TITLE: The adaptive maintenance of phenotypic polymorphism

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ABSTRACT: Phenotypic polymorphisms have fascinated evolutionary biologists since the field's inception, providing easily observable and quantifiable variation amenable to both empirical and theoretical study. However, a clear method for developing alternative hypotheses for the adaptive processes by which multiple morphs are maintained remains elusive. Here we review hypotheses for the maintenance of polymorphisms and propose a framework in which polymorphisms can be described by (1) a type of balancing selection and (2) the ecological and social context through which balancing selection acts. We argue that a complete hypothesis for the maintenance of polymorphism should describe both variables, offering a simple method for generating testable alternatives. To demonstrate this, we explore the case of female-limited polymorphism, a class of polymorphisms with diverse explanations, yet little unifying theory across taxa. We show that, in most cases, social competition drives the maintenance of female-limited polymorphism. Applying this framework to both within-sex and species-wide polymorphism reveals distinctions and commonalities across disparate taxa, provides a clear structure for developing hypotheses, and reveals new paths for future research in the adaptive maintenance of polymorphism.

KEYWORDS: polymorphism, balancing selection, social selection, adaptation, female-limited polymorphism

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I. Introduction

The maintenance of phenotypic variation in the face of selection is one of evolutionary biology's most enduring questions (Wallace, 1865; Ford, 1945; Levene, 1953; Hedrick, 2007). Within a population, selection should fix phenotypes with the highest fitness, and drift can also stochastically eliminate variants over time. Yet, phenotypic variation is ubiquitous in most organisms. Particularly puzzling are *polymorphisms,* wherein within-population variation is discrete (Ford, 1945). Polymorphism can also occur within a single sex within a population. Although these "sex-limited" polymorphisms are more studied in males (male-limited polymorphism), they also occur among females (female-limited polymorphism) in a large number of taxa (Mank, 2022). Yet, despite enduring interest in polymorphism, understanding why multiple phenotypic morphs are maintained over time in organisms as diverse as birds and plants has been an ongoing challenge. In part, this is because different types of polymorphism (e.g., morphological, behavioral) have been studied by different fields, and hypotheses are typically discussed within species, hampering comparison and discussion across taxa and sexes.

The definition of polymorphism has changed over time, reflecting shifting frameworks in our understandings of biological variation. Darwin and his contemporaries used the term loosely, including variation due to life-stage, within-species variants, and inter-species differences. Ford (1940) provided a more concrete within-species definition, and presented a framework that distinguished between transient polymorphism in which a directionally selected variant is in the process of sweeping to fixation, or balanced polymorphism in which variation is selected to persist. Later frameworks (Michener, 1961; Mayr, 1963) focused on heritability, splitting terminology such that *polymorphism* referred to morphs associated with genetic differences while *polyphenism* (synonymous with "conditional" tactics) referred to variants that were environmentally determined. This dichotomy between polymorphism and polyphenism, which is based largely on trait development, has been highly influential and remains a primary framework for understanding and categorizing discrete traits (Gross, 1996; West-Eberhard, 2003a; Oliveira, Taborsky & Brockmann, 2008; Mank, 2022).

While this developmental categorization of phenotypes as either polymorphism or polyphenism has value in many contexts, there are also drawbacks. First, researchers rarely know the heritability of phenotypic variation in their study organism (i.e., those with long generation times, that are difficult to observe in the wild, etc.). Second, all phenotypic variation reflects both genetic and environmental effects (Huxley, 1942), and the distinction automatically excludes cases of intermediate heritability and gene-by-environment interactions (e.g. Geffroy et al. 2021). Third, some definitions of polyphenism only include discrete variation, whereas others include all forms of environmentally determined variation regardless of trait distribution (Canfield & Greene, 2009). Reality is more complex than this simple dichotomy suggests, overlooking critical details—such as the fact that environmental sensitivity can vary within populations and evolve over time (Lively, 1986; Plaistow *et al.*, 2004). We therefore suggest the re-adoption of Ford's (1945) usage of the term *polymorphism* in all cases of discrete variation, regardless of trait heritability. When necessary, polymorphisms should be referred to as heritable or non-heritable, with *polyphenism* simply referring to a type *polymorphism* that is at less heritable. We use this generalized definition of polymorphism to describe all discrete variation.

Development relates to proximate mechanisms of trait production, yet natural selection acts on traits while blind to the mechanisms that produce them during an individual's development (Sherman, 1988; MacDougall-Shackleton, 2011). It follows that over-reliance on an ontogeny-based framework might limit the development and comparison of alternative *adaptive* hypotheses for the maintenance of polymorphism. This is especially apparent in the male-limited polymorphism literature. For example, Gross's (1996) classic review of male-limited polymorphism is divided into two sections – evolutionary studies and proximate studies. Confusingly, hypotheses for the "evolution" of male polymorphism were classified as either alternative, mixed, or conditional strategies. Yet, these categorizations are based on differences in the developmental origin of morphs, not the type of selection that maintains the polymorphism. Certainly, the consequences of selection depend a great deal on heritability, but this should not be confused with the causative type of selection that maintains variation. The confounding of adaptive and developmental mechanisms has also led to incorrect dichotomies, such as a distinction between negative-frequency dependent selected and condition-dependent traits. Yet these are not in fact distinct explanations, because condition-dependent traits can be balanced under negative-frequency dependent selection (Shuster, 2010).

The lack of a clear framework for distinguishing and forming adaptive hypotheses for polymorphism has at times led to confusion, a limitation of crosstalk between fields, and untested alternative hypotheses. For example, the hypothesis that male-limited polymorphism is often related to alternative reproductive tactics for access to mates has ample support (Gross, 1996; Oliveira *et al.*, 2008; Mank, 2022), yet alternatives to this hypothesis are rarely articulated or tested. The term "mimicry" is often used loosely, and sometimes only based on resemblance to females by human standards (Jukema & Piersma, 2006). Furthermore, as we discuss below, mimicry and alternative reproductive tactics are in fact two independent ways in which balancing selection can maintain the coexistence of multiple morphs. Both involve negative frequency dependence, but the theoretical parameters that govern stable levels of each morph are distinct. It is certainly possible and likely that these two mechanisms can interact in tandem. However, when a part of an alternative tactics, critical aspects of mimicry are often ignored, with little regard to the influence of parameters such as the model-to-mimic ratio and the encounter rates between alternative morphs and females.

Though the ontogeny-based framework is useful for answering a broad scope of questions about polymorphism, it is not useful for distinguishing hypotheses on the adaptive maintenance of polymorphism, and an additional framework is necessary. Here, we review hypotheses and outline a simple conceptual framework for developing and distinguishing hypotheses for the adaptive maintenance of polymorphism (Figure 1). We propose that a complete hypothesis for the maintenance of polymorphism must be described by two distinct factors: (1) a type of **balancing selection** – the form of selection that maintains multiple morphs within a population; and (2) a selective **context** – the aspect of the organism's life history upon which balancing selection acts (e.g. competition for food or for mates—ecological and social context). Both factors are necessary to describe independent and alternative hypotheses for the maintenance of polymorphism, but should be thought of as separate axes. Just as directional selection can function under many contexts (e.g. ecological, social, sexual, or sexual conflict), so too can balancing selection. This framework pertains to adaptive explanations for how polymorphisms are maintained rather than the evolutionary origins of polymorphism or their developmental bases. Although we see no particular reason why this framework should be limited to animals, this paper is centered around animal taxa. Our purpose is not to assign cases of polymorphism to rigid categories, but instead to define, refine, and clarify major axes by which hypotheses for polymorphism can be described.

In the last section, we use our framework to categorize instances of female-limited polymorphism, a class of polymorphisms with diverse and varied explanations. We highlight similarities and differences between male- and female-limited polymorphism, and demonstrate that female-limited polymorphism, much like female ornamentation, is driven by strong social competition for resources other than mates. Both balancing selection and selective context have long been aspects of a vibrant discussion on polymorphism. Ultimately, formalizing the distinction between these descriptive axes helps to clarify similarities and differences in polymorphism across animal taxa, allows for simple construction of testable alternative hypotheses, and reveals the many ways in which selection maintains phenotypic diversity.

Why two axes?

To begin, we use two examples of polymorphism in nature to demonstrate why both a type of balancing selection and a selective context are necessary for a complete adaptive hypothesis. In both damselflies and hummingbirds, female-limited polymorphism has evolved multiple times. Females of many damselfly species have two or three morphs – one which appears like the male in coloration (androchrome), while the others do not (heterochromes) (Verhaar, 1985; Askew, 2004; Willink, Ho & Svensson, 2025). Androchrome females might deceive males by mimicking them, thereby mating less frequently than heterochromes and giving them a negative frequency-dependent advantage (Robertson, 1985). In this hypothesis, *deceptive mimicry* is what balances the polymorphism, and *mating avoidance* is the selective context in which mimicry acts. Many forms of this hypothesis have been proposed for polymorphisms in damselflies (reviewed in Fincke 2004; Van Gossum et al. 2008). An alternative is that male damselflies learn to recognize potential female mates, and female polymorphism makes it difficult for males to cue in on *any* particular female morph (Miller & Fincke, 1999; Fincke, 2004). In this case the balancing selection type (Axis 1, Figure 1) would be *basic rarity* advantage rather than mimicry, but mating avoidance is still the context (Axis 2, Figure 1). It is important to note that these two mechanisms, *deceptive mimicry* and *basic rarity*, both involve negative-frequency dependence. However, the prediction of each hypothesis is distinct: under deceptive mimicry, the male to male-mimic ratio governs the balancing dynamics of the system, whereas under a basic rarity hypothesis, the male to male-mimic ratio is irrelevant, and it is the ratio between all female morphs that matters for the strength of selection and equilibrium frequencies of each morph.

Like damselflies, white-necked jacobins (*Florisuga mellivora*) and some other hummingbird species can either be androchromic or heterochromic (Diamant, Falk & Rubenstein, 2021; Falk, Webster & Rubenstein, 2021). Rather than involving the context of mating avoidance, androchrome female white-necked jacobins appear to be *avoiding aggression* from other hummingbirds (both conspecific and heterospecific) around food resources. Appearing like the more aggressive male white-necked jacobins gives androchromic females access to more nectar resources (Falk *et al.*, 2021, 2022). Like damselflies, the balancing selection type (Axis 1, Figure 1) involves *deceptive mimicry* of males, but it’s the selective context that differs. *Mating avoidance* is the context for male mimicry in damselflies, whereas males are mimicked to *avoid aggression* and to gain access to food resources in hummingbirds.

Thus, damselflies and hummingbirds demonstrate how a framework that includes a balancing selection type and a selective context allows for simple and intuitive comparisons between similar phenomena in different taxa. Next, we detail these concepts and the major forms of each axis, balancing selection and selective context.

II. Two Descriptive Axes of Polymorphism Maintenance

(1) Axis 1: Balancing Selection and the Maintenance of Polymorphism

Unlike directional selection that favors fixation of alleles and single phenotypes, balancing selection favors the maintenance of multiple phenotypes within a population and thus the coexistence of multiple morphs. Three types of balancing selection are generally recognized: (i) negative frequency-dependence; (ii) heterogenous environments; and (iii) heterozygote advantage (Hedrick, 2007). However, we propose that three distinct forms of negative frequency-dependence should be recognized, in addition to the two frequency-neutral forms. Negative frequency-dependent selection occurs when the fitness benefit to a morph decreases as its prevalence increases (Figure 2). As we detail below, most forms of negative-frequency dependence appear to fall under the distinct categories of: (i) basic rarity, (ii) deceptive mimicry, and (iii) alternative tactics (Figure 1). Our descriptions of these categories are not novel, but this delineation simplifies and clarifies the important variables by which each is governed. The other two types of balancing selection, heterogeneous environments and heterozygote advantage, are frequency-neutral, meaning that the average fitness of a morph does not depend on its frequency in the population (Figure 1). We emphasize these five categories of balancing selection as distinct because each is theoretically sufficient to maintain a polymorphism on its own. However, individual examples of polymorphism need not fall neatly into a single category (see section: Multiple Truths: The Rule rather than the Exception)

a. Negative Frequency-dependent Selection

i. Basic rarity: Selection may directly favor rare phenotypes (Fisher, 1930) for no reason other than that they are rare. These cases are frequency-dependent since rare phenotypes will increase in frequency until they are no longer rare, at which point alternative rarer morphs are favored. For example, basic rarity advantage may appear if predators develop search images for common prey and rare prey morphs benefit by not resembling those types (Endler, 1978; Bond, 2007), or when signal receivers prefer rare phenotypes, such as female mate preference for novel male phenotypes (Hughes *et al.*, 2013).

All forms of negative frequency-dependent selection benefit rare phenotypes, but unlike the other forms discussed below, *the fitness advantage of one morph over others in this type of selection rests on its relative frequency to other morphs*. External factors can affect the precise equilibrium point, including the cognitive or sensory biases of direct competitors or mediators of selection (e.g. predators, prey, mates, etc.) (Fincke, 2004), but relative rarity to other morphs is still the factor that drives morph maintenance.

As an example, Fisher's early theory for the maintenance of a balanced sex ratio exemplifies rarity advantage (Fisher, 1930). Under a skewed ratio for either sex, the average fitness of the rare sex will be higher, assuming a diploid sexually reproducing species (Fisher, 1930; Conover & Van Voorhees, 1990). Individuals that produce more of the rare sex will have increased fitness. In this model, no other properties of females or males *per se* are necessary to explain the maintenance of a balanced sex ratio – it is simply the fitness advantage of the rare sex. In the same vein, we also expect to see basic rarity advantage in any form of disassortative mating between distinct morphs. For example, in white-throated sparrows (*Zonotrichia albicollis*), white-stripe and tan-stripe morphs tend to mate with each other resulting in balanced offspring ratios of these two morphs (Hedrick, Tuttle & Gonser, 2018). Apostatic selection, in which a predator develops a search image for common prey forms and rarer forms resist detection, is another well-studied example of how this type of basic rarity advantage might manifest (Clarke, 1962; Bond, 2007). For example, adder snakes (*Vipera berus*) can be either patterned or melanistic, and the maintenance of these morphs are likely due to increased predation from crows on more common morphs (Madsen *et al.*, 2022).

ii. Deceptive mimicry: Deceptive mimicry occurs when one group of animals (mimics) appear similar to another group (models) such that a mimic is misinterpreted to be a model, resulting in a benefit to the mimic (Fisher, 1930). Batesian mimicry refers to a form of deceptive mimicry where the model is toxic or distasteful to a predator, but the mimic is not. In this case, selection is imposed by a predator that learns to avoid the prey with the model's appearance (Bates, 1862; Fisher, 1930). However, similar principles may apply in other scenarios when one class of individuals deceptively mimics another, such as when one species mimics a socially dominant species to gain access to food resources (Rainey & Grether, 2007; Prum, 2014; Miller *et al.*, 2019; Falk *et al.*, 2021). Although in many cases all individuals of a species or population mimic another sex or species, this need not be the case, and mimicry can manifest as a polymorphism if mean mimic and non-mimic fitness reach equilibrium before mimic frequency reaches fixation (Clarke, 1964; Barrett, 1976; Kunte, 2009; Shine, Brown & Goiran, 2022).

Unlike basic rarity, in deceptive mimicry *the average fitness of a morph depends on the relative frequency of the mimic to the model*, not the frequency of one morph to another morph. The frequency of mimics may also depend on several factors including the degree of model-mimic resemblance, the rate of encounter between the operator and the model, and the relative costs of deception to the receiver (Fisher, 1930; Pfennig, Harcombe & Pfennig, 2001).

Deceptive mimicry has been experimentally modeled, such as Brower's (Brower, 1960) classic demonstration using the European starling (*Sturnus vulgaris*) as a predator and painted mealworms as prey. In non-venomous turtle-headed sea snakes (*Emydocephalus annulatus*), banded individuals mimic several species of venomous snakes, and this morph fluctuates with a black morph as expected under negative frequency-dependence (Shine *et al.*, 2022). Similar principles will apply in any deceptive mimicry system (Jamie, 2017). For example, male bluegill sunfish (*Lepomis macrochirus*) sometimes mimic females to access egg fertilizations at the nests of non-mimic males (Dominey, 1980). In this case mimics advertise a benefit rather than a danger to the receiver, a non-mimic male (Jamie, 2017).

iii. Alternative tactics: Alternative tactics are consistent and discrete behavioral morphs that occur within a population (Gross, 1996; Oliveira *et al.*, 2008). Specifically, one morph uses a tactic to monopolize a resource, while another increases its fitness by exploiting or competing against the monopolizing tactic with a different tactic (Oliveira *et al.*, 2008). Morphological associations with behavioral tactics may facilitate these differences in behavior, such as enlarged weaponry in monopolizing morphs or color signals that display behavioral type.

The stability and negative frequency-dependence of alternative tactics have been explored extensively (reviewed in Shuster 2010). In short, high frequencies of the monopolizing tactic create conditions in which few individuals exclude many other individuals from access to a critical resource or social interaction (e.g. matings). Alternative tactics that do not engage in the monopolizing tactic are successful at low frequency, but as their numbers increase, their average success decreases. The resulting stable frequencies of each morph that are maintained by alternative tactics include *the relative ability of the monopolizing morph to restrict access from other individuals, as well as the rate and degree of success of the alternative tactics in competing against the monopolizing morph* (Shuster & Wade, 2003; Shuster, 2010).

A classic example of alternative tactics are the three alternative morphs of marine isopods (*Paracerceis sculpta*). Females associate and live inside sponges, and α-males compete for exclusive access to these female aggregations. Female-resembling β-males and small γ-males use non-exclusionary behaviors to access females that are guarded by α-males (Shuster, 1992). As aggregations increase in size, β- and γ-males are able to escape detection by α-males and mate more often, resulting in equal lifetime fitness of each male morph (Shuster & Wade, 1991).

b. Frequency-neutral Selection

i. Heterogeneous environments: Fluctuating environmental conditions over space or time may favor the existence of multiple morphs through specialization for certain environmental conditions (Hedrick, Ginevan & Ewing, 1976; Hedrick, 1986). For example, a morph may exist in relatively low frequencies in most years, but under certain environmental conditions it may be favored. Fluctuating conditions may be either biotic or abiotic and include fluctuations in population density of conspecifics. Density fluctuations, however, are rarely independent from frequency fluctuations so care should be taken to distinguish the two. Under heterogeneous environmental conditions, polymorphisms are maintained by the prevalence of different environmental types. For example, the bill sizes of black-bellied seedcrackers (*Pyrenestes ostrinus*) are bimodally distributed – large bills are better at processing hard seeds, and narrow bills are better for soft seeds (Smith, 1993). Juvenile seedcrackers with intermediate bills have lower survival rates to adulthood than those with either large or small bills (Smith, 1993).

Although there are few unambiguous examples of genetic polymorphisms maintained through heterogeneous environments (Brisson, 2018), polymorphisms induced through phenotypic plasticity during development in heterogeneous environments are numerous (Nijhout, 2003; West-Eberhard, 2003b). For instance, larval tiger salamanders (*Ambystoma tigrinum*) can develop into a cannibalistic morph that feeds mostly on other salamanders, swims faster, and has a larger head and teeth than the non-cannibalistic morph, which feeds mostly on insects (Collins

& Holomuzki, 1984). The morph is plastically induced through increased tactile stimulation from conspecifics when densities are high (Hoffman & Pfennig, 1999).

ii. Heterozygote advantage: A heritable polymorphism can be maintained through overdominance or any scenario where parents are of different types. In overdominance, individual fitness is higher for heterozygotes compared to homozygotes at a genetic locus (Fisher, 1923; Dobzhansky, 1955). In this type of selection, the stable phenotype frequency depends on the relative fitness advantage of heterozygotes over homozygotes (Fisher, 1923). Overdominance and disassortative mating (see above, Basic rarity) are not necessarily linked but may often be found together because overdominance creates conditions that favor the evolution of disassortative mating, which would reduce mate pairings that result in lower fecundity or offspring survival.

There are few examples in which heterozygote advantage unambiguously maintains a polymorphism with no influence from other types of balancing selection. In one example, Neotropical tortoise beetles (*Chelymorpha alternans*) are polymorphic with five different color morphs related to variation at a single gene (Strickland *et al.*, 2019). Captive beetles mate randomly, but clutch hatching and pupal eclosion rates were both lower between parents of the same morph (Strickland *et al.*, 2021). Overdominance may play a role in maintaining this polymorphism, but the reason for reduced survival rates is currently unknown.

c. Non-adaptive null

An alternative to these adaptive hypotheses is that the polymorphism is not actively maintained by selection, but rather a mutation-selection balance or relaxed selection allows for the existence of multiple types (Kimura, 2020). While possible, a neutral or non-adaptive polymorphism should be unstable in the presence of drift. Some studies explicitly examine morph frequencies under null models to test the explanatory power of drift (e.g. Madsen et al. 2022). This hypothesis should also be considered if adaptive hypotheses are refuted. Our focus here is on the adaptive maintenance of within-population polymorphism, so we do not discuss hypotheses involving migratory gene flow and hybridization, even though this has been proposed and is supported in some studies (e.g. Cooper 2010; Cooper et al. 2016). However, we note that this type of non-adaptive evolution may exist on a spectrum with heterogeneous patchy environments described above (e.g. Rosenblum 2006).

d. Multiple Truths: The Rule rather than the Exception

The five types of balancing selection that we describe above are theoretically capable of maintaining a polymorphism on their own. However, evidence for multiple types of balancing selection acting on the same polymorphism is common (see Table 1). Multiple interacting forms of balancing selection may be the rule rather than the exception (Jones, Leith & Rawlings, 1977). The white-throated sparrow (*Zonotrichia albicollis*) is a prime example. This species is polymorphic (Lowther, 1961) due to a large chromosomal inversion (Huynh, Maney & Thomas, 2010), exhibiting either a white-stripe or tan-stripe morph that are distinct in color and behavior (Watt, Ralph & Atkinson, 1984). Nesting pairs and mating occur almost entirely between males and females from opposite morphs with same-type pairings suffering reduced fitness, demonstrating strong disassortative mating and therefore rarity advantage, along with heterozygote advantage (Tuttle *et al.*, 2016). The two morphs also exhibit consistent behavioral differences reminiscent of alternative tactics, with white-stripe morphs exhibiting higher levels of social dominance, less parental care, and higher extra-pair copulation. Thus, basic rarity, alternative tactics, and heterozygote advantage all may be playing a role. In another complex example, males of *Poecilia parae* guppies have five different morphs. All three types of frequency-dependent balancing selection may be acting on the different morphs through the context of intrasexual competition for access to mates (Hurtado-Gonzales & Uy, 2009, 2010; Hurtado-Gonzales, Baldassarre & Uy, 2010).

If each type of balancing selection can maintain polymorphism independently, it is curious that so many polymorphisms appear to involve multiple types occurring at the same time. Above we noted that in many cases of male-limited polymorphism, both mimicry and alternative tactics have been implicated, and that an exclusive role for overdominance appears to be rare. However, in several suspected instances of alternative tactics, overdominance also appears to be at play (e.g. Küpper et al. 2015). Perhaps the combination of both frequency-dependent and frequency-neutral forms of balancing selection can result in highly stable polymorphism. Does the strength of balancing selection increase additively when multiple types are involved? Ultimately, studying interactions may be key to understanding why some polymorphisms persist while others do not, though surprisingly little empirical or theoretical work has been done in this arena.

(2) Axis 2: Selective Context: Ecological and Social Selection

Balancing selection acts through the fitness of individuals, but fitness itself is multifaceted and the various processes by which natural selection occurs are numerous. Therefore, while the type of balancing selection (Axis 1) describes the mechanism of trait maintenance, Axis 2 completes the hypothesis by describing the natural history context by which balancing selection acts. Recall in our initial example comparing female polymorphism in damselflies and hummingbirds: both examples involve deceptive mimicry of males, but it is the selective context that differs, and this is crucial to understanding the distinction between these two hypotheses. In damselflies, *mating avoidance* is the context for male mimicry, whereas in hummingbirds, males are mimicked to *avoid aggression* and to gain access to food resources. In another comparison, damselfly and white-throated sparrow polymorphisms, basic rarity may both play a role. In the former, the selective context is mate avoidance, whereas in the latter it is mate attraction.

Although Axis 1 can be divided into a discrete number of forms, this is not so easily done with Axis 2. How can hypotheses be categorized in a way that would allow for useful comparisons across taxa? Darwin (1896) recognized that there are fundamental differences between the expectations of selection involved in competition for mates (sexual selection) versus competition to survive (ecological selection). This distinction is powerful for explaining conspicuously ornamented or exaggerated traits (Andersson, 1994; Hare & Simmons, 2019), but it also leaves many exaggerated traits unaccounted for, such as those expressed during non-breeding stages of an animal's life, and in females or males experiencing low levels of competition for mates (e.g. monogamous species) (West-Eberhard, 1983; Lyon & Montgomerie, 2012).

We suggest that the social selection framework, developed by West-Eberhard, offers a broader and more inclusive structuring of the modes of natural selection than Darwin's natural-sexual selection framework (West-Eberhard, 1983; Lyon & Montgomerie, 2012). Social selection is distinct from ecological selection, the latter of which derives from abiotic factors, prey capture ability, and interspecific interactions such as predation. In contrast, social selection arises from an individual's ability to compete with conspecifics (and sometimes heterospecifics) over any type of resource important for survival or reproduction, and views sexual section as one of several types of social selection (West-Eberhard, 1983). Darwin's sexual selection theory is therefore subsumed within the social selection framework. However, any type of competition induced by an individual's social environment may produce similar patterns as sexual selection, including weaponry or conspicuous ornamentation (West-Eberhard, 1983). Examples of non-sexual social selection include competition for access to non-mating breeding resources, critical food resources, or the attention of parents (West-Eberhard, 1983; Lyon & Montgomerie, 2012; Tobias, Montgomerie & Lyon, 2012). Competition in this sense broadly encompasses both direct competition such as territorial aggression, as well as indirect competition mediated by a third party such as mate choice, mating avoidance, or parental choice in attention toward offspring (Lyon & Montgomerie, 2012). We note that while the social selection framework can be used to categorize and compare contexts, the lines between different contexts is not always clearly cut, and multiple contexts may compound on each other (Wang *et al.*, 2024). For example, access to food could have indirect implications for the ability to attract mates, or the ability to defend high-resource territories could affect resource allocation during parental care.

While social selection provides a framework for identifying types of competition, it is not typically used as an explanation for adaptive polymorphism (Sinervo, Bleay & Adamopoulou, 2001). We argue, however, that pairing the social selection framework with balancing selection creates a surprisingly simple structure by which hypotheses for seemingly disparate types of polymorphism can be linked. Most discussion of polymorphism focuses primarily on the influence of ecology (Clarke, 1962; Endler, 1978) or male competition for mates (Gross, 1996; Oliveira *et al.*, 2008). Yet, there are many other forms of competition through which balancing selection can work to maintain polymorphism, such as mating avoidance (Fincke, 2004) and access to food (Falk *et al.*, 2022). By considering both the type of balancing selection and the selective context through which balancing selection acts, we can develop a more general framework for understanding the maintenance of polymorphism.

III. The Puzzle of Female-limited Polymorphism

We demonstrate the utility of this framework by considering female-limited polymorphisms, where females are polymorphic but males are not. Cases of female-limited polymorphism are sometimes considered less numerous than those in males (Oliveira *et al.*, 2008), and occasionally are left out of discussions of sex-limited polymorphism altogether (Gross, 1996), yet female-limited polymorphisms can be common in at least some taxa (Mank, 2022). Sexual conflict and mating avoidance have been proposed as a possible context for the evolution of female-limited polymorphism (Suzanne H Alonzo, 2008; Svensson *et al.*, 2009), but alternative explanations abound across taxa. It is therefore unclear whether the function of female-limited polymorphisms can also be generalized in the same way that male-limited polymorphisms have been (Oliveira *et al.*, 2008), and whether both female- and male-limited polymorphisms can be discussed under the same conceptual framework. We believe that applying our framework—considering both the type of balancing selection and the selective context—will help explain the evolution of female-limited polymorphism.

We surveyed existing hypotheses for the maintenance of female-limited polymorphisms by identifying the type of balancing selection and the selective context (Table 1). Our focus was on phenotypic variation, and we did not include purely cellular, molecular, or entirely behavioral variants (see Wang *et al.* 2024). Polymorphisms in eusocial species were also excluded due to complex multi-level selection in these systems, as were examples in which expression is impossible in males (e.g. egg polymorphisms). We do not seek to discredit or obviate the many hypotheses that have been suggested for female-limited polymorphisms within specific taxa (e.g. damselflies: Fincke 1994, 2004; Andrés et al. 2002; Svensson et al. 2005; Cooper 2010; Xu and Fincke 2011; Willink and Svensson 2017). Indeed, accounting for life history is critical for developing predictions that are specific to each case of polymorphism. However, a framework for categorizing hypotheses is necessary for finding generalities, commonalities, and distinctions between different types of polymorphism.

The Role of Social Competition

What can be learned about female-limited polymorphism by using our proposed framework? By mapping examples onto Table 1, we see that female-limited polymorphisms occur over a wide range of categories but are most highly concentrated under non-sexual social competition. Others have noted that mating avoidance and sexual conflict frequently appear to underly female-limited polymorphism (Svensson *et al.*, 2009; Lee *et al.*, 2019). Our findings supports this observation while also broadening the explanatory scope to include various forms of competition for social dominance. Not every case of female-limited polymorphism is driven by social interactions, as ecological contexts are also supported in some species, most notably in aposematic butterflies (reviewed in Kunte 2009). In contrast to polymorphism in females, reviews of male-limited polymorphism have indicated a strong association with intrasexual competition for mates (Gross, 1996; Taborsky, 2008). Therefore, most sex-limited polymorphisms, including female-limited polymorphism, fall under the broader category of social competition (i.e. social selection), with male-limited polymorphism primarily found more narrowly under social competition for mates (i.e. sexual selection).

Our hypothesis that strong social competition is an important prerequisite or facilitator of the evolution of sex-limited polymorphism in both males and females is consistent with other observations. For instance, why exactly are sex-limited polymorphisms "limited" to a single sex? One potential explanation is that competition between members of the same sex can reach very high and consistent levels over generations (West-Eberhard, 1983; Andersson, 1994; Kokko & Jennions, 2008; Cain & Rosvall, 2014). Furthermore, especially strong social competition for mating opportunities is often found in males due to higher operational sex ratios and steeper Bateman gradients (Jennions & Kokko, 2010). This may explain why male-limited polymorphism is more common than female-limited polymorphism (Shuster & Wade, 2003; Svensson *et al.*, 2009; Shuster, 2010; Mank, 2022), though Wang et al. (2024) point out that many female alternative reproductive tactics could be mostly behavioral, which we have addressed to a lesser degree here. It is interesting to note that a similar paradigm has been proposed for ornamentation and weaponry, with diverse forms of social competition driving the evolution of these phenomena in females, and strong competition for mating opportunities typically invoked to explain male-biased expression of exaggerated traits (West-Eberhard, 1983; Tobias *et al.*, 2012). However, non-mating contexts are rarely tested or considered in male-limited polymorphisms.

Another pattern revealed in our mapping is that few examples of female-limited polymorphism are categorized as being maintained entirely through frequency-neutral balancing selection. Fluctuating social environments has been proposed (for butterflies, reviewed in Kunte 2009) and has support in at least one case (Sinervo, Svensson & Comendant, 2000), but even there, frequency-dependent selection is likely also at play (Sinervo *et al.*, 2000). Interestingly, reviews of male-limited polymorphism also rarely find support for frequency-neutral explanations (but see Mérot et al. 2020). This is likely because frequency-dependent selection is inherently social and rarely exists without the interaction of individuals (Smith, 1982). If social competition is a primary force in the evolution of sex-limited polymorphism, then sex-limited polymorphism should go hand-in-hand with the most socially relevant types of balancing selection. Indeed, strong sexual selection has long been considered an evolutionary driver of polymorphism associated with alternative mating strategies in males (Gadgil, 1972; Shuster, 2010). Using our framework, we show that this expectation can be broadened to include polymorphism in females simply by considering competition for mates to be just one of many types of social competition for resources.

IV. Future Questions

In addition to providing a simple method for developing alternative hypotheses, and for comparing classes of polymorphism across sexes and taxa, using this framework raises questions and avenues for future study. We briefly highlight two of these questions for consideration.

First, how does the genetic mechanism of production of polymorphism influence the types of balancing selection at play? Although we have focused primarily on the function of polymorphisms, a number of recent studies have identified large inversion mutations as the genetic basis for genetic polymorphism in female-limited polymorphism (Kunte *et al.*, 2014; Nishikawa *et al.*, 2015; Willink *et al.*, 2024), male-limited polymorphism (Küpper *et al.*, 2015; Dodge *et al.*, 2024), and in species-wide polymorphism (Huynh, Maney & Thomas, 2011; Sanchez-Donoso *et al.*, 2022). It will be interesting to explore whether there are particular types of inversions that lead to balancing selection, and if there are aspects of inversion mutations that can predict the type of balancing selection. By preventing recombination, inversions may create conditions for the evolution and maintenance of polymorphisms, but other genetic mechanisms that are more difficult to detect (e.g., copy number variants and transposable elements) have also recently been implicated (Bijl *et al.*, 2023; Willink *et al.*, 2024).

Second, how are polymorphisms that derive from cooperative interactions related to those derived from competitive interactions? Although we have ignored polymorphism in eusocial animals that may derive primarily from cooperation rather than competition, others have noted the similarities between models of alternative tactics and cooperative breeding strategies (Koenig & Dickinson, 2008). Theoretical and empirical work suggests that morphs of alternative tactics contain elements of cooperation and competition (Hugie & Lank, 1997; Watters, 2005; Taborsky, 2008). These ideas suggest an intriguing possibility that perhaps the evolution of castes in highly social insects could be unified under a common framework with alternative tactics.

V. Conclusion

(1) Rigorous testing of hypotheses for the maintenance of polymorphism is limited by the lack of a common framework for discussing across taxa and types of polymorphism.

(2) Standard frameworks center ontogeny—whether variation is determined by environment or genetic—but can create confusion when developing alternative hypotheses for the maintenance of polymorphism.

(3) We demonstrate a simple method for developing complete alternative hypotheses for the maintenance of polymorphism: Both a type of balancing selection (Axis 1), as well as the context (Axis 2) in which the balancing selection acts must be described.

(4) We identify 5 distinct types of balancing selection (Axis 1): basic rarity, deceptive mimicry, and alternative tactics, heterogeneous environments, and heterozygote advantage. Though all types of balancing selection can function independently, there is often evidence for multiple types acting simultaneously.

(5) The selective context (Axis 2) in which balancing selection acts is best viewed through the social selection framework, which provides a useful structure for categorizing and comparing modes of ecological and social competition.

(6) We demonstrate this method by reviewing female-limited polymorphism, and find that many, but not all, examples are maintained by basic rarity and deceptive mimicry, through the context of non-sexual social selection.

(7) This method aids in comparison between seemingly disparate taxa, allows researchers to identify understudied topics regarding polymorphism, and clarifies distinctions between hypotheses to better understand the numerous and complex polymorphic systems found across animals.

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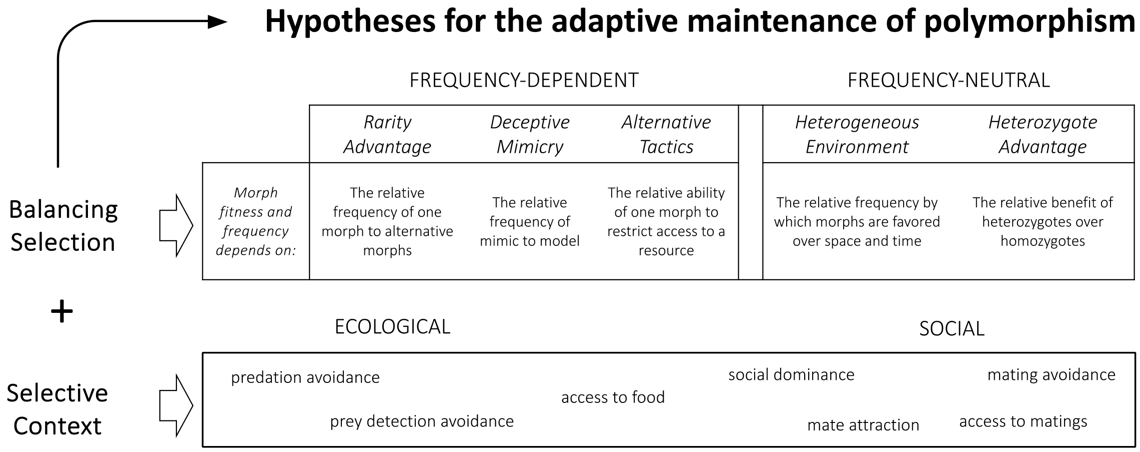

Figure 1: **A simple method for developing hypotheses for the adaptive maintenance of polymorphism.** A complete adaptive hypothesis should involve at least one type of *balancing selection* (either frequency-dependent, or frequency-neutral), and the selective *context* through which the balancing selection acts (both ecological and social). Each type of balancing selection paired with a selective context is theoretically capable of maintaining a polymorphism, but actual polymorphisms may involve multiple types of balancing selection or contexts.

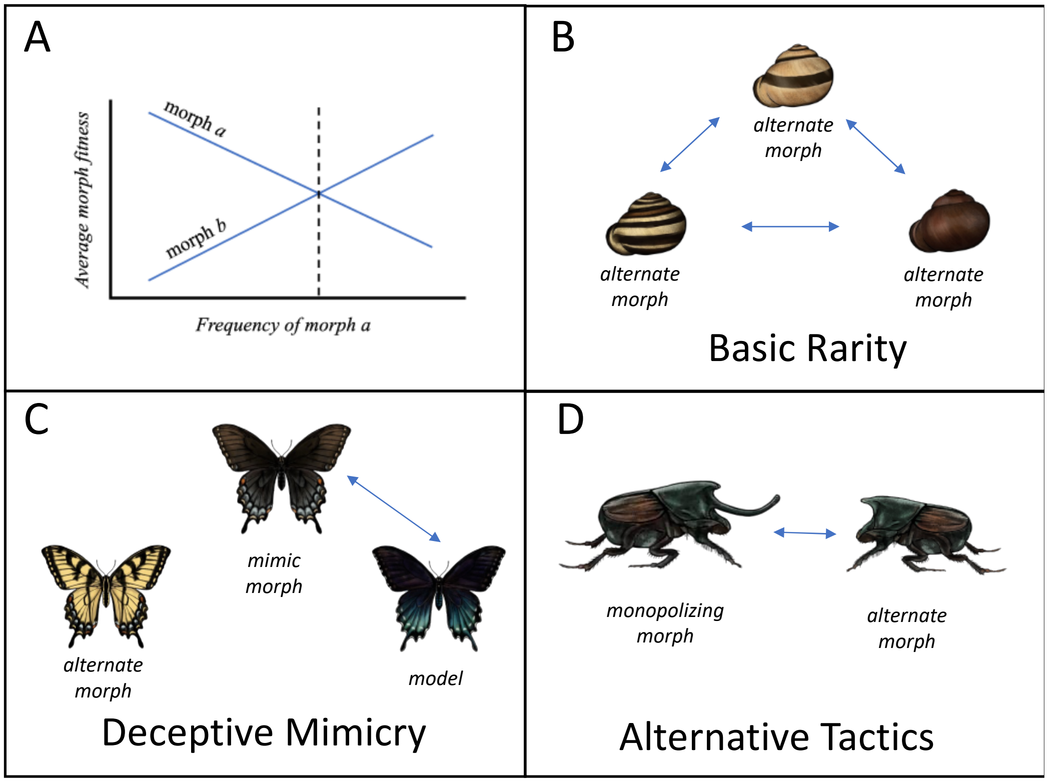

Figure 2: Negative frequency-dependent selection: (A) A graphical depiction of negative frequency-dependent fitness which will favor a polymorphism of two morphs, *a* and *b*. The relative fitness of *a* over *b* decreases as its frequency in the population increases. Since *a* has higher fitness when at lower frequencies, its prevalence in the population should increase until it reaches an equilibrium frequency (dotted line). At frequencies greater than equilibrium, *b* outcompetes *a*. A stable polymorphism with equilibrium can result so long as fitness curves for *a* and *b* intersect such that *a* has greater relative fitness at lower frequencies of *a*, and *b* has greater relative fitness at higher frequencies of *a*. These conditions can be met in variety of ways, only one of which is depicted here. (B-D) Representative species of the three forms of negative frequency-dependent selection. Arrows indicate interaction pairs that influence morph frequency and fitness. (B) Polymorphism in grove snail (*Cepaea nemoralis*) shell patterning has been suggested to arise from a variety of selective pressures, including rarity advantage (Clarke, 1962). (C) Female eastern tiger swallowtails (*Pailio glaucus*) are polymorphic. One morph (left) has wing coloration similar to males, while the other (right) mimics a sympatric species which sequesters toxic compounds (Kunte, 2009). (D) Male dung beetles (*Onthophagus nigriventris*)

have male polymorphism in horn size that represents alternative tactics for accessing mating opportunities (Simmons & Emlen, 2006). Illustrations by Liz Wahid.

			Negative Frequency-dependent Balancing Selection		
			Rarity Advantage	**Deceptive Mimicry**	**Alternative Tactics**
Selective Context	**Ecological**	**Predation avoidance**		♀ Butterflies, e.g. *Papilio glaucus*	
		Prey/host detection avoidance	♀ Crab spider, *Synema globosum*; ♀ Common cuckoo, *Cuculus canorus*	♀ Common cuckoo, *Cuculus canorus*	
	Social	**Mating Avoidance**	♀ Damselflies, e.g. *Ischnura* sp.; ♀ Dytiscid beetle, *Graphoderus zonatus*	♀ Damselflies, e.g. *Ischnura* sp.; ♀ African bat bug, *Afrocimex constrictus*; ♀ Brown anole, *Anolis sagrei*; ♀ Common cuckoo, *Cuculus canorus*; ♀ Butterflies, e.g. *Papilio Dardanus, Colias sp.*	
		Social Dominance	♀ Cichlid fish, *Neochromis omnicaeruleus*	♀ White-necked jacobin, *Florisuga mellivora*	♀ *Megalopta* sp. bees; ♀ Side-blotched lizard, *Uta stansburiana*
		Competition for mates		♂	♂

Table 1: We compiled representative species or groups of species in which the adaptive function of female-limited polymorphisms has been studied. Hypotheses for polymorphism maintenance may not fall neatly into any single box, as demonstrated by examples that appear repeatedly. Most examples of female-limited polymorphism fall into the selective context of non-sexual social selection. We do not include the frequency-neutral types of balancing selection here because there is little support for purely frequency-neutral adaptive functions for sex-limited polymorphism (but see (Schoener & Schoener, 1976) for proposed heterogeneous environment hypothesis in females of *Anolis sagrei*). Male-limed polymorphism have been reviewed previously, and these polymorphisms are typically attributed to alternative tactics and mimicry related to competition for mates (indicated by ♂). References included in this table: (Emlen, 1994; Cook *et al.*, 1994; Lank *et al.*, 1995; Sinervo *et al.*, 2000; Nielsen & Watt, 2000; Fincke, 2004; Jukema & Piersma, 2006; Reinhardt *et al.*, 2007; Dijkstra, Seehausen & Groothuis, 2008; Van Gossum *et al.*, 2008; Kunte, 2009; Rose Thorogood & Nicholas B. Davies, 2012; Karlsson Green *et al.*, 2013; Trnka, Trnka & Grim, 2015; Steitz *et al.*, 2018; Moon & Kamath, 2019; Ajuria Ibarra *et al.*, 2019; Lee *et al.*, 2019; Falk *et al.*, 2022)