



Sexual selection and social context: Web-building spiders as emerging models for adaptive plasticity

Maydianne C.B. Andrade*

Departments of Biological Sciences and Ecology and Evolutionary Biology, University of Toronto
Scarborough, Toronto, ON, Canada

*Corresponding author: e-mail address: maydianne.andrade@utoronto.ca

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1. Introduction

1.1 Adaptive phenotypic plasticity

Phenotypic plasticity refers to the ability of individuals with a given genotype to show variation in phenotypes under different conditions (e.g., Kelly, Panhuis, & Stoeck, 2012; Pigliucci, 2001; West-Eberhard, 2003), an ability that may be adaptive if plastic phenotypes have higher fitness than those that are inflexible in the face of environmental variation (Nettle & Bateson, 2015). Understanding the evolution, nature, and optimization of adaptive phenotypic plasticity is a major goal of modern research in evolutionary ecology, behavior, and conservation. Adaptive plasticity encompasses a wide range of responses that differ in the time-scale of integration of environmental variation with phenotypic changes, and whether those changes are permanent or transient (Beaman, White, & Seebacher, 2016; Charmantier et al., 2008; Fawcett & Frankenhuis, 2015; Groothuis & Taborsky, 2015; Guerrero-Bosagna et al., 2018; Kasumovic, 2013; Nyman, Fischer, Aubin-Horth, & Taborsky, 2017; Snell-Rood, 2013; Taborsky, 2017). Most relevant to this review is the considerable effort aimed at understanding how trait expression is affected by information acquired during ontogeny (developmental plasticity, Kasumovic, 2013; Pigliucci, 2001; West-Eberhard, 2003) or during adult life stages (activational plasticity, Snell-Rood, 2013). The evolution of these forms of adaptive plasticity is most likely when environmental conditions vary on a scale that ensures the phenotypes and life histories that confer high fitness for adults are different from those that were advantageous in the previous generation, but are detectable by juveniles (developmental plasticity), or that these conditions change throughout the lifetime of the adult (activational plasticity, Nettle & Bateson, 2015). Even under these conditions, however, plasticity is only expected if reliable information is available to the individual regarding the changing state of the environment on a time-scale that allows phenotype-environment matching (Dore et al., 2018; Nettle & Bateson, 2015; Pigliucci, 2001). Here I provide an overview of adaptive plasticity, particularly how links between changing social context and sexual selection can shape the evolution of plasticity (Section 2). I then discuss the utility of testing hypotheses for such socially-linked adaptive plasticity in taxa with extreme mating behaviors (Section 3). I conclude with empirical examples of plasticity in web-building spiders in which severe limits on male mating frequency arise from high rates of sexual cannibalism, male genital

mutilation at mating, arduous, high-mortality mate searching, and where first male sperm precedence places a premium on finding unmated females before rivals (Sections 3 and 4).

Not all traits are plastic (Palacio-Lopez, Beckage, Scheiner, & Molofsky, 2015), and thus the physiological (e.g., metabolic or neural capacities) and morphological (e.g., body size, ornaments, gonad size) traits of mature organisms have often been studied as a “toolbox” which animals employ via flexible behavioral capacities to overcome the challenges of their current environment. This is often a reasonable approach since, for any one individual, the range of possible behavioral responses to a given situation will have limits defined by the potential of their phenotypic traits and underlying mechanisms (Fawcett, Hamblin, & Giraldeau, 2013). A simple example is the negative correlation between body size and the lower limit of call frequency for male frogs and toads (McClelland, Wilczynski, & Ryan, 1996; Zweifel, 1968). Understanding when we expect to find constitutively expressed (fixed) traits vs plasticity (e.g., Levis & Pfennig, 2016) is important because, for plastic traits, the nature of the phenotypic toolbox can change (West-Eberhard, 2003), as can the behavioral capacities that utilize them (Ghalambor, Angeloni, & Carroll, 2010) with important implications for adaptation and population persistence (Levins, 1962, 1963). Plasticity can evolve when variation in the behavioral tasks that are required for survival and reproduction in a particular context creates selection for links between individual detection of environmental cues and the development, adult form, and behavioral use of phenotypic traits (West-Eberhard, 2003). For example, for male frogs, the presence of noise that masks low frequencies (e.g., flowing water, Grafe et al., 2012; traffic, Parris, Velik-Lord, & North, 2009) can trigger an increase in call frequency across body sizes. Higher frequency calls are less likely to be masked by low-frequency noise, but they are less preferred by females in the absence of noise, and attenuate more rapidly (Grafe et al., 2012; Parris et al., 2009). Whether calls are plastic in the presence of noise should depend on the net effect of this trade-off on male fitness. Indeed, while one species with narrowly-tuned, predominantly low-frequency call components showed this shift in the presence of noise, another with more broad-band calls showed little evidence of a shift, possibly because other components of the call could still carry information and so plasticity was not beneficial overall (see Parris et al., 2009).

Selection for phenotypic plasticity is thus expected when there is predictable variation in phenotype–fitness associations (Stearns, 1989a), which is expected to create links between ecological challenges, phenotypic

variation, and the evolution of trait expression (Levis & Pfennig, 2016). In some organisms, this manifests as information-cued variation in ontogeny yielding changes in adult traits (developmental plasticity, Nettle & Bateson, 2015). In others, information can trigger activational plasticity whereby adult experience shifts the “tools” available (e.g., neural changes via learning), or life history allocations to competing functions (e.g., gamete production, courtship effort, Snell-Rood, 2013). These changes can increase fitness under variable conditions, including facilitating adaptive alterations in the intensity or form of behavioral outputs (Badyaev, 2005). While developmental changes are usually fixed at adulthood, activational changes may remain in place throughout life, or may remain flexible with continuous updating relative to current conditions (English, Fawcett, Higginson, Trimmer, & Uller, 2016; Groothuis & Taborsky, 2015; Stamps & Frankenhuys, 2016; Taborsky, 2009).

The study of adaptive plasticity has substantively changed our understanding of the causes of phenotypic variation in nature (Price, 2006; West-Eberhard, 2003), and how this may be iteratively linked to behavioral performance across generations through eco-evolutionary feedback loops (e.g., Kokko & López-Sepulcre, 2007). Feedback is particularly likely when variation in phenotype–fitness relationships ultimately derives from variation in population density. If the performance of particular phenotypes is density dependent, then the outcome of interactions among conspecifics may favor the evolution of adaptive plasticity cued to demographic information, and changes in performance may in turn alter demography (Kokko & López-Sepulcre, 2007). This may be particularly likely for traits under sexual selection, where population density and related demographic variables (sex ratio, proximity, and availability of mates) are expected to drive the direction and intensity of selection on traits related to pre- and post-copulatory selection. Understanding these dynamics is important as it may underlie our ability to infer processes of diversification in nature (Gomez-Mestre & Buchholz, 2006; West-Eberhard, 2005), and the capacity of organisms to adapt to novel conditions related to environmental change or biological invasions (Ghalambor et al., 2015; Lande, 2015; West-Eberhard, 2003; Zimova et al., 2018). It also challenges us to rethink how we envision the evolutionary role of behavior (e.g., Noonan et al., 2018).

Considering behavior through the lens of plasticity can unify insights from decades of behavioral research with the body of theory and empirical work on plasticity (Bretman, Gage, & Chapman, 2011; Ghalambor et al., 2010). It has long been clear that organisms show flexibility in behavior

and this can be predicted by variation in their environment or internal state. Nevertheless, explicit considerations of behavioral flexibility under the same theory as other forms of phenotypic plasticity is relatively recent (Bretman et al., 2011; Danchin, Giraldeau, & Cezilly, 2008; Ghalambor et al., 2010). Behavioral plasticity may exist even when the decision rules or algorithms that lead to behavioral outputs remain static. This can arise with shifts in the inputs—the external or internal variables that affect the fitness effect of behavioral options, or shifts in the detectable information (cues) regarding these variables (e.g., see Danchin et al., 2008). Behavioral plasticity may also arise through changes in the underlying algorithms that alter the probability of particular outputs under a given set of informational inputs. Consider that a predatory web-building spider may show a range of possible responses to vibrations in a web that may arise from prey (or a potential threat), including retreat, approach/investigate, or attack (e.g., Nelson & Jackson, 2011). A short-term change in the internal state of the predator, like decreased energy reserves, may lead to an increased probability that potential prey will be attacked after a rapid approach (activational plasticity). Predatory behavior may also be altered by variation in prey availability experienced in early adulthood (e.g., via learning, Jakob, Skow, & Long, 2011). So, an adult in an environment with scarce prey may attack more quickly than an individual with the same body condition in a habitat where prey has been plentiful. This form of activational plasticity may be fixed or may change over time (Nelson & Jackson, 2011; Stamps & Frankenhuis, 2016). Finally, variable food availability can also produce developmental effects, where individuals that experience unpredictable or low food availability during ontogeny may attack potential prey more readily as adults, regardless of body condition or current prey availability (developmental plasticity, e.g., Schneider & Elgar, 2002). This change may be fixed in adulthood. Moreover, for all of these pathways, the change in behavior may be associated with a range of connected changes in physiology or morphology (Levis, de la Serna Buzón, & Pfennig, 2015; Relyea, 2002; Snell-Rood, 2012) that may also show sustained flexibility (Gabriel, 2005), or may be fixed after maturity (Nijhout, 2003).

1.2 Why spiders? Leveraging extreme mating for studies of plasticity

Here I join others in advocating an integrative approach to testing hypotheses regarding adaptive developmental and activational plasticity and consider the pivotal role of behavior and the integrated phenotypes

supporting behavior. I focus on the phenotype–environmental matching required for success under variable sexual selection linked to fluctuating demographic variables that determine the social context for reproduction (Elias, Andrade, & Kasumovic, 2011; McLain, 1992; Oh & Badyaev, 2006; Sachser, Kaiser, & Hennessy, 2013). Such dynamics are likely to be important across taxa (reviewed in Kasumovic & Brooks, 2011) and impose selection on plasticity across generations (Kokko & López-Sepulcre, 2007). Significant advances in our understanding of plasticity are being made in work on relatively long-lived vertebrates, such as fish (e.g., Taborsky, 2017), amphibians (e.g., Becker, Tolley, Measey, & Altwegg, 2018; Relyea et al., 2018), birds (e.g., Drummond & Ancona, 2015; Guerrero-Bosagna et al., 2018), and mammals (e.g., Noonan et al., 2018; Sachser et al., 2013). Such models are valuable because of the range of genomic and physiological tools available (Kelly et al., 2012), and considerable information on how variable phenotypes affect fitness across complex gradients of social demography (e.g., Taborsky, 2017). This work is important, but also challenging. Understanding the complexity of social, behavioral, and environmental factors affecting fitness is a significant task for long-lived animals. Moreover, the existence of trade-offs in trait development (Nylin & Gotthard, 1998) and among behavioral outputs across variable lifespans can confound the development of clear predictions. A complementary approach is to seek foundational understanding of processes underlying the evolutionary dynamics of adaptive phenotypic plasticity using more short-lived taxa in which there is a natural simplification of some of these complexities. Studies of short-lived invertebrates have provided critical insights into a wide range of different processes in evolutionary behavioral ecology, with broad implications for other taxa (e.g., sex roles, Gwynne, 1985; sperm competition, Parker & Simmons, 1996; Parker, 1970). The advantage of work on invertebrates for questions related to plasticity includes the tractability of work in the laboratory and field that would allow characterizing and manipulating (1) environmental variables that are most salient to phenotype–fitness associations (Chevin & Lande, 2015) on different timescales (McLain, 1992), (2) complex cues that may indicate the relevant environmental context (Dore et al., 2018), and (3) development of plastic phenotypes (Kasumovic & Andrade, 2006). Finally, (4) phylogenetic tests of hypotheses for the evolution of plasticity across populations or closely-related species that differ in key demographic predictors are likely to be feasible (Rodriguez, Rebar, & Fowler-Finn, 2013) because of the relative ease of creating replicable assays.

Among invertebrates, spiders present an interesting opportunity for studies of adaptive plasticity in traits related to reproductive fitness under variable demography, particularly as it relates to males under sexual selection. Spiders are remarkable for their diverse mating behaviors (Schneider & Andrade, 2011), and this, together with features of their ecology and biology outlined here, make them attractive subjects for studying various aspects of sexual selection (Eberhard, 2004; Huber, 2005; Schneider & Andrade, 2011). Our current understanding of phenotype–fitness relationships under sexual selection and how these are affected by demography suggests the potential importance of adaptive plasticity for males in nature (e.g., Elias et al., 2011). Here I discuss three focal genera of web-building spiders which present a good balance between reduction of some of the axes of complexity within species, and sufficient variation across species, or populations for informative studies of the evolution of plasticity—*Nephila* (family Nephilidae), *Argiope* (family Araneidae), and *Latrodectus* (family Theridiidae, see reviews in Andrade & MacLeod, 2015; Elias et al., 2011; Herberstein, Painting, & Holwell, 2017; Herberstein, Schneider, Uhl, & Michalik, 2011; Robinson & Robinson, 1980; Schneider & Andrade, 2011; Schneider & Fromhage, 2010; Schneider, Uhl, & Herberstein, 2015). Critical features predicting plasticity vary between populations in some species, or across species within genera in others (Section 3.2). Species level phylogenies are available for each genus to support comparative studies (Cheng & Kuntner, 2014; Garb, Gonzalez, & Gillespie, 2004; Kuntner, Coddington, & Hormiga, 2008), and rapidly expanding work on gene flow, along with the development of molecular tools useful for spider taxa can provide the underpinning for comparative analyses at the level of adaptive patterns or mechanisms (Dimassi, Ben Khadra, Ben Othmen, Ezzine, & Said, 2017; Krehenwinkel, Rodder, & Tautz, 2015; Krehenwinkel & Tautz, 2013; Kuntner et al., 2016; Miles, Johnson, Dyer, & Verrelli, 2018; Sawadro, Bednarek, & Babczynska, 2017). Within each genus, I review our current understanding of sexual selection and natural history with a focus on why these taxa would be valuable comparative models for understanding adaptive plasticity (Section 3). To date, there have been a handful of laboratory and field studies of adaptive plasticity linked to social context in each genus (Section 4). I end by reviewing the intriguing, and sometimes unexpected results from this work with an eye to interesting areas for future study.

Spiders in the focal genera are notorious for their extreme mating behaviors and traits. This includes sexual cannibalism, genital mutilation (of males), and genital plugging (of females), severely restricted male mating

opportunities, protandry (males maturing before females), and extreme female-biased sexual size dimorphism (Andrade & Kasumovic, 2005; Andrade & MacLeod, 2015; Kuntner et al., 2016; Schneider et al., 2015; Schneider & Fromhage, 2010; Schneider & Michalik, 2011; Uhl, Nessler, & Schneider, 2010). All of these may be related to selection for plasticity. In particular, the relatively short lifespan of adult males in all three genera (and in web-building spiders in general, Foelix, 2011) provides a narrow window of opportunity for acquiring fitness, and this is particularly true for the numerous species in which males are likely to mate only once (Section 3.2.2). For such males, a match between their phenotypic traits and the particular challenges likely to be encountered during that narrow window should be strongly advantageous, relative to a phenotype that is unresponsive to cues of context. Moreover, males' relatively rapid development means that information acquired late in ontogeny could provide salient information about the competitive arena after maturity (Section 3.1). This is particularly true because females of many web-building species are relatively sedentary, so information about spatial distribution of mates may have long-term relevance to male competition. This same feature is also useful for researchers, since it facilitates observational or manipulative studies of variation in the distribution and availability of potential mates, and assessment of reproductive fitness in the field.

There are at least two additional aspects of web-building spider biology and natural history that underlie predictions of adaptive plasticity linked to demography. First, the challenges encountered by adult males seeking to reproduce are relatively discrete and episodic, and the form of selection operating across these episodes varies (Section 3.2.1). Since spiders are solitary through most of their lifespan, males must find sedentary females for mating. Mate searching can impose strong selection on male traits, including sensory abilities, mobility, endurance, and maturation rate (Section 3.2.3). The intensity of selection imposed by mate searching will be shaped by the density, proximity, and spatial distribution of receptive females (Sections 2.1 and 3.1). The next, relatively discrete episode of selection occurs after males reach female's webs, where direct competition and/or female choice can determine mating success (Section 3.2.4). The final episode, as with many species, are the post-copulatory processes that ultimately determine paternity differences among males that do mate successfully and that can be affected by male traits or pre-copulatory behaviors (reviewed in Schneider & Andrade, 2011). Phenotypic traits mediating mating success at the web are not necessarily the same as those important during mate

searching, nor will they necessarily have a positive effect on post-copulatory sexual selection. Moreover, development of traits important in one episode may handicap other traits. The optimal balance for these trade-offs will depend on variable demographic factors that affect the relative importance of each episode of selection to fitness (Section 3.1).

Second, spiders use airborne and contact chemicals for communication, and in web-building spiders these are released from the body of the spider as well as from the spider's silk (Gaskett, 2007; Schulz, 2013; Scott, Anderson, & Andrade, 2018). Pheromones or chemical cues can provide information about the presence and proximity of potential mates and competitors, along with the traits of those conspecifics (Section 3.1.2). Pheromones produced by female web-building spiders attract mates and trigger courtship (Gaskett, 2007), and males apparently also release chemical cues (Scott et al., 2018). These signals and cues provide the possibility for assessment of the proximity and relative number of males and females from a distance, both for developing males and for adults. Critically, experimental manipulation of exposure to pheromones also allows researchers to probe effects on plasticity directly (Section 4).

1.3 Tests of adaptive plasticity: Empirical challenges

Rigorous studies of plasticity using tractable models are necessary. Not all forms of plasticity in response to environmental changes are adaptive (e.g., Kelly et al., 2012; Velotta & Cheviron, 2018), and responses to conditions outside the normal range of experience will frequently have adverse effects on fitness (Hale, Morrongiello, & Swearer, 2016). Being able to predict when adaptive plasticity will evolve and produce populations resilient to change (e.g., Charmantier et al., 2008; Noonan et al., 2018) is a major challenge in the field. Arguably, theory regarding the evolution of adaptive plasticity currently outstrips rigorous empirical support (Uller, Nakagawa, & English, 2013), which, at its most stringent, requires comparison of the fitnesses of plastic and static phenotypes under conditions that trigger plasticity, as well as those that do not (Bretman et al., 2011; Doughty & Reznick, 2004; Groothuis & Taborsky, 2015; Nettle & Bateson, 2015). Additional challenges are introduced by the tendency to experimental reductionism, driven by the need for tractability. For example, experiments rarely capture the complexity of aspects of the natural environment that are relevant to fitness (Groothuis & Taborsky, 2015; Kasumovic & Brooks, 2011; Miller & Svensson, 2014; Taborsky, 2017), the multivariate cues that

may provide information on the state of that environmental complexity (Dore et al., 2018; McNamara, Dall, Hammerstein, & Leimar, 2016), nor how plasticity may cause integrated shifts in a range of phenotypic traits that affect net fitness (reviewed in Kasumovic, 2013).

To highlight the challenges, it is instructive to consider conclusions from a recent meta-analysis (Uller et al., 2013) examining effects of transgenerational plasticity on offspring phenotypes. Transgenerational plasticity includes anticipatory parental effects through which cues derived from parents “prime” the offspring to develop phenotypes matched to current conditions (Guillaume, Monro, & Marshall, 2016; Holeski, Jander, & Agrawal, 2012; Uller, 2008). There are numerous studies of parental effects on adaptive phenotypic plasticity in offspring, including some convincing, well-known empirical examples, particularly in the context of predation risk and herbivory (Agrawal, Laforch, & Tollrian, 1999; Badyaev & Oh, 2008; Galloway, 2005; Galloway & Etterson, 2007; Holeski et al., 2012). Nevertheless, Uller et al.’ (2013) meta-analysis of experimental studies in plants and animals showed very little effect of parental environment on offspring fitness correlates, although there was a strong direct effect of the environment experienced by the individual themselves. Their conclusion is that, surprisingly, transgenerational plasticity may be of limited importance in nature. These results may suggest that transgenerational plasticity is weak, but may also suggest a pervasive failure of methodology that makes detection unlikely (Badyaev & Oh, 2008; Donelson, Salinas, Munday, & Shama, 2018; Uller et al., 2013). The latter encompasses considerations relevant to tests of other forms of plasticity (Taborsky, 2017).

First, for most studies in the meta-analysis, environmental factors were simplified, and it was unclear whether the cues manipulated or assessed were field relevant, reliable indicators of the changing environmental context for offspring (Burgess & Marshall, 2014; Chevin & Lande, 2015; Dore et al., 2018; Scheiner, 2013). Second, most of the studies focused on one or a few phenotypic traits measured in isolation, rather than the multivariate plastic phenotype. Since fitness is expected to be related to the net effect of trade-offs among traits that are shifted by plasticity, this is problematic (Doughty & Reznick, 2004; Kasumovic, 2013; West-Eberhard, 2003). Third, the use of incomplete experimental designs required the exclusion of some studies which otherwise might be strong candidates for plasticity. For example, the omission of one or more cells in a fully-crossed design of parental and offspring environment was common (Uller et al., 2013). This can lead to inferences of transgenerational plasticity of offspring based on

parental cues (information detected during development that arises from parents) when in fact a more parsimonious explanation is differential resource allocation by parents (somatic provisioning of offspring, [Uller, 2008](#)). This study suggests analogous cautions for the study of other forms of plasticity by illustrating the necessity of testing both plastic and unchanged phenotypes in both phenotype-matched and phenotype mismatched contexts ([Kassen, 2002](#); [Murren et al., 2015](#); [Nettle & Bateson, 2015](#)). Mismatches occur in nature because plasticity involves a risk of misreading cues, or integrating those cues over suboptimal timescales ([Siljestam & Ostman, 2017](#)). If these mismatches occur at sufficiently high frequency, selection for plasticity will decline. Researchers can probe mismatches by manipulating phenotypes and environments, or through transplant experiments. This is critical because demonstrating a benefit of plasticity under phenotype-environment matching alone is insufficient. We expect plasticity precisely because there is also a fitness cost to the induced phenotype if it is mismatched to the environment ([Auld, Agrawal, & Relyea, 2010](#); [Murren et al., 2015](#)). Otherwise we would expect an inflexible phenotype that does well across environments on average ([Nettle & Bateson, 2015](#)), whether through direct selection on trait values, or via genetic assimilation of a previously plastic trait ([Waddington, 1953](#)).

A common approach to studying adaptive plasticity in animals is to seek species in which current theory suggests the evolution of plasticity is likely. Reviews often outline features of species in which studies of plasticity are likely to be productive and tractable ([Holeski et al., 2012](#); [Kasumovic, 2013](#); [Kasumovic & Brooks, 2011](#); [Kelly et al., 2012](#); [Levis & Pfennig, 2016](#); [Taborsky, 2017](#)). This is a reasonable approach given the importance of sufficient knowledge of species' natural history for making realistic predictions from hypotheses about plasticity ([Groothuis & Taborsky, 2015](#)), and the need for replicable studies of development and performance. However, a "focal species" approach can handicap the development of comparative tests of evolutionary hypotheses which are essential for moving the field forward ([Doughty, 1995](#); [Murren et al., 2015](#); [Pigliucci, 2001](#)). The long-term impact of focal species work could be improved if chosen species are those for which there are groups of related taxa that vary in predicted determinants of plasticity (or in measured plasticity), for which a phylogenetic framework is available, and for which replicable methods of testing for plasticity and its fitness effects ([Blanckenhorn, 2010](#)) are possible.

The power (and challenge) of comparative approaches to plasticity is clear from the relatively few phylogenetic analyses of plasticity in animals,

two of which have focused on developmental responses to predation and/or abiotic challenges (flooding) by embryonic amphibians (Gomez-Mestre, Wiens, & Warkentin, 2008; Relyea et al., 2018). Relyea et al. (2018) examined the evolution of life history traits and developmental plasticity of embryos in response to chemical cues of egg predation across three families of amphibians (20 species) using a common garden approach. This ambitious analysis involved 25 authors from labs across the United States. Their work showed a low phylogenetic signal for plasticity, much less so than for life history traits per se, suggesting relatively little phylogenetic constraint on the evolution of plasticity (Relyea et al., 2018). On a smaller phylogenetic scale (six species across two genera), Gomez-Mestre et al.' (2008) comparative analysis of hatching plasticity in frogs had high resolution for ecological and phenological factors predicted to affect hatching plasticity, and combined field studies with laboratory experiments. Their work showed that the capacity for plasticity in hatching time (hatching acceleration) was highly evolutionarily conserved, as was accelerated hatching in response to flooding. In these frogs, the same plastic response can be triggered by cues from foraging snakes (Warkentin, 1995). Intriguingly, this trigger did not show a strong phylogenetic signal. Instead, the subset of species with a weak plastic response to predation cues were those for which breeding phenology generally decreases predation risk, and thus for which predation-triggered plasticity might not increase fitness. This example is also intriguing because it appears that the plastic response initially evolved in response to a broadly experienced ecological trigger (flooding) with later evolution of predation cues triggering the same response, but only in those species for which the risk was salient.



2. Variable sexual selection linked to social context

I now turn to a consideration of why and how variation in demography may drive phenotypic plasticity in traits related to reproductive success in nature, particularly for males under strong sexual selection. It is well established that demographic features of populations show spatio-temporal variation and have strong effects on the evolution and dynamics of mating systems (Andersson, 1994; see Elias et al., 2011 for a review with a focus on spiders; Emlen & Oring, 1977), partly through effects on the intensity, direction, and form of sexual selection (Ah-King & Gowaty, 2015; Gillespie, Tudor, Moore, & Miller, 2014; Herberstein et al., 2017;

Kasumovic, Bruce, Andrade, & Herberstein, 2008; Kasumovic, Bruce, Herberstein, & Andrade, 2009; Kokko & Monaghan, 2001; Kokko & Rankin, 2006). Key demographic variables affecting sexual selection include age structure, population density, spatial distribution, and operational sex ratio (ratio of males to sexually active females, Andersson, 1994). Together these define the social context in which individuals must find or choose mates, secure matings, and produce offspring. I define the social context as the distribution and frequency of potential mates and potential competitors in space and time. Social context is a complex environmental variable in which different components may vary independently with additive or interactive effects on phenotype–fitness relationships.

2.1 Demography, social context, and sexual selection

One advantage to studying adaptive plasticity related to mating behavior is leveraging the considerable literature on sexual selection to predict how shifting social context can affect sexual competition in a taxon of interest. In a classic example from the perspective of males, if females are spatially clustered, then males may be able to defend and mate with multiple females (female- or resource-defense polygyny, Emlen & Oring, 1977; Herberstein et al., 2017). Male success will then depend on the ability to defend these clusters, which is often positively correlated with body size or weaponry (Andersson, 1994). Positive relationships between fitness and male phenotypic traits such as fighting ability and physical dominance are expected, and the slope of these relationships (the intensity of sexual selection) will increase as the number of competitors increases (i.e., as the operational sex ratio become more male biased). In contrast, if females are sparsely or widely distributed, then males may engage in scramble competition, and high fitness may be acquired primarily by males with acute sensory abilities and/or traits related to increased mobility, such as speed, or endurance (Herberstein et al., 2017). In this situation, weaponry, relatively large body size, and the time and resources required to develop these traits may be costly since they will often trade-off against traits related to successful mate searching (Brandt & Andrade, 2007; Foellmer & Fairbairn, 2005b; Foellmer, Marson, & Moya-Larano, 2011).

For females, social context can affect choice via effects on the timing and nature of mating opportunities and thus the risk of costly delays to reproduction, of remaining unmated, or of stochastic variation in the quality of the potential mates (Ah-King & Gowaty, 2015, 2016; De Jong & Sabelis, 1991;

Kokko & Mappes, 2005). Since sparse population distributions may decrease or delay mating opportunities, female reproductive fitness in this context may depend on minimizing choosiness by decreasing preference thresholds or reducing the expression of choice (e.g., “wallflower” effects, De Jong & Sabelis, 1991; Kokko & Mappes, 2005). Female fitness considerations may lead to alterations in the efficacy or intensity of female-initiated sexual signaling (Barry, 2015). In contrast, when populations are more dense and/or operational sex ratios strongly skewed toward males, choice is expected to be an important aspect of female reproductive tactics, and effort expended on signaling may decrease, or be limited to defined windows that balance the costs of male approach and courtship (Herberstein, Schneider, & Elgar, 2002) against the benefit of creating sufficient opportunity for choice (Watson, 1990). These effects could reduce (sparse populations) or reinforce (dense populations, male-biased operational sex ratios) the intensity of sexual selection on traits of males that are preferred by females. Thus, it is desirable to simultaneously consider effects on both sexes (Ah-King & Gowaty, 2015, 2016) to make realistic predictions about changing relationships between phenotypes and fitness in different social contexts.

Although these pre-copulatory dynamics may shape phenotype-fitness associations, the net effect of sexual selection will often depend on post-copulatory processes (Parker, 1970; Thornhill, 1983) that also link to social context. Since post-copulatory sexual selection mediates fertilization success, it can have strong effects on phenotype-fitness associations (Evans & Garcia-Gonzalez, 2016). In addition to mate choice, post-copulatory tactics of females may also affect net sexual selection. For example, although “wallflower” effects may reduce choosiness of females in low-density populations (De Jong & Sabelis, 1991; Kokko & Mappes, 2005), once fertilization is assured females may actively seek to “trade-up” by copulating with and affording paternity to higher quality mates (Pitcher, Neff, Rodd, & Rowe, 2003). This can rescue effects of selection on female-preferred traits despite the dampening of pre-copulatory choice at lower population densities, particularly if later-mating males have high fertilization success. More generally, optimal mating frequencies of females, and the extent to which females control mating access, can affect the extent to which variation in male tactics over sperm competition can increase paternity (Fromhage, McNamara, & Houston, 2008).

Post-copulatory selection may augment or decrement selection on male traits favored by pre-copulatory mate choice (Cordes, Yiğit, Engqvist, & Schmoll, 2013) or competition over mating (Buzatto, Roberts, & Simmons, 2015; Danielsson, 2001; Evans & Garcia-Gonzalez, 2016),

particularly when there are trade-offs in the development or expression of traits that confer high success in each of these episodes of selection (Cattelan, Evans, Pilastro, & Gasparini, 2016; Fisher, Rodriguez-Munoz, & Tregenza, 2016; Jordan & Brooks, 2010; Simmons & Emlen, 2006; Tomkins, Radwan, Kotiaho, & Tregenza, 2004; Yasui, 1997). Such trade-offs are a fundamental feature of life history decisions regarding allocation of time and energy to growth (and thus adult size or morphological traits related to mobility), reproduction (including gamete investment), and maintenance (Gadgil & Bossert, 1970; Parker, Ramm, Lehtonen, & Henshaw, 2018; Schaffer, 1983; Stearns, 1989b). For example, increased sperm competition can drive relative investment in reproductive function across taxa, as suggested by commonly-found correlations between sperm competition and the ratio of gonadal to somatic tissues (Bailey, Gray, & Zuk, 2010; Harcourt, Harvey, Larson, & Short, 1981; Harcourt, Purvis, & Liles, 1995; Hayward & Gillooly, 2011; Hosken, 1997; Moller, 1991; Parker et al., 2018) or the rate of gamete production (Allen, Barry, Holwell, & Herberstein, 2011; Firman, Garcia-Gonzalez, Simmons, & Andre, 2018). Gametic investment can show activational or developmental plasticity linked to the likelihood of polyandry (females mating with more than one male). For example, sperm production or release can be altered on short timescales (Kelly & Jennions, 2011; Pizzari, Cornwallis, Lovlie, Jakobsson, & Birkhead, 2003) but is also affected by gonadal tissue investment (Hayward & Gillooly, 2011), which itself is determined during development, but may shift after maturity (e.g., in seasonal breeders DeFalco & Capel, 2009; Kenagy & Trombulak, 1986). Social context (presence and density of potential mates, competitors, and/or the operational sex ratio) has been shown trigger variation in both variables related to gamete production (Firman et al., 2018; Gage, 1991; Gage & Baker, 1991; Geiger, Beaulieu, Franke, & Fischer, 2018; Pizzari et al., 2003). In turn, investment in gonads and gametes can limit the development of traits related to pre-copulatory success (e.g., horns vs gonads in dung beetles; Simmons & Emlen, 2006), and thus have cascading effects on the integrated adult phenotype (Kasumovic, 2013; Pigliucci, 2003).

2.2 Sliding, overlapping scales of variation in social context

In most species, social context is variable and can fluctuate over a variety of spatio-temporal scales (reviewed in Kasumovic & Brooks, 2011). The causes of this variation will depend on the natural history of the species under study,

and may include seasonal phenology, sex-differences in maturity rates, longevity, or mating frequency (Elias et al., 2011; Kasumovic & Brooks, 2011) or, particularly in small populations, demographic stochasticity (Danchin et al., 2008). Here, I focus on “coarse-grained variation,” in which each generation is likely to experience a different set of conditions and “fine-grained” variation in which change occurs within the lifetime of one animal (as per Snell-Rood, 2013). Plasticity is unlikely to evolve or be maintained when variation is over longer (multi-generation) timescales, as under these circumstances, a standard set of phenotypic trade-offs that lead to high average fitness may be fixed in the population (Nettle & Bateson, 2015; West-Eberhard, 2003). However, for coarse or fine-scale variation, there may be critical periods during the life of an organism when detectable information (Wagner & Danchin, 2010) can be used to predict future competitive conditions (Pigliucci, 2001; West-Eberhard, 2003).

Critical periods define spans when adaptive updating occurs, with the acquisition of new information being used to adjust plastic phenotypes (Fawcett & Frankenhuis, 2015). The organism can be considered an integrator in a Bayesian process; using newly acquired information to update posterior probabilities for predicting some fitness-linked aspect of the environment (Stamps & Frankenhuis, 2016). One can imagine a sliding window of opportunity for attention to environmental information that starts at the time of fertilization and ends at the time of the last fitness-affecting actions of an aging adult. Updating is expected only insofar as the addition of new information can significantly improve prediction of the phenotype that will match the competitive environment (Fawcett & Frankenhuis, 2015; Stamps & Frankenhuis, 2016). Critical periods may be limited to early or later life stages, or occur throughout life (Fawcett & Frankenhuis, 2015). As with the evolution of plasticity itself, the evolution of critical periods will depend on the scale of environmental change affecting the success of traits underlying fitness-enhancing activities of individuals, and the time required to integrate this information and create appropriate changes in the relevant phenotype (Stomp et al., 2008).

The sliding window analogy is useful for temporal fluctuations in social context, but comparable effects arise from spatial variation, with complex interactions likely between the two (Scheiner, 2013). Interactive effects are possible for any species with temporal variation in demography and where animals move through their habitat, because non-uniform distributions of conspecifics are common. Scheiner's (2013) models integrate both forms of variation and suggest that spatial heterogeneity may more reliably

favor plasticity. For sexually-selected traits, spatial variation in social context may be predictably structured in some taxa and can clearly have substantial effects on fitness. For example, spatial variation in population density may depend on clustering or irregular distribution of resources, suitable refuges, or micro-habitat variations in temperature or exposure profiles. Physical proximity to clusters of potential mates may be detected through spatially informative cues associated either with the clusters of conspecifics themselves, or the preferred features of the environment underlying those clusters (Kasumovic & Brooks, 2011; Kasumovic et al., 2008; Kasumovic, Bruce, et al., 2009).

2.2.1 Environmental and individual social context

When critical periods occur early in ontogeny for information relevant to sexual competition, developmental plasticity will often result in canalization of morphology or physiology (Kasumovic & Brooks, 2011) and this can shape the range of behavioral options available to adults (Snell-Rood, 2013). This should be most likely under coarse-grained environmental variation, when the social context sensed during development is still relevant at maturity. However, this does not exclude the concurrent use of other cues on finer scales by that mature adult (Scheiner, 2013). In fact, understanding adaptive plasticity requires consideration of both the complexities of fluctuations in the natural environment (Elias et al., 2011), and the layering of cues that can provide information at the different scales of variation that may be relevant to phenotype-environment matching (e.g., Danks, 2007; Dore et al., 2018). Social context may provide information that affects plasticity of traits in different ways during different critical periods, and together these will contribute to an integrated set of phenotypic traits that may be employed in a particular set of conditions. These will inevitably also involve trade-offs in function in other conditions. To fine-tune predictions about adaptive plasticity, it may be helpful to consider how, at the coarse-grained level of variation, the *environmental social context* might indicate the average set of traits that will be favored by sexual selection within a given cohort (divergent from that in their parents). Adaptive developmental plasticity may be most likely in response to such variation, and individuals will mature with a set of traits that will, on average, match the environment. However, since any given set of interactions can be displaced from the average for that environment due to fine-grained heterogeneity, the *individual social context* relevant to local performance can also trigger plasticity. Individual social context could tune broader developmental effects and is also likely to affect

activational plasticity either through transient responses, or adaptive updating that can have longer term effects on behavioral and other phenotypes (Fawcett & Frankenhuis, 2015; Stamps & Frankenhuis, 2016). Similarly, layering of responses to temporal and spatial effects may be important in some species or populations, where broader-scale cues (e.g., seasonal patterns of variation, overall population density) set the range of phenotypes that are possible, while individual cues specific to a given micro-habitat (e.g., proximity of potential mates) tune the phenotype to fit spatially explicit variables (e.g., Danks, 2007; Scheiner, 2013). Such interactive effects can also lead to plastic responses that appear to be maladaptive if considered outside the natural context (Scheiner, 2013). For example if there is a reliable, negative correlation between the social context at the time of perception and the context at the time of selection, then reaction norms (phenotype \times environment curves) may be opposite to that expected when the focus is on perceived cues only. Considering layering of effects of environmental heterogeneity, given the natural history of the species under study, is thus critical for designing realistic studies of plasticity that allow strong inference about links between context and phenotype (Kasumovic, Bruce, et al., 2009).

As an example of how such layering of response can be beneficial to the animal, consider plasticity in development and behavior of crickets in response to exposure to calling song. In *Tellegryllus* crickets, juvenile males exposed to cues of a high density of adult competitors (calling song) develop more slowly and mature at larger body sizes, in better condition, and with higher investment in gonadal tissue than males reared without such cues (Bailey et al., 2010; Kasumovic, Hall, Try, & Brooks, 2011). On average, these traits, (particularly body size) can confer success in the environmental social context indicated by the presence of male songs—intense inter-male competition, including fighting (Hack, 1997). In many taxa, including crickets however, although larger males are typically more aggressive, males that have lost fights in the past are more likely to avoid, rather than confront, newly encountered rival males (e.g., “loser effects,” Kasumovic, Elias, Punzalan, Mason, & Andrade, 2009; Reaney, Drayton, & Jennions, 2011). Even a large male may shift to less dominant behavior in the face of repeated losses (Hsu & Wolf, 2001). Such activational plasticity may arise because fight performance provides information on the individual social context, and thus a more fine-grained estimate of an individual’s rank in the local hierarchy of competitors than body size alone. Males that update their assessment of the optimal behavioral response with new, local, information (Fawcett & Frankenhuis, 2015; Stamps & Frankenhuis, 2016)

will save energy, time, and risk on fights they are statistically unlikely to win. Interestingly, for crickets, one bout of flying resets aggressive behavior to a level predicted by body size (reverses the behavioral plasticity). Presumably, movement to a new competitive micro-habitat with a new constellation of competitors (Hofmann & Stevenson, 2000) negates the value of the previously-acquired individual social information. Self-assessed body size may once again be the best predictor of fighting outcomes given the reality of spatial heterogeneity in competitive landscape.

Another analogy is suggested by game theory models for sperm allocation. Allocation to gonads and sperm production increases across species based on the *risk* of sperm competition (overall likelihood of occurrence)—an evolutionary effect (Harcourt et al., 1981; Hosken, 1997). For a given mating within a species, however, the perceived *intensity* of sperm competition (number of ejaculates competing in this particular mating) can be the best predictor of sperm and ejaculate investment (Parker, 1998; Parker, Ball, Stockley, & Gage, 1996; Parker, Immler, Pitnick, & Birkhead, 2010). The distinction is important because, unlike the cross-species relationship, game theory predicts that sperm allocation may decrease as the number of perceived competitors for a given mating (individual social context) increases past the average expectation (environmental social context), although this depends on various features of natural history of the species being considered (Parker et al., 1996). We can translate this insight into speculation about how developmental decisions may affect the nature of activational effects on sperm allocation in the wild. Juvenile males that detect a high risk of sperm competition on average (e.g., male-biased sex ratio in a species where females mate multiply) may show elevated gonadal investment and have the capacity at adulthood to produce more sperm at a higher frequency than males that perceive a low risk of sperm competition. As adults, however, allocation decisions in a particular mating will depend on the perception of cues related to the local socio-sexual context (Cornwallis & Birkhead, 2006; Kelly & Jennions, 2011). Thus allocation can change across mating opportunities despite an overall ramping up of capacity in response to environmental context.

Consider a hypothetical example of a male that encounters a solitary, unmated female with no rivals present. If that male has developed under cues indicating a high prevalence of competition on average, the current context may suggest the female is of particularly high reproductive value compared to the average female in the population. The result of adaptive updating (Stamps & Frankenhuys, 2016) in this case might be higher than average

mating investment by the male in terms of courtship effort, sperm allocation, and other mediators of mating and fertilization success, despite the apparent absence of competition. In contrast, if the same male encounters a female with rivals present, that female might accrue only average mating investment, despite males having developed the capacity to invest more, and despite the higher risk of sperm competition in that context.

Thus, plasticity of a set of related traits may be shaped across more than one critical period, based on spatial or temporal heterogeneity, and developmental and/or activational effects may combine to affect the same trait. Complex responses to environmental heterogeneity at different scales are possible, and may present considerable challenges to experimental design, and particularly to interpretation if these complexities are not considered. Below I outline how individual and environmental social context affect fitness components for male spiders in the focal genera *Nephila*, *Argiope*, and *Latrodectus*. I consider these different determinants of variation may be used to provide an integrative lens on our understanding of plasticity in these developing models. I start by reviewing relevant features of phenology and natural history that relate to sexual selection and variable social context in these spiders, and the types of cues that may be used to detect relevant scales of environmental variation.



3. Sexual selection and social context in (some) web-building spiders

3.1 Spatial distribution, phenology, and development of focal spider taxa

This section provides a general outline of the biology and ecology of *Argiope*, *Nephila*, and *Latrodectus*, with reference to key considerations for testing ideas about adaptive plasticity. I touch on variables that are likely to affect selection for plasticity by shaping variation in social context: overwintering patterns and phenology, seasonality, female web distributions, and website persistence. Readers seeking additional information about spider biology and ecology are referred to a range of useful reviews and books (Andrade & MacLeod, 2015; Eberhard, 2004; Foelix, 2011; Herberstein et al., 2017; Herberstein & Wignall, 2011; Huber, 2005; Sawadro et al., 2017; Schneider et al., 2015; Schneider & Andrade, 2011; Schneider & Fromhage, 2010; Scott et al., 2018; Uhl, 2000; Uhl & Elias, 2011).

Web-building spiders are good candidates for the evolution of adaptive plasticity partly because juveniles disperse and are likely to settle in habitats

very different from that experienced by their parents. Ballooning is the main mode of dispersal, a process by which a silk strand or sail is reeled out and the spider flies on wind currents, assisted by electrical fields (Cho, Neubauer, Fahrenson, & Rechenberg, 2018; Morley & Robert, 2018; Suter, 1991). Ballooning spiders may settle in environments that pose novel challenges (e.g., in the middle of the ocean, Darwin, 1934; on recently-active volcanoes, Crawford, Sugg, & Edwards, 1995), and they do not seem to settle near to relatives (e.g., Zimmer & Schneider, 2016). Moreover for spiders, considerable fluctuations in population size and distribution are possible because sex-specific development, population growth rates, and spatial distribution depend heavily on prey availability, which itself is affected by a range of variable biotic and abiotic factors (Wise, 1993). This can introduce considerable coarse and fine-grained heterogeneity in social contexts.

Phenological patterns can also affect the strength of selection for plasticity, particularly if there is variation in male time at maturity and temporal variation in the operational sex ratio. *Nephila*, *Argiope*, and *Latrodectus* spiders are all protandrous, with males from a given cohort developing more rapidly than females and leaving their webs to seek out mates at sexual maturity. In many species, the availability of receptive females (or the operational sex ratio) changes predictably over the season. In temperate (or even subtropical) populations of *Nephila* and *Argiope* for example, reproduction is seasonal, and typically, only egg sacs overwinter. Thus sex-specific development is usually synchronous over the active season, shifting from a population dominated by juvenile spiders, to one dominated by adult males and penultimate instar females, and finally to a population consisting primarily of adults (e.g., *Nephila fenestrata*, Fromhage, Jacobs, & Schneider, 2007; *N. plumipes*, Kasumovic et al., 2008; *N. clavata*, Miyashita, 1993; *A. aurantia*, Foellmer & Fairbairn, 2005a). The mating season in some of these species can be brief and intense (e.g., 3 weeks, with the majority of males arriving at females' webs and attempting to mate within a 5-day period; *Argiope bruennichi*, Schulte, Uhl, & Schneider, 2010). These seasonal patterns in environmental social context determine variation in competitive environments for males of univoltine species (a single reproductive bout per year as in many *Argiope* and *Nephila*), and, to a more moderate extent, multivoltine species in which few life history stages overwinter. In species with these phenological patterns, cues indicating the time of season at which a male is maturing (environmental social context) may be the key to phenotype-environment matching.

At the opposite extreme, there are species in which females and/or males mature throughout the season with little clear temporal pattern—because in addition to egg sacs, spiders may overwinter at a variety of developmental stages. Population age structure, and variation in the availability of mates, may thus be complex. In this case, plasticity, if it exists, should be cued to indicators of the current, local conditions (individual social context). Among the multivoltine *Latrodectus* spiders, even in temperate and subtropical species, both types of patterns are found, with variation possible across and within species (reviewed in [Andrade & MacLeod, 2015](#)). For example, *Latrodectus revivensis* (Negev Desert, Israel) has an annual life cycle ([Segev, Ziv, & Lubin, 2003](#)), and larger juveniles, subadults, and egg sacs are able to overwinter. Patterns of change in age structure for *L. revivensis* are similar to *Nephila* and *Argiope* in that most mature females encountered by males near the peak of the season are newly matured and unmated ([Anava & Lubin, 1993](#)), and the proportion of mated females increases as the seasons progresses. In comparison, in North American populations of *Latrodectus hesperus*, in addition to juveniles, subadults and egg sacs, adult females can also overwinter (S. Fry, unpublished data; Scott, McCann, & Andrade, submitted). Since females often copulate before the end of the season in which they mature, most adult females present at the start of the active season are already mated and producing egg sacs ([D'Amour, Becker, & Van Riper, 1936](#)). As the juveniles in the population begin to mature, the proportion of unmated females increases over time so that social context at the end of the season is very different from that at the start. Seasonal variation in the density of males in *L. hesperus* also partly depends on whether adult or subadult males are able to overwinter, which varies among populations (S. Fry, unpublished data; Scott, McCann, & Andrade, unpublished data; [D'Amour et al., 1936](#)), and the time-course of egg sac production during the active season (since cohorts of rapidly-developing males could mature in one season). Finally, in the subtropical *L. hasselti*, all life stages can overwinter, and the proportion of mated and unmated females, and adult males stay relatively constant through much of the active season (Andrade, unpublished data). In species such as this one, detection of the individual social context is likely to be more informative than seasonal or broad-scale information.

Regardless of which phenological pattern is seen, at any given point in the season, spatial heterogeneity will also be an important determinant of sexual selection. Each male's proximity to potential mates and competitors may predict local mating opportunities and challenges. Juvenile or adult males may be able to assess local mate availability, or whether they are near

the temporal peak of female availability by detecting airborne pheromones released from females' webs and their bodies (individual social context, [Section 3.1.2](#), [Fig. 1A](#)). These local cues may be particularly important in species where when females' webs are clustered, rather than broadly distributed, and where females show high website persistence. Females' decisions about website location, and thus web distributions, are affected by many factors, including prey availability, frequency of web damage, availability of refugia, and micro-climate ([Lubin, Ellner, & Kotzman, 1993](#); [Salomon, 2009](#); [Wise, 1993](#)). In some species of solitary web-builders, females' webs are not uniformly distributed and may be found clustered in suitable habitats, in some cases with peripheral overlap of adjacent webs (e.g., several species of *Nephila*, [Elgar, 1989](#); [Kasumovic, Bruce, et al., 2009](#); [Kasumovic & Jordan, 2013](#); *Argiope radon*, [Rao, Webster, Heiling, Bruce, & Herberstein, 2009](#); *Latrodectus hesperus*, [Salomon, Vibert, & Bennett, 2010](#)). Clustered webs may have prey capture benefits for females, but may also attract more rival males than solitary webs (*A. radon*, [Rao et al., 2009](#)). A male's location relative to widely distributed or clustered females may thus have significant effects on his expected number of mating opportunities and the phenotypes and development patterns that yield highest fitness (see [Section 3.2.3](#)). For males that mature and search for mates within aggregations (e.g., *Nephila plumipes*, [Kasumovic et al., 2008](#); [Kasumovic, Brooks, & Andrade, 2009](#); [Kasumovic, Bruce, et al., 2009](#); [Kasumovic, Elias, Punzalan, Mason, & Andrade, 2009](#)), selection will favor different traits than for males that develop on solitary webs and need to detect females at a distance (e.g., *Argiope keyserlingi*, [Kasumovic et al., 2008](#); [Kasumovic, Brooks, et al., 2009](#); [Kasumovic, Bruce, et al., 2009](#); [Kasumovic, Elias, et al., 2009](#); *L. hasselti*, [Andrade, 2003](#)). Thus fitness benefits of shifting development or behavior as a function of proximity to clustered females may favor plasticity cued to local context.

Whether cues of local variation in female proximity or web density are useful for males depends on the interval between cue detection and male mating attempts, and the persistence of female's webs. Mismatches will be more likely, and plasticity in response to local cues less likely, if females frequently relocate their webs. Females of some web-building spiders relocate their webs when habitat quality is poor, when there is frequent web disturbance/damage, low prey availability, low rates of mate attraction ([Chmiel, Herberstein, & Elgar, 2000](#); [Enders, 1975](#); [Janetos, 1982](#); [Kasumovic & Jordan, 2013](#); [McNett & Rypstra, 1997](#); [Riechert & Gillespie, 1986](#); [Salomon, 2009](#)) or as the suitability of web support

A



B



C



D



Fig. 1 Episodes of selection related to mating for *Latrodectus hesperus* males. Adult male *Latrodectus hesperus* spiders (A and B) and males with females (C and D). (A) An adult *L. hesperus* male perches on vegetation while mate searching. The first pair of sensory-hair-laden legs are waved through the air while perched, a behavior that may facilitate detection and localization of females' airborne pheromones (C. E. Scott & S. McCann, pers. comm.). (B) Direct competition between *L. hesperus* males can be fatal; the male above has been partly wrapped in silk by the rival male below. (C) Approaching females can be risky. *L. hesperus* male (above) is being wrapped in silk (and eventually cannibalized) by a penultimate instar female. The male had been living (cohabiting) on the juvenile female's web. Photos (A–C) courtesy of Sean McCann. (D) Adult *L. hesperus* female (left) with two courting males (right), showing female-biased size dimorphism, and wide variation in male body size, with larger male (above, right) and smaller male (below, right) courting simultaneously. Photo courtesy of Ken Jones.

structures changes as the spider grows (Lubin et al., 1993; Lubin, Kotzman, & Ellner, 1991). Web relocation is relatively common among females of many *Argiope* species that rebuild their web each day and may move web locations as often as every 2 days (Janetos, 1982). In contrast, web relocation is rare among many species of *Nephila* and *Latrodectus* in which females retain, add to, and repair their webs each day (e.g., *Nephila edulis*, Austin & Anderson, 1978; *N. fenestrata*, Fromhage et al., 2007; *Latrodectus hasselti*, Andrade & Banta, 2002; *L. hesperus*, Salomon, 2009; but see *Nephila plimipes*, Danielson-Francois, Hou, Cole, & Tso, 2012). There are some examples of web relocation among adult *Latrodectus*, but on a much more limited scale than is found in *Argiope* (e.g., *L. revivensis* females move every ~44 days, within 5 m of original web location, Lubin et al., 1993).

3.1.1 Relevance for adaptive plasticity

Dispersal by ballooning virtually ensures the environment of web-building spiders will differ from that of their parents in a way that is not predictable by parental experience, and such that traits that increase reproductive success for parents may not do the same for their offspring.

Species differences in website persistence of females can affect the salience of cues based on detecting female proximity. Although cues about population parameters may be available throughout juvenile development, it seems most likely that the critical period for integrating social information will be during the male's final instar (developmental plasticity), or in the immediate context of social interactions (activational plasticity). The high website tenacity of female *Nephila* and *Latrodectus* spiders suggests cues detected in that final instar may accurately predict whether males are in a habitat with sparse webs or dense webs, and a high or low frequency of potential competitors. In *Argiope*, where females move web locations more frequently, locally-cued developmental plasticity could be less likely, although direct cues of female density, or indirect, seasonal cues may be important if they indicate when males are maturing relative to peak female availability.

Phenology is clearly key to predictions about plasticity in these taxa. In univoltine species (typical for temperate/subtropical *Nephila* and *Argiope*), environmental social context will closely track the progression of the season. For species in which few life stages overwinter, and synchronous development results, there may be little need for broad plastic responses to environmental social context within populations—since male development will be predictably linked to female maturity. Plasticity in response to individual

social context is still likely to be beneficial if there is spatial variation in web distribution, such as in species where females cluster their webs (some *Nephila*). Even in species with synchronous development, phenology may vary across populations along latitudinal clines, along with changes in the timing or duration of the active season, or average population density (Woodman, Ash, & Rowell, 2006; Yamamoto & Sota, 2009). Thus developmental plasticity in response to environmental context may be beneficial, even in synchronous, univoltine species if they are distributed across broad latitudinal clines with dispersal common between populations, or if they are in a period of range expansion (e.g., *Argiope bruennichi*, Krehenwinkel et al., 2015). In multivoltine species (typical for *Latrodectus*), and those in which a broader range of life history stages overwinter, detection of changing environmental and individual social context will both be important, and both developmental and activational plasticity are likely to be beneficial. These opposite extremes in phenological synchrony suggest very different predictions about plasticity, suggesting the importance of understanding the natural history of the species under study and integrating this into predictions (Scheiner, 2013).

3.1.2 Detectable information and complex cues of shifting social context

Information about social context can be derived from abiotic (photoperiod, humidity, temperature) and biotic (conspecifics or heterospecifics) sources where the latter may include signals, or cues that have not evolved in the context of communication, but nonetheless provide information (Danchin et al., 2008). Abiotic factors such as photoperiod and temperature may provide indirect indicators of invertebrate phenology (Joschinski, Hovestadt, & Krauss, 2015; Nahrung, Allen, & Patel, 2004). In insects, photoperiod has pervasive effects on life cycles and predicts seasonal progression in population structure (Danks, 1994, 2007). For spider populations with predictable seasonal changes in age structure, photoperiod may be sufficient to indicate average social context. Seasonal patterns in development, reproduction, and activity level have been experimentally linked to photoperiod in some spiders (a Theridiid, Tanaka, 1992) and (a Sicariid, Vetter, Penas, & Hoddle, 2017). These links are not necessarily static, as relationships between growth, maturation rates, and photoperiod can evolve in response to the degree of seasonality of the habitat (Gotthard, Nylin, & Wiklund, 1999; Tanaka, 1992).

Direct detection of social context may be based on the perception of signals or cues from conspecifics in a variety of modalities (chemical, vibratory, visual, tactile; reviewed in Kasumovic & Brooks, 2011; Thomas, 2011).

These differ in their range and persistence and thus can provide information with different degrees of spatial and temporal resolution (Scheiner, 2013). For web-building spiders, sensory systems are well suited to the detection of chemical, vibratory, and tactile information, and of these, chemical information arguably provides the broadest range of possible information, both in terms of content and spatio-temporal sampling (reviews in Gaskett, 2007; Schulz, 2013; Symonds & Elgar, 2008). Female web-building spiders produce sex pheromones released from their bodies and their silk which may have airborne or contact components (Gaskett, 2007; Huber, 2005; Schulz, 2013). Mate attraction is mediated by airborne pheromones and contact pheromones trigger courtship and mating behavior in many species of spiders (Chinta et al., 2010; Jerhot, Stoltz, Andrade, & Schulz, 2010; Miyashita & Hayashi, 1996; Olive, 1982; Perampaladas, Stoltz, & Andrade, 2008; Ross & Smith, 1979; Scott, Kirk, McCann, & Gries, 2015; Scott, McCann, Gries, Khaskin, & Gries, 2015; Stoltz, McNeil, & Andrade, 2007; Uhl & Elias, 2011). Sex pheromones can allow males to determine many characteristics of the signaler, including female sexual maturity, age, mating or reproductive status, and recent feeding history (Anava & Lubin, 1993; Andrade & Kasumovic, 2005; Baruffaldi & Andrade, 2015; Baruffaldi & Costa, 2010; Cory & Schneider, 2016; Henneken et al., 2015; Henneken, Goodger, Jones, & Elgar, 2017; Johnson, Trubl, Blackmore, & Miles, 2011; Kasumovic & Andrade, 2004; Kasumovic, Bruce, Herberstein, & Andrade, 2007; Nessler, Uhl, & Schneider, 2009a, 2009b; Perampaladas et al., 2008; Stoltz et al., 2007; Tuni & Berger-Tal, 2012). There is accumulating evidence that males also produce chemical cues, and these may also be detected by potential rivals (Scott et al., 2018).

Although the effective zone for spider chemical cues or signals has not yet been identified (Gaskett, 2007), airborne chemicals clearly provide the opportunity for the assessment, at a distance, of the presence of male and female conspecifics, and possibly also their relative density (sex ratio). This information about the average environmental social context would be available to males throughout development, during mate searching, and during interactions with conspecifics. Moreover, since females of many species cease pheromone production after copulation (Chinta et al., 2010; Gaskett, 2007; Jerhot et al., 2010; Perampaladas et al., 2008; Stoltz et al., 2007), chemical cues from females are likely to reliably indicate current socio-sexual conditions with a lag reflecting the persistence of pheromones in a particular habitat (e.g., Andrade & Kasumovic, 2005; Baruffaldi, Costa, Rodriguez, & Gonzalez, 2010; Watson, 1986). This lag is likely to be short

in *Latrodectus* and *Argiope*. In *Latrodectus*, males damage female's webs during courtship in ways that reduce attractiveness of the silk (Scott, Kirk, et al., 2015; Scott, Vibert, & Gries, 2012; Watson, 1986). When mated females rebuild their webs, they will no longer contain pheromones (Stoltz et al., 2007). In *Argiope*, webs are rebuilt daily, so the lag will be a maximum of 24h.

Once spiders are in close proximity to each other, contact chemicals, vibrations, and tactile cues can provide additional information about individual social contexts, including the presence and relative size of competitors, or the receptivity of females (Dutto, Calbacho-Rosa, & Peretti, 2011; Stoltz, Elias, & Andrade, 2008). These forms of information may be used by males to adjust their behavior (activational plasticity). For example, male *Argiope bruennichi* avoid otherwise high quality females in the presence of silk cues left behind by rivals (Schneider, Lucass, Brandler, & Fromhage, 2011). Male *Latrodectus hesperus* increase courtship effort with females on webs with cues associated with a recent meal (well-fed females are less likely to attempt pre-copulatory cannibalism, Johnson et al., 2011), and male *L. hasselti* cease courtship signaling and shift to a "sneaker" tactic after detecting the silk or vibrational signals of a larger competitor on a female's web (Stoltz et al., 2008).

3.2 Extreme mating systems and sexual selection

For *Nephila*, *Argiope*, and *Latrodectus* spiders, the mating system will intersect with phenology and spatial distributions to shape fitness effects of plasticity. A given environmental social context will also include distinct variation in individual social contexts (e.g., proximity to clustered or widely distributed webs, Section 3.1), and these factors may vary in importance within or across species (Kasumovic & Brooks, 2011). For example, for males that mate with only one female (monogyny, Schneider & Fromhage, 2010), the individual social context at the time of maturity is key and may be the trigger for developmental and activational plasticity. For males of polygynous species, however, particularly those in which males are relatively long lived, the environmental context will be the best predictor of the traits that will increase fitness across a range of mating opportunities and local competitive conditions. Adaptive updating of environmental information based on individual context is likely to trigger relatively transient, activational effects (e.g., behavioral tactic changes), and this form of plasticity will be increasingly important in habitats where the spatio-temporal variance in social context is high.

This section provides an overview of the dynamics of pre- and post-copulatory sexual selection on males in focal taxa, and how these dynamics may be related to social context (Evans & Garcia-Gonzalez, 2016). I discuss the traits that increase success in the episodes of selection encountered by adult males (Fig. 1), and how demography and mating system are necessary to determine which episodes will have the strongest effects on fitness.

3.2.1 Episodes of selection and trade-offs in performance

For web-building spiders, pre-copulatory sexual selection is initially mediated by success at mate searching. Once a potential mate is located, processes of competition and choice, which generally occur on a female's web, determine mating success (Fig. 1B). Post-copulatory processes that affect fertilization success include female remating behavior, the efficacy of genital plugging, and sperm competition. The outcome of each of these processes may be linked to pre-copulatory male performance and traits (Elgar & Fahey, 1996; Schneider & Andrade, 2011). When traits favored by each episode of selection differ, then developmental allocation and behavioral decisions tuned to one phase of the mating attempt will inevitably lead to trade-offs in performance in other episodes (Cattelan et al., 2016; Geiger et al., 2018). These trade-offs are an important component of selection on plasticity.

3.2.2 Genital mutilation and terminal investment: Severe limits on male mating

Mating systems of males and females (Emlen & Oring, 1977; Herberstein et al., 2017) will have strong effects on the relative importance of different episodes of selection in a given social context. The female mating system sets the stage for the forms of inter-male competition that will yield the highest success. In most species of *Nephila*, *Argiope*, and *Latrodectus*, females are capable of polyandry (Schneider & Michalik, 2011), although mating frequencies in nature are apparently variable and females of some species may rarely remate (Andrade & Banta, 2002; Andrade & MacLeod, 2015). Even in species in which polyandry occurs, the majority of females may mate only once on average (Foellmer, 2008; Kuntner et al., 2016; Zimmer, Welke, & Schneider, 2012). Realized mating rates may depend on both male and female interests, and sexual conflict is likely to play a strong role (e.g., *Nephila*, Fromhage & Schneider, 2005; Kuntner et al., 2016; *Argiope*, Foellmer & Fairbairn, 2005a, 2005b; *Latrodectus*, Neumann & Schneider, 2011). Regardless of actual mating rates, however, females of

Nephila, *Argiope*, and *Latrodectus* often have the opportunity for polyandrous mating, as it is common for multiple males to visit or cohabit with individual females (Foellmer, 2008; Miller, 2007; Schneider & Andrade, 2011). The opportunity for polyandry has led to selection for male paternity protection traits that affect both pre- and post-copulatory dynamics (Fromhage, Elgar, & Schneider, 2005; Kuntner et al., 2016; Miller, 2007).

Male *Nephila*, *Argiope*, and *Latrodectus* are unusual among non-social invertebrates in the prevalence of severe restrictions on male mating frequency, and this is one of the key features that makes them attractive for studies of plasticity. Monogyny is common, and together with the risk of sperm competition, leads to extremely strong selection on males to maximize fertilization success in their single mating (Fromhage et al., 2005; Schneider & Fromhage, 2010). In this situation, while phenotypes may respond to coarse-scale environmental context, fine-tuning of phenotypes to variable individual context may be of central importance, as performance in a single mating constitutes the male's lifetime reproductive effort (Andrade & Kasumovic, 2005; Fromhage et al., 2005; Kasumovic & Andrade, 2006). Moreover, developmental plasticity tuned to individual (local) social context could yield high fitness since males that gamble on fixed phenotypic traits matched to local conditions do not risk potential mismatches under changed future circumstances.

While monogyny is very common in these taxa, males of some species are polygynous (mate with multiple females). Like all web-building spiders, males have paired copulatory organs (the palps) which are used to inseminate the female's paired, independent sperm storage organs (spermathecae). In *Nephila* and *Argiope*, polygyny is restricted to a maximum of two females, with a single copulation with each palp (bigyny, Schneider et al., 2015; Schneider & Michalik, 2011), but in some *Latrodectus* species, multiple mating may involve many females with each palp being used more than once (e.g., *L. mactans*, Breene & Sweet, 1985; *L. hesperus*, MacLeod, 2013). Polygynous males are likely to encounter a range of contexts as they seek sequential mating opportunities, and optimal tactics would include reserving resources for iterative rounds of mate searching and courtship or competition. Environmental social context gleaned from coarse-scale cues would provide information on the average challenges across a range of expected mating opportunities for polygynous males, and should thus be the trigger for developmental plasticity if it exists. This may, for example, affect development time, body size, condition, or allocation to gonads. Assessment of individual social context will also affect performance within the broader

developmental tactic and is expected to lead to fine-tuning of behavior at each mating opportunity (e.g., decisions about allocation of resources to sperm or courtship effort).

Understanding the causes of variation in limitations on male mating frequency may be leveraged by researchers to design studies of plasticity that capture salient species-specific contexts. In monogynous and bigynous species, male mating frequency is limited due to routine damage of copulatory organs at mating, terminal mating adaptations of males (=investing maximally in a single mating, [Andrade & Kasumovic, 2005](#)), high rates of sexual cannibalism, and permanent sperm depletion ([Andrade & MacLeod, 2015](#); [Christenson, 1989](#); [Kuntner et al., 2016](#); [Michalik & Rittschof, 2011](#); [Miller, 2007](#); [Schneider & Andrade, 2011](#); [Uhl et al., 2010](#)). Mate searching may also constrain mating opportunities, but this is a result of ecological factors, and so is considered separately ([Section 3.2.3](#)).

Nephila, *Argiope*, and *Latrodectus* are among the many taxa of spiders where males leave broken portions of their palps lodged in the female's reproductive tract after mating ([Uhl et al., 2010](#)). There is a separate fertilization duct by which sperm exits from storage, so these plugs can theoretically remain in place for long periods without preventing reproduction, which has led to them being called “plugs,” presumed to prevent mating or insemination by rival males ([Foelix, 2011](#); [Uhl et al., 2010](#)). Whether the broken palp is in fact effective as a plug is highly variable, as is the nature of the breakage. In *Nephila* and *Argiope*, palp damage has been called genital mutilation as the portion that breaks is often irregular and may be quite large ([Uhl et al., 2010](#)). A mutilated palp is non-functional after one copulation, so genital mutilation often co-occurs with monogyny ([Miller, 2007](#)). Polygyny, when it occurs in species with genital mutilation, involves copulating with a maximum of two females, once with each palp ([Herberstein, Gaskett, Schneider, Vella, & Elgar, 2005](#); [Kuntner et al., 2016](#); [Schneider & Michalik, 2011](#); [Uhl et al., 2010](#)).

The typical form and effect of genital mutilation varies across species. Some male *Argiope* spiders die spontaneously during their first mating, and a portion of their copulatory organ blocks the female's genital opening after death, with the broken organ deterring copulation by subsequent males (*A. aurantia*, [Foellmer, 2008](#); [Foellmer & Fairbairn, 2003](#); *A. argentata*, [Ghione & Costa, 2011](#); *A. lobata*, [Hirt, Ruch, & Schneider, 2017](#)). The copulatory organs of male *A. bruennichi* are often severely damaged during mating and each organ can only be used once, but males choose whether to attempt to mate twice with one female (=monogyny) or mate once each

with two females (=bigyny; [Fromhage & Schneider, 2012](#)), although the high frequency of sexual cannibalism can restrict the latter option ([Nessler, Uhl, & Schneider, 2007](#); [Schneider, Gilberg, Fromhage, & Uhl, 2006](#)). Broken palps placed in the female's reproductive tract reduce copulation duration of subsequent mates in this species, which protects paternity of the first male ([Nessler et al., 2007](#)). Male *A. keyserlingi* appear to be obligately bigynous, using one palp with their first mate, then, if they survive cannibalism, they typically seek out a second female after guarding their first against rivals ([Herberstein et al., 2005](#); [Zimmer, Schneider, & Herberstein, 2014](#)). The broken palp can act as an effective mating plug, but only if placed correctly, and it remains in place for a variable period ([Herberstein, Wignall, Nessler, Harmer, & Schneider, 2012](#)). Variation in genital mutilation also exists in *Nephila* species. Male *N. fenestrata*, *N. plumipes*, and *N. pilipes* frequently damage their genitalia during mating, but not *N. clavipes*, *N. edulis*, nor *N. senegalensis* ([Schneider & Michalik, 2011](#)). While plugs in *N. fenestrata* are effective as plugs against rivals ([Fromhage & Schneider, 2006](#)), they are apparently an exception, as broken palps in other *Nephila* spiders are ineffective (e.g., *Nephila plumipes*, reviewed in [Schneider & Michalik, 2011](#)), and it is common to find multiple "plugs" in the same genital tract ([Kuntner, Kralj-Fiser, Schneider, & Li, 2009](#)). The question of how genital mutilation evolved despite ineffective plugging is fascinating, but beyond the scope of this chapter (see [Kuntner, Kralj-Fiser, et al., 2009](#); [Schneider & Michalik, 2011](#)).

All *Latrodectus* males experience organ breakage at mating ([Knoflach & van Harten, 2002](#)), but for these, (as well as a few species of *Nephila* and *Argiope*, [Schneider et al., 2015](#); [Schneider & Michalik, 2011](#)), the break involves a relatively small, discrete sclerite whose loss does not prevent future mating by the male ([Andrade & Banta, 2002](#); [Breene & Sweet, 1985](#); [Segoli, Lubin, & Harari, 2008](#); [Uhl et al., 2010](#)). These sclerites are placed deep in the female's reproductive tract and can be effective as long-term sperm plugs if positioned so they block the entrance to the spermatheca (*Latrodectus tredecimguttatus*, [Neumann & Schneider, 2011](#); *L. hasselti*, [Snow, Abdel-Mesih, & Andrade, 2006](#); *L. hesperus*, [MacLeod, 2013](#)). In some *Latrodectus* species however (as with *Nephila*), the discovery of multiple sclerites in each spermatheca suggests they are not effective in blocking insemination by rival males, an effect that may reflect antagonistic coevolution with females over control of fertilization ([Andrade & MacLeod, 2015](#); [Berendonck & Greven, 2005](#); [Bhatnagar & Rempel, 1962](#); [Knoflach & van Harten, 2002](#)). Independent of the effect of sclerite loss,

there is variation in the genus in whether males are monogynous or able to be polygynous, but this rests on the occurrence of cannibalism rather than genital mutilation. *L. hasselti* and *L. geometricus* males typically mate only once since they facilitate sexual cannibalism by their mates by twisting their bodies onto the female's fangs during copulation, where this behavior is obligate in *L. hasselti* but facultative in *L. geometricus* (Forster, 1992; Segoli, Arieli, Sierwald, Harari, & Lubin, 2008). In *L. mirabilis*, males are frequently killed by females during mating although there is no evidence of facilitation (L. Baruffaldi, pers. comm.). In contrast, males of other *Latrodectus* species do not engage in terminal investment, are rarely cannibalized, and can mate multiple times (e.g., *L. hesperus*, *L. mactans*, *L. variolus*, Andrade & MacLeod, 2015). These polygynous males may range widely to seek sequential mating opportunities (C.E. Scott, pers. comm.).

Another example of a “terminal investment” trait that restricts male mating in *Nephila* and *Argiope* is permanent sperm depletion. Depletion arises because testes are degenerate in adult males, spermatogenesis occurs only prior to sexual maturity, so males have a single, non-renewable sperm load to expend in mating (Herberstein et al., 2005; Michalik & Rittschof, 2011; Schneider & Michalik, 2011). Males with functioning (non-mutilated) palps may be able to mate more than once nonetheless, but this requires partitioning their limited sperm stores across relatively few productive matings (as shown in the lab with *Nephila senegalensis* Schneider & Michalik, 2011). Since not all species of *Nephila* and *Argiope* experience palp damage (Uhl et al., 2010), there is some interesting potential to ask how this variation affects links between plasticity and local social context (see Kuntner, Kralj-Fiser, et al., 2009; Schneider et al., 2015).

Recently, an opportunistic mating tactic of male *L. hasselti* and *L. geometricus* was reported which could allow typically “terminally investing” males (Andrade, 1996; Andrade, Gu, & Stoltz, 2005; Forster, 1992; Segoli, Arieli, et al., 2008) to be polygynous (Baruffaldi & Andrade, 2017; Biaggio, Sandomirsky, Lubin, Harari, & Andrade, 2016; Waner, Motro, Lubin, & Harari, 2018). Males of both species are able to inseminate immature females near the end of the female's final instar by accessing female's developing spermathecae through tears made in their exoskeleton; and males who mate immatures are never cannibalized (Biaggio et al., 2016). “Immature mated” females retain stored sperm after their final molt and show normal fertility, fecundity, and longevity without mating as adults (Baruffaldi & Andrade, 2017; Biaggio et al., 2016; Waner et al., 2018). Although males are apparently unable to detect immature females using pheromones

(Waner et al., 2018), *Latrodectus* males are frequently found cohabiting with immature females in nature (Segev et al., 2003; Segoli, Harari, & Lubin, 2006) and may encounter these females by chance while seeking signaling adults. Such opportunities occur at higher frequency in dense populations (Andrade, unpublished data), although this tactic can be risky if males approach immature females that are not receptive (Fig. 1C). Males recognize a potential mate once they are on immature webs, and show activational plasticity, including altering their copulatory posture (no self-sacrifice) and a substantial reduction in courtship effort (Baruffaldi & Andrade, 2017; Biaggio et al., 2016). Males always survive immature matings and could thus mate again (Biaggio et al., 2016). This may explain why these typically monogynous *Latrodectus* males retain the capacity for spermatogenesis after adulthood and do not show the permanent sperm depletion common in *Argiope* and *Nephila* (Biaggio et al., 2016; Modanu, Michalik, & Andrade, 2013).

3.2.3 Scrambling to find females

In the species highlighted here, and most web-building species, males engage in scramble competition, where the search for potential mates precedes mating (Herberstein et al., 2017). Mate searching is often risky, and this may be particularly true for spiders. Male spiders are solitary prior to maturity, females are largely sedentary, and webs may have patchy distributions with males maturing at variable distances from females. Male fitness may hinge on performance at mate searching, since males that fail will not reproduce. Field estimates of mortality during mate searching are high in *Latrodectus* and some *Nephila*: ~80% mortality in four species of *Latrodectus* (*Latrodectus hasselti*, Andrade, 2003; *L. revivensis*, Segev et al., 2003; *L. pallidus*, Segoli et al., 2006; *L. hesperus*, C.E. Scott, pers. comm.) and for *Nephila*, between 36% (*Nephila fenestrata*, Fromhage et al., 2007) and ~88% (*Nephila plumipes*, Kasumovic et al., 2007; *N. clavipes*, Vollrath, 1980; and see Danielson-Francois et al., 2012; *N. pilipes*). Some males successfully reach more than one female in both genera in nature, but this is not common (Andrade, 2003; Fromhage et al., 2007; Segev et al., 2003). In *Argiope*, while mortality during mate search has not been measured directly, indirect evidence suggests the risk could be lower. In *A. keyserlingi*, males typically seek a second female if they survive their first mating, suggesting searching for a new female can yield fitness payoffs rather than mating twice with one female (Herberstein et al., 2005). Studies of *A. bruennichi* also suggest that mate searching may not be risky because in the field, because choosy males abandon some females

without attempting copulation after reaching their webs in nature (Schulte et al., 2010), or show long delays in courtship initiation in no-choice pairings in the lab (Schneider et al., 2015). Measurements of mate-searching mortality in *Argiope* would be welcome however, as the high-mortality rate during mate searching in *N. plumipes* occurs despite the existence of high-density web aggregations and was proposed to be partly a result of male choosiness (Kasumovic et al., 2007).

Even if the mortality risk of mate searching is low, selection imposed by scramble competition may still be intensified as the importance of finding unmated females increases; for example, if female mating rates are low, if mated females are cryptic (e.g., cessation of pheromone production) or less receptive than unmated females, if the first male to mate has the highest fertilization success (first male sperm precedence, Elgar, 1998), and/or if the operational sex ratio is biased toward males. Some or all of these conditions have been found in all *Nephila*, *Argiope*, and *Latrodectus* species that have been studied to date (reviewed in Andrade & MacLeod, 2015; Kuntner et al., 2016; Kuntner, Coddington, & Schneider, 2009; Schneider & Andrade, 2011; Schneider & Fromhage, 2010). The result is that the scramble is a true race for unmated females in most species. Numerous aspects of the physiology and morphology of male web-building spiders, such as leg-body allometry and leg length (Brandt & Andrade, 2007; Foellmer et al., 2011; Foellmer & Fairbairn, 2005b), metabolic capacities (Kasumovic & Seebacher, 2018), and chemosensory abilities (Ganske & Uhl, 2018) are likely adaptations to locating and reaching potential mates first (Herberstein et al., 2017).

Protandry, an adaptive response to the evolutionary persistence of this race (Herberstein et al., 2017), is another common feature of *Nephila*, *Argiope*, and *Latrodectus*. In addition to this evolutionary response, there may be selection for individual males to show developmental acceleration as a function of their individual or environmental social context; for example, to mature rapidly and capitalize on nearby unmated females before the females are reached by rivals (Kasumovic & Andrade, 2006). However, rapid development may be costly if there is a mismatch, because of trade-offs with morphological or physiological traits that could increase success at longer-distance mate searching. Costs may also arise from trade-offs with traits that are required for successful mating after females are reached (via competition or choice), but may require longer periods for optimal development (e.g., large size, Nijhout, 2015). Monogynous males in particular may have the highest success if they are able to detect whether the best tactic is to allocate

more resources to rapid development (if there is an opportunity to reach nearby unmated females quickly), even at the cost of smaller size, lower body condition, or reduced spermatogenesis (where the latter is arguably the cause of permanent sperm depletion in *Nephila* and *Argiope* Michalik & Rittschof, 2011). If there are no cues of nearby unmated females, males may do better to spend a longer period developing to allow sufficient time and resource acquisition to develop a phenotype that is well equipped for a more arduous mate search.

Shifts in development that prioritize maturation speed can affect the integrated phenotype of males, particularly those developing with limited resources (Neumann, Ruppel, & Schneider, 2017; Nijhout, 2015; Pigliucci, 2003; Stearns, 1989a). The trade-offs inherent in accelerated development suggest that developmental plasticity should be adjusted based on other informational inputs that are relevant for a given species. Some of these will be intrinsic to the male, such as male “quality,” or the inherent ability to acquire and utilize resources and maintain condition (Rowe & Houle, 1996; Van Noordwijk & Dejong, 1986), as this will affect the extent to which shifts in development time handicap trait development. Others will depend on other aspects of social context, such as indicators of the risk or intensity of inter-male competition, which is likely to be reflected in variation in operational sex ratio (Kasumovic et al., 2008) and could be detected by the overlaying of cues of male proximity with those of female proximity. For example, in species where aggressive dominance and first male sperm precedence are common, the detection of females nearby in the presence of rival males may still lead to developmental acceleration, but the adaptive trade-off may be to retain relatively large body size, but reduce investment elsewhere (e.g., gonadal tissues). In contrast, if sperm mixing is common, males may maintain allocation to spermatogenesis at the cost of body size (Nylin & Gotthard, 1998).

3.2.4 Competition, choice, and fertilization success with sexual cannibals

Although mate searching success is the first filter, males will often be in direct competition over choosy, potentially cannibalistic females once they reach a web (Schneider & Andrade, 2011). Moreover, they may be competing against males that did not have the same developmental trade-offs, either because of variation in male quality or because they have arrived from different microhabitats (Kasumovic & Andrade, 2009). The accumulation of males on the webs of females is pervasive in *Nephila*, *Argiope*, and

Latrodectus (Anava & Lubin, 1993; Andrade, 1996; Fromhage et al., 2007; Kasumovic et al., 2008; Miller, 2007; Miyashita, 1993; Scott, Kirk, et al., 2015) and reflects the male-biased sex ratios often measured across these taxa, particularly during peak mating periods (Foellmer & Fairbairn, 2005b; Fromhage et al., 2005; Fromhage et al., 2007; Kasumovic et al., 2008; Miyashita, 1993). Another contributor to male aggregation may be biased attraction to females with preferred traits, or those that are more detectable due to micro-habitat characteristics or web clustering (Hirt et al., 2017; Kasumovic & Jordan, 2013; MacLeod & Andrade, 2014). Regardless, inter-male competition can be intense, and this is a recurrent feature of monogynous species in particular (Miller, 2007; Schneider & Fromhage, 2010). Since female mating rates are often low (Section 2.1) although polyandry is possible, this imposes strong intra-sexual selection on males (Andersson, 1994). Moreover, when females are polyandrous, the two most common patterns of sperm use are sperm mixing and first male sperm precedence (Elgar, Schneider, & Herberstein, 2000; Neumann & Schneider, 2011; Snow & Andrade, 2005). The latter primarily occurs if the first male is able to copulate twice, and place two effective plugs (Andrade & MacLeod, 2015; Schneider & Andrade, 2011; Schneider & Fromhage, 2010; Snow et al., 2006), which imposes strong selection on males to achieve this outcome. Both forms of selection will depend on the relative density of rival males.

For spiders in these focal taxa, studies suggest some common themes in sexual selection, including the importance of male size, courtship effort, copulation duration, copulation frequency (with the same female), and sexual cannibalism in determining the fitness outcome of a given mating interaction (reviewed in Schneider & Andrade, 2011). Although some of the discussion below deals with these separately, the effects of each of these factors are likely to arise from the interaction of male and female behaviors and traits. Activational plasticity in mating tactics is pervasive (Schneider & Andrade, 2011), and so, for spiders on a web with a given individual history and current context, the outcome depends on considering all the players present. The complexity in these interactive effects must be considered when inferring how individuals of a given species might trade-off allocation to development, scramble competition, and web-based performance.

An important determinant of male fitness across these taxa is the risk of cannibalism by physically dominant females (Fig. 1C). Cannibalism rates and female propensity to attack vary widely but can be substantial (reviewed in Schneider & Andrade, 2011). In *Latrodectus* and some *Nephila* spiders,

cannibalism can occur during courtship (most costly to males), or during mating, which is also costly, but with variation in implications for male fitness (Elgar, 1992). In *Argiope*, cannibalism usually causes the termination of copulation, so cannibalized males may fertilize eggs with their current mate, but will not mate again (Schneider et al., 2015; Schneider & Fromhage, 2010). Cannibalism can severely limit male reproductive success and impose strong selection on males (particularly if females attack males during courtship). Cannibalism risk may impose selection for rapid sperm transfer and relatively short copulation duration (Foellmer & Fairbairn, 2004; Schneider et al., 2006; Schneider & Elgar, 2001; Schneider, Fromhage, & Uhl, 2005), even though this can be costly in terms of paternity. Behavioral adaptations to avoid cannibalism are widespread, including mating with hunting, feeding, or molting females, tactics that are common in *Nephila* and *Argiope* (Austin & Anderson, 1978; Christenson, Brown, Wenzl, Hill, & Goist, 1985; Fromhage & Schneider, 2005; Schneider & Andrade, 2011; Uhl, Zimmer, Renner, & Schneider, 2015). While these are opportunistic tactics in some species, in others, males mate primarily during these periods (Danielson-Francois et al., 2012; Elgar & Fahey, 1996; Miyashita, 1993). In *Latrodectus*, despite the risk of pre-copulatory cannibalism in some species (reviewed in Andrade & MacLeod, 2015), these tactics have not been reported. However, male *L. hesperus* do detect and avoid females that have had food withheld and thus represent an elevated risk of a cannibalistic attack during courtship (Johnson et al., 2011; MacLeod & Andrade, 2014).

In species where cannibalism occurs during or after copulation, females seem to control duration, and males that are cannibalized may copulate for longer (*L. hasselti*, Andrade, 1996; *N. plumipes*, Elgar et al., 2000a; *A. keyserlingi*, Schneider & Elgar, 2001; *L. hasselti*, Snow & Andrade, 2004). The act of cannibalism may also be beneficial to males if it facilitates the process of plugging the female, with a related increase in paternity, as has been found in *Argiope lobata* (Nessler et al., 2009a). Copulation duration (across one or both copulations) is correlated with paternity in many web-building spiders (see Elgar, 1998). This may arise from increased sperm transfer conferring advantages in a raffle competition (Parker, 1990; Schneider et al., 2006), creating selection for males to increase the number of sperm produced and transferred. In some species, however, sperm is released very rapidly relative to mating durations (*Argiope*, Foellmer & Fairbairn, 2004; *Nephila*, Schneider et al., 2005; *Latrodectus*, Snow & Andrade, 2004) and so the cause of the relationship to paternity is less clear. Moreover, in some of these rapid-release species, there is no detectable

correlation between the widely variable number of sperm stored by females or released by males, and male body size (*Latrodectus hasselti*, [Snow & Andrade, 2004](#)). Substances in the ejaculatory fluid could mediate the outcome of competition, but such effects have not been well studied ([Herberstein et al., 2011](#)). Regardless of the cause, these effects may link to body size because of established connections between copulation duration and male size in general ([Assis & Foellmer, 2016](#); [Elgar, 1998](#)). These effects are primarily a large male advantage, but there may be exceptions (see below).

One of the key traits thought to trade-off against development time of males is size ([Nylin & Gotthard, 1998](#)). Size is consistently found to mediate access to mating opportunities for males ([Blanckenhorn, 2000](#)). In orb-weaving spiders, males often arrive on webs of immature females, guard them until they are sexually mature, and may also guard them against rivals after mating ([Hill & Christenson, 1988](#); [Miyashita, 1993](#); [Schneider & Andrade, 2011](#)). In *Nephila* and *Argiope* for example, females build orb-webs, typically reside near the hub (center), and are sexually receptive shortly after molting ([Christenson et al., 1985](#); [Miyashita, 1993](#)). Male positions on the web are notably size dependent, with larger males often having a mating advantage because they hold positions closer to the female and hub ([Christenson & Goist, 1979](#); [Elgar, Champion de Crespigny, & Ramamurthy, 2003](#); [Elgar & Fahey, 1996](#); [Foellmer & Fairbairn, 2005a](#); [Miyashita, 1993](#); [Neumann & Schneider, 2015](#); [Robinson & Robinson, 1976](#); [Robinson & Robinson, 1980](#); [Vollrath, 1980](#)). In *Latrodectus* spiders, females rest in a refuge or on a sheet within a cobweb ([Foelix, 2011](#)), and there are no clear positional effects on mating success. There is evidence for a large male advantage in finding and mating with females when males compete simultaneously ([Kasumovic & Andrade, 2009](#)), larger males will typically win aggressive interactions on the female's web when smaller males retreat ([Stoltz et al., 2008](#)), and larger males are apparently more successful than smaller males at successfully placing plugs ([MacLeod, 2013](#); [Neumann & Schneider, 2011](#)).

Body size advantages, such as those seen in combat, can be offset by interactive effects of size-dependent male mating tactics (e.g., sneaking vs defense), the risk of sexual cannibalism (which may affect hub-resident males, or larger males, more), and variation in copulation duration (which can be affected by male tactics and by sexual cannibalism; [Elgar & Jones, 2008](#); [Foellmer & Fairbairn, 2004](#); [Fromhage, Uhl, & Schneider, 2003](#); [Neumann & Schneider, 2015](#)). In *Nephila*, *Argiope*, and *Latrodectus* species

where it has been studied, total copulation duration is positively correlated with paternity (Andrade & MacLeod, 2015; Schneider et al., 2015; Schneider & Andrade, 2011; Schneider & Fromhage, 2010). Copulation frequency has a similar effect, as males that copulate only once leave one sperm storage organ (spermatheca) empty and vulnerable for a competitor (Stoltz et al., 2008). When rival males inseminate opposite spermathecae, the outcome is often variable sperm use patterns (Snow & Andrade, 2005). Females can thus affect paternity not only through overt pre-copulatory choice but also through behaviors that affect male copulation duration or copulation frequency (post-copulatory choice; Andrade & MacLeod, 2015; Elgar et al., 2000; Schneider et al., 2015). In some species, such post-copulatory mechanisms of females appear to be more common than pre-copulatory mate rejection (Stoltz et al., 2008; Stoltz & Andrade, 2010; Welke & Schneider, 2009), perhaps because delays to reproduction can be costly for females (Kokko & Mappes, 2005; Stoltz, Hanna, & Andrade, 2010).

Thus, despite apparent advantages for large males in direct competition, fertilization success cannot be inferred to be size dependent, and outcomes vary across species in ways that affect male fitness. For example, in *A. keyserlingi*, where cannibalism results in the cessation of copulation, females do cannibalize small males, but delay it sufficiently that small males have longer copulation duration than larger males (Elgar et al., 2000). In *A. aurantia*, there is no effect of size on cannibalism (Foellmer & Fairbairn, 2004). Similarly, there is variation in *Nephila*, where some laboratory trials with *N. edulis* show small males copulate for longer when mating is sequential (and fertilize more eggs than large males when mated sequentially; Schneider, Herberstein, De Crespigny, Ramamurthy, & Elgar, 2000), but fertilization success is size independent when competition is simultaneous (Elgar & Jones, 2008). However, a more recent study in the same species found copulation duration increased with male size (Ceballos, Jones, & Elgar, 2015), so patterns are currently unclear. In *N. plumipes* larger males are at higher risk of cannibalism than small males when approaching unmated females (Schneider & Elgar, 2001), which could balance positional advantages. Similarly, in *Latrodectus*, in general, direct effects of male size on mating outcomes appear to be less important than effects of courtship and female post-copulatory choice (Snow & Andrade, 2005; Stoltz et al., 2008). Courtship is prolonged in many *Latrodectus* species (several hours) and affects mating and fertilization success (Anava & Lubin, 1993; Andrade & MacLeod, 2015; Harari, Ziv, & Lubin, 2009; Schneider & Lesmono, 2009). In *Latrodectus hasselti*, although larger males typically have

higher mating success, smaller males can mate successfully if they sneak copulations after the female has already experienced courtship from a competitor (Stoltz & Andrade, 2010). When males compete directly, females will cannibalize males who provide a short courtship after a single copulation, while allowing longer-courting males to copulate twice (Stoltz et al., 2008; Stoltz, Elias, & Andrade, 2009). In addition, it is males of intermediate (rather than large) size classes that are best at creating the energetic signals preferred by females (De Luca, Stoltz, Andrade, & Mason, 2015).

Overall, then, even males that trade-off size for rapid development may still be competitive if they encounter larger competitors, and this may mean that fluctuating selection in earlier contexts can be compensated at the point of mating. In *Nephila*, size-specific tactics are common (Elgar & Fahey, 1996), whereas in *Latrodectus* there is evidence for male mating tactics to shift as a function of size relative to competitors once males reach a web (i.e., activational plasticity based on individual social context, Stoltz et al., 2008). This may reflect the form of male size variation in nature—*Nephila* males tend to sort into relatively distinct size classes (Elgar & Fahey, 1996), whereas in *Latrodectus* species variation in male body size approximates a normal distribution (Andrade, 2003). These are intriguing results since (another) one of the striking features of *Nephila* and *Latrodectus* species is the puzzling maintenance of significant variation in male size in the field, where male size may differ by an order of magnitude (Andrade, 2003; Brandt & Andrade, 2007; Neumann & Schneider, 2015, Fig. 1D). For example, field-collected males show a 10-fold difference in body mass in *L. hasselti* (Andrade, 2003, Fig. 2), and in many species of *Nephila* (Christenson & Goist, 1979; Elgar & Fahey, 1996; Schneider & Elgar, 2001); a 20-fold difference in *L. hesperus* (Fry & Andrade, unpublished data) and, incredibly, a 100-fold difference in size in *Nephila edulis* (Elgar, 1991). This puts these spiders near (and *N. edulis* at) the upper end of the distribution of intraspecific variation in male mass reported in a meta-analysis of 210 animal species across six classes (Mckellar & Hendry, 2009). It is tempting to speculate that developmental plasticity underlies much of this variation, and the availability of plastic mating behaviors that can offset any disadvantages of small size is critical to the persistence of this impressive level of variation (Neumann & Schneider, 2015).

Thus, patterns of post-copulatory sexual selection vary widely across taxa, but there are a few generalizations relevant to questions of plasticity: (1) females are at least moderately polyandrous and choosy, and operational sex ratios should provide a gauge of the risk of losing paternity and (2) male

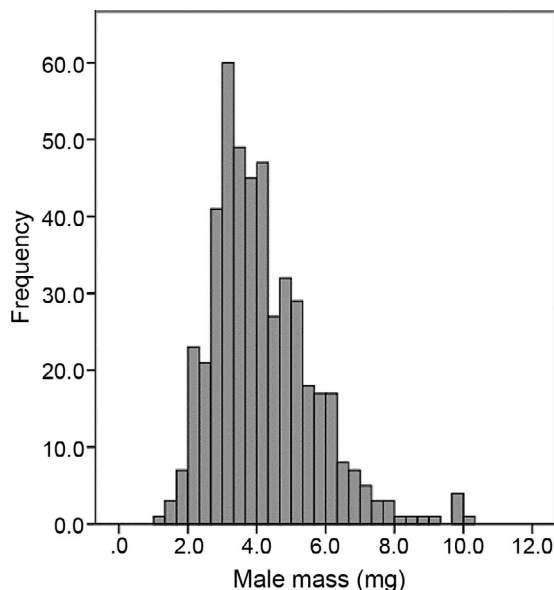


Fig. 2 Frequency histogram of the mass (mg) of 472 *L. hasselti* adult males collected in Perth WA in a single field season (for field site details, see [Andrade, 2003](#)). The coefficient of variation for mass is 0.37.

morphologies and behaviors can affect paternity, although the key traits will depend on the characteristics of male competitors and species-typical features of mating and fertilization.



4. Tests of adaptive plasticity in *Nephila*, *Argiope*, and *Latrodectus* spiders

Behavioral plasticity during mating is widespread, well studied in some spider taxa ([Schneider & Andrade, 2011](#)), and some of this variation has been reviewed above. Studies of adaptive developmental plasticity are much less common. Here I focus on a handful of studies in *Nephila*, *Argiope*, and *Latrodectus* spiders that have approached key questions in the study of adaptive plasticity in different ways. First ([Section 4.1](#)), there is an examination of a critical assumption of developmental plasticity and social context, the measurement of fluctuations in demographic factors and correlations with sexual selection in natural populations of *N. plumipes* ([Kasumovic et al., 2008](#)). Second ([Section 4.2](#)), is another observational study from the field, which examines correlations between phenotypic distributions of males and social context at different spatio-temporal scales, where

divergent predictions are derived from differences in the natural history of *A. keyserlingi* compared to *N. plumipes* (Kasumovic, Bruce, et al., 2009). The third (Section 4.3) includes three experimental examinations of developmental and activational plasticity in *A. bruennichi*. These studies ask how cues of social context affect the decision to attempt monogynous or bigynous mating (Cory & Schneider, 2018a, 2018b; Nessler et al., 2009b). These vary in the periods when males are expected to pheromones: across the juvenile and adult stages, only in the juvenile stages, or only in the adult stage. The fourth (Section 4.4) includes studies that manipulate cues of social context to examine developmental plasticity and male phenotypes in *N. senegalensis* and *N. fenestrata*, sympatric species which differ in key features of their mating systems (Neumann & Schneider, 2016). The fifth (Section 4.5) is a set of studies on *L. hasselti*, including: (1) tests of how cues of social context trigger developmental plasticity and alter male phenotypes under different levels of resource availability in manipulative experiments (Kasumovic & Andrade, 2006; Kasumovic, Brooks, et al., 2009; Stoltz, Andrade, & Kasumovic, 2012) and (2) estimation of the fitness effect of plastic phenotypes in a semi-natural field enclosure (Kasumovic & Andrade, 2009). While none of these studies provide comprehensive demonstrations of adaptive plasticity, they are all useful entries to the field which illustrate the range of approaches that may yield meaningful insights. They also serve as proof of concept for study designs that could be expanded to the approaches required for convincing tests of theory (Section 1.2).

4.1 Direction and intensity of sexual selection fluctuates with social context

Nephila plumipes males typically mature at or near aggregations of females, and male fitness typically depends on one mating due to genital mutilation and high mate-searching mortality. Fitness may be increased by protandry since early-maturing males may reach an unmated, receptive female before rivals. In the presence of rivals, male fitness is increased by large size, since larger males hold the hub of the web, are more likely to mate first, can also be effective guards, and are more likely to gain high paternity. Kasumovic et al. (2008) conducted a longitudinal study of two field populations of *Nephila plumipes* that differed in overall density to determine whether there were conditions that might favor the evolution of developmental plasticity—within-season fluctuations in social context, and correlated variation in selection on male traits. They measured female density and OSR, predicting these would fluctuate during the breeding season at a scale relevant to the

spiders—at the level of web aggregations. They also expected fluctuations in selection on male body size through the season along with variation in density and OSR, which would predict the relative importance of protandry (rapid development) vs direct intra-male competition (body size).

During *N. plumipes*' 2-month breeding season (Sydney, Australia), males and females were counted, males were weighed and measured, and the location of males within marked aggregations was recorded, as was their proximity to the hub of the female's web. As a proxy for fitness, expected paternity was estimated for each male based on published studies of sperm use patterns as a function of proximity to the hub when two or three males compete for fertilization (Elgar et al., 2003; Schneider & Elgar, 2001). Selection gradients were used to describe how estimated fitness of males was related to male size, where differences in the direction and intensity of selection can be assessed as a function of the sign and the slope of the relationship of the phenotype–fitness association (Arnold & Duvall, 1994; Grafen, 1988).

Nephila plumipes populations showed significant changes in female density and OSR over the course of the 2-month season, with the density of females increasing and OSR shifting from slightly male-biased (1.2) to female-biased (0.6) over time at the level of aggregations, where most male activity was centered. This spatial scale was important—when data were averaged across broader scales, the result was a female-biased OSR throughout the season. This was likely driven by the scattered solitary female webs found throughout the site, but since very few males were located outside of aggregations, this type of averaging blurs salient levels of variation for individual males.

In the entire sample, about 36% of over 300 males collected were found in direct competition with at least one other male on the web of a single female. Male density peaked at mid-season, so although there were relatively few adult females present early in the season, there were also relatively few males. Selection on male size tended to be negative early in the season at both sites, when inter-male competition would be least important. This shifted to positive selection on size by mid-season (peak male abundance), then remained positive at the high-density site but shifted back to negative at the low-density site by the end of the season. While the selection gradients themselves were not significant at any one time of the season, there were significant differences among gradients between the two populations and over time. Although correlative, this study provides evidence for how selection gradients can fluctuate at a fine-grained scale even within seasonal pattern of change, and how fluctuations can differ between populations. I suggest three take-home messages from this work.

First, this type of analysis can provide insight into the scale of demographic fluctuation that might be relevant to individual fitness. For males in this spatially structured population, seasonal cues of social context (i.e., broad-scale estimates of OSR) would not provide reliable information about the form of selection that is likely to mediate most interactions (fine-scale OSR, within aggregations). Second, this study highlights one of the major challenges with measuring selection gradients—the need for a very large sample size to make an accurate and statistically rigorous estimate (Kingsolver et al., 2001). However, approaches like this one can still be informative if the study design incorporates a comparative element (here, comparing between sites, across seasons, across scales), rather than resting on an absolute assessment. Third, it is clear from their relative scarcity in the literature that longitudinal field studies are challenging. Careful curating of the types of data that will be collected are often required. Here, the measurement of male somatic traits (size and mass) allowed focus on the proposed trade-off between development time and inter-male competition. In general, however, studies of this type might benefit from also examining correlates of investment in gonads/sperm production in addition to somatic investment. Although not practical in this case due to permanent sperm depletion of male *N. plumipes*, (Parker et al., 2018), measurements of gonadal tissue can be taken from preserved specimens, and provide insight into broader life history trade-offs.

4.2 Phenotypic distributions correlate with social context in nature

Developmental plasticity may allow males to capitalize on the opportunities presented by different social contexts, switching between rapid development when protandry is key to fitness, and slower development when body size is more critical. Kasumovic, Bruce, et al. (2009) predict that this process should lead to correlations between male phenotypic distributions for size and mass and female or male density in field populations. This longitudinal field study of *Argiope keyserlingi* and *Nephila plumipes* begins with the elucidation of different predictions regarding the nature and scale of social cues that should be relevant to each species given its natural history and mating system.

As was made clear in Section 4.1, *N. plumipes* males experience fluctuating sexual selection within semi-permanent aggregations of female's webs, including periods when there is relaxed selection on body size, but likely to be increased selection on rapid development (Kasumovic et al., 2008). If male development responds to this in nature, then male body size should

decrease with the density of immature females (benefit of protandry) but increase with the density of adult males (potential rivals, benefits via competition). The situation is different for *A. keyserlingi*, a species in which males copulate once with their first mate, and if they survive, guard her for a day and then wander to seek a second mate. In addition to this, females rebuild their web each day, do not have high website tenacity, and do not create aggregations. Thus cues of female presence are transient and will not provide a reliable source of information about the local availability of potential mates. However, inter-male competition can be intense in this species and broad-scale recognition of the density of competing males could be an important indicator of the extent to which body size will confer increased fitness. The prediction for *A. keyserlingi* then, is that male body size will increase with the broad-scale density of adult males in the population, but will not depend on the density of adult females.

In this field study, populations of both species were surveyed with a focus on the size of males and the developmental stage and number of all conspecifics surrounding every male that was collected at two spatial scales (local = within 2 m or in the same aggregation; and broad = within 5 m of the aggregation). As predicted, male size was negatively correlated with the density of adult females, and positively correlated with the density of rival males at the local, but not at the broad scale for *N. plumipes*. For *A. keyserlingi*, also as predicted, male body size was positively correlated with the density of adult males, but only at broad scales. Although this study is correlative, examining expected population-level effects of individual developmental plasticity is a good approach to grounding these studies in biological reality. Pairing this type of observational study with manipulative laboratory experiments would significantly increase the impact of this work.

4.3 Divergent critical periods for developmental and activational plasticity

Argiope bruennichi males are able to copulate only twice due to genital mutilation during mating. They may choose to copulate with one female (monogyny), or attempt to leave their first mating after one copulation and mate with a second female (bigyny, see [Schneider et al., 2015](#)). Female cannibalistic attacks are common, and males are only able to attempt bigyny if they severely truncate the duration of their first copulation to allow their escape ([Schneider et al., 2005](#)). However, this reduces expected paternity under sperm competition since only one spermatheca is filled. Social context and individual state may affect this behavioral decision

(Fromhage & Schneider, 2012), which could be determined during the final juvenile instar, or based on the information detected by adults. The likelihood of a male attempting bigyny should increase as a function of: (1) decreased quality (reproductive potential) of the first mate relative to the average for females in the population (Welke, Zimmer, & Schneider, 2012), (2) the likelihood the male will be successful at finding and copulating with a second female (Fromhage & Schneider, 2012), which should increase with the availability of unmated females, decrease with the density of rival males, and increase with male quality or condition. As with other protandrous spiders with limited male mating frequency and plugs, plasticity in development rate may also be favored in *A. bruennichi* as a function of fine-grained variation in the density of unmated females. The rich understanding of the mating behavior, ecology, and population structure of this species makes it a promising model for studies of plasticity.

In the first of three laboratory experiments, Nessler et al. (2009a, 2009b) examined the effect of exposure to unmated females' airborne pheromones on the occurrence of cannibalism during the first copulation of male *A. bruennichi*. Females always attempt to kill males during mating. Males that attempt bigyny must copulate once for a very brief period, and spring away from the female; longer matings result in death by cannibalism. Thus, in *A. bruennichi*, whether males survive or are cannibalized is primarily due to variation in male behavior. In this experiment, males were exposed to pheromones (or not) throughout their final juvenile instar, exposure was continued for adults for up to 28 days, and during mating trials (effects of variation in male age was a second focus of this experiment). There was no effect of male age on cannibalism and thus on the male attempts at bigyny, but males that had been exposed to pheromones were much *more* likely to be cannibalized at their first copulation, and thus constrained to monogyny, than males who had been held in isolation from females. This demonstrates that male mating tactics can be affected by social context information, an effect that may be developmental or activational. The male response is puzzling however, as pheromones would be predicted to indicate a high density of available, unmated females, and thus the a priori prediction would be that males should increase attempts to avoid cannibalism in the presence of such cues to allow an attempt at bigyny.

One possible explanation, not yet explored, is that the sustained period of exposure to female pheromones used in this experiment primarily communicates information about the imminent end to the mating season and rapid decrease in the availability of unmated females. The mating season in nature

lasts for about 1 month, with the majority of females becoming sexually mature and mating within a 2-week period (Zimmer et al., 2012). An adult male that is unmated but has been exposed to pheromones for weeks may well opt for the low-risk monogyny tactic and thus not attempt to avoid cannibalism, but maximize paternity with one female. On the other hand, a male who does not detect females for weeks may well be near the start of the mating season, when relatively few females are currently available, but that should soon change. That is, this could be a case where the environment at the time of mating is predictable from juvenile cues, but is the opposite of the context detected during development, leading to a plastic response that appears counter-intuitive outside the natural context (e.g., see Scheiner, 2013). This might be an intriguing opportunity to assess how the information content of a cue depends heavily on the evolved meaning in natural populations, and how environmental social information (sustained exposure to female's pheromones) might intersect with personal information (the context of the mating) to affect male behavior. Examining this idea would require experimental adjustments to the duration and timing of exposure to pheromones. Moreover, if this is the case, it may represent the use of direct cues of social context rather than indirect, seasonal cues, despite a univoltine life cycle in which female maturity is relatively synchronous.

The population studied here is invasive, part of a Northern-expanding invasion front (Krehenwinkel et al., 2015) which may be undergoing rapid evolutionary change. These Northern populations have a shorter, time-shifted breeding season relative to the native population to the South (Krehenwinkel & Tautz, 2013), and so may be uncoupled from seasonal cues. Consistent with this, a field study on a German population showed no effect of time of season on male mating tactic, despite seasonal changes in OSR (Welke et al., 2012), males in this population apparently mature at two points during the season, rather than showing a single seasonal peak as is seen for females (Zimmer et al., 2012), and males from Northern, but not (native) Southern populations, are more likely to attempt bigyny if their first mate is relatively small (Cory & Schneider, 2018a; Welke et al., 2012).

A second study on *A. bruennichi* explored whether social cues affect developmental plasticity in male maturation time, as predicted by scramble competition, but also whether male mating tactics are shaped by information acquired during ontogeny. In an elegant experiment, Cory and Schneider (2018a) reared final-instar males from Northern (invasive) and Southern (native) populations of *A. bruennichi* in a "common garden"

laboratory experiment in the presence or absence of female silk and (contact and airborne) pheromones. Development time was noted as was mass of adult males (highly correlated with size). Female pheromones were removed at the male's adult molt, so any effects noted would arise from juvenile exposure. Males were then paired with females in mating trials, and females were prevented from cannibalizing males. The mating arena allowed males to retreat after mating (as expected for a bigynous tactic), or return to the female to copulate again (a monogynous tactic).

There were differences between the two populations in overall development time and size. Northern males are smaller (also see [Krehenwinkel & Tautz, 2013](#)) and developed more quickly than Southern males. Moreover, consistent with the scramble competition hypothesis, males of both populations accelerated their development in the presence of female pheromones. There was only a minimal effect of pheromone exposure on male mating tactic, however. The strongest predictors of monogyny were low male condition (which might affect the likelihood of achieving a second mating) and large female size (high reproductive value).

The third study ([Cory & Schneider, 2018b](#)) examined the effect on male mating behavior when pheromone exposure was restricted to the adult stage. This study used *A. bruennichi* originating from a more Southern population (France). Naïve adult males were placed in an arena containing females, in which they freely searched for and copulated with experimental females. High pheromone exposure arenas enclosed four unmated adult females, while low pheromone exposure arenas had three penultimate instar females and only one adult. Males initiated mate searching sooner in cages with more pheromone sources, but there was no effect on the frequency of monogynous or bigynous mating.

Taken together, these studies show that male *A. bruennichi* are responsive to pheromonal cues of the availability of unmated females. When detected in the juvenile stage, this can trigger developmental plasticity in the timing of maturation. When detected as an adult (or with prolonged exposure), this can affect male mating tactics, including the initiating of mate searching. There is a fascinating opportunity to study these dynamics in a rapidly-adapting invasion front ([Krehenwinkel et al., 2015](#)). New field studies that assess how seasonal changes in social context affect male tactics, development, and sexual selection would be helpful additions, as would 2×2 laboratory studies that examine whether there are interactive effects of juvenile and adult exposure to female cues.

4.4 Developmental acceleration: Monogyny is not sufficient

Nephila fenestrata and *N. senegalensis* are sympatric congeners which differ in the degree of limitation of male mating opportunities. The palps of *N. fenestrata* males break during copulation, with broken pieces deposited in their only mate where they are largely effective as mating plugs (first male sperm precedence). Male *N. senegalensis* do not undergo palp damage at mating and are able to mate with multiple females. However permanent sperm depletion is typical of both species, so *N. senegalensis* males can copulate effectively with multiple females only by division of a limited sperm load among mates (Schneider & Michalik, 2011). Moreover, *N. senegalensis* actually invest less in sperm production than do *N. fenestrata*, suggesting a practical upper limit to mating frequency in terms of fitness payoffs (Preik, Schneider, Uhl, & Michalik, 2016; Schneider & Michalik, 2011). Nevertheless, the possibility of polygyny in *N. senegalensis* combined with the lack of effective plugging suggests scramble competition for unmated female is less critical than it is for male *N. fenestrata*. In this study, Neumann and Schneider (2016) harness this difference to test whether developmental acceleration in response to cues of female presence occurs in these species, and to test the prediction that the effect will be augmented in the monogynous species (*N. fenestrata*).

Males from each species were reared in the presence or absence of female silk, which could include tactile cues as well as airborne or contact pheromones, as in the studies in Section 4.3. Data showed that *N. senegalensis*, but not *N. fenestrata*, shifted to more rapid development when exposed to silk cues of unmated females. Most of this response occurred during the subadult instar, which supports that idea that this might be the critical period for this type of effect.

The lack of a response in *N. fenestrata* requires additional consideration since, all things being equal, monogyny should generate stronger selection for context-phenotype matching than would polygyny. The authors suggest that the restricted habitat types favored by *N. fenestrata* and a tendency to form dense aggregations in areas with relatively consistent temperature and humidity may minimize local fluctuations in population parameters. If this is true, they predict that broad-scale seasonal changes in demography might be best indicated by abiotic cues, rather than males detecting and responding to pheromones. However, *N. plumipes* also lives in aggregations and nevertheless fluctuations in female density, OSR, and selection on male traits at the level of those aggregations was demonstrated (Section 4.1, Kasumovic et al., 2008). Evaluating whether there is

significantly greater homogeneity in social context for *N. fenestrata* will require additional longitudinal field studies.

Another interesting dimension of these data lies in comparing developmental patterns in the two species as reported in this study. Whereas *N. senegalensis* subadult instars ranged from 23 days (no cues) to ~17.5 days (with cues), the range of variation in *N. fenestrata* was close to the lower limit of the *N. senegalensis* range, at ~19 days to ~18 days (Neumann & Schneider, 2016). Total development time for *N. fenestrata* was also ~10 days shorter, although males are slightly larger at adulthood (Neumann & Schneider, 2016). This raises the interesting possibility that *N. fenestrata* may already be near the lower limit for rapid development for a spider of this size. Finally, as for all the studies of plasticity discussed here, there was no assessment of gonadal investment or sperm count, although this is another area that might be predicted to see elevated investment in a dense aggregation.

4.5 Mate searching, developmental plasticity, and the integrated phenotype

Latrodectus hasselti has monogynous males that facilitate cannibalism during mating by moving into a vulnerable copulatory posture (Forster, 1992). Males deposit sperm plugs that effectively block paternity of rivals, so finding unmated females is critical to male success (Snow et al., 2006). When the density of males is high, males accumulate on the webs of females so that direct competition and female choosiness based on prolonged, energetically expensive courtship, will mediate fitness (Stoltz et al., 2009; Stoltz & Andrade, 2010). Larger males have some advantages in this context. Populations have complex age structures such that there is significant micro-habitat variation in the availability of unmated females, but very little seasonal variation (Andrade, unpublished data). The high website tenacity of females and relatively short-distance movement of mate-searching males (Andrade, 2003) predicts that local cues of OSR, and the density of males and females could provide salient information to tune plasticity.

In a series of replicated laboratory experiments, Kasumovic and colleagues (Kasumovic & Andrade, 2006; Kasumovic, Brooks, et al., 2009; Stoltz et al., 2012) tested for developmental plasticity of final-instar males reared in the presence or absence of airborne pheromones produced by females, where these treatments were crossed with three different diet levels to probe life history trade-offs. The experimental procedure housed males and pheromone-producing females in screen cages that allowed the free

spread of pheromones, including any produced by males (e.g., Scott et al., 2018). The density of males in the treatments changed over time as males that matured were removed from the experiment, and new males were added from the general laboratory population when they reached their final instar. Analyses of these experiments could thus examine effects of female presence, (average) male density, and diet on male development and adult phenotypes. As in Section 4.2, the prediction tested in the first replicate of this experiment (Kasumovic & Andrade, 2006) was that males would delay development and be smaller (or poorer condition) in the presence of females, develop for longer and be larger (or in better condition) in the absence of females, and that the trade-offs between development time and size/condition would be most extreme under resource restriction (low diets). A complementary field component of this study included an assessment of the body size and condition of newly-matured males in nature as a function of the distance to the web of their nearest female neighbor. Subsequent replicates of the laboratory experiment also examined other phenotypic traits that might affect male performance—longevity (Kasumovic, Brooks, et al., 2009) and metabolic rate (Stoltz et al., 2012).

As predicted, males reared in the presence of females mature more quickly than those reared in the absence, and these males were smaller and in poorer body condition when they matured. These results were strongest for males on a restricted diet. The studies outlined in Section 4.3 (*A. bruennichi*) and Section 4.4 (*N. senegalensis*, *N. fenestrata*) also examined whether there were trade-offs with male size (or mass) as a function of development time, but found no such effects. However, in these cases, males were fed ad libitum, which can mask the effects of trade-offs since higher quality, larger males may develop faster under such a regime (Van Noordwijk & Dejong, 1986).

In the *L. hasselti* studies, there was also an effect of the density of rival males on allocation. In addition to the effects of female's presence and diet on adult phenotypes, male body condition increased with the density of potential rivals. These main results were repeated in subsequent replicates, and supported by the field data, in which male size and condition at adulthood showed a negative correlation with proximity to females (Fig. 3). Finally, there were also treatment effects on male longevity and routine metabolic rates, suggesting plasticity leads to a suite of integrated phenotypic changes. Understanding the fitness effects of these physiological changes requires more study.

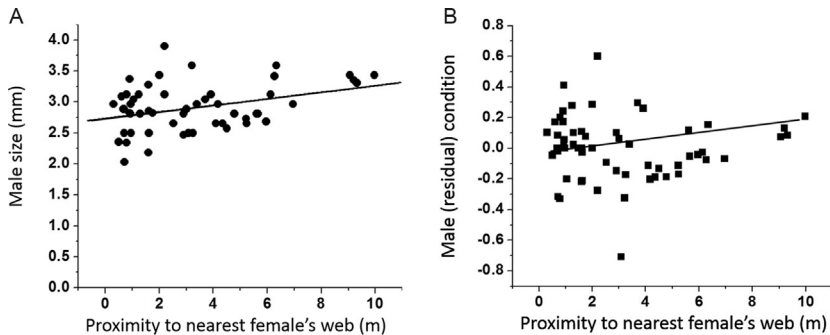


Fig. 3 (A) The size (mm, measured as the average size of the patella-tibia of the first pair of legs) and (B) condition (residuals from a regression of mass on size) of male *Latrodectus hasselti* that were captured on their juvenile webs just after molting, and prior to mate searching, as a function of the distance (m) to the closest web of an adult or penultimate instar female at a field site in Perth, WA (see [Andrade, 2003](#) for information on the field site). Proximity to the nearest female's web, used as a proxy for the local density of females during male development, was a significant predictor of size ($F=5.14$, $P=0.028$) and condition ($F=8.96$, $P=0.004$) in a two-way ANCOVA with maturity date as a covariate. Figure drawn from data reported in [Kasumovic, M. M., & Andrade, M. C. \(2006\). Male development tracks rapidly shifting sexual versus natural selection pressures. *Current Biology*, 16\(7\), R242–R243.](#)

At the heart of the hypothesis for plasticity in protandrous males with limited mating opportunities is the idea that accelerated development will allow males to reach and mate with newly-matured females before rivals. However, particularly in a patchy environment, males that are responding to one set of social cues might be competing with searching males who arrive from a different micro-habitat with a different set of potential trade-offs. This form of plasticity will only be favored if rapidly-developing males who pay the cost in terms of other phenotypic traits can still win in the competition for mates. This condition is not trivial, as the developmental advantage of plastic *L. hasselti* males is typically on the order of only 1–3 days (note that this is comparable the magnitude of developmental shifts found in *Nephila senegalensis*, [Neumann & Schneider, 2016](#); and *Argiope bruennichi*, [Cory & Schneider, 2018a](#)). The potential advantage of this developmental shift was tested in a field-enclosure study in which the distribution of immature and mature females in the field was mimicked, then unrestrained males were released and allowed to search for females and compete naturally for copulations ([Kasumovic & Andrade, 2009](#)). In this experiment, large and small males were either released simultaneously (no advantage) or small males were released just 1 day earlier than their larger counterparts.

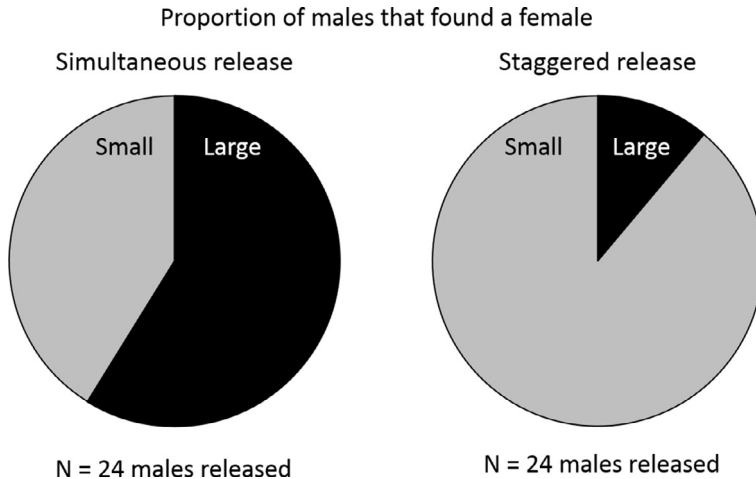


Fig. 4 Proportion of large or small *L. hasselti* males that found a female when released into one of two enclosures containing six adult and six juvenile females with inter-web distances approximating that in the field (Andrade, 2003). Released males were either relatively small (mean leg length = 2.67 mm, SD 0.24) or relatively large (mean 3.03 mm, SD 0.25), with three of each size class released in each enclosure in four replicates. When males of both size classes were released simultaneously (A), larger males were more likely to find a female, but when smaller males were released 1 day earlier, simulating their more rapid development, very few large males found females (B, treatment \times size interaction, $P = 0.016$). Redrawn from data in Kasumovic, M. M., & Andrade, M. C. (2009). A change in competitive context reverses sexual selection on male size. *Journal of Evolutionary Biology*, 22(2), 324–333.

When males of different sizes were released at the same time, larger males dominated the competition. Large and small males were equally likely to find females, but larger males were much more likely to mate first and had higher predicted paternity. If small males were released 1 day early, however, the outcome completely reversed, and small males were more successful at finding females (Fig. 4) and almost always mated first. Small males win the scramble to find females because of their more rapid (simulated) development. Most females accept matings from these males relatively quickly, largely in the absence of a rival, and then cease producing pheromones after they mate. By the time larger males enter the arena on day two, it is too late.

These results show that smaller males can benefit overall from developmental acceleration and suggest that an advantage in one episode of selection may carry over to other episodes. One challenge with this study, however, is that the males used were individuals that happened to mature at relatively

large or small size in a laboratory population (in *Latrodectus*, variation in male size is maintained, even in the laboratory). Although the sizes of experimental males were comparable to males found in the field, they were not necessarily males that had switched to longer or shorter development times in response to female cues. So while this experiment shows that small males with a time advantage can have higher fitness than larger males, it does not incorporate other aspects of the plastic phenotype that might have been altered with shifted development. Future work on this species that examines performance of plastic males would be beneficial.



5. Adaptive plasticity: Where are we now?

5.1 Summing it up for cannibalistic, mate-limited spiders

These studies of *Argiope bruennichi* (Section 4.3) and *L. hasselti* (Section 4.5) are arguably the most comprehensive examinations of adaptive developmental plasticity in web-building spiders to date. The probing of the critical period in *A. bruennichi* suggests gaps in our understanding of critical periods, and how cues may differentially affect developmental and activational plasticity. The studies of *L. hasselti* support some key predictions regarding social triggers of plasticity, life history trade-offs of the integrated phenotype, and effects on fitness in nature. Nevertheless, as with the other studies described, all studies to date omit measures of gonadal investment, which may provide an important part of the picture with respect to allocation shifts during development. Moreover, the work falls short of the criteria for demonstrating adaptive plasticity that was described at the start of this chapter (Section 1.2). The tractability of open field studies, microcosm/field-enclosure work and laboratory studies should make it feasible to test for adaptive plasticity more rigorously. With much of the ground-work done, such an approach may help establish these as important models for plasticity.

In general, these studies make clear the potential of spider taxa to advance the field. The extreme restrictions on male mating opportunities paired with first male precedence leads to a common prediction across a wide range of ecologies—accelerated development in the presence of unmated females, although the cues that should trigger these effects may vary. These studies show that developmental shifts in response to cues of social context have evolved in three different families of spiders (Nephilidae, Araneidae, Theridiidae), consistent with broad predictions regarding benefits of protandry and plastic development. Clearly, a simple focus on mating system

is not sufficient, however (Section 4.4), and puzzles remain. Nevertheless, these represent a useful start, demonstrating that a variety of approaches to testing theory in the field and laboratory are possible. This is critical because of the need to “reality check” predictions that are often based on a range of studies, completed in other contexts, that are used to form a sometimes-foggy picture of how the natural history, ecology, and mating system of the focal species are expected to give rise to adaptive plasticity. The risk of “just so” stories is high in the absence of systematic approaches.

Efforts to move toward more comprehensive tests will be facilitated by the routine adoption of standardized, replicable assessments of variables that are relevant to rigorous tests of predictions (e.g., Relyea et al., 2018), by estimates of environmental variation at various scales in nature, and assessment of how those are related to variation in sexually-selected behaviors and related traits. These should be a starting point for the rigorous design of experimental and comparative tests. Although to date the focus has been on how cues and signals from conspecifics shape plasticity, understanding the interaction of these with abiotic indicators of the time of the season may be particularly fruitful in temperate species. Exciting possibilities include the integration of this work with invasion biology in species like *A. bruennichi*, and exploration of the relative importance of spatial structure, seasonal variation, and restricted mating opportunities on the evolution of adaptive plasticity.

5.2 Needed: Detailed empiricism welded to an evolutionary framework

Plasticity is widespread, and may be of critical importance to our understanding of the evolution of phenotypic distributions and responses of populations to environmental heterogeneity (Pigliucci, 2001; Sanger & Rajakumar, 2019; Stearns, 1989a; West-Eberhard, 2003). Although many organisms show some level of plasticity, it may not be the case that most traits are adaptively plastic. A recent meta-analysis of reciprocal transplant experiments in plants (31 studies across 15 families of plants) concludes that most traits are not plastic in response to environmental heterogeneity, and 1/3 of the traits that are plastic are non-adaptive (Palacio-Lopez et al., 2015). Does this hold for animal populations? It is currently unclear (see Scheiner, 2018), and there are insufficient studies of this type in animals to allow a similar analysis. We urgently need comprehensive studies of adaptive plasticity (Nettle & Bateson, 2015) in animal populations across broad taxonomic groups.

An integrative framework would consider how plasticity may arise from the interplay of behavioral, morphological and life history trade-offs across variable ecological contexts (Johansson, Stoks, Rowe, & De Block, 2001; Nylin & Gotthard, 1998), an approach that is particularly challenging due to the complexity of natural systems. Although modeling approaches can be powerful for creating testable predictions, even here, the explicit integration of animal movement, spatial and temporal heterogeneity into comprehensive predictive frameworks has been slow (but see Scheiner, 2013), as has the consideration of the interconnected nature of phenotypic traits (Scheiner, 2018). For empiricists, the need to explicitly test the key predictions of adaptive plasticity models cannot be understated (e.g., Uller, 2008; Uller et al., 2013). This will require overcoming the many challenges to studying adaptive plasticity.

One of the most pressing challenges is achieving a balance between complexity and generality. It is important to develop a strong understanding of what aspects of environmental variation affect individual fitness in the species we study, the cues that may indicate the status of that variation, and critical periods for integrating new information into phenotypes. Creating a realistic predictive framework for a focal species is not trivial, and may require substantial background knowledge and studies of basic behavior, life history, ecology, and natural history. Only these will allow a focus on heterogeneity and cues that are salient to the animal in nature. The second half of this challenge is seeking generalizable inferences that emerge from the nuanced details of such studies (Doughty & Reznick, 2004; Scheiner, 2013), a goal best met through comparative analyses (Doughty, 1995; Pigliucci, Cammell, & Schmitt, 1999). A productive approach to acquiring the empirical underpinnings of comparative tests would consider not a focal “model species,” but rather ensure that the focal species belongs to a “model clade” (see Sanger & Rajakumar, 2019). A model clade approach can simplify the legwork required to determine salient heterogeneity, cues, and tests of plasticity because similarity across closely-related species allows commonality of understanding and methodology (e.g., Section 3; Relyea et al., 2018). Thus the ultimate goal of understanding the evolution of adaptive plasticity, and moving the field forward globally, depends not only on advances in theory but also careful empirical work conducted with rigor within a known phylogenetic framework, on carefully chosen taxa.

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