants, reproductives have wings, while workers are wingless. There are important similarities between the evolution of a single-sex work force and a sex-limited polymorphism for niche use. Both are characterized by the amplification of initially small differences between sexes. Furthermore, the rarer-sex effect is essential to understanding both of them, albeit for opposite reasons: it fixes sex-ratios to 1:1 in the case of sex-limited polymorphism for niche use, and it promotes the evolution of strongly biased sex-ratios during the evolution of eusociality.

In conclusion, the divers behind female-limited diversity are diverse and differ between taxa. Insights gained on one system can not simply be applied to a different system. At the same time, it is often possible to find important similarities between different cases of female-limited diversity, such as the role of learning or the rarer-sex effect. A thorough understanding of one system can therefore help derive hypotheses about a different system. Furthermore, conceptual frameworks constructed in one context can often also aid understanding of other systems, sometimes in surprising ways.

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A

TREE review: "Female alternative reproductive tactics: diversity and drivers"

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Abstract

It is often argued that anisogamy causes alternative reproductive tactics (ARTs) to be more common in males than females. We challenge this view by pointing out logical flaws in the argument. We then review recent work on the diversity of female ARTs, listing several understudied types such as solitary versus com- munal breeding and facultative parthenogenesis. We highlight an important dif- ference between male and female ARTs that caused female ARTs to be overlooked: male ARTs tend to focus on successful fertilization, whereas female ARTs occur at many stages of reproduction and often form complex networks of decision points. We propose to study correlated female ARTs as a whole to better understand their drivers and eco-evolutionary dynamics.

Highlights

Alternative reproductive tactics (ARTs) are thought to be more abundant in males than in females owing to higher fitness variance in males and higher female investment in reproduction, but there are no strong empirical or theoretical studies that support this.

Whereas male ARTs tend to act pre-mating (focusing on fertilization), female ARTs can occur at various stages of re- production (from mate finding to brood care) and form complex networks of decision points.

The evolutionary dynamics of female ARTs can be condition- and frequency-dependent, and can be influenced by factors including sexual antagonism and intralocus tactical conflict.

Evidence for female ARTs is abundant, and they are more common than is often appreciated. However, their eco-evolutionary drivers are not well understood, calling for future research.

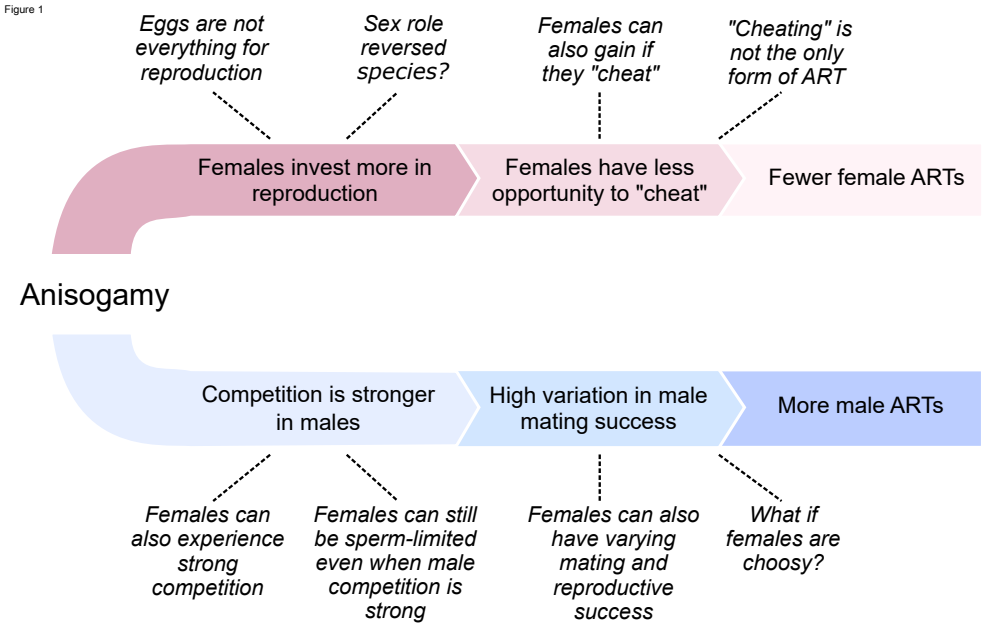

Figure 1.1: An illustration of the commonly cited logic chains leading from anisogamy to fewer alternative reproductive tactics (ARTs) in females (top) than in males (bottom). We identify several caveats that deserve further investigation (indicated by dotted lines and italics).

Do ARTs evolve more easily in males than in females?

Alternative reproductive tactics (**ARTs**; see Glossary) refer to discrete variations in a reproductive behavior that occur within the same sex in a population of the same species. The different variations must serve the same functional end and directly contribute to the production of off-spring. Continuous behavioral variations (e.g., biased resource allocation to sons and daughters) and those that indirectly influence fitness (e.g., dispersal, infanticide, or reproductive suppression) are not considered to be ARTs. ARTs are often thought to evolve in response to intense reproductive competition and are a means for individuals who might not succeed through conventional tactics (e.g., fighting for territories or singing to attract partners) to reproduce [1]. Although in both sexes there are examples of ARTs, as well as less clear-cut variable reproductive tactics such as continuous offspring sex allocation by female ungulates [2] and different types of 'sneaker' tactics in male fish [3], the existing literature has focused on discrete ARTs in males. ARTs have been predicted to evolve more easily in males because **anisogamy** biases the intensity of sexual selection between the sexes [1]. Because there does not appear to be any theoretical work linking anisogamy to the evolution of ARTs, current literature generally relies on limited evidence to explain why ARTs may evolve more easily in males than in females [4,5]. The arguments generally follow two chains of logic: either through females investing more heavily in reproduction, leading them to have less opportunity to 'cheat', or through stronger intrasexual competition and consequent higher fitness variance in males, causing them to explore alternative ways to achieve fertilization (Figure 1, shaded arrows)

Does anisogamy necessarily lead to fewer ARTs in females because of their greater investment in reproduction? A closer examination of the proposed logic chain reveals several important caveats that undermine this common view (Figure 1, upper dotted lines). For many species, egg production represents only a small proportion of the entire investment needed to produce independent offspring, and the relative contributions of the male and female parents can vary greatly across breeding stages [6]. In sex role-reversed species such as pipefishes and jacanas, males often invest more in reproduction than females. Although such cases are relatively rare in the animal kingdom [7], it is still peculiar that we do not seem to have any examples of female ARTs in sex role-reversed species. Furthermore, because females usually invest heavily in reproduction, natural selection can favor a tactic that parasitizes the investment of others to reduce reproductive costs. Indeed, conspecific brood parasitism, where some females lay eggs in the nests of others, is abundant across taxa (e.g., the burying beetle *Nicrophorus vespilloides* [8] and many species of birds [9]) and is a well-recognized type of female ART. There are also ways other than 'cheating' that females could use to increase their reproductive fitness. For example, female striped mice *Rhabdomys pumilio* and house mice *Mus musculus domesticus* can breed solitarily or in groups [10,11].

Similarly, the argument that ARTs are more abundant in males because of stronger competition for fertilization between them does not always hold (Figure 1, lower dotted lines). For example, in **lekking** species, where sexual selection on males is particularly strong, females can still be sperm-limited and compete aggressively for mating with preferred males (reviewed in [12]). Females can also suffer from sperm limitation due to cryptic male mate choice, where more sperm are allocated to high-quality females [13,14]. In a remarkable case, female triplefin blennies *Tripterygion melanurus* were observed to intrude on a mating pair and displace the spawning female to gain priority in accessing the male, resembling the 'sneaker' male tactic [15]. In addition, female competition and aggression, although often cryptic and indirect, are abundant in animals [12,16]. Substantial female reproductive skew has been found in many cooperatively breeding species where a high proportion of females have no or very low direct fitness [17]. Female mating failure because of a shortage of males has also been found in non-cooperative breeding species with conventional sex roles [18]. If high fitness variance promotes the evolution of ARTs, we should expect to find female ARTs in those species. However, theoretical work has also shown that high variance in male mating success through the conventional tactic does not necessarily lead to the maintenance of ARTs which can be disrupted by female choice and sexual conflict [19].

Given the abundant caveats in these logic chains (Figure 1), further empirical and theoretical studies will be necessary to clarify the evolution of ARTs and examine the causal relationship between differences in investment or fitness variance and the abundance of ARTs in males and females.

Diverse forms of female ARTs

In the following we provide examples of ARTs in females, including many recent studies supporting our conjecture that female ARTs are abundant in nature but have been overlooked in the literature so far.

Intraspecific parasitism
Similar to the 'sneaker' tactic in males, females across diverse taxa are found to parasitize the reproductive investment of other females. For example, conspecific brood parasitism has been found in ¿250 avian species and is particularly abundant in precocial and colonial birds with female philopatry and large clutches (reviewed in [9,20]). It has also been found in the largemouth bass *Micropterus salmoides* [21] and several species of wasps [22,23]. Furthermore, female insects are known to steal resources vital for reproduction from others [24].

Polymorphism with distinct reproductive behavior patterns
In several species, females have genetically determined distinct morphs and associated behavioral patterns. In the fire ant *Solenopsis invicta*, the queens have two distinct morphs that are determined by a single genomic element with two variants, commonly referred to as the social B and social b chromosomes (SB and Sb) [25]. SB/SB homozygotes form single-queen colonies, SB/Sb heterozygotes form polygynous colonies, and Sb/Sb homozygotes are not viable. Another example is the white-throated sparrow *Zonotrichia albicollis*, where females have genetically determined white- or tan-colored median crown stripes. The white females are more aggressive, have higher mating rates, and provide less parental care than the tan females [26]. In the side-blotched lizard *Uta stansburiana*, females have genetically determined orange and yellow morphs, corresponding to r- and K-strategies in reproduction, respectively [27].

Independent mate choice versus mate choice copying
When choosing a mate, some individuals make their decisions independently, whereas others copy the preferences of others. For example, in the deer mouse *Peromyscus maniculatus*, some females copy the odor preference of other females, independently of their familiarity and kinship [28]. This type of ART has been found in both sexes but seems to be more common or better-studied in females. A recent meta-analysis containing 22 species of females (149 effect sizes) and nine species of males (14 effect sizes), including arthropods, fishes, birds, and mammals, found that the strength of copying did not differ significantly between the sexes [29].

Female morph versus male-mimicry
Analogous to the 'female-mimic' tactic in males, some females resemble the color pattern and morphology of males. This type of ART has been identified in ¿100 species of damselflies and dragonflies (reviewed in [30]). In addition, female andromorphs have also been found in several butterfly species such as the bog fritillary butterfly *Boloria eunomia*, where the gynomorphs have an advantage in daily survival and precocious emergence, whereas the andromorphs have higher fecundity, lower predation risk, and suffer less from male harassment [31]. Note that not all female color polymorphisms are ARTs. For example, the andromorph female hummingbirds resemble males to reap the benefit of reduced resource competition [32], which does not directly contribute to the production of offspring and is thus not considered to be an ART.

Solitary versus colonial breeding
Females can breed alone or in colonies. The behavioral choice can be genetically determined (such as the aforementioned single- or multiple-queen colonies of fire ants)

or condition-dependent. For example, in the tree sparrow *Passer montanus* [33], females can shift between these two ARTs between subsequent broods within the same breeding season. These types of female ARTs have also been found in several mouse species [10,11,34].

Facultative parthenogenesis
Some females can either reproduce sexually by fertilizing their eggs with sperm or asexually by letting their eggs develop into offspring without being fertilized. This type of ART has been found in various invertebrates [35-37], cartilaginous fishes [38-40], reptiles [41,42] and birds [43,44]. Interestingly, California condor *Gymnogyps californianus* [44] and zebra shark *Stegostoma tigrinium* [40] females have been found to reproduce by parthenogenesis, even when they are in regular contact with fertile males. In the remarkable case of the tropical night lizard *Lepidophyma smithii*, offspring produced in the same clutch can be a mixture of individuals produced sexually and parthenogenetically [45]. These new findings indicate that facultative parthenogenesis can be very cryptic and more abundant in nature than was previously thought. More information on the evolutionary dynamics of this female-specific ART is provided in Box 1.

Discrete sex allocation
The offspring sex ratio is usually continuous, but in some species, particularly Hymenoptera and some families of Diptera, females can specialize in producing either only sons or only daughters (reviewed in [46,47]).

The different types of female ARTs listed above are non-exhaustive, given the diverse ways in which females reproduce in nature. We list polymorphisms with distinct reproductive behavior patterns as a conspicuous type of ART, but it is important to note that, in both sexes, only a fraction of ARTs are associated with distinct morphs. For example, in the green-veined white butterfly *Pieris napi*, female monandry and polyandry are genetically determined, but the two types of females do not seem to differ in morphology [48]. In this case the distinct female mating patterns were referred to as 'alternative lifestyles' rather than ARTs. Such terminology differences across subfields could also contribute to many female ARTs remaining hidden in the literature.

Box 1. Evolutionary dynamics of facultative parthenogenesis
Facultative parthenogenesis is a special type of ART that occurs only in females. It describes any system where sexual and parthenogenetic reproduction co-occur in the same population. One type of facultative parthenogenesis is cyclical parthenogenesis, which is characterized by periods of asexual reproduction and short bouts of sexual reproduction. Examples include Daphnia [92], aphids [93], and rotifers [94]. The period of asexual reproduction allows cyclical parthenogenesis to quickly populate an environment under favorable conditions (e.g., in spring and summer), whereas sexual reproduction is often associated with the production of resting eggs that can survive unfavorable conditions (e.g., winter or drought). The lifespan of such species is often short such that some individuals reproduce only sexually or asexually during their entire life. In cyclical parthenogens it is crucial for females to be able to predict when the environment becomes unfavorable, and several cues are used for this purpose, such as population density [95] and day length [96]. Females differ in their responses to these environmental cues, and therefore sexual and asexual generations typically overlap.
Cyclical parthenogens have attracted much attention from both empiricists and modelers, but cyclical environments are not the only factor that can maintain facultative parthenogenesis. Another mechanism is mate-limitation: a female can fail to find a mate at low population densities. In this case, she benefits from asexual reproduction even if it produces far fewer offspring compared to sexual reproduction. For example, mate-limitation is an essential factor in mayflies [97]. The decision between sexual and asexual reproduction in species of facultative parthenogenesis can also be condition-dependent, where poor condition individuals reproduce sexually to increase genetic variation among offspring such that at least some of them might have a favorable genetic makeup. Condition-dependent parthenogenesis occurs in Daphnia [92] and also in species that are not cyclical parthenogens, for example in nematodes [98]. Furthermore, facultative parthenogenesis can

Proximate and ultimate drivers of female ARTs

The proximate and ultimate drivers of female ARTs provide insights into the immediate inducement and the long-term evolutionary causes underlying their evolution and maintenance. Studies on male ARTs have identified hormones, neuroendocrine mechanisms, and genetic and environmental interactions (GEIs) as important proximate drivers (reviewed in part II of [49]). Because males and females share a large part of their genomes, we expect that these factors also play a role in triggering the expression of female ARTs. For example, in the white-throated sparrow, ARTs in both sexes seem to be driven by changes in steroid hormone pathways caused by a chromosomal inversion [26,50]. The steroid hormones not only activate sexual behaviors that directly mediate mate choice, aggressive competition, and mating but also help to steer the development of neural and physical systems that underlie these reproductive traits. At the ultimate level, ARTs can potentially evolve whenever there is fitness to be gained by pursuing divergent reproductive behaviors, and this should also apply to both sexes. For example, large variance in breeding success through the 'conventional tactic', such as aggressive male mate competition or females laying eggs exclusively into their own

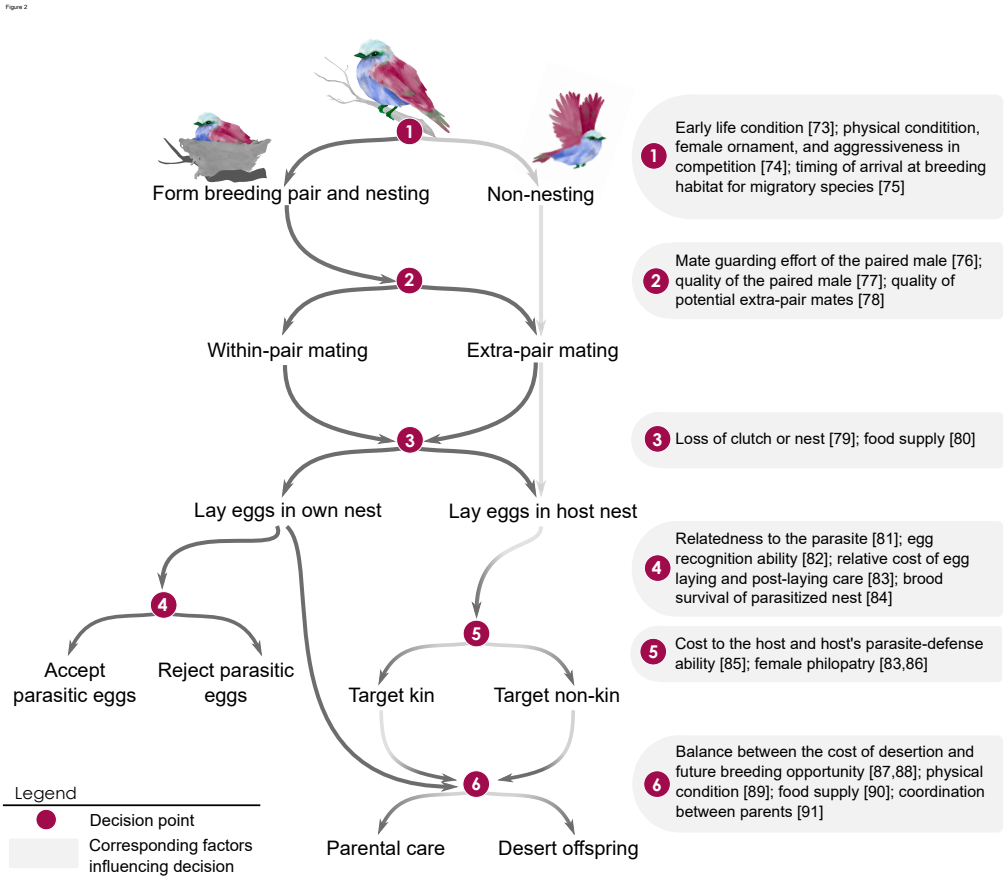

Figure 1.2: The diverse female reproductive tactics (using birds as an example) often cannot be clearly characterized into small sets of discrete alternative reproductive tactics (ARTs), such as 'territorials' and 'sneakers' as in males, and instead comprise a complex network of decision points. Each decision point can be influenced by multiple (possibly interacting) factors, and some factors can influence multiple decision points. The list of factors influencing each decision point is not exhaustive. See refs [73-91].

nest, sets the stage for alternative tactics such as sneaky mating and conspecific brood parasitism in males and females, respectively.

Despite the similarities, the evolution and development of ARTs also have important differences between the sexes. In males, ARTs often only occur pre-mating to achieve fertilization (although other strategies such as providing parental care versus abandoning offspring are viable male ARTs in some species). Therefore, males can often be sorted into categories such as 'fighter versus scrambler', or guarder versus sneaker', etc. It is thus easier to form hypotheses and study the proximate and ultimate drivers of male ARTs, both empirically and theoretically. By contrast, female ARTs can occur in all breeding stages, thus forming a complex network of splitting and merging decision points that can be temporally intermixed. Using breeding female birds as an example (illustrated in Figure 2), although nesting and non-nesting are clear-cut female ARTs, both types of females could subsequently engage in extra-pair mating, lay eggs in conspecific nests, and/or take care of or desert their offspring. Furthermore, the ART of

a female in a specific breeding activity can often be influenced by her previous behavior choices, including those that are not ARTs (e.g., whether she has experienced natal dispersal). To understand the drivers of a specific female ART it is often not useful to categorize females solely according to their ARTs at that focal event because the same behavioral choice can have different drivers. For example, conspecific brood parasitism can be caused by floater females doing the 'best of a bad job', by nesting females trying to enhance their reproductive fitness by spreading the predation risk of their offspring, or as a response to nest loss [51,52].

Some correlated female behavior patterns are genetically determined. For example, in the side-blotched lizard, female color morph, territoriality, and the number and size of eggs are determined by linked genetic components [27], and in the white-throated sparrow female aggressiveness, mating rate, and parental care investment are influenced by the same chromosomal inversion [26]. Other female behavior patterns can be correlated because their expression depends on the same aspects of individual condition. For example, in birds, physical condition (i.e., characterized by body mass, parasite load, or stress levels) not only influences the choice between nesting and non-nesting but also influences whether a female deserts her offspring or provides care. Similarly, food supply influences whether a nesting female will lay extra eggs in the nests of other females and whether she will desert her offspring (Figure 2). In many primates, dominant females often suppress the reproduction of subordinates and reduce the survival of their offspring by causing consistent stress through mild but repeated harassment and aggression [53]. These behaviors are not considered to be ARTs because they usually do not feature discrete alternatives, but they are indispensable for understanding the maintenance and interactions of female behavioral variations in social mammals [12,16,53].

Finally, the interactions between males and females that adopt diverse tactics are crucial in driving the evolution of male and female ARTs [5,19]. A recent study following the establishment of a spotless starling colony and its development over the following 2 years illustrates the feedback between male and female ARTs [54]. As population density and the quality of potential mates and same-sex competitors increased, more males switched from polygyny to monogamy, and the frequency of conspecific brood parasitism also increased in females.

Evolutionary dynamics of female ARTs

Status-dependent selection and **negative frequency-dependent selection** are the two most studied types of evolutionary dynamics that underlie the maintenance of ARTs. The former can produce ARTs in populations of genetically identical individuals. In this case the expression of ARTs is triggered by the condition of an individual instead of their genetic background. For example, female house mice in high condition breed solitarily, whereas those in low condition breed communally and suffer from reduced pup survival [11,34]. In this case, the communally breeding females have likely been doing the 'best of a bad job' given their poor condition. Different female ARTs can also result from polymorphic genotypes and be maintained by negative frequency-dependent selection. For example, color polymorphism associated with ARTs is controlled by a single locus with female-limited expression in several damselfly and butterfly species

[55-57]. The coexistence of gynomorphic and andromorphic females is proposed to be maintained by frequency-dependent selection through mechanisms such as learned mate recognition and/or male mimicry [31].

The relative importance of status-dependent and negative frequency-dependent selection has been extensively debated because the two mechanisms are based on different assumptions of the genetic basis of ARTs and have different implications for their evolutionary dynamics (reviewed in [1,58]). In short, if the determination of ARTs is purely status-dependent and not heritable, natural selection cannot act on this response. Therefore, individuals adopting different ARTs can have unequal fitness, and the frequencies of different ARTs should be independent of their relative success. By contrast, if the different ARTs correspond to different genotypes (i.e., **alternative reproductive strategies** [59]), they should be heritable and subject to natural selection. Consequently, negative frequency-dependent selection is expected to lead to a fitness equilibrium between ARTs, and their relative frequencies should be stable or oscillate in cycles. The two idealized mechanisms also respond very differently to changing environments. For example, status-dependent ARTs can be less efficient in purging maladaptive genes than ARTs maintained through frequency-dependent selection in environments that change directionally or in large steps [60].

It is important to note that these two idealized mechanisms can independently or jointly produce the same set of ARTs, such as conspecific brood parasitism [61,62]. Furthermore, the two mechanisms cannot be distinguished solely by comparing the fitness between the ARTs because status-dependent selection may also lead to equal average fitness of different ARTs when there are multiple status-dependent tactic 'switch points' [63]. Similarly, genetically controlled ARTs maintained by negative frequency-dependent selection in the long term can have large frequency fluctuations and very different fitness on the timescales amenable to empirical measurements [64]. In natural populations, the fitness of ARTs can be influenced by diverse environmental factors that change both spatially and temporally, making it even more difficult to pin down the mechanisms maintaining the ARTs over long timescales [65]. It is now widely accepted that status- and frequency-dependent selection are not mutually exclusive. For example, many ARTs seem to be threshold traits where the status-dependent 'switch point' between tactics is influenced by quantitative trait loci. For example, in female striped mice, the choice between solitary and communal breeding can be predicted from their baseline blood corticosterone levels [8], and the expression of stress hormones and stress-related genes has been found to be controlled by quantitative trait loci in various species [66-68]. Such ARTs controlled by evolving reaction norms can be captured theoretically by environmentally cued threshold models. These ARTs are simultaneously status-dependent and heritable, and can be subject to negative frequency-dependent selection (reviewed in [58]).

In addition to status- and frequency-dependent selection, the evolutionary dynamics of ARTs can also be influenced by genetic constraints, leading to **intralocus tactical conflicts** [69,70]. Analogous to the effect of **sexually antagonistic** genes that prevent males and females from reaching their sex-specific fitness optima, constraints of a shared genome can prevent ARTs from reaching their respective phenotypic optima [70]. Empirical evidence consistent with this prediction has been found in bulb mites and swordtail fish [71,72]. All research to date on intralocus tactical conflict is, to our knowledge, focused on male ARTs. However, there is no reason to think that the phe-

nomenon should be restricted to males, and such conflict is therefore worth considering in the context of female ARTs. Genetic constraints such as **sexual antagonism** and intralocus tactical conflict are expected to impact on eco-evolutionary dynamics and speciation, for example by altering equilibrium frequencies of ARTs among populations or by causing rapid phenotypic evolution after the loss of an ART [69].

Concluding remarks

ARTs illustrate the variety of solutions that species have evolved to achieve reproductive success among same-sex individuals in a population. In this review we draw attention to the diversity of ARTs in females and question the widespread notion that ARTs are more common in males than females. We show that female ARTs can occur throughout the breeding cycle, often forming a network of splitting and merging points of behavioral choices. The drivers and evolutionary dynamics of ARTs have similarities and important differences between the sexes, and our understanding of how ARTs evolve in each sex is still limited.

To expand our knowledge on this important topic, we need a thorough survey of the diversity and prevalence of different types of ARTs in males and females across taxa, and the use of meta-analysis, modeling, and experiments (e.g., by removing a specific ART, changing the frequency distribution of ARTs, or varying the strength of a selection force) to clarify the driving factors and their interactions. Furthermore, the feedback between female and male ARTs and their impact on evolution needs to be studied at both the genetic and behavioral levels. Addressing the unresolved issues (see Outstanding questions) provides a starting point to fill in this knowledge gap.

Outstanding questions

Which factors increase or decrease the likelihood of evolving female ARTs?

Are female ARTs more likely to be plastic or genetically determined? Is this relationship different in males?

Are ARTs more likely to evolve as a de novo behavior or from a continuous trait under disruptive selection? Is this different between the sexes?

Does the presence of ARTs in one sex influence the likelihood that ARTs will evolve in the other sex?

Can studying correlated reproductive behaviors as a whole help us to understand the causes and consequences of female ART choices in different breeding activities and stages?

Are there cases of intralocus tactical conflict in females? What are the roles of genetic constraints in the evolution of female ARTs?

Does the prevalence of female ARTs differ between major taxonomic groups? Does the type of mating system influence the evolution of female ARTs?

Many plants also have polymorphic reproductive organs, such as color polymorphism of the flowers. Do they serve as ARTs and share the same ultimate drivers as the ARTs in animals? Is there a sex bias regarding the diversity and prevalence of ARTs in plants?

Glossary

Alternative reproductive strategies: genetically determined rather than condition-dependent ARTs; for example the distinct male morphology and mating strategies determined by the OBY locus alleles in the side-blotched lizard Uta stansburiana.

Alternative reproductive tactics (ARTs): discontinuous alternative phenotypes directly associated with reproduction that can be observed within the same sex in the same population (e.g., solitary or communal breeding).

Anisogamy: the condition in which the male and female gametes are of different sizes. The smaller gamete, a sperm cell, is produced by the male sex, whereas the larger gamete, an egg cell, is produced by the female sex.

Intralocus tactical conflict: similar to intralocus sexual conflict, this occurs when ARTs have different optima for traits that are genetically correlated across tactics.

Lekking species: in such species males provide females with no resources except gametes, male distribution is clumped in space during the mating season, and females choose males based on criteria other than territorial quality and parental care.

Negative frequency-dependent selection: a form of selection that occurs when rare alleles have higher fitness than common alleles. This process can maintain genetic variation within populations.

Parthenogenesis: a form of asexual reproduction where offspring are formed without genetic material from a male.

Precocial: young animals of a precocial species show a high level of maturity and typically can feed and move independently almost immediately after birth or hatching.

Sexual antagonism: conflict arising from traits or genes that are beneficial to one sex but harmful to the other.

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B

Supplement for "Sex ratio theory for facultative parthenogens: from fortuitously optimal stick insects to the origin of haplodiploidy in Hymenoptera"

B.1 Glossary

term	definition
parthenogenesis	A type of asexual reproduction where offspring develop from unfertilized eggs. Hence, only females can reproduce parthenogenetically.
automixis	A type of parthenogenesis where recombination takes place, and offspring are diploid. This results in high rates of homozygosity in the offspring, although the degree of homozygosity can differ greatly between different types of automixis.
apomixis	A type of parthenogenesis where offspring are full clones of their mother and heterozygosity is retained.
thelytoky	the parthenogenetic production of female offspring
haplodiploidy	A system where parthenogenetically produced offspring are haploid and male and sexually produced offspring are diploid and female (arrhenotoky). Haplodiploidy can also refer to similar systems where all offspring are produced sexually, but sons do not transmit their father's alleles to the next generation (paternal genome elimination).

(haplodiploid) CSD	A sex determination system found in many Hymenoptera. Usually, there is a single sex-determining locus. Individuals that are heterozygous at this locus develop into females. Hemi- and homozygous individuals develop into males. Males are usually haploid and produced parthenogenetically. However, inbreeding can also cause the production of diploid males. These diploid males are usually inviable.
diplodiploid CSD	A plausible sex determination system suggested by Bull (1981) that has not (yet) been reliably shown to be present in any natural system. In this system, all individuals are diploid and produced sexually. There is a single sex-determining locus with two alleles. Heterozygous individuals develop into females and homozygous individuals develop into males. Superficially, this system resembles a ZW system. However, under diplodiploid CSD, parthenogenesis through automixis produces an all-male brood. Diplodiploid CSD with three sex-determining loci has been proposed for the rice frog, but molecular proof is still lacking (Miura et al. 2015).
cyclic parthenogenesis	A life cycle where some generations reproduce exclusively parthenogenetically, while other generations (usually towards the end of a season) reproduce sexually.

B.2 Hatching failures and reduced fecundity as two types of costs of parthenogenesis

For theoreticians

In the main text, we define δ as the cost of asexuality reflecting hatching failures of parthenogenetically produced eggs. However, costs of asexuality can also be due to deleterious recessive allleles that only become apparent in adults in the form of reduced fecundity or mortality after hatching. Here, we add additional costs of asexuality that occur after hatching: δ_1 captures hatching failures of parthenogenetically produced eggs, while δ_2 captures reduced fecundity as well as mortality after hatching.

In order to separate these two effects, it is also necessary to consider each generation at two different time points: $P_{1,t+1}$ considers generation $t+1$ just after hatching. As in the main text, $z_{a,t}$, $z_{s,t}$, and $\overline{z}_t$ (with $\overline{z}_t := P_{1,t+1}(\male)$) will also refer to this point in time, denoting the sex ratio among asexually produced hatchlings, sexually produced hatchlings, and the entire population of hatchlings, respectively. $P_{2,t+1}$ denotes the eggs laid by generation $t+1$ after additional viability and fecundity costs of asexuality have taken effect.

$P_{1,t+1}(\male)$, $P_{1,t+1}(asex\|\male)$, and $P_{1,t+1}(asex\|\female)$ are calculated in the same way as in the main text:

$$\overline{z}_t := P_{1,t+1}(\male) = \frac{(1-\delta_1)\overline{\alpha}_t z_{a,t} + (1-\overline{\alpha}_t) z_{s,t}}{1-\delta_1\overline{\alpha}_t} \tag{S2.1}$$

$$P_{1,t+1}(asex\|\male) = \frac{(1-\delta_1)\overline{\alpha}_t z_{a,t}}{(1-\delta_1\overline{\alpha}_t)\overline{z}_t} = \frac{(1-\delta_1)\overline{\alpha}_t z_{a,t}}{(1-\delta_1)\overline{\alpha}_t z_{a,t} + (1-\overline{\alpha}_t) z_{s,t}} \tag{S2.2}$$

$$P_{1,t+1}(asex\|\female) = \frac{(1-\delta_1)\overline{\alpha}_t (1-z_{a,t})}{(1-\delta_1\overline{\alpha}_t)(1-\overline{z}_t)} = \frac{(1-\delta_1)\overline{\alpha}_t (1-z_{a,t})}{(1-\delta_1)\overline{\alpha}_t (1-z_{a,t}) + (1-\overline{\alpha}_t)(1-z_{s,t})} \tag{S2.3}$$

As mentioned above, $P_{2,t+1}(asex\|\male)$ and $P_{2,t+1}(asex\|\female)$ will take into account other costs of asexuality, such as increased mortality and decreased fecundity of parthenogenetically produced offspring. These additional costs are denoted by δ_2, giving us:

$$P_{2,t+1}(asex\|\male) = \frac{(1-\delta_2) P_{1,t+1}(asex\|\male)}{(1-\delta_2) P_{1,t+1}(asex\|\male) + (1 - P_{1,t+1}(asex\|\male))} \tag{S2.4}$$

$$P_{2,t+1}(asex\|\female) = \frac{(1-\delta_2) P_{1,t+1}(asex\|\female)}{(1-\delta_2) P_{1,t+1}(asex\|\female) + (1 - P_{1,t+1}(asex\|\female))} \tag{S2.5}$$

For $P_{2,t+1}(asex\|\female)$, we consider all eggs produced by generation $t+1$ (including eggs that never hatch) and ask what proportion of these have a mother who was herself parthenogenetically produced. For $P_{2,t+1}(asex\|male)$, we consider fertilized eggs (i.e. eggs that have a father) produced by generation $t+1$ and ask what proportion of these have a father who was himself parthenogenetically produced.

The class reproductive values of males and females are then calculated as

$$V_t^m = \left(\frac{1 - P_{2,t+1}(asex\|\female)}{2}\right) V_{t+1}^f + \left(\frac{1 - P_{2,t+1}(asex\|\male)}{2}\right) V_{t+1}^m \tag{S2.6}$$

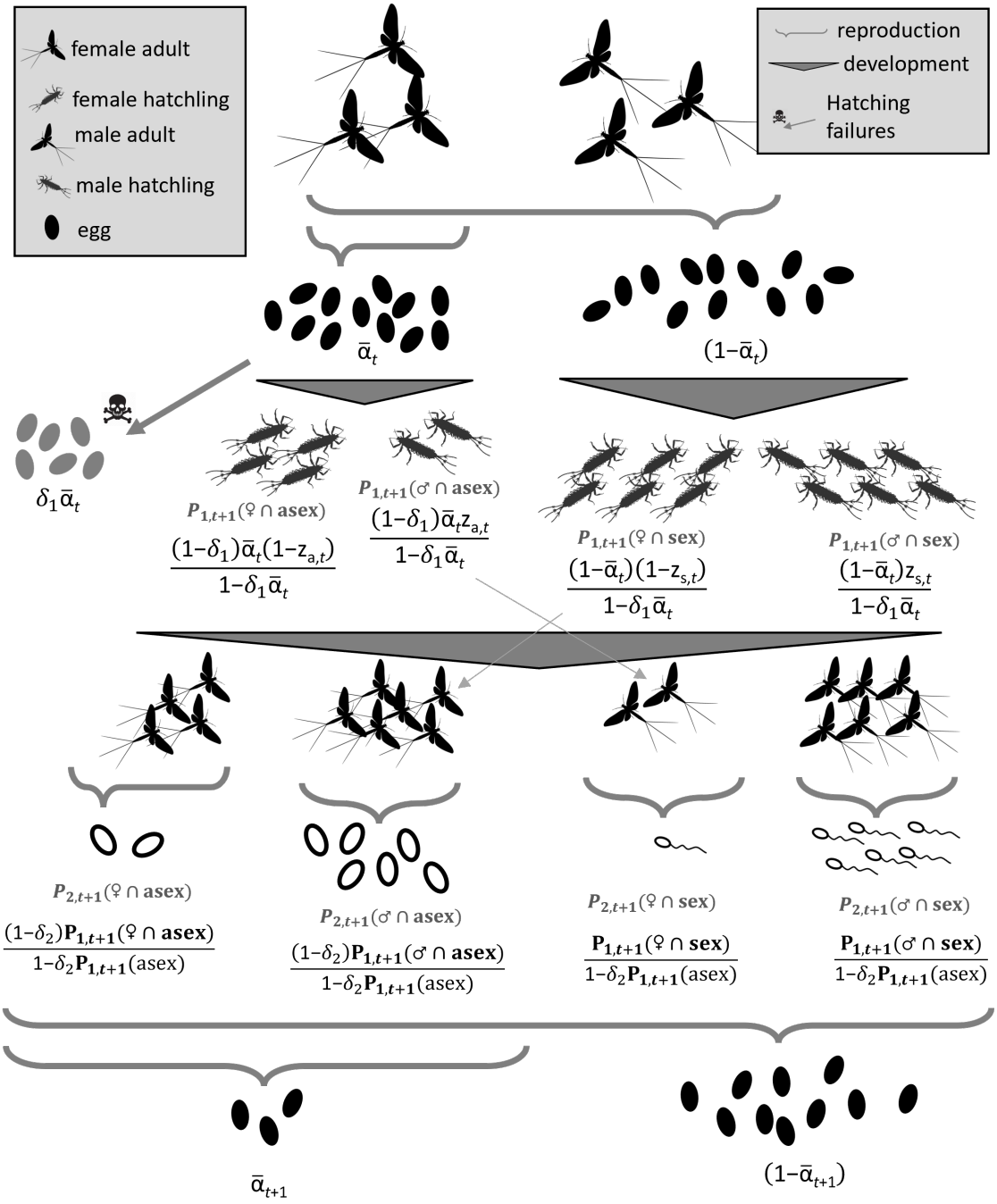

Figure S2.1: **Conceptual illustration including both costs of asexuality: δ_1, hatching failures of parthenogenetically produced eggs, as well as δ_2, reduced fecundity and/or mortality after hatching**

and

$$V_t^f = 1 - V_t^m \tag{S2.7}$$

In the Maple Code (Supplement S4), we show three aspects in which the model described above gives the exact same result as the simpler model described in the main text when choosing $\delta = \delta_1 + (1 - \delta_1)\delta_2$. Firstly, the class reproductive values are the same for both models. In other words, for the class reproductive value of males and females, it does not matter whether the cost of asexuality takes the form of hatching failures or reduced fecundity due to recessive alleles. Secondly, if $z_s = z_a$ (i.e. if the sexual reproduction and parthenogenesis produce the same sex ratio among offspring), then the prescient optimal sex ratio, $\bar{z}*$ predicted here equals that predicted by the simpler model in the main text. Lastly, the model here also gives the result reported in the main text that the stick insect system ($z_a = 0$, $z_s = 0.5$, and constant $\bar{\alpha}$) generates prescient optimality.

An explicit distinction between the two types of costs becomes necessary for those cases where $z_s \neq z_a$, $\delta_2 > 0$, and $0 < \bar{\alpha} < 1$. In this case, calculating the optimal $\bar{z}*$ becomes more tedious. Recall that optimality is achieved if the individual reproductive value of parthenogenetically produced sons equals that of parthenogenetically produced daughters and the same is true for sexually produced sons and daughters. In the main text, the individual reproductive value of parthenogenetically produced males equaled that of sexually produced males and the same was true for females. This made it sufficient to calculate the mean individual reproductive value of males and females. However, when some costs of parthenogenesis occur after hatching, it becomes necessary to separately calculate the mean individual reproductive values for four groups of hatchlings: parthenogenetically produced daughters, sexually produced daughters, parthenogenetically produced sons, and sexually produced sons. These individual reproductive values of hatchlings are denoted as $v^{f,a}$, $v^{f,s}$, $v^{m,a}$, and $v^{m,s}$, respectively, and are calculated as:

$$v_t^{f,a} = \frac{P_{2,t}(asex \| ♀) V_t^f}{P_{1,t}(asex \cap ♀) N} \tag{S2.8}$$

$$v_t^{f,s} = \frac{P_{2,t}(sex \| ♀) V_t^f}{P_{1,t}(sex \cap ♀) N} \tag{S2.9}$$

$$v_t^{m,a} = \frac{P_{2,t}(asex \| ♂) V_t^m}{P_{1,t}(asex \cap ♂) N} \tag{S2.10}$$

$$v_t^{m,s} = \frac{P_{2,t}(sex \| ♂) V_t^m}{P_{1,t}(sex \cap ♂) N} \tag{S2.11}$$

The prescient optimal value $\bar{z}^*$ is achieved when $v^{f,a} = v^{m,a}$ and $v^{f,s} = v^{m,s}$.
It is useful to first introduce the term $P_{2,t}(♂)$:

$$P_{2,t}(♂) = \frac{(1 - \delta_2)(1 - \delta_1)\bar{\alpha} z_a + (1 - \bar{\alpha}) z_s}{1 - \delta_1 \bar{\alpha} - (1 - \delta_1)\delta_2 \bar{\alpha}} \tag{S2.12}$$

While $P_{2,t}(\male)$ is not measurable in nature, it is nevertheless useful for the calculations that are to follow, and we will use it in order to calculate results in terms of the optimal sex ratio at hatching, $\overline{z}^*$.

Prescient optimality is achieved if and only if $V_t^m = P_{2,t}(\male)$ (see calculation below):

$$v_t^{f,a} = v_t^{m,a}$$

$$\frac{P_{2,t}(asex \| \female) V_t^f}{P_{1,t}(asex \cap \female) N} = \frac{P_{2,t}(asex \| \male) V_t^m}{P_{1,t}(asex \cap \male) N}$$

$$\frac{P_{2,t}(asex \| \female)(1 - V_t^m)}{P_{1,t}(asex \cap \female)} = \frac{P_{2,t}(asex \| \male) V_t^m}{P_{1,t}(asex \cap \male)}$$

$$\frac{P_{2,t}(asex \cap \female)(1 - V_t^m)}{P_{2,t}(\female) P_{1,t}(asex \cap \female)} = \frac{P_{2,t}(asex \cap \male) V_t^m}{P_{2,t}(\male) P_{1,t}(asex \cap \male)}$$

$$\frac{P_{2,t}(asex \cap \female)}{P_{1,t}(asex \cap \female)} \frac{(1 - V_t^m)}{P_{2,t}(\female)} = \frac{P_{2,t}(asex \cap \male)}{P_{1,t}(asex \cap \male)} \frac{V_t^m}{P_{2,t}(\male)} \tag{S2.13}$$

$$\frac{1 - \delta_2}{1 - \delta_2 P_{1,t}(asex)} \frac{(1 - V_t^m)}{1 - P_{2,t}(\male)} = \frac{1 - \delta_2}{1 - \delta_2 P_{1,t}(asex)} \frac{V_t^m}{P_{2,t}(\male)}$$

$$\frac{(1 - V_t^m)}{1 - P_{2,t}(\male)} = \frac{V_t^m}{P_{2,t}(\male)}$$

$$V_t^m = P_{2,t}(\male)$$

Using this result, equation S2.6, and the assumption that generation $t+1$ makes optimal decisions, we can derive what value $P_{2,t+1}(\male)$ needs to take for $\overline{z}_t^*$ to be optimal:

$$P_{2,t+1}^*(\male) = V_{t+1}^m = \left(\frac{1 - P_{2,t+2}(asex \| \female)}{2} \right) (1 - P_{2,t+2}(\male)) + \left(\frac{1 - P_{2,t+2}(asex \| \male)}{2} \right) P_{2,t+2}(\male) \tag{S2.14}$$

In our Maple Code, we use this equation to derive the optimal value for $\overline{z}_t^*$. Here, we simply present this result:

$$\overline{z}_t^* = \frac{(1 - \overline{\alpha}_{t+1})(\delta_1 \delta_2 \overline{\alpha}_t - \delta_1 \overline{\alpha}_t - \delta_2 \overline{\alpha}_t + 1)(\delta_1 z_{a,t} \overline{\alpha}_t - z_{a,t} \overline{\alpha}_t + z_{s,t} \overline{\alpha}_t - z_{s,t})}{(2(\overline{\alpha}_{t+1} \delta_1 \delta_2 - \overline{\alpha}_{t+1} \delta_1 - \overline{\alpha}_{t+1} \delta_2 + 1)(\delta_1 \overline{\alpha}_t - 1)(\delta_1 \delta_2 z_{a,t} \overline{\alpha}_t - \delta_1 z_{a,t} \overline{\alpha}_t - \delta_2 z_{a,t} \overline{\alpha}_t + z_{a,t} \overline{\alpha}_t - z_{s,t} \overline{\alpha}_t + z_{s,t}))} \tag{S2.15}$$

Unlike the simpler model presented in the main manuscript, $\overline{z}_t^*$ does not depend solely on $\overline{\alpha}_{t+1}$, but also on $\overline{\alpha}_t$, $z_{a,t}$, and $z_{s,t}$.

As can be seen in our Maple Code, this complication disappears when we additionally assume that $z_{a,t} = z_{s,t}$, in which case we recover the same result as in the main

manuscript (if choosing $\delta = \delta_1 + (1 - \delta_1)\delta_2$). Furthermore, we can recover the result that stick insect thelytoky results in prescient optimality if the rate of parthenogenesis is constant over time: If $\overline{\alpha}_t = \overline{\alpha}_{t+1}$, and $z_s = 0.5$, then prescient optimality can be achieved if all parthenogenetically produced offspring are female (i.e. if $z_a = 0$).

For empiricists

Above, we showed that some results generalize from the model in the main text when including costs of parthenogenesis that occur after hatching. However, there is one important scenario in which the model presented in this supplement has a different prediction from that in the main text. This scenario occurs when a number of factors come together: the sex ratio of parthenogenetically offspring is different from that of sexually produced offspring ($z_{s,t} \neq z_{a,t}$), the rate of parthenogenesis, $\overline{\alpha}$, is not constant over time, and there are some post-hatching costs (or benefits) of parthenogenesis ($\delta_2 \neq 0$). Post-hatching costs of parthenogenesis include increased mortality of reduced fecundity in parthenogenetically produced young. We have phrased δ_2 as a cost, but our model also allows for negative values of δ_2 in cases when parthenogenetically produced offspring have higher fecundity or lower mortality than their sexually produced siblings.

This subsection will focus on one important case in which it is necessary to distinguish between hatching failures and post-hatching costs: In multiple cyclic parthenogens (e.g. *Daphnia* and aphids), sexually produced offspring are always female, while the sex of parthenogenetically produced offspring is under maternal control. Our model captures this by setting $z_s = 0$.

We still assume that individuals have perfect information about what the rate of parthenogenesis both in their own generation and in the next generation, and that the sex ratio of parthenogenetically produced offspring can be adjusted plastically.

Assuming that all parthenogenetically produced offspring are female ($z_s = 0$) and that the sex ratio of parthenogenetically produced offspring can be adjusted freely, we get the result

$$\overline{z}_t^* = \frac{(1 - \overline{\alpha}_t(1 - \delta_1)\delta_2 - \delta_1\overline{\alpha}_t)}{(1 - \delta_1\overline{\alpha}_t)(1 - \delta_2)} \frac{\frac{1}{2}(1 - \overline{\alpha}_{t+1})}{(1 - \delta_2(1 - \delta_1)\overline{\alpha}_{t+1} - \delta_1\overline{\alpha}_{t+1})} \tag{S2.16}$$

Importantly, this result is in principle measurable in nature and can be used as a model to test real populations against.

B.3 Why does Diplodiploid CSD evolve towards 1/3 asexual reproduction

As shown in the main text, when parthenogenesis produces only males and sexual reproduction is unbiased and if $\delta = 0$, then parthenogenesis can spread until one third of offspring are produced parthenogenetically. Here, we give a verbal (and partially mathematical) explanation for this using the concepts of class and individual reproductive value. For the argument below, we will consider a population where one third of offspring are produced parthenogenetically, and we will show why this remains stable. Very briefly, the argument can be summarized like this: We will first show that the class reproductive value of males is $V^m = 0.4$ and that the sex ratio is $\bar{z} = 2/3$ (proportion of males). We then show that this causes the individual reproductive values of females to be three times that of males. Finally, we show that this three-fold advantage of females cancels out the two-fold advantage of asexual vs. sexual reproduction, and that, therefore, mothers gain equally from asexual and sexual reproduction.

The class reproductive value of females is 0.6 (and the class reproductive value of males is 0.4): Calculating the class reproductive values of males and females is not trivial when asexually produced offspring are all male. In this case, an increased rate of parthenogenesis has two consequences: The class reproductive value of females becomes higher than that of males and the sex ratio becomes more male-biased. Both of these factors cause the individual reproductive values of males to be lower than that of females. In other words, sons can be viewed as "low-quality" offspring compared to daughters who are "high-quality" offspring (daughters give more grand-offspring than sons). However, males only reproduce sexually, and therefore produce comparatively many "high-quality" (female) offspring. Females, on the other hand, produce many "low-quality" (male) offspring. This doesn't fully cancel out that the class reproductive value of females is higher than that of males, but it does reduce the magnitude of that difference. Note that this argument does not apply when asexually produced offspring are female because the individual reproductive value of females always equals that of males (only the class reproductive values differ, but these are canceled out by the female-biased sex-ratios).

The class reproductive value of females describes what percentage of alleles in a generation in the distant future are currently residing in a female. In the main text it was sufficient to look only one generation into the future to determine the class reproductive value of males and females. However, when asexually produced offspring are male, then it becomes necessary to look farther into the future.

We are interested in the class reproductive values of females in generation 0. To calculate this, we need to look at a generation in the distant future, denoted as generation n, where n is a natural number. From generation n we then track the ancestry of alleles.

Let t be a natural number between 0 and n, and let F_t denote what percentage of alleles in generation n descend from alleles that reside in females in generation t. F_n simply derives from the sex ratio: $F_n = 1 - \bar{z} = 2/3$. Note that F_t is an approximation of the class reproductive value of females, V_t^f, and that this approximation becomes more accurate if n is much larger than t. We can now construct a simple equation to move backwards in time:

$$F_{t-1} = 0.5F_t + 0.75(1 - F_t) \tag{S2.17}$$

The term $0.5F_t$ indicates that alleles residing in a female in generation t have a 50% chance to be derived maternally, and the term $0.75(1 - F_t)$ indicates that alleles residing in a male in generation t have a 75% chance to be derived maternally. This sequence converges for $t \to -\infty$ (readers are welcome to check this themselves). A simple way to get the result of what it converges to is by solving $F_{t-1} = F_t$ which gives the result of $F_t = 0.6$. Hence, as n goes to ∞, F_0 goes to 0.6, giving the class reproductive value of females, $V^f = 0.6$. The class reproductive value of males is simply $1 - F_0 = V^m = 0.4$.

The sex ratio (female:male) is 1:2: Two thirds of offspring are produced sexually and half of these are female. The remaining two thirds of offspring are male. Hence, $\overline{z} = 2/3$, i.e. two third are male and one third of offspring are female.

The individual reproductive value of females is three times that of males: The individual reproductive values of males and females depend on the class reproductive values of males and females and on the sex ratio of the population. If N denotes the population size, then the mean individual reproductive value of males is

$$v^m = \frac{V^m}{N\overline{z}} = \frac{0.6}{N} \tag{S2.18}$$

and the mean individual reproductive value of females is

$$v^f = \frac{V^f}{N(1 - \overline{z})} = \frac{1.8}{N} \tag{S2.19}$$

Hence, the individual reproductive value of females is three times that of males.

Mothers gain equally from asexual and sexual reproduction: Asexually produced offspring are always male and these offspring are 100% related to their mother. Sexually produced offspring can be male or female (in equal proportion) and these offspring are 50% related to their mother. Daughters are "worth" three times as much as sons (in terms of individual reproductive value). Therefore, a mother gains equally many grand-grand-[...]-offspring (descendants in the distant future) by parthenogenetically producing two sons compared to sexually producing one daughter and one son.

B.4 PDF of Maple Code

General

```
> with(Student[MultivariateCalculus]):
> with(LinearAlgebra):
> with(DocumentTools):
>
```

Model 1: unconstrained optimal sex allocation using only delta1

This section only uses delta to refer to hatching failures as presented in the manuscript.
delta1: percentage of parthenogenetically produced eggs that fail to hatch
alpha: mean rate of parthenogenesis in generation t+1 (percentage of eggs that are parthenogenenetically produced, including eggs that fail to hatch)
za: sex ratio (percentage male) among parthenogenetically produced hatchings of generation t+2 (hence, sex allocation by generation t+1)
zs: sex ratio (percentage male) among sexually produced hatchings of generation t+2 (hence, sex allocation by generation t+1)
mean_z: mean sex ratio (percentage male) among all hatchlings of generation t+2 (derived from the other parameters)

Vmnext and Vfnext denote the class reproductive values of males and females, respectively, in generation t+2 (the "next" generation)
simple_Vmnow denotes the same for males of generation t+1. (it is "simple" because delta only reflects hatching failures)
P1_ace_given_male is P(asex | male) in generation t+2, i.e. the percentage of male hatchlings that are produced parthenogenetically.
P1_ace_given_female is P(asex | female) in generation t+2, i.e. the same as above, but for females instead of males

```
> P1_ace_given_male := (1 - delta1) · alpha · za / (1 - delta1 · alpha) · mean_z :
> P1_ace_given_female := (1 - delta1) · alpha · (1 - za) / (1 - delta1 · alpha) · (1 - mean_z) :
> simple_Vmnow := (1 - P1_ace_given_male)/2 · Vmnext + (1 - P1_ace_given_female)/2 · (1
      - Vmnext)
```

$$simple\_Vmnow := \frac{\left(1 - \frac{(1-\delta 1)\,\alpha\, za}{(-\delta 1\,\alpha + 1)\,mean\_z}\right) Vmnext}{2} + \frac{\left(1 - \frac{(1-\delta 1)\,\alpha\,(1-za)}{(-\delta 1\,\alpha+1)\,(1-mean\_z)}\right)(1 - Vmnext)}{2} \tag{2.1}$$

In this model, mean_z is often used as a variable because it has a clear biological meaning. However, it

is also derived from the other parameters. Maple therefore needs to know how it relates to the other parameters:

```
> definition_of_mean_z := ((1 - delta1)·alpha·za + (1 - alpha)·zs) / (1 - delta1·alpha)
```

$$definition\_of\_mean\_z := \frac{(1-\delta 1)\,\alpha\, za + (1-\alpha)\, zs}{-\delta 1\,\alpha + 1} \tag{2.2}$$

Below, we add the assumption that generation t+1 achieves optimal sex allocation, by assuming that Vmnext = mean_z.
We denote the sex allocation of generation t as "old_mean_z" to differentiate it from the mean sex ratio of genetaion t+1 "mean_z"

```
> simple_Optimal_Sex_allocation := simplify(old_mean_z = subs({Vmnext
      = definition_of_mean_z, mean_z = definition_of_mean_z}, simple_Vmnow))
```

$$simple\_Optimal\_Sex\_allocation := old\_mean\_z = \frac{-1+\alpha}{2\,\delta 1\,\alpha - 2} \tag{2.3}$$

Below, we make the assumption that the rate of parthenogenesis is constant over time, and that zs = 1/2, in order to ask what the optimal sex allocation among parthenogenetically produced offspring is. We find that the optimal strategy is simply for all parthenogenetically produced offspring to be female:

```
> subs(old_mean_z = definition_of_mean_z, simple_Optimal_Sex_allocation):
> subs(zs = 1/2, %):
> za = solve(%, za)
```

$$za = 0 \tag{2.4}$$

Model 1: unconstrained optimal sex allocation using delta1 and delta2

In this section we allow for two types of costs of parthenogenesis.

delta1: percentage of parthenogenetically produced eggs that fail to hatch
delta2: cost to parthenogenesis that occur after hatching, including both mortality after hatching and reduced fertility.
alpha: mean rate of parthenogenesis in generation t+1
za: sex ratio (percentage male) among parthenogenetically produced hatchings of generation t+2 (hence, sex allocation by generation t+1)
zs: sex ratio (percentage male) among sexually produced hatchings of generation t+2 (hence, sex allocation by generation t+1)
mean_z: mean sex ratio (percentage male) among all hatchlings of generation t+2 (derived from the other parameters)

Vmnext and Vfnext denote the class reproductive values of males and females, respectively, in generation t+2 (the "next" generation)

Vmnow denotes the same for males of generation t+1. (they are "simple" because delta only reflects hatching failures)
P1_ace_given_male is P(asex | male), i.e. the percentage of male hatchlings that are produced parthenogenetically.
P1_ace_given_female is P(asex | female), i.e. the same as above, but for females instead of males
P2_ace_given_male and P2_ace_given_female also take into account costs of asexuality that occur after hatching.

$$> P1\_ace\_given\_male := \frac{(1 - delta1) \cdot \text{alpha} \cdot za}{(1 - delta1 \cdot \text{alpha}) \cdot mean\_z} :$$

$$> P1\_ace\_given\_female := \frac{(1 - delta1) \cdot \text{alpha} \cdot (1 - za)}{(1 - delta1 \cdot \text{alpha}) \cdot (1 - mean\_z)} :$$

$$> P2\_ace\_given\_male := \frac{(1 - delta2) \cdot P1\_ace\_given\_male}{(1 - delta2) \cdot P1\_ace\_given\_male + (1 - P1\_ace\_given\_male)} :$$

$$> P2\_ace\_given\_female := \frac{(1 - delta2) \cdot P1\_ace\_given\_female}{(1 - delta2) \cdot P1\_ace\_given\_female + (1 - P1\_ace\_given\_female)} :$$

$$> P2\_sex\_given\_male := 1 - P2\_ace\_given\_male :$$

$$> P2\_sex\_given\_female := 1 - P2\_ace\_given\_female :$$

$$> Vmnow := \frac{(1 - P2\_ace\_given\_male)}{2} \cdot Vmnext + \frac{(1 - P2\_ace\_given\_female)}{2} \cdot (1 - Vmnext)$$

$$Vmnow := \frac{1}{2}\left(\left(1 - \frac{(1 - \delta 2)\,(1 - \delta 1)\,\alpha\, za}{(-\delta 1\,\alpha + 1)\,mean\_z\left(\frac{(1 - \delta 2)\,(1 - \delta 1)\,\alpha\, za}{(-\delta 1\,\alpha + 1)\,mean\_z} + 1 - \frac{(1 - \delta 1)\,\alpha\, za}{(-\delta 1\,\alpha + 1)\,mean\_z}\right)}\right) Vmnext\right) + \frac{1}{2}\left(\left(1 - \left((1 - \delta 2)\,(1 - \delta 1)\,\alpha\,(1 - za)\right) \Big/ \left((-\delta 1\,\alpha + 1)\,(1 - mean\_z)\left(\frac{(1 - \delta 2)\,(1 - \delta 1)\,\alpha\,(1 - za)}{(-\delta 1\,\alpha + 1)\,(1 - mean\_z)} + 1 - \frac{(1 - \delta 1)\,\alpha\,(1 - za)}{(-\delta 1\,\alpha + 1)\,(1 - mean\_z)}\right)\right)\right)(1 - Vmnext)\right) \quad \textbf{(3.1)}$$

The definition of mean_z is still the same as in the simpler model above because it is ment to reflect the sex ratio at hatching and therefore isn't affected by delta2.

$$> definition\_of\_mean\_z := \frac{((1 - delta1) \cdot \text{alpha} \cdot za + (1 - \text{alpha}) \cdot zs)}{1 - delta1 \cdot \text{alpha}} \quad \textbf{(3.2)}$$

$$definition\_of\_mean\_z := \frac{(1-\delta l)\,\alpha\, za + (1-\alpha)\, zs}{-\delta l\,\alpha + 1} \tag{3.2}$$

Below is a simple sanity check to examine whether the reproduce values calculated by the more complex model match those calculated by the simple model above when choosing delta = delta1 + (1-delta1)*delta2 . Thankfully, this is the case:

```
> full_Vmnow := subs(mean_z = definition_of_mean_z, Vmnow):
> full_simple_Vmnow := subs(mean_z = definition_of_mean_z, simple_Vmnow):
> is(subs({delta2 = 0, delta1 = delta1 + (1 - delta1)·delta2}, full_Vmnow) = full_Vmnow)
> is(subs({delta2 = 0, delta1 = delta1 + (1 - delta1)·delta2}, full_simple_Vmnow)
      = full_Vmnow)
```

$$true$$

$$true \tag{3.3}$$

Below, we first calculate the class reproductive values for four groups of hatchlings in generation t+2: parthenogenetically produced males (Vmanow), parthenogenetically produced females (Vfanow), sexually produced males (Vmsnow), and sexually produced females (Vfsnow).
In order to calculate these class reproductive values, we use the class reproductive value of males. We want Maple to treat the male class reproductive value as a variable, and therefore, we call it "Vmnow_as_variable", instead of Vmnow:

```
> Vmanow := P2_ace_given_male · Vmnow_as_variable:
> Vfanow := P2_ace_given_female · (1 - Vmnow_as_variable):
> Vmsnow := (1 - P2_ace_given_male) · Vmnow_as_variable:
> Vfsnow := (1 - P2_ace_given_female) · (1 - Vmnow_as_variable):
```

We then use these class reproductive values to calculate the individual reproductive values for each type of offspring:

```
> v_m_a_now := Vmanow / (P1_ace_given_male ·mean_z):
> v_f_a_now := Vfanow / (P1_ace_given_female · (1 - mean_z)):
> v_m_s_now := Vmsnow / ((1 - P1_ace_given_male)·mean_z):
> v_f_s_now := Vfsnow / ((1 - P1_ace_given_female)·(1 - mean_z)):
```

ace_Vm_term, annd sex_Vm_term now calculate what values Vmnow_as_variable needs to be for parthenogenetically produced males to have the same individual reproductive value as parthenogenetically produced females, and what values Vmnow_as_variable needs to take for the same to be true for sexually produced offspring. The condition actually turns out to be identical for both types of reproduction:

```
> ace_Vm_term := solve(v_m_a_now = v_f_a_now, Vmnow_as_variable)
```

```
> sex_Vm_term := solve(v_m_s_now = v_f_s_now, Vmnow_as_variable)
> is(ace_Vm_term = sex_Vm_term)
```

$$ace\_Vm\_term := \frac{\alpha\,\delta l\,\delta 2\,za - \alpha\,\delta l\,mean\_z - \alpha\,\delta 2\,za + mean\_z}{\alpha\,\delta l\,\delta 2 - \delta l\,\alpha - \alpha\,\delta 2 + 1}$$

$$sex\_Vm\_term := \frac{\alpha\,\delta l\,\delta 2\,za - \alpha\,\delta l\,mean\_z - \alpha\,\delta 2\,za + mean\_z}{\alpha\,\delta l\,\delta 2 - \delta l\,\alpha - \alpha\,\delta 2 + 1}$$

$$true \tag{3.4}$$

```
> Vm_requirement := subs(mean_z = definition_of_mean_z, ace_Vm_term)
```

$$Vm\_requirement := \frac{1}{\alpha\,\delta l\,\delta 2 - \delta l\,\alpha - \alpha\,\delta 2 + 1}\left(\alpha\,\delta l\,\delta 2\,za - \frac{\alpha\,\delta l\,\left(\left(1-\delta l\right)\alpha\,za + \left(1-\alpha\right)zs\right)}{-\delta l\,\alpha + 1} - \alpha\,\delta 2\,za + \frac{\left(1-\delta l\right)\alpha\,za + \left(1-\alpha\right)zs}{-\delta l\,\alpha + 1}\right) \tag{3.5}$$

Vm_requirement specifies what value Vmnow (generation t+2) takes when generation t+1 achieves optimal sex allocation. In the supplementary text, we write that Vmnow equals P2,t+2(male). To confirm this again, we show below that this does indeed equal Vm_requirement:

```
> full_P2m := (1 - delta2)·(1 - delta1)·alpha·za + (1 - alpha)·zs / (1 - delta1·alpha - (1 - delta1)·delta2·alpha)
```

$$full\_P2m := \frac{\left(1-\delta 2\right)\left(1-\delta l\right)\alpha\,za + \left(1-\alpha\right)zs}{1 - \delta l\,\alpha - \left(1-\delta l\right)\delta 2\,\alpha} \tag{3.6}$$

```
> is(full_P2m = Vm_requirement)
```

$$true \tag{3.7}$$

Unlike the simpler model, it is not easily possible to express the optimal sex allocation in terms of the sex ratio at hatching. Instead, we define it in terms of P2,t+1(male) which we refer to as "old_P2m" here.

```
> Optimal_Sex_allocation := simplify(old_P2m = subs({Vmnext = Vm_requirement, mean_z
      = definition_of_mean_z}, Vmnow))
```

$$Optimal\_Sex\_allocation := old\_P2m = \frac{1-\alpha}{2 + \left(\left(2\,\delta 2 - 2\right)\delta l - 2\,\delta 2\right)\alpha} \tag{3.8}$$

```
> is(rhs(Optimal_Sex_allocation) = subs(delta1 = delta1 + (1 - delta1)·delta2,
      rhs(simple_Optimal_Sex_allocation)))
```

$$true \tag{3.9}$$

Unlike the simpler model, we have to take into account the values for alpha, za, ans zs not only for generation t+1, but also for the generation prior to this. Here, these parameters of generation t are notated as old_alpha, old_za, and old_zs.
old_alpha refers to alpha in generation t. old_za and old_zs refer to the sex ratios in generation t+1 (and hence to the sex allocation by generation t).
Hence, the three parameters refer to one generation earlier than alpha, za, and zs.

```
> oldP2m := subs({za = old_za, zs = old_zs, alpha = old_alpha}, full_P2m)
```

$$oldP2m := \frac{(1-\delta 2)\,(1-\delta 1)\,old\_alpha\,old\_za + (1-old\_alpha)\,old\_zs}{1-\delta 1\,old\_alpha-(1-\delta 1)\,\delta 2\,old\_alpha} \tag{3.10}$$

We can use the parameters defined above to find a general solution for the optimal sex allocation t (i.e. z*_t). For this, we need to include z_t as a variable into the equation for oldP2m. We do this below, by asking Maple to first devide by z_t (in the form of old_definition_of_mean_z) and then multiplying by it again (in the shape of old_mean_z, which is simply a variable):

```
> old_definition_of_mean_z := subs({za = old_za, zs = old_zs, alpha = old_alpha},
    definition_of_mean_z)
```

$$old\_definition\_of\_mean\_z := \frac{(1-\delta 1)\,old\_alpha\,old\_za + (1-old\_alpha)\,old\_zs}{-\delta 1\,old\_alpha+1} \tag{3.11}$$

```
> oldP2m_with_mean_z := oldP2m / old_definition_of_mean_z * old_mean_z
```

$$oldP2m\_with\_mean\_z := (((1-\delta 2)\,(1-\delta 1)\,old\_alpha\,old\_za + (1-old\_alpha)\,old\_zs)\,(-\delta 1\,old\_alpha+1)\,old\_mean\_z) / ((1-\delta 1\,old\_alpha-(1-\delta 1)\,\delta 2\,old\_alpha)\,((1-\delta 1)\,old\_alpha\,old\_za+(1-old\_alpha)\,old\_zs)) \tag{3.12}$$

```
> solve(oldP2m_with_mean_z = rhs(Optimal_Sex_allocation), old_mean_z)
```

$$-((-1+\alpha)\,(\delta 2\,old\_alpha\,\delta 1-\delta 1\,old\_alpha-\delta 2\,old\_alpha+1)\,(old\_alpha\,old\_za\,\delta 1-old\_alpha\,old\_za+old\_zs\,old\_alpha-old\_zs)) / (2\,(\alpha\,\delta 1\,\delta 2-\delta 1\,\alpha-\alpha\,\delta 2+1)\,(\delta 1\,old\_alpha-1)\,(\delta 1\,\delta 2\,old\_za\,old\_alpha-old\_alpha\,old\_za\,\delta 1-\delta 2\,old\_za\,old\_alpha+old\_alpha\,old\_za-old\_zs\,old\_alpha+old\_zs)) \tag{3.13}$$

The (somewhat awkward) term above gives the optimal sex allocation for generation t. It is easy to see that unlike the simpler model, it depends not only on the rate of parthenogenesis in the next generation, alpha, but also on the rate of parthenogenesis in the current generation, t, as well as the sex allocation of generation t among sexually and asexually produced offspring. Note, however, that it does not depend on the sex allocation of the next generation (za and zs don't appear in the term).

Below, we go through some relevant examples.

Firstly, if we assume that the sex ratio among sexually produced offspring always equals that among parthenogenetically produced offspring, then the complications above disappear, and we get same result as we did in the simpler model:

```
> subs({old_zs = old_za}, oldP2m = rhs(Optimal_Sex_allocation)) :
> solve(%, {old_za, old_zs})
```

$$\left\{old\_za = -\frac{-1+\alpha}{2\,(\alpha\,\delta 1\,\delta 2-\delta 1\,\alpha-\alpha\,\delta 2+1)},\ old\_zs = old\_zs\right\} \tag{3.14}$$

If we assume that the rate of parthenogenesis is constant over time, and that sexually produced broods

have a sex ratio of 0.5, then optimal sex allocation is achieved if za=0. This recovers the result that the system seen in stick insects achieves optimal sex allocation.

We first calculate the value that zs needs to take for optimal sex allocation to be achieved. When then use this to calculate what this optimal sex allocation is:

```
> subs({old_zs = 1/2, old_alpha = alpha}, oldP2m = rhs(Optimal_Sex_allocation)) :
> solve(%, {old_za, old_zs})
> subs(%, old_definition_of_mean_z) :
> old_mean_z = simplify(subs({old_zs = 1/2, old_alpha = alpha}, %))
```

$$\{old\_za = 0,\ old\_zs = old\_zs\}$$

$$old\_mean\_z = \frac{-1+\alpha}{2\,\delta 1\,\alpha - 2} \tag{3.15}$$

Below, we assume that parthenogenesis only produces daughters, but remove the assumption that the rate of parthenogenesis is constant over time. We first calculate the value that zs needs to take for optimal sex allocation to be achieved. When then use this to calculate what this optimal sex allocation is:

```
> subs({old_za = 0}, oldP2m = rhs(Optimal_Sex_allocation)) :
> solve(%, {old_za, old_zs})
> subs(%, old_definition_of_mean_z) :
> old_mean_z = simplify(subs(old_za = 0, %))
```

$$\{old\_za = old\_za,\ old\_zs = (\alpha\,\delta 1\,\delta 2\,old\_alpha - \alpha\,\delta 1\,old\_alpha - \alpha\,\delta 2\,old\_alpha - \delta 1\,\delta 2\,old\_alpha + \delta 1\,old\_alpha + \delta 2\,old\_alpha + \alpha - 1)\,/\,(2\,(\alpha\,\delta 1\,\delta 2\,old\_alpha - \alpha\,\delta 1\,\delta 2 - \alpha\,\delta 1\,old\_alpha - \alpha\,\delta 2\,old\_alpha + \delta 1\,\alpha + \alpha\,\delta 2 + old\_alpha - 1))\}$$

$$old\_mean\_z = \frac{(-1+\alpha)\,(1+((-1+\delta 2)\,\delta 1 - \delta 2)\,old\_alpha)}{2\,(\delta 1\,old\_alpha - 1)\,((-1+\delta 2)\,\delta 1\,\alpha - \alpha\,\delta 2 + 1)} \tag{3.16}$$

Below, we do the same when assuming that sexual reproduction only produces daughters (as is the case in Daphina or aphids). Similarly to above, we first calculate what value za needs to take to achieve optimal sex allocation, and then we use this to calculate what that optimal sex allocation is:

```
> subs({old_zs = 0}, oldP2m = rhs(Optimal_Sex_allocation)) :
> solve(%, {old_za, old_zs})
> subs(%, old_definition_of_mean_z) :
> old_mean_z = simplify(subs(old_zs = 0, %))
```

$$\{old\_za = -(\alpha\,\delta 1\,\delta 2\,old\_alpha - \alpha\,\delta 1\,old\_alpha - \alpha\,\delta 2\,old\_alpha - \delta 1\,\delta 2\,old\_alpha + \delta 1\,old\_alpha + \delta 2\,old\_alpha + \alpha - 1)\,/\,(2\,old\_alpha\,(\alpha\,\delta 1^2\,\delta 2^2 - 2\,\alpha\,\delta 1^2\,\delta 2 - 2\,\alpha\,\delta 1\,\delta 2^2 + \alpha\,\delta 1^2 + 3\,\alpha\,\delta 1\,\delta 2 + \alpha\,\delta 2^2 - \delta 1\,\alpha - \alpha\,\delta 2 + \delta 2\,\delta 1 - \delta 1 - \delta 2 + 1)),\ old\_zs = old\_zs\}$$

$$old\_mean\_z = -\frac{(-1+\alpha)\,(old\_alpha\,(-1+\delta 1)\,\delta 2-\delta 1\,old\_alpha+1)}{2\,(\delta 1\,old\_alpha-1)\,(-1+\delta 2)\,(\delta 2\,(-1+\delta 1)\,\alpha-\delta 1\,\alpha+1)} \tag{3.17}$$

Model 2: the model

pm = 1-qm Allele frequency of asexuality allele in males (between 0 and 1)
pf = 1-qf Allele frequency of asexuality allele in females (between 0 and 1)
alpha: percentage to which facultative individuals reproduce asexually (between 0 and 1)
Sa: Sex ratio among asexually produced offspring (percantage that are males) (between 0 and 1)
delta: disadvantage of asexuality (between 0 and 1)

```
> FacultativeSex_female_pretty := ((1/4)·pm·qf + (1/2)·pm·pf·(1 − alpha) + (1/4)·qm·pf
      ·(1 − alpha) + (1 − Sa)·alpha·pf·(1 − delta)) / ((1/2)·qf + (1/2)·pf·(1 − alpha)
      + (1 − Sa)·pf·alpha·(1 − delta));
> FacultativeSex[f] := subs({qf = 1 − pf, qm = 1 − pm}, FacultativeSex_female_pretty):
> FacultativeSex_male_pretty := ((1/4)·pm·qf + (1/2)·pm·pf·(1 − alpha) + (1/4)·qm·pf·(1
      − alpha) + Sa·alpha·pf·(1 − delta)) / ((1/2)·qf + (1/2)·pf·(1 − alpha) + Sa·pf
      ·alpha·(1 − delta));
> FacultativeSex[m] := subs({qf = 1 − pf, qm = 1 − pm}, FacultativeSex_male_pretty):
```

$$FacultativeSex\_female\_pretty := \frac{\frac{pm\,qf}{4}+\frac{pm\,pf\,(1-\alpha)}{2}+\frac{qm\,pf\,(1-\alpha)}{4}+(1-Sa)\,\alpha\,pf\,(1-\delta)}{\frac{qf}{2}+\frac{pf\,(1-\alpha)}{2}+(1-Sa)\,\alpha\,pf\,(1-\delta)}$$

$$FacultativeSex\_male\_pretty := \frac{\frac{pm\,qf}{4}+\frac{pm\,pf\,(1-\alpha)}{2}+\frac{qm\,pf\,(1-\alpha)}{4}+Sa\,\alpha\,pf\,(1-\delta)}{\frac{qf}{2}+\frac{pf\,(1-\alpha)}{2}+Sa\,\alpha\,pf\,(1-\delta)} \tag{4.1}$$

Model 2: Jacobian Matrices at (0, 0) and (1, 1)

We derive the Jacobian Matices at the two trivial equilibria. These are later used to investigate the invasion and fixation of alleles:

```
> FacultativeSex[invasion] := simplify(subs({pf = 0, pm = 0}, Jacobian([FacultativeSex[f],
      FacultativeSex[m]], [pf, pm])));
> FacultativeSex[fixation] := simplify(subs({pf = 1, pm = 1}, Jacobian([FacultativeSex[f],
```

```
    FacultativeSex[m]], [pf, pm]) ));
```

$$FacultativeSex_{invasion} := \begin{bmatrix} \frac{1}{2} + \frac{((4\,Sa-4)\,\delta - 4\,Sa + 3)\,\alpha}{2} & \frac{1}{2} \\ \frac{1}{2} + \frac{(-1 + (-4\,\delta + 4)\,Sa)\,\alpha}{2} & \frac{1}{2} \end{bmatrix}$$

$$FacultativeSex_{fixation} := \begin{bmatrix} \frac{1}{2 + ((4\,Sa-4)\,\delta - 4\,Sa + 2)\,\alpha} & \frac{1-\alpha}{2 + ((4\,Sa-4)\,\delta - 4\,Sa + 2)\,\alpha} \\ -\frac{1}{-2 + (2 + (4\,\delta - 4)\,Sa)\,\alpha} & \frac{-1+\alpha}{-2 + (2 + (4\,\delta - 4)\,Sa)\,\alpha} \end{bmatrix} \quad \textbf{(5.1)}$$

```
>
```

As shown below, we need to take two Eigenvalues into account when investigating the invasion of alleles, but only one Eigenvalue for the fixation (because the other Eigenvalue is 0)

```
> Eigenvalues(FacultativeSex[invasion])
```

$$\left[\left[Sa\,\alpha\,\delta - Sa\,\alpha - \alpha\,\delta + \frac{3\,\alpha}{4} + \frac{1}{2} + \frac{1}{4}\left(16\,Sa^2\,\alpha^2\,\delta^2 - 32\,Sa^2\,\alpha^2\,\delta - 32\,Sa\,\alpha^2\,\delta^2 + 16\,Sa^2\,\alpha^2 + 56\,Sa\,\alpha^2\,\delta + 16\,\alpha^2\,\delta^2 - 24\,Sa\,\alpha^2 - 16\,Sa\,\alpha\,\delta - 24\,\alpha^2\,\delta + 16\,Sa\,\alpha + 9\,\alpha^2 - 4\,\alpha + 4\right)^{1/2} \right], \left[Sa\,\alpha\,\delta - Sa\,\alpha - \alpha\,\delta + \frac{3\,\alpha}{4} + \frac{1}{2} - \frac{1}{4}\left(16\,Sa^2\,\alpha^2\,\delta^2 - 32\,Sa^2\,\alpha^2\,\delta - 32\,Sa\,\alpha^2\,\delta^2 + 16\,Sa^2\,\alpha^2 + 56\,Sa\,\alpha^2\,\delta + 16\,\alpha^2\,\delta^2 - 24\,Sa\,\alpha^2 - 16\,Sa\,\alpha\,\delta - 24\,\alpha^2\,\delta + 16\,Sa\,\alpha + 9\,\alpha^2 - 4\,\alpha + 4\right)^{1/2} \right] \right] \quad \textbf{(5.2)}$$

```
> Eigenvalues(FacultativeSex[fixation])
```

$$\left[\left[0 \right], \left[\left(2\,Sa\,\alpha^2\,\delta - 2\,Sa\,\alpha^2 - 2\,\alpha^2\,\delta + \alpha^2 + 2\,\alpha\,\delta + \alpha - 2\right) \Big/ \left(2\left(4\,Sa^2\,\alpha^2\,\delta^2 - 8\,Sa^2\,\alpha^2\,\delta - 4\,Sa\,\alpha^2\,\delta^2 + 4\,Sa^2\,\alpha^2 + 8\,Sa\,\alpha^2\,\delta - 4\,Sa\,\alpha^2 - 2\,\alpha^2\,\delta + \alpha^2 + 2\,\alpha\,\delta - 1\right)\right) \right] \right] \quad \textbf{(5.3)}$$

Model 2: Invasion and Fixation when parthenogenesis produces only daughters (Sa = 0)

```
> solve(subs({Sa = 0}, Eigenvalues(FacultativeSex[invasion])[1]) = 1, {delta, alpha})
```

$$\{\alpha = 0, \delta = \delta\}, \left\{\alpha = \alpha, \delta = \frac{1}{2}\right\} \quad \textbf{(6.1)}$$

> $solve(subs(\{Sa = 0\}, Eigenvalues(FacultativeSex[invasion])[2]) = 1, \{delta, alpha\})$

$$\left\{\alpha = \alpha, \delta = \frac{1}{2}\right\} \quad \textbf{(6.2)}$$

> $solve(subs(\{Sa = 0\}, Eigenvalues(FacultativeSex[fixation])[2]) = 1, \{delta, alpha\})$

$$\{\alpha = 0, \delta = \delta\}, \left\{\alpha = \alpha, \delta = \frac{1}{2}\right\} \quad \textbf{(6.3)}$$

Model 2: Invasion and Fixation when parthenogenesis produces only sons (Sa = 1)

> $solve(subs(\{Sa = 1\}, Eigenvalues(FacultativeSex[invasion])[1]) = 1, \{delta, alpha\})$

$$\{\alpha = 0, \delta = \delta\}, \left\{\alpha = \alpha, \delta = \frac{1}{2}\right\} \quad \textbf{(7.1)}$$

> $solve(subs(\{Sa = 1\}, Eigenvalues(FacultativeSex[invasion])[2]) = 1, \{delta, alpha\})$

$$\left\{\alpha = \alpha, \delta = \frac{1}{2}\right\} \quad \textbf{(7.2)}$$

> $solve(subs(\{Sa = 1\}, Eigenvalues(FacultativeSex[fixation])[2]) = 1, \{delta, alpha\})$

$$\{\alpha = 0, \delta = \delta\}, \left\{\alpha = \frac{2\delta - 1}{4\delta - 3}, \delta = \delta\right\} \quad \textbf{(7.3)}$$

Model 2: Equilibrium Frequency when parthenogenesis produces only sons (Sa = 1)

An equilibrium frequency is reached when pf = pf(t+1) and pm=pm(t+1).

As shown below, this is the case if pf = 0, pf = 1, or $pf = \frac{2\delta - 1}{(4\delta - 3)\alpha}$

Below, the corresponding values for pm are also shown, but we omit these in the manuscript

> $solve(\{pm = subs(Sa = 1, FacultativeSex[m]), pf = subs(Sa = 1, FacultativeSex[f])\}, \{pf, pm\})$

$$\{pf = 0, pm = 0\}, \{pf = 1, pm = 1\}, \left\{pf = \frac{2\delta - 1}{\alpha(4\delta - 3)}, pm = \frac{(2\delta - 1)(4\alpha\delta - 3\alpha - 1)}{2(\delta - 1)\alpha(4\delta - 3)}\right\} \quad \textbf{(8.1)}$$

Model 2: Invasion and Fixation for intermediate Sa

These results are omitted in the manuscript because we can not think of an organism to which these results would apply. Intermediate sex ratios in parthenogenetically produced young are conceivable under environmental sex determination, but in this case mothers are also able to manipulate the sex of their young, therefore contradicting our assumption that Sa is the result of an evolutionary constraint.

Nevertheless, the results below are interesting due to their underlying logic.

```
> solve(subs({Sa = 0.5}, Eigenvalues(FacultativeSex[invasion])[1]) = 1, {delta, alpha})
```

Warning, solutions may have been lost

$$\left\{\alpha = \alpha, \delta = RootOf\left(2\_Z\alpha - \sqrt{(2\_Z\alpha - \alpha - 2)^2} - \alpha + 2\right)\right\} \quad \textbf{(9.1)}$$

```
> solve(subs({Sa = 0.5}, Eigenvalues(FacultativeSex[invasion])[2]) = 1, {delta, alpha})
```

Warning, solutions may have been lost

$$\left\{\alpha = \alpha, \delta = RootOf\left(2\_Z\alpha + \sqrt{(2\_Z\alpha - \alpha - 2)^2} - \alpha + 2\right)\right\} \quad \textbf{(9.2)}$$

```
> solve(subs({Sa = 0.5}, Eigenvalues(FacultativeSex[fixation])[2]) = 1, {delta, alpha})
```

$$\{\alpha = 0., \delta = \delta\}, \{\alpha = \alpha, \delta = 0.5000000000\} \quad \textbf{(9.3)}$$

Above, we can see that for Sa=0.5, asexuality can reach fixation as long as delta < 0.5 (which is the same result as when asexuality only produces females). Unfortunately, Maple is unable to find solutions the invasion if Sa=0.5. Therefore, we investigate Sa=0.49 and Sa=0.51 instead.

```
> solve(subs({Sa = 0.49}, Eigenvalues(FacultativeSex[invasion])[1]) = 1, {delta, alpha})
```

$$\{\alpha = 0., \delta = \delta\}, \{\alpha = \alpha, \delta = 0.5000000000\} \quad \textbf{(9.4)}$$

```
> solve(subs({Sa = 0.49}, Eigenvalues(FacultativeSex[invasion])[2]) = 1, {delta, alpha})
```

$$\{\alpha = \alpha, \delta = 0.5000000000\} \quad \textbf{(9.5)}$$

```
> solve(subs({alpha = 1, Sa = 0.49}, Eigenvalues(FacultativeSex[fixation])[2]) = 1, {delta})
    # this shows that for Sa = 0.49, the allele can reach fixation if δ < 0.5098039216 This is
    always the case if the allele can invade (because δ < 0.5)
```

$$\{\delta = 0.5098039216\} \quad \textbf{(9.6)}$$

```
> solve(subs({Sa = 0.51}, Eigenvalues(FacultativeSex[invasion])[1]) = 1, {delta, alpha})
```

$$\{\alpha = 0., \delta = \delta\}, \{\alpha = \alpha, \delta = 0.5000000000\} \quad \textbf{(9.7)}$$

```
> solve(subs({Sa = 0.51}, Eigenvalues(FacultativeSex[invasion])[2]) = 1, {delta, alpha})
```

$$\{\alpha = \alpha, \delta = 0.5000000000\} \quad \textbf{(9.8)}$$

```
> solve(subs({alpha = 1, Sa = 0.51}, Eigenvalues(FacultativeSex[fixation])[2]) = 1, {delta})
    # this shows that for Sa = 0.51, the allele can reach fixation if δ < 0.4897959184. Hence,
    equilibrium frequencies of asexuality are possible if 0.4897959184 < δ < 0.5)
```

$$\{\delta = 0.4897959184\} \quad \textbf{(9.9)}$$

The results for invasion with Sa=0.49 and Sa=0.51 are both the same: the allele can invade if $\delta < 0.5$. This is the same result as when asexual reproduction only produces females or only males.
However, the result for fixation is different if Sa > 0.5 (compared to Sa < 0.5 where asexuality either invades or fixes) :
If Sa > 0.5, then equilibrium frequencies are possible for the right values of δ
Of course, if Sa =1, then fixation is impossible for any δ. This leads to the interesting question of how high the Sa must be to make fixation impossible even if $\delta = 0$. We further assume that alpha = 1, because this allows for the establishment of obligate asexuality.

```
> solve(subs({delta = 0, alpha = 1}, Eigenvalues(FacultativeSex[fixation])[2]) = 1, {Sa})
```

(9.10)

$$\left\{ Sa = \frac{3}{4} \right\} \tag{9.10}$$

The result above shows that fixation becomes impossible when more than 75% of asexually produced offspring are male.
This result surprised us because it shows that asexuality can fix even if a very large proportion of the parthenogenetically produced offspring are male.
Our explanation for this result is the following:
For the fixation of asexuality, only the production of female offspring is important, while males are unable to reproduce when asexuality is ubiquitous. If sexual reproduction produces unbiased sex ratios, then half or their offspring are female, and these have a relatedness of 0.5 to their mother. Hence a sexual female must produce 4 offspring (2 females and 2 males) to fully replicate herself. For an asexually reproducing female with Sa = 0.75, only 25% of her offspring are female, but she has a relatedness of 1 to these daughters. Hence, she must also produce 4 offspring (1 female and 3 males) to fully replicate herself.

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Education:

01.07.2020 – 30.06.2024

Employed as PhD student at the *Universität Zurich* (01.07.2020 – 31.12.2022) and at *Johannes Gutenberg-Universität Mainz* (01.01.2023 – 31.06.2024), defense in Aug 2024

- Topic: the various drivers of female-limited diversity
- Main Supervisor: Hanna Kokko (JGU Mainz)
- Second Supervisor: Chris Wheat (Stockholm University)

01.10. 2017 – 22.04.2020

Master of Biology at *Freie Universität* in Berlin

Thesis: 15.07.2019 – 20.12.2019 at the University of Zurich (*UZH*)

- "Disentangling Verbal Arguments: Intralocus Sexual Conflict in Haplodiploids"
- Supervisors in Zurich: Hanna Kokko and Hanna ten Brink
- Supervisor in Berlin: Jens Rolff

01.10.2014 - 21.12.2017

Bachelor of Biology at *Freie Universität* in Berlin

Thesis: "Testing the Evolution of Termite External Immunity in a Comparative Framework"
Supervisor: Dino McMahon

2014

Finished Abitur at the *Heinrich-Schliemann-Gymnasium* (high school) in Berlin

Teaching:

06.10.2017 – 31.03.2020

Employed as a Tutor (teaching assistant) for Zoology and Ecology at *Freie Universität Berlin*

- 41h/month (06.10.2017 – 05.10.2019)
- 20h/month (06.10.2019 – 31. 03.2020)

01.07.2020 – 31.12.2022

A total of 315 hours of teaching at the University of Zurich while employed as a PhD student

Publications:

Klein, K., Kokko, H., & Ten Brink, H. (2021). Disentangling Verbal Arguments: Intralocus Sexual Conflict in Haplodiploids. *The American Naturalist*, *198*(6), 678-693.

Wang, D., Abbott, J., Brenninger, F.A., Klein, K., Nava-Balaños, A., Yong, L., & Li Richter, XY. (2024). Female alternative reproductive tactics: diversity and drivers. Accepted in *Trends in Ecology and Evolution*

CV of Kora Klein July 2024

Email: koraklein@protonmail.com

Awards and Research Funding:

2022: Jahrespreis (annual award) of the faculty of science at the University of Zurich (usually awarded for best PhD thesis of the year)
2022: Honorary mention for (one of the) best student papers published in the American Naturalist
2023: awarded 4000€ research funding by the Sibylle Kalkhof-Rose-Stiftung (main applicant) for a project on the evolution of floral traits (hermaphroditism vs. monoecy)

Conference and workshop participation:

Biology20 (06.-07.02.2020, Fribourg, Switzerland) – Poster presentation
Biology22 (17.-18.02.2022, Basel, Switzerland) – Talk
Guarda Workshop (18.-25.06.2022, Guarda, Switzerland)
ISBE (28.07.-02.08.2022, Stockholm, Sweden) – Talk
ESEB (15.-19.08.2022, Prague, Czech Republic) – Talk
Biology23 (16.-17.02.2023, Geneva, Switzerland) – Poster presentation
STN workshop on sex differences & local adaptation (21.-24.03.2023, Ingelheim, Germany)
EMPSEB (29.05.-02.06.2023, FSC Millport, UK) – Talk + alternative presentation
Gutenberg workshop on unisexual reproduction (11.-13.07.2023, Ingelheim, Germany) – Talk
Biology of Sperm (04.-08.09.2023, Stockholm, Sweden) – Talk
Simultanious hermaphroditic organisms workshop (23-24.04.2024, Rennes, France) – talk

Reviewing:

Reviewed five papers (for the Journal of Evolutionary Biology, Oikos, Evolution, PLOS ONE, and the European Journal of Taxonomy)

Outreach:

Lectures at the “Tag der Naturwissenschaften” at the Heinrich-Schliemann-Gymnasium (former high school in Berlin) about sex ratio theory and sex chromosome evolution, in Jan 2023 and Jan 2024, respectively.