

Chapter 2

Potential for CFC in Black Widows (Genus *Latrodectus*): Mechanisms and Social Context

Maydianne C.B. Andrade and Emily C. MacLeod

Abstract Understanding the causes of variation in paternity is an important goal of research in sexual selection. While much progress has been made in understanding the dynamics of pre-copulatory mate choice and competition, post-copulatory processes that affect paternity are much less well understood. Distinguishing cryptic female choice (CFC, biases in paternity due to female post-copulatory preferences) from sperm competition (SC, competition among ejaculates for fertilization) and particularly from sexual antagonistic coevolution (SAC, intersexual conflict over mating frequency or fertilization) is at best challenging, and at worst, may be impossible. One way forward is to identify taxa in which comparative approaches, field studies, and detailed mechanistic study are all tractable, as these may allow the design of critical tests of distinguishing predictions of these intertwined hypotheses at different levels of analysis. Here, we focus on the widow spiders, the approximately 30 species in the genus *Latrodectus*, as a promising group for future work on CFC. *Latrodectus* spiders are distributed worldwide and show a fascinating range of mating systems set in variable ecological and social contexts. We outline how some of the aspects of *Latrodectus* natural history and biology may favor CFC rather than (or in addition to) pre-copulatory choice. Moreover, inter- and intraspecific variation in the benefits of CFC may provide the opportunity for comparative and intraspecific studies. We then identify likely mechanisms of CFC in this genus and end by providing suggestive evidence for CFC in a few of the species that have been studied in detail. Although there is no evidence for sperm selection in the *Latrodectus* to date, female behavior can lead to biases in paternity via changes in copulation frequency, duration, and remating as a function of male courtship effort. In addition, although first-male sperm precedence mediated by the deposit of sperm plugs is common in this genus, females may be able to manipulate the success of this internal plug and

M.C.B. Andrade (✉) · E.C. MacLeod
Department of Biological Sciences and Department of Ecology & Evolutionary Biology,
University of Toronto Scarborough, Toronto, ON, Canada
e-mail: mandrade@utsc.utoronto.ca

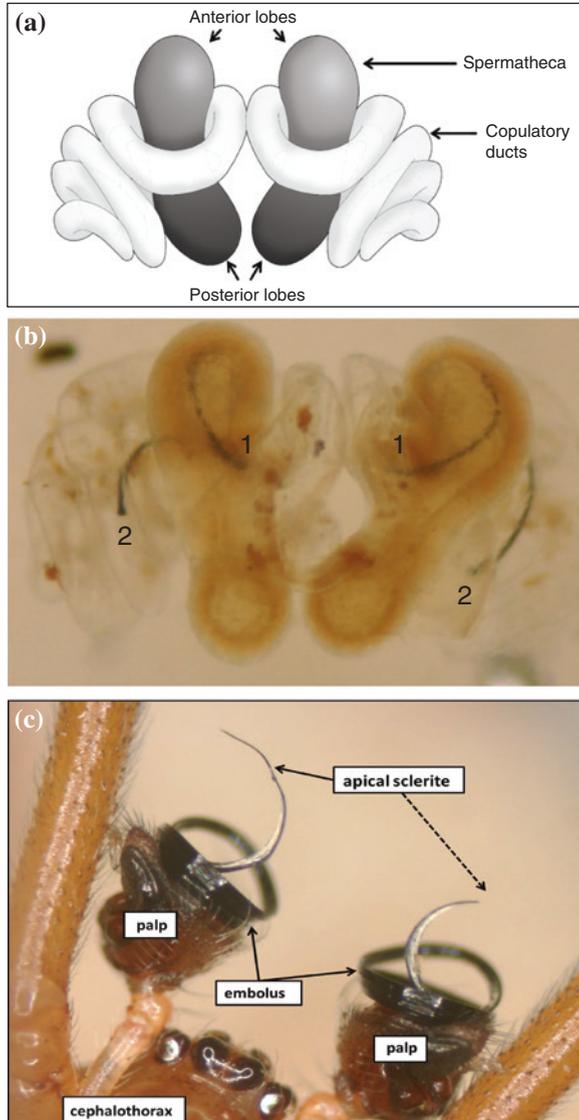
retain the ability to cede paternity to later mates. Since relatively few *Latrodectus* species have been studied in detail, this discussion is necessarily suggestive, rather than conclusive. Nevertheless, the available data suggest increased focus on this genus may prove productive for examining causes and consequences of CFC.

2.1 Introduction

Cryptic female choice (CFC) may be defined as the occurrence of paternity biases among males that arise as a result of behavioral, physiological, or morphological traits of females that favor certain mates over others (Eberhard 1996). The question of how to identify CFC and distinguish it from other post-copulatory processes that may cause biased paternity has led to considerable debate and disagreement (see Chap. 1 for an overview; Eberhard 1993; Arnqvist and Rowe 1995, 2005; Birkhead 1998, 2000; Eberhard 2000; Kokko et al. 2003, 2006). For example, direct competition between the ejaculates of males within females (sperm competition, SC, Parker 1970; Birkhead 2000; Simmons 2001) and CFC could both shape sperm use patterns in similar ways since sperm competitiveness may be linked to other aspects of male phenotype (Birkhead 2000; Evans et al. 2013). Similarly, when there is sexual conflict over mating frequency and fertilization, sexually antagonistic coevolution (SAC) may lead females to resist male mating attempts and male adaptations for controlling fertilization (Arnqvist and Rowe 2005). Since males with certain phenotypes may be more likely to overcome this resistance, biases in fertilization linked to male phenotypes may result, and the outcomes may resemble those expected under CFC (Birkhead 1998, 2000). Although these processes may be intertwined in reality, assessing how mating outcomes affect the fitness of females and their offspring in nature may be informative since only CFC explicitly predicts net genetic benefits to offspring of choosy females (Chap. 1, Kokko et al. 2003, 2006). Similarly, comparative analyses of morphology and behavior may allow identification of intersexual evolutionary arms races (SAC, e.g., Arnqvist and Rowe 2002), the evolution of sensory adaptations of females that enhance assessment of or stimulation by males (CFC, Eberhard 1994, 2000), or the evolution of male traits that increase competitive fertilization success (SC, Simmons 2001). A review of these debates and possible resolutions is beyond the scope of this chapter. While acknowledging the challenges inherent in identifying CFC, the primary goal of this chapter is to discuss existing evidence for the importance of CFC in one taxon: the widow spiders (genus *Latrodectus*), and to argue that several features of this group may make it a good subject for tests of theory regarding the evolution and effects of post-copulatory processes affecting paternity. There are currently few empirical studies that directly examine paternity biases in *Latrodectus*, so this review does not include distinguishing tests, but is rather a review of aspects of the available literature that suggests the potential importance of CFC. We start by suggesting three general features of taxa in which studies of CFC are feasible and likely to be productive for testing distinguishing predictions of CFC, SAC, and SC.

First, it is desirable to identify species in which paternity biases arising from SC can be distinguished from biases induced by female-directed processes such as

Fig. 2.1 Reproductive organs of *Latrodectus hesperus* female (a, b) and male (c), which are representative of genital morphology in this genus. A line drawing of the ventral view of the internal genitalia shows the anterior and posterior lobes of the two spermathecae and the coiled copulatory ducts (a). The dissected, cleared reproductive organs of a field-caught female (b) contains four sclerites (bases labeled with numbers). Two sclerites are placed at the entrance to the spermathecae and are likely to be successful sperm plugs (1), and two sclerites are deposited within the copulatory ducts and will not function as plugs (2). Sclerites are the broken apical portions of the embolus of the male's pedipalp (*palp*, c), which is inserted in the copulatory ducts. Arrows indicate the base of the apical sclerite (which is missing on the *right* palp, dotted arrow). The membranous *pars pendula* is visible in the terminal coil of each embolus. Line drawing (a) created by Simon Ford



variation in sperm storage or differential sperm use at fertilization. In many spiders, sperm are transferred in a non-motile (encapsulated) state, (Michalik and Ramírez 2014), ejaculates from different copulations are stored in separate storage organs (spermathecae, e.g., Fig. 2.1, Levi 1959; Bhatnagar and Rempel 1962; Snow and Andrade 2004; Berendonck and Greven 2005; Neumann and Schneider 2011), and direct SC is thus minimized, making spiders attractive subjects for studying (other) post-copulatory processes (Eberhard 2004). *Latrodectus* have independent spermathecae, each of which is filled in independent copulations (see Sect. 2.2.3.1), so the influence of SC on sperm use patterns is likely to be low (Berendonck and Greven 2005).

Second, one can identify species (or contexts) in which post-copulatory choice is likely to be more advantageous for females than pre-copulatory (mate) choice. Although there are debates about the strength of selection on female choice for indirect (genetic) benefits (the only source of benefits for CFC), females commonly show mate preferences in species in which males do not provide resources, but there is significant phenotypic variation among potential sires (Andersson 1994; Kokko et al. 2003, 2006). Preferences in these species arise if the fitness of choosy females is high compared to that of females that mate indiscriminately (Jennions and Petrie 1997; Kokko et al. 2003, 2006). However, even if females show strong mate preferences, these may not be expressed in (pre-copulatory) mate choice in nature if costs of choice are sufficiently high (De Jong and Sabelis 1991; Jennions and Petrie 1997; Kokko and Mappes 2005). This may be the case if, for example, rejecting a potential mate leads to costly delays in offspring production or a high risk of infertility for virgin females (De Jong and Sabelis 1991), such as when the encounter rate with males is low (Kokko et al. 2003, 2005; Heubel et al. 2008). In cases like these, females may mate relatively indiscriminately to ensure fertilization, but selection may favor females that can adjust paternity independent of male mating success (e.g., De Jong and Sabelis 1991; Kokko and Mappes 2005; Bleu et al. 2012).

Third, it is useful to examine taxa in which studies are tractable at different levels of analysis to allow tests of predictions at ecological and evolutionary time-scales. Mechanistic and behavioral experiments in the laboratory are invaluable, and it is equally important to be able to identify proxies for fitness in nature. Such species-level studies would ideally occur in a taxon with a well-resolved phylogeny and sufficient inter-specific variation in ecology and social behavior to provide the raw material for comparative analyses of evolutionary predictions of CFC, SAC, and SC (e.g., Arnqvist and Rowe 2002).

Below, we outline aspects of the biology and natural history of *Latrodectus* spiders that are consistent with these latter two features (since the advantages of these types of spiders with respect to minimizing SC have been established elsewhere, Eberhard 2004) and thus suggest these spiders may be good models for studies of CFC. We then outline the reproductive biology of *Latrodectus* spiders to identify potential mechanisms of CFC in this genus (see Sect. 2.2.3). Finally, we summarize data from existing studies that may suggest females are employing CFC in a few of the well-studied species (see Sect. 2.3). One goal of this chapter was to highlight avenues for research that is likely to produce fruitful studies of sexual selection within *Latrodectus* species while contributing to a larger comparative data set. Currently, empirical investigations of mating behavior, ecology, and reproductive success are rare in *Latrodectus*, with experiments reported in just 7 of the 30 species in the genus (*L. geometricus*, *L. hasselti*, *L. hesperus*, *L. mactans*, *L. pallidus*, *L. revivensis*, and *L. tredecimguttatus*). These studies include investigations of intersexual and intra-sexual interactions as well as their outcomes (correlates of mating success, sperm use patterns, sperm plugs, courtship behaviors, intersexual aggression, and cannibalism), studies of female distribution and success in the field, as well as analyses of how changes in ecological or social context that affect female fitness are linked to mating outcomes. It is our hope that more such work on additional species will eventually

allow leveraging of the variation found in this genus to test distinguishing predictions of CFC compared to other post-copulatory mechanisms (particularly SAC).

2.2 Natural History and Biology of *Latrodectus* Spiders in the Context of CFC

Here, we review features of *Latrodectus* natural history and biology that appear to be common to most species that have been studied to date, and highlight areas of known variability as well features that may be relevant to understanding post-copulatory processes. What follows is a piecing together of likely patterns from studies or descriptions from different species, with leading superscripts on citations indicating the *Latrodectus* species from which each description is derived (Table 2.1).

2.2.1 Comparative Context and Variation

Spiders in the genus *Latrodectus* (informally, the ‘widow’ spiders, family Theridiidae) comprise approximately 30 recognized species with worldwide distribution (Levi 1959; Garb et al. 2004), living under a wide range of ecological conditions (Lubin et al. 1993; Carrel 2001; Salomon et al. 2010; Trubl et al. 2012; Simo et al. 2013). Widows are well known in popular culture because of their neurotoxic venom (Jelinek 1997; Ushkaryov et al. 2004), the tendency of several species to thrive in anthropogenically disturbed habitats (Trubl et al. 2012; Vetter et al. 2012), and

Table 2.1 *Latrodectus* species for which information is reported in the chapter with their associated in-text reference numbers (noted as leading superscripts on the relevant citations^a)

Species	Superscript reference number
<i>L. mirabilis</i>	1
<i>L. antheratus</i>	2
<i>L. corallinus</i>	3
<i>L. diaguita</i>	4
<i>L. mactans</i>	5
<i>L. hesperus</i>	6
<i>L. variolus</i>	7
<i>L. revivensis</i>	8
<i>L. bishopi</i>	9
<i>L. hasselti</i>	10
<i>L. curacaviensis</i>	11
<i>L. pallidus</i>	12
<i>L. tredecimguttatus</i>	13
<i>L. geometricus</i>	14
<i>L. indistinctus</i>	15

^aSpecies notes are not provided for review papers comparing more than 4 species

because of their lurid reputation for females that kill and consume courting males (D'Amour et al. 1936). In reality, there is a wide range of mating systems in this genus (e.g., Breene and Sweet 1985; Forster 1992; Andrade 1996; Knoflach and van Harten 2002; Segev et al. 2003; Segoli et al. 2006), ranging from polygyny and polyandry to the most extreme examples of male monogyny enforced by polyandrous female cannibals (observed in two species to date: Forster 1992; Segoli et al. 2008a). For example, in the Australian *L. hasselti*, males are monogynous and facilitate cannibalism by females (Forster 1992; Andrade 1996), but neither of these behaviors is found in the sister taxon *L. katipo* (Kavale 1986; Forster 1992). Similarly, there is variation in the frequency of polyandry, with females of some species rarely remating (Herms et al. 1935) but others mating with multiple males (Andrade 1996; Knoflach and van Harten 2002; Segoli et al. 2006; MacLeod 2013). In the absence of polyandry, CFC and SC do not exist, but SAC may be intense (Arnqvist and Rowe 2005). Thus, this type of variation may provide a strong basis for using phylogenetically independent contrasts to infer causes and consequences of CFC, SC, and SAC (e.g., Harvey and Pagel 1991 and see suggestions below).

Recent analyses suggest *Latrodectus* spiders may have undergone relatively recent, rapid speciation. The latter is consistent with the broadly similar morphological (e.g., Levi 1959, 1983), behavioral (Kaston 1970; Ross and Smith 1979a; Breene and Sweet 1985; Forster 1992; Neumann and Schneider 2011), and venom (Garb and Hayashi 2013) characteristics across most species in the genus. While genital morphology is unusually (for spiders) similar across species (Levi 1959, 1966; Knoflach and van Harten 2002), there is subtle, but potentially important interspecific variation in the relative diameter of male compared to female genital structures (Bhatnagar and Rempel 1962; Knoflach and van Harten 2002). Since these variations are likely to affect the success of cuticular sperm plugs often left inside females by mating males in all *Latrodectus* species (see Fig. 2.1 and Sect. 2.2.3.1 below, Levi 1959, 1961; Bhatnagar and Rempel 1962; Knoflach and van Harten 2002; Berendonck and Greven 2005), these could reflect a history of CFC, SC, and/or SAC (e.g., Eberhard 1985, 1996; Arnqvist and Rowe 2005). This genus could thus allow comparative study of hypotheses regarding links between the evolution of post-copulatory sexual selection, genitalic structures, mating systems, and ecology (Eberhard 1985, 1996; Simmons 2001; Arnqvist and Rowe 2005). Although the phylogenetic topology of the genus is not yet completely clear (Garb et al. 2004), recent work (Garb and Hayashi 2013) including sequencing of the genome of *L. hesperus* (BCM-HGSC i5 k Pilot Project, Accession: PRJNA168123 ID: 168123) suggests a more well-resolved phylogenetic analysis based on robust molecular data will soon be available.

2.2.2 Ecology and Phenology: CFC May Be More Likely that Mate Choice

Latrodectus are multivoltine with an annual (males, some females) or biennial (some females) life cycles and overlapping generations (^{5,6,7}Kaston 1970; ^{1,2,3,4}

Estévez and González 1991; ⁶Salomon et al. 2010). Males develop more rapidly (in fewer instars) and have much shorter life spans than females (typically, weeks compared to a year or more, ^{14,15}Smithers 1944; ^{5,6,7}Kaston 1970; ¹⁰Andrade and Banta 2002). Females are sedentary, but males are nomadic and search for potential mates as adults. Most reproductive activity occurs over the course of a few months, the duration and timing of which varies with geographic region (^{14,15}Smithers 1944; ^{5,6,7}Kaston 1970; ^{5,6,13,14}Levy and Amitai 1983; ⁸Anava and Lubin 1993; ⁹Carrel 2001; ⁸Segev et al. 2003; ⁶Salomon et al. 2010; ⁶Salomon 2011), but which encompass ‘spring through fall’ in temperate environments. All developmental stages of both sexes may be present in populations throughout their active season (¹²Segoli et al. 2006; ⁶Salomon 2011). Nevertheless, population structure often changes in predictable ways over time (Elias et al. 2011), such that the number of mate-searching males (⁸Anava and Lubin 1993; ⁸Segev et al. 2003) and thus the potential for and cost of pre-copulatory choice would vary over time for virgin females (De Jong and Sabelis 1991; Kokko et al. 2003; Kokko and Mappes 2005; Heubel et al. 2008; Bleu et al. 2012). For example, challenging climatic conditions combined with minimal prey availability (e.g., hot dry weather, winter, ⁶Salomon 2011) characterize ‘low’ activity periods where spider development may be retarded (⁵D’Amour et al. 1936; ¹⁰Downes 1987), and males or juveniles may be more likely to die than adult or subadult females. In the same habitats, seasonal changes associated with increased prey abundance (i.e., spring, wet season) correspond with increased spider activity and density and thus the availability of potential mates (⁶Salomon et al. 2010; ⁶Salomon 2011). Thus, there may be cyclical variation in the net fitness effects of pre-copulatory compared to post-copulatory choice for females, mediated by the risk of remaining unmated (De Jong and Sabelis 1991). Mate rejection (pre-copulatory choice) at times of year when there are relatively few males (⁸Anava and Lubin 1993; ⁶Salomon et al. 2010) could lead to significant delays in mating, or the risk of not mating at all (De Jong and Sabelis 1991; Kokko and Mappes 2005; Elias et al. 2011; Bleu et al. 2012). In contrast, under the same conditions, females that permit the first-arriving male to mate but bias paternity toward better males that are encountered later will have secured fertility insurance while also ‘trading up’ to preferred sires for their offspring (e.g., De Jong and Sabelis 1991; Pitcher et al. 2003; Bleu et al. 2012). In addition, if there are seasonal shifts in the frequency of preferred males, this may also make CFC beneficial. For example, in at least two *Latrodectus* species, male body size, mass, or condition show significant differences between the early and late season (⁸Segev et al. 2003; S. Fry, personnel communication), and wide variation in male body size has been reported in many species (^{5,6,7}Kaston 1970; ⁸Segev et al. 2003; ⁶Brandt and Andrade 2007). Some of this variation arises from developmental plasticity (¹⁰Kasumovic and Andrade 2006; ¹⁰Stoltz et al. 2012). However, the maintenance of considerable phenotypic variation under standardized laboratory rearing (e.g., males range from 6.1 to 27.1 mg in *L. hesperus*) suggests additive genetic variance underlies some of these differences, and this may represent a source of indirect benefits for choosy females (¹⁰Brandt and Andrade 2007). Thus, mechanisms of CFC may arise because there

are benefits to manipulating paternity for females that become sexually mature at a time of year when males with less-preferred phenotypes are common.

There is evidence that the risk of remaining unmated is significant in nature for females of several species of *Latrodectus* (¹²Segoli et al. 2006). Even when males are numerous, a patchy distribution of males on females' webs is common (¹⁰Kasumovic and Andrade 2009). Whereas some females have more than five (and up to 8) males present simultaneously in the field (⁸Anava and Lubin 1993; ¹⁰Andrade 1996), the median in most species appears to be 1 or 2 males per female, and observations include many females with no males on their webs (^{5,7,9,11}McCrone and Levi 1964; ⁸Anava and Lubin 1993; ¹⁰Andrade 1996; ⁸Segev et al. 2003; ¹²Segoli et al. 2006). Even in enclosures with experimental release of males, some females do not attract any mates (e.g., ¹⁰Kasumovic and Andrade 2009) and this risk is higher for females on poor diets (⁶MacLeod and Andrade 2014). Consistent with this, among field-collected females in two species, 12 % (¹²Segoli et al. 2006) to 17 % (Andrade and Kasumovic 2005) were unmated. Even if these data represent delayed mating of some females (rather than no mating), this also entails a significant risk in nature, where mortality from extrinsic sources is unpredictable and even relatively small mating disadvantages can affect female fitness (Kokko and Mappes 2005). Moreover, virgin females suffer from decreased longevity relative to mated females in at least one species (¹⁰Stoltz et al. 2010), which adds to the risk of forgoing mating. We predict that these risks will lead to the evolution of mechanisms for CFC rather than pre-copulatory mate choice in some *Latrodectus* species.

Since the risk of remaining unmated is likely to vary with the local or seasonal availability of males, the occurrence of CFC could vary in predictable ways within or across species. This variability provides the opportunity for interesting comparative or intraspecific tests of links between variation in male availability and CFC (Kokko and Mappes 2005) that we have suggested here. For example, in species where male density is relatively invariable across the mating season (¹²Segoli et al. 2006), or where the risk of not mating is negligible, the evolution of CFC may be less likely than in species with variation in the density of males (or of those males with preferred phenotypes; ⁸Anava and Lubin 1993) and a higher risk of not mating. Moreover, within species with variable male density, we would predict females would employ CFC more commonly at times of year or in microhabitats where males are scarce (e.g., Elias et al. 2011), but may more frequently reject their first suitor when the local density of males is high. *Latrodectus* females have access to cues of mate availability since males frequently cohabit with immature females in nature (⁸Segev et al. 2003; ¹²Segoli et al. 2006), multiple males may be present on an adult female's web simultaneously (⁵D'Amour et al. 1936; ⁸Anava and Lubin 1993; ¹⁰Andrade 1996), and females may detect chemical cues released by nearby males (Elias et al. 2011). In other spiders, females adjust their mating behavior as a function of their juvenile experience with males via direct social interactions or cohabitation (Hebets 2003; Johnson 2005). In *Latrodectus* however, first-male sperm precedence is common (see Sect. 2.2.3.3) and so 'trading up' would require cryptic mechanisms (CFC) for shifting paternity to favor better males that are encountered later (see Sect. 2.3).

2.2.3 *Reproductive Biology and Possible Mechanisms of CFC*

Here, we describe *Latrodectus* genitalia and focus on those features that may be relevant to post-copulatory processes. *Latrodectus* genitalia show relatively small differences among species, so our description of common structures is likely to apply broadly across the genus (^{8,12,13}Levi 1966; Knoflach and van Harten 2002). We then describe mating behavior (Sect. 2.2.3.2), which seems to be quite similar across the genus in terms of sequence and elements. Finally, we discuss paternity (Sect. 2.2.3.3) and mechanisms that females might employ to effect paternity biases if they mate initially with a non-preferred male (Sect. 2.3).

2.2.3.1 *Genital Morphology and Possible Mechanisms of CFC*

Latrodectus females have paired, independent spermathecae (sperm storage organs, Fig. 2.1), each of which is entered through a coiled copulatory duct that is accessed via one of two copulatory pores (⁶Bhatnagar and Rempel 1962). Sperm exits each spermatheca via a separate fertilization duct (⁶Bhatnagar and Rempel 1962; Austad 1984). Males have paired intromittent organs (pedipalps, Fig. 2.1) with a heavily sclerotized, coiled structure (the embolus) that completely penetrates one of the female's copulatory ducts during separate (ipsilateral) copulatory insertions (Knoflach and van Harten 2002). The copulatory pores are located on a ventral abdominal sclerotized genital plate (epigynum) which has numerous mechanoreceptive hairs overhanging the genital opening (^{5,6,7}Kaston 1970; ⁸Berendonck and Greven 2002, ⁸2005). Spermathecae are 'dumbbell' shaped with a relatively narrow medial channel joining the anterior and posterior lobes (Fig. 2.1). During copulation, the embolus is usually threaded through the copulatory duct until the tip extends into the anterior spermathecal lumen (⁶Bhatnagar and Rempel 1962). SC and morphology studies suggest that fertilization success is maximized if males ejaculate in this location, whereas sperm storage is less likely if males fail to fully insert the embolus and instead ejaculate in the copulatory ducts (⁵Abalos and Baez 1963; ¹⁰Snow and Andrade 2004).

The embolus consists of two parts: the heavily sclerotized but flexible truncus (⁶Bhatnagar and Rempel 1962) with a median channel along its length into which is fused the membranous pars pendula (or ejaculatory duct, ⁶Bhatnagar and Rempel 1962), through which sperm flows. The pars pendula terminates at a rounded hump or recurved tooth which marks the base of the apical sclerite, the distal-most part of the truncus through which sperm is released. The hump or tooth at the base of the sclerite marks a point at which the embolus will often break during copulation (reviewed in: Uhl et al. 2010), leaving the apical sclerite lodged inside the female's genitalia (Fig. 1.1, ⁶Bhatnagar and Rempel 1962; ⁸Berendonck and Greven 2002). The sclerite could function as a sperm plug, blocking insemination (but not mating) by subsequent males, if its base is lodged in the end of the

copulatory duct (⁶Bhatnagar and Rempel 1962; ¹⁰Snow and Andrade 2005; ¹⁰Snow et al. 2006; ¹³Neumann and Schneider 2011). However, male success at plugging females is variable. Although in some species males always lose one sclerite with each copulation (¹⁴Segoli et al. 2008a), in others sclerite loss is variable (¹²Segoli et al. 2008b; ¹³Neumann and Schneider 2011; ⁶MacLeod 2013). Moreover, even when sclerites are lost, males sometimes place them in the copulatory ducts or entirely inside the spermatheca, locations where they fail to block rivals (¹²Segoli et al. 2006, 2008b; ¹⁰Snow et al. 2006; ⁶MacLeod 2013). The rate of plug placement failure apparently varies among species, with failure rates approaching 50 % of copulations in some species (Knoflach and van Harten 2002; ¹⁰Snow and Andrade 2004; ¹³Neumann and Schneider 2011; ⁶MacLeod and Andrade 2014). Thus, although plug-mediated first-male sperm precedence does occur in *Latrodectus*, paternity outcomes are variable and male or female traits, or their interaction could affect this variability (see Sect. 2.2.3.3, ¹⁰Andrade 1996; ¹⁰Snow and Andrade 2005; ¹⁰Snow et al. 2006; ¹³Neumann and Schneider 2011).

Some of the variation in plugging success in *Latrodectus* is likely related to interspecific variation in the size and structure of the copulatory ducts at their point of entrance into the spermathecal lumen (Knoflach and van Harten 2002). In some species, the point of entry of the copulatory ducts to the spermatheca is a narrow, well-defined collar that is sufficiently small relative to the size of the sclerite to make blockage of the entrance likely (⁶Bhatnagar and Rempel 1962; ⁸Berendonck and Greven 2005). In other species, the point of entry is relatively broad and much less likely to be plugged by a single sclerite (Uhl 2002; Knoflach and van Harten 2002). This is consistent with the observation that mated females of some species are typically found with only one sclerite lodged at the entrance to each spermatheca (e.g., ^{5,6,13,14}Levy and Amitai 1983; ⁸Berendonck and Greven 2002; Knoflach and van Harten 2002; ⁶MacLeod 2013) and any other sclerites present are located in the copulatory ducts (⁶Bhatnagar and Rempel 1962; ¹⁰Snow et al. 2006; ⁶MacLeod 2013). In contrast, in other species, the rate at which multiple sclerites are found in the same spermathecal opening ('failed plugs') is high; at least 50 % of field-collected *L. pallidus* females had at least one failed plug (¹²Segoli et al. 2008b). Although not systematically documented, illustrations of the genitalia of field-caught females show failed plugs in several other species which also appear to have relatively wide points of entry to the spermathecae (*L. renivulvatus*, *L. geometricus*, *L. dahli*, Knoflach and van Harten 2002). Variation in this aspect of female morphology across species is likely to have a significant effect on whether plugs can affect sperm use patterns, but this has never been tested. A comparative analysis of the rate of plug failure as well as the relative size of male and female genital structures across species may reveal past selection via sexual conflict over the control of fertilization (SAC) or via sexual selection (CFC or SC). Such an analysis would also identify those species in which plugging failure rates are relatively high and in which CFC may thus be more likely. This type of study would be facilitated by the fact that sclerites are not disturbed by fertilization and remain lodged in females even after their death (e.g., sclerites are visible in the dissected spermathecae of females preserved for decades in alcohol).

There has long been speculation that having independent sperm storage organs that are inseminated in separate copulations could make sperm selection particularly feasible in some invertebrates (Siva-Jothy and Hooper 1996; Simmons 2001). Berendonck and Greven (2005) looked in *L. revivensis* for internal structures that might permit differential sperm usage from the two spermathecae and thus suggest a mechanistic basis for CFC. At fertilization, sperm empties from the posterior lobe of the spermatheca through a common fertilization duct into the uterus externus, the site of fertilization (⁶Bhatnagar and Rempel 1962; ^{1,3,11}De La Serna De Esteban et al. 1987; ⁸Berendonck and Greven 2005), via a process that is not well understood in spiders (Foelix 1982). In *L. revivensis*, the tube through which sperm enters the common fertilization duct is heavily sclerotized on one side and membranous on the other side and may function as a valve that controls the movement of sperm at fertilization (⁸Berendonck and Greven 2005). In its neutral state, the valve is closed, but muscle contractions could pull it open, theoretically creating negative pressure in the fertilization duct, and drawing sperm out of the spermathecae (⁸Berendonck and Greven 2005). This may be achieved by a band of muscle that connects the internal surface of the epigynum to the terminal portion of the copulatory duct and the ventral side of the common fertilization duct, and/or by a second, paired muscle that extends from the epigynal plate to the common fertilization duct (^{2,3}Lauriade Cidre 1988; ⁸Berendonck and Greven 2005). However, this valve would draw sperm from both spermathecae simultaneously, and in the absence of any recognizable mechanisms for differential sperm release, Berendonck and Greven (2005) argued that CFC by sperm selection is unlikely in *L. revivensis* or other species with comparable morphology.

However, we suggest there are other ways that the fertilization valve could affect paternity. For example, since the spermathecae often contain proteins and fluids even before mating (⁸Berendonck and Greven 2002 ⁸2005; Useta et al. 2007; Michalik and Ramírez 2014), females that opened this valve during copulation (rather than during fertilization) might draw fluids out of the spermatheca, thus affecting pressure in the spermathecae and copulatory ducts. Such a change could alter the likelihood of effective insemination or even plug placement by the female's current mate. Since males insert in one spermatheca at a time, such a mechanism could allow females differential control over sperm storage and plugging, and thus over first-male sperm precedence (Sect. 2.2.3.3). The possibility that these contractions could be triggered by male stimulation of the epigynal hairs during courtship and mating is particularly intriguing. Since males typically move the embolus across the epigynum multiple times before insertion is achieved, repeated contact between the pedipalps and these hairs is common (^{5,6,7}Kaston 1970) and may serve a stimulatory function ('copulatory courtship,' e.g., Huber 2005; Eberhard and Huber 2010). Whether the fertilization valve is activated during copulation, is linked to stimulation of the epigynal hairs, and whether paternity is affected could be studied with a combination of mating trials, sensory-hair ablation (e.g., Aisenberg et al. 2015), muscle physiology, and freeze-fixation (Huber 1993).

2.2.3.2 Mating Behavior and Possible Mechanisms of CFC

At sexual maturity, males abandon the webs on which they developed and localize females using airborne pheromones released from the female's silk (⁸Anava and Lubin 1993; ⁶Kasumovic and Andrade 2004; ¹⁰Andrade and Kasumovic 2005; ⁶MacLeod and Andrade 2014). Female production of sex pheromones varies with mating status, age or developmental stage (¹⁰Stoltz et al. 2007; ¹⁰Perampaladas et al. 2008; ¹⁰Jerhot et al. 2010), and diet (⁶MacLeod and Andrade 2014). This likely explains why females attract fewer males when they are immature than when they are mated (¹⁰Andrade and Kasumovic 2005; Kasumovic et al. 2009b; ⁶MacLeod 2013), and (in some species) when they have had food withheld (⁶Johnson et al. 2011; ⁶MacLeod and Andrade 2014). Nevertheless, in nature, males also mate with previously mated females (⁸Segev et al. 2003; ¹²Segoli et al. 2008b; ⁶MacLeod 2013) and are often found cohabiting with subadult females (⁵D'Amour et al. 1936; ⁸Anava and Lubin 1993; ¹⁰Andrade and Kasumovic 2005). Males may encounter juveniles by chance while searching for adult females (subadults do not produce sex pheromones in some species, ⁸Anava and Lubin 1993; ¹⁰Jerhot et al. 2010), or they may respond to chemical cues produced by juveniles (⁶Ross and Smith 1979b).

Despite guidance from chemical signals, male mortality is very high during mate searching (>80 %) in some species (¹⁰Andrade 2003; ⁸Segev et al. 2003; ¹²Segoli et al. 2006), and it seems likely to be costly in others where spiders that change web location suffer approximately 40 % mortality (⁸Lubin et al. 1993). The challenges of seeking females may thus impose strong selection on males (e.g., Foellmer and Fairbairn 2005). If so, mate searching may act as a 'first filter' that narrows the types of males to which virgin females are exposed, decreasing the benefits of CFC. Laboratory studies show that larger *Latrodectus* males have a mobility advantage over smaller males (¹⁰Brandt and Andrade 2007; but see Moya-Larano 2002), but field studies show no clear effect of male phenotype (size, mass, or condition) on mate-searching success (¹⁰Andrade 2003; ⁸Segev et al. 2003; size: ¹²Segoli et al. 2006). This may be an issue of statistical power since few males are successful (e.g., ¹⁰Andrade 2003; ¹²Segoli et al. 2006) or it may be that the most relevant phenotypic traits for searching success were not assessed (e.g., intermediate-sized males have the highest metabolic efficiency, ¹⁰De Luca et al. 2015). However, regardless of any possible phenotypic advantages of intermediate or large-sized males, the more rapid development of relatively small males may allow them to reach newly matured females more rapidly (¹⁰Kasumovic and Andrade 2006, 2009; Elias et al. 2011). Thus, it is not yet clear whether females are courted by a restricted subset of males in nature.

After reaching a female, males may cohabit on or near the female's web for a variable period, particularly if the female is not yet sexually mature or receptive (^{5,7,9,11}McCrone and Levi 1964; ⁸Segev et al. 2003; ¹²Segoli et al. 2006). Most descriptions of mating are based on laboratory pairings of single males and females, which is common in the field (but see ¹⁰Stoltz et al. 2008; ¹²Harari et al. 2009; ¹⁰Stoltz et al. 2009; ¹⁰Stoltz and Andrade 2010). In these cases, males often

begin courtship shortly after contacting the web (triggered by contact pheromones on the silk, ⁶Ross and Smith 1979b; ¹⁰Stoltz et al. 2007; ¹⁰Jerhot et al. 2010; ⁶Scott et al. 2012). Courtship provides ample opportunity for female assessment of males and for male stimulation of females in more than one modality (e.g., tactile, vibratory, and chemical). Courtship has a number of vibratory elements common to all species thus far described (for details see ^{5,6,7}Kaston 1970; ⁶Ross and Smith 1979a; ¹⁰Forster 1992). Males may also cut and bind portions of the female's web (web reduction), which may reduce pheromone release or alter the female's response to the courting male (Watson 1986; ⁶Scott et al. 2012). In some species, males loosely string silk across the dorsal surface of the female's abdomen ('the bridal veil'), a behavior whose function is unclear (see speculations in ^{5,6,7}Kaston 1970; ⁶Ross and Smith 1979a).

During courtship, females are typically quiescent, hanging dorsal-side-down from the underside of the horizontal snare of their webs with their legs flexed. Females may eventually straighten their legs and allow their body to sag away from the web, a receptive posture that facilitates the male mounting their ventral surface. Males may then begin a period of courtship that includes vibratory and tactile movements while on the female's abdomen (¹⁰Forster 1995). Eventually, males scrape one pedipalp against the female's epigynum, eventually loosening the coil of the embolus and attempting to insert it into one of the female's copulatory pores (Fig. 2.1). There may be multiple copulation attempts, with intervening periods of courtship on the web and abdomen before the male is successful. Courtship duration is impressively long in some species (e.g., mean of 5 h in *L. hasselti*), but on the order of 10 min or less in other species (¹⁰Forster 1995; Knoflach and van Harten 2002). Intersexual interactions during extended courtships could reflect selection via CFC, or could be due to SAC if male stimulation is met with female resistance. However, under SAC, we might expect consistent, overt signs of aggression rather than quiescence in *Latrodectus* since extreme female-biased size dimorphism (females at least 100× heavier than males: ^{5,6,7}Kaston 1970) minimizes the cost of aggression to females. Non-receptive females can (and do) easily knock males out of their webs with no risk of injury (¹⁰Andrade 1996; ¹⁰Stoltz et al. 2008).

After copulating with one palp, males of many species return to the web and court again before attempting to mount the female a second time and insert their second palp (^{5,6,7}Kaston 1970; ⁶Ross and Smith 1979a; ¹⁰Forster 1992; ¹⁰Andrade 1995; ¹⁴Segoli et al. 2008a). The duration and occurrence of the inter-copulatory dismount varies. In some species (and perhaps under some circumstances), males insert both palps in sequence without leaving the female's abdomen (⁵D'Amour et al. 1936; ^{5,7,9,11}McCrone and Levi 1964). The presence of an inter-copulatory interval in some species is intriguing as it is likely to be costly to males given the risk of the appearance of a competitor at any time (¹⁰Stoltz and Andrade 2010). From the female's perspective, however, this period provides an additional opportunity for assessment and discrimination at a point when her mate has inseminated only one of the female's two spermathecae (Snow and Andrade 2005). As we argue below (Sect. 2.3.1), this provides one opportunity for females to bias paternity.

Females receive ample sperm at a single copulation to fertilize their lifetime supply of eggs (¹⁰Andrade and Banta 2002; ⁸Berendonck and Greven 2005) and repeatedly mating with the same male does not increase their fertility (¹⁰Andrade and Banta 2002; ¹²Segoli et al. 2008b). This means virgin females have the option of mating once and leaving one spermatheca empty to accept future mates without suffering any fertility costs. Perhaps this explains why, once mated (even after just one copulation), females' sexual receptivity decreases (¹⁰Andrade 1996; Segoli et al. 2008b; ¹³Neumann and Schneider 2011; ⁶MacLeod 2013). Nevertheless, females clearly copulate more than once in many species, which includes repeated mating with individual males (most often, once with each palp) and multiple mating with more than one male (¹⁰Andrade 1996; ¹⁰Andrade and Banta 2002). Conservative estimates of multiple mating can be derived from assessing the number and position of sclerites inside females' genitalia given that each male can deposit a maximum of two, with one within each tract (¹⁰Andrade 1996; ¹²Segoli et al. 2008b; ¹³Neumann and Schneider 2011; ⁶MacLeod 2013). Studies with systematic sampling of females suggest at least 12–47 % of females are polyandrous (¹²Segoli et al. 2006; ⁶MacLeod 2013), and this is consistent with descriptive studies in which a subset of females collected across species show patterns of sclerite deposition consistent with polyandry (⁶Bhatnagar and Rempel 1962; ⁵Abalos and Baez 1963; Mueller 1985; Knoflach and van Harten 2002; ¹²Segoli et al. 2008b). Molecular studies of paternity would be invaluable to estimate polyandry more precisely, but no such studies are available for any *Latrodectus* species (see Sect. 2.2.3.3).

2.2.3.3 Sperm Use Patterns

The few studies of paternity in *Latrodectus* use sterile male techniques in the laboratory, in which females are mated to irradiated males as well as unmanipulated males, and paternity pattern is inferred from the hatch rate of eggs (Boorman and Parker 1976; Sillen-Tullberg 1981). These studies show that, when two males inseminate the same spermatheca, first-male sperm precedence is the dominant pattern (100–80 % first-male paternity) as expected for species with sperm plugs (¹⁰Snow and Andrade 2005; ¹⁰Snow et al. 2006; ¹³Neumann and Schneider 2011; ⁶MacLeod 2013). However, reversals to second-male precedence (0–20 % paternity of first male) are not uncommon (e.g., found in 18.8 % of cases, ¹⁰Snow and Andrade 2005; 33.6 %, ⁶MacLeod 2013), although sperm mixing (20 to 80 % paternity) is rare (¹⁰Snow and Andrade 2005; ⁶MacLeod 2013). There is some evidence that reversals of first-male priority occur when the first male is unsuccessful at leaving his sclerite in a plug position (¹⁰Snow et al. 2006), but in other studies, there is no straightforward relationship between sclerite loss and paternity (¹³Neumann and Schneider 2011; ⁶MacLeod 2013). This suggests other mechanisms may also determine paternity. One possible explanation for first-male precedence is the relative position of the ejaculates inside the female. The female's spermatheca contains proteins that may form a matrix that holds the first ejaculate in each spermatheca closer to the fertilization duct (⁸Berendonck and Greven

2005). Some of the variation in SC results may arise because the sterile male technique leads to erroneous inferences when baseline levels of male sterility are high and/or sample sizes are small (Rugman-Jones and Eady 2001; Garcia-Gonzalez 2004). This makes even clearer the necessity of paternity studies using molecular methods to corroborate or challenge these apparent patterns.

Although first-male precedence is common when competing males inseminate the same spermathecae, when matings proceed naturally, sperm use patterns may vary considerably (e.g., ranging from 0 to 100 % paternity of the first male to mate, ¹⁰Andrade 1996). In *L. hasselti*, paternity was positively correlated with copulation duration (Andrade 1996), even though sperm transfer required only a fraction of the time spent in longer copulations (Snow and Andrade 2004). Such a result suggests paternity could be mediated by the activity of ejaculatory proteins transferred during longer copulations (Michalik and Ramírez 2014), as these can affect fertilization in other taxa (SC, e.g., Chapman et al. 1995). Another possibility is that females permit longer copulations with preferred males (e.g., ¹³Neumann and Schneider 2011) and these males are then more likely to place plugs successfully, or females later bias paternity in their favor (¹⁰Snow and Andrade 2004). However, the wide range of variation in paternity may also be attributable to the range of different mating outcomes that are possible when two males attempt to mate with the same female. This includes variation in copulation frequency of each male (inseminating both or only one spermatheca), which male inseminates each spermatheca first, and whether first-mating males in each spermatheca deposit an effective plug. Attempts to disentangle these sources of variation are often hampered by relatively small sample sizes. However, experimental matings with manipulated insemination patterns (males forced to inseminate the same or opposite organs, ¹⁰Snow and Andrade 2005) corroborate inferences from morphological studies (⁸Berendonck and Greven 2005) that suggest sperm/ejaculates are released from both spermathecae equally and thus enter the uterus internus without bias at fertilization (also see Sect. 2.2.3.1). Thus, if each male inseminates a different spermatheca, the expectation is a fair raffle paternity pattern (Parker 1990) with an average near 50 % (regardless of plug deposition). Experiments of this type do show paternity is centered on 50 %, but variation is still common (¹⁰Snow and Andrade 2005). Deviations from shared paternity under a fair raffle likely arise from differences in the number of sperm inseminated by each male (Parker 1990) since sperm loads are variable among individuals and within individuals over time (¹⁰Snow and Andrade 2004; ^{6,10}Modanu et al. 2013). Examining links between patterns of deposition and positioning of sclerites within females (Sect. 2.2.3.1) and paternity also reveals sources of variation. In *L. tredecimguttatus* and *L. hesperus*, relatively large males more frequently place successful plugs (¹³Neumann and Schneider 2011; ⁶MacLeod 2013), perhaps because they have longer emboli. Alternatively, females may prefer larger males and affect plug placement success using either a physiological mechanism like the one suggested above (Sect. 2.2.3.1), or behavioral mechanisms. For example, if female quiescence during mating is necessary for successful threading of the embolus into the spermatheca (Sect. 2.2.3.2), then agitation may interfere with plug placement (¹⁰Snow et al. 2006; but see ¹³Neumann and Schneider 2011).

2.3 CFC in *Latrodectus*: Potential Mechanisms and Evidence

Despite the gaps in our knowledge, the reproductive biology of *Latrodectus* spiders suggests at least three possible mechanisms of CFC. These may be employed most commonly if virgin females mate indiscriminately with the first male they encounter (for reasons outlined in Sect. 2.2.2) and then utilize one or more of these mechanisms to allow later-mating males to have higher paternity than would be expected given the common occurrence of first-male sperm precedence (Sect. 2.2.3.3).

First, females may adjust the frequency with which they copulate with particular males. When insemination of the two spermathecae occurs in two discrete copulations separated by an intervening period of additional courtship, females mating with non-preferred males can terminate mating after one, rather than two copulations with relatively little cost or risk. With one spermatheca filled, females will have fertility insurance (¹⁰Andrade and Banta 2002). If the first mate places a successful plug, a later mate can achieve at least 50 % paternity if they inseminate the opposite organ (¹⁰Snow and Andrade 2005; ¹⁰Snow et al. 2006). Moreover, if the first male fails to place a plug (Sect. 2.2.3.1), and the female's second mate inseminates both spermathecae, paternity will then favor the second male overall (e.g., see calculations in ¹⁰Kasumovic and Andrade 2009). Second, females may adjust the duration of copulation with a particular male and affect paternity (¹⁰Snow and Andrade 2005). While the mechanism by which this functions is not yet clear, paternity is correlated with copulation duration in at least one species in the genus (¹⁰Andrade 1996), and a positive correlation between copulation and paternity is common in spiders and other invertebrates (Simmons 2001; Schneider and Andrade 2011). Third, females may be able to affect the positioning of the embolus during ejaculation and sclerite loss. If the first mate is not of a preferred phenotype, females could block plug placement to ensure later males have higher paternity.

2.3.1 CFC and Control of Copulation Frequency

If females restrict first mates to one copulation and subsequently remate only with preferred males, they not only avoid the risk of remaining unmated and retain the option of 'trading up' to more preferred males (Bleu et al. 2012), but they also employ this mechanism after acquiring significant information derived from male courtship behavior, copulatory behavior, and potentially sperm or ejaculate characteristics. This is particularly true because the ability of males to sustain prolonged, vigorous vibratory courtship prior to the first mating attempt may provide significant information about male traits such as metabolic competence, body condition, and juvenile provisioning (which reflects both development history and diet ¹⁰Kasumovic et al. 2009a; ¹⁰Stoltz et al. 2012; Kasumovic and Seebacher 2013;

¹⁰De Luca et al. 2015). Thus, CFC in *Latrodectus* may occur when female-mediated variation in male copulation frequency (equivalent to repeated mating success) is linked to some aspect of male phenotype, and those same traits are linked to the likelihood or frequency of the females copulating with a subsequent suitor. Below, we consider two ways this may manifest: (1) decreased female receptivity to second copulation attempts from some, but not all males; (2) female cannibalism of some males after a single mating, preventing subsequent copulations.

2.3.1.1 Remating and Receptivity to Second Males

While this has not been studied specifically from the perspective of CFC in *Latrodectus*, it is clear that the 2 copulations with each male is not necessarily the norm (¹⁵Smithers 1944; ^{5,6,7}Kaston 1970; ⁸Anava and Lubin 1993; ¹⁴Segoli et al. 2008a; ¹²Harari et al. 2009; ¹⁰Stoltz et al. 2009; ⁶MacLeod 2013). For example Kaston (1970) reports that females become aggressive toward males after one copulation in 2/3 of matings, causing males to retreat and fail to accomplish a second copulation (based on observations in *L. variolus* and *L. hesperus*). Experimental studies of *L. hesperus* and *L. hasselti* suggest that in both species, courtship duration predicts the copulation frequency permitted by females. In recent work, *L. hesperus* females were more likely to copulate twice with males that courted for longer (compared to shorter) durations (⁶MacLeod and Andrade in preparation). As the first step in a SC study (detailed methods in ¹⁰Snow and Andrade 2005; ⁶MacLeod 2013), naive virgin males and females were paired in the laboratory, and mating sequences recorded. Among the 182 males that mated in these trials, 19 % ($n = 38$) copulated only once despite their repeated attempts at second copulations. There was no relationship between copulation frequency and male mass or duration of the first copulation (all $p > 0.05$), but the males with which females copulated only once spent significantly less time courting prior to their first copulation attempt (7.7 ± 0.72 min, $n = 34$) than did males with which females copulated twice (15.0 ± 0.97 min, $n = 146$; generalized linear model with logit link function: Wald $\chi^2 = 19.177$, $p < 0.001$). Moreover, when females from this study were paired with a second male on the next day, females that allowed only one copulation with their first mate were more likely to copulate with a second male (62 % remated, $n = 34$) than were females that allowed two copulations with their first mate (26 % remated, $n = 146$; Fisher's exact test, $p = 0.0002$). This is the opposite of what would be expected if some females simply had low receptivity to male mating attempts in general (e.g., as may be expected from SAC).

2.3.1.2 Premature Cannibalism and Receptivity to Second Males

In *L. hasselti*, a similar effect of courtship duration on female behavior was observed, but the mechanism was more extreme; males were wrapped in silk and killed by females during or after the first copulation ('premature cannibalism,'

¹⁰Snow and Andrade 2005; ¹⁰Stoltz et al. 2008, 2009; ¹⁰Stoltz and Andrade 2010). This could occur in any *Latrodectus* species where cannibalism occurs after the commencement of copulation (^{14,15}Smithers 1944). *L. hasselti* females were more likely to mate twice with her first mate if he courted for longer, or was relatively large (¹⁰Snow and Andrade 2005; ¹⁰Stoltz et al. 2008, ¹⁰2009; ¹⁰Stoltz and Andrade 2010). In these experiments, females were presented with two males simultaneously, so an alternative mate was available for evaluation while females made decisions about premature cannibalism of their first mate. However, as was seen in *L. hesperus*, cryptic preferences in *L. hasselti* also operate in the absence of direct comparisons or competition. In pairings of individual males with naive virgin females, males that were prematurely cannibalized were those with significantly shorter courtships (¹⁰Stoltz et al. 2008) or smaller body size (¹⁰Snow and Andrade 2005) than males that survived their first mating. Thus, CFC may be triggered by some absolute rather than relative criterion with respect to male size and courtship duration. As was the case with *L. hesperus*, remating behavior of *L. hasselti* females was also affected by interactions with their first mate. In *L. hasselti*, this manifested as a strong inverse relationship between the courtship duration of the first male and the female's copulation frequency with a second male (¹⁰Stoltz et al. 2008). Thus, smaller males who invest less in courtship are more likely to be cannibalized after just one copulation, and their mates are more likely to copulate multiple times with a rival.

In *L. hasselti*, decreased receptivity to new males has also been linked to female cannibalism of first males that succeed in mating twice. In a laboratory study, females that consumed their first mate during and after their second copulation were less likely to copulate with a subsequent male compared to females that did not cannibalize their first mate (¹⁰Andrade 1996). This result has not been replicated, however, and it is unclear whether such an effect might arise as a female decision or via chemical manipulation by males (e.g., Andersson et al. 2004; Aisenberg and Costa 2005), particularly since cannibalistic matings are longer and thus may include the transfer of more ejaculatory substances. Chemical manipulation is not likely to explain premature cannibalism, however, as males are often wrapped in silk and disabled, but not consumed by females when attacked during the inter-copulatory interval. Additional study of these aspects of mating and reproduction in this species and in *L. geometricus* (the only other *Latrodectus* in which this type of cannibalism has been reported: ¹⁴Segoli et al. 2008a) would be valuable.

2.3.2 CFC and Control of Copulation Duration

There have been no direct demonstrations of female control over copulation duration in *Latrodectus*, and it seems likely that copulation duration is affected by both male and female behaviors. Nevertheless, observations suggest female behavior may be primarily responsible for limiting the duration of relatively brief copulations (¹³Neumann and Schneider 2011). While females are generally quiescent following

embolus insertion in successful matings, females may also become agitated during copulation and strike at the male, move their legs across the male's body (^{5,6,7}Kaston 1970; ¹³Neumann and Schneider 2011; MCB pers. obs.; ECM pers. obs.), or attempt to bite the male's legs (*L. mirabilis*, L. Baruffaldi, pers. comm.). In copulations involving agitated females, males typically pull the embolus free and retreat shortly after female activity commences (^{5,6,7}Kaston 1970; ¹⁴Segoli et al. 2008a). In *L. tredecimguttatus*, the occurrence of female attacks was linked to significantly shorter copulations (14 vs. 23 min, ¹³Neumann and Schneider 2011). In *L. hasselti*, there is also evidence for female control over copulation duration; males are able to survive partial cannibalism (¹⁰Andrade et al. 2005) during their first copulation, continue to copulate as they are consumed, and in fact copulate for longer as they are being cannibalized (11 vs. 25 min: ¹⁰Andrade 1996; 13 vs. 19 min: ¹⁰Snow and Andrade 2004; 13 vs. 17 min: ¹⁰Snow and Andrade 2005). Copulation typically ends when the female wraps the male in silk. Thus, in this case, it appears that females permit longer copulations when they choose to cannibalize a male.

The mechanism underlying links between paternity benefits and longer copulation durations may be more complex than a direct relationship with sperm transfer. In *L. hasselti*, complete sperm transfer occurs well before the termination of most copulations (¹⁰Snow and Andrade 2004), an effect also shown in another spider where copulation duration is positively related to paternity (*A. bruennichi*: Schneider et al. 2006). Thus, increased paternity shares are not simply due to having more sperm in the 'raffle' (Parker 1990) after longer copulations. This leaves several possible explanations for the link to paternity. First, the additional time may allow males to transfer more ejaculatory fluids or proteins (e.g., Vocking et al. 2013), and these may mediate fertilization success (e.g., via SC or SAC: Simmons and Siva-Jothy 1998). Second, females may preferentially store more sperm (Useta et al. 2007) or preferentially use sperm from males that copulate for longer (CFC, e.g., Argiopidae: Welke and Schneider 2009) and perhaps are better at stimulating the female through copulatory courtship (Eberhard 1994). Third, males that copulate for longer may be higher 'quality' spiders with a range of traits that reflect superior resource acquisition and allocation, including more sperm (¹⁰Snow and Andrade 2005). The mechanisms underlying the relationship between copulation duration, sperm transfer, and paternity is thus ambiguous and would benefit from additional study.

Even if rapid sperm transfer is the rule for *Latrodectus* males (which has not yet been established), there may be species in which there is sufficient female-mediated limitations on sperm transfer to make this an important mechanism affecting paternity. For example, Kaston (1970) reported that copulation durations for *L. hesperus*, *L. mactans*, and *L. variolus* range from 1 to 32 min, with a median between 4 and 8 min. In Neumann and Schneider's (2011) study of *L. tredecimguttatus*, some copulations were also extremely brief (<1 min). Even in *L. hasselti*, a copulation of 2 min predicts transfer of only 67 % of the male's sperm load (calculated from equation provided in Fig. 2 legend in ¹⁰Snow and Andrade 2004). Given the wide variation in the number of sperm carried by males (<500 to >120,000 per palp in *L. hasselti* and *L. hesperus*: ¹⁰Snow and Andrade 2004; ^{6,10}Modanu

et al. 2013), this could lead to a substantial disadvantage in paternity for some males. Studies that focus on the details of these potential mechanisms could provide significant insight into whether female truncation of some copulations might be a mechanism of CFC (see Herberstein et al. 2011). Such studies would elucidate how variation in sperm storage and paternity is related to male traits in natural copulations, and when copulation duration is manipulated to mimic the range of natural variation. This is particularly true if such studies take advantage of the ‘double-barreled’ nature of the genital tracts and apparent correlation between the number of sperm in the male’s two palps (¹⁰Snow and Andrade 2004; ^{6,10}Modanu et al. 2013) to assess and manipulate factors affecting sperm transfer, storage, and copulation duration (see ¹⁰Snow and Andrade 2004 for possible methods).

2.3.3 CFC and the Mechanics of Ejaculation and Plug Placement

In order to ejaculate into female spermatheca and place apical sclerites at the spermathecal lumen, males must fully insert their coiled embolus (2–4 coils depending on the species: Levi 1959) into the female’s insemination ducts (⁵Abalos and Baez 1963; ⁸Berendonck and Greven 2002, ⁸2005; ¹⁰Snow et al. 2006). This apparent structural challenge has led to the hypothesis that brief copulations, or other female-based disruptions to the process, might significantly decrease male insemination or plugging success (⁸Berendonck and Greven 2002; ¹³Neumann and Schneider 2011). This idea has not been well studied, but insights can be gained from two sources. First, Neumann and Schneider (2011) found a significant negative relationship between copulation duration and successful sclerite placement in *L. tredecimguttatus*, where copulation duration was shortened by female attacks. Interpreting the effect of this result on paternity is complicated because SC data from this study were equivocal, and so it is not yet clear whether correctly placed sclerites function as plugs in *L. tredecimguttatus* (¹³Neumann and Schneider 2011). Second, in an experimental study, when Snow and Andrade (2004) artificially terminated copulations of *L. hasselti* after 5 min, the female’s spermatheca already contained about 90 % of the male’s total sperm load. Males apparently had no difficulty reaching into the spermatheca in that time despite having three coils in their embolus (the maximum recorded in the genus is four in *L. geometricus*, the minimum is one in *L. dahli*: ^{5,6,13,14}Levy and Amitai 1983; Knoflach and van Harten 2002). It would be valuable to have additional research that combines observational study with manipulated copulation duration with SC studies and post hoc dissection of genitalia. A focus on the location of sperm masses and sclerites would also be useful. Comparative study could capitalize on such studies since males vary across species in the number of coils (complexity) of their embolus and thus presumably in the mechanical challenge of mating.

We speculate above that females may have internal mechanisms that affect male success at placing plugs, or perhaps the location of ejaculation

(Sect. 2.2.3.1). We close by describing one study that, while not examining polyandry, suggests that virgin females are able to manipulate plug placement by males and may do so as a function of the perceived availability of potential mates (see Sect. 2.2.2, ¹⁰Biaggio 2007). In a laboratory study of the effects of cohabitation on female behavior, subadult females were held alone or with another spider (a male or an early-instar juvenile) for the duration of their penultimate instar to mimic cohabitation (¹⁰Biaggio 2007). Cohabitation cages allowed vibrational and chemical cues to be transmitted between cohabitants, but no direct contact. After their adult molt, focal females were placed in a mating trial with a naïve adult male. Regardless of cohabitation history, females mated readily across all treatments and there was no difference in the number of copulations achieved by males (General Linear Model, $F_{2,55} = 1.371$; $p = 0.262$). However, the number of sclerites in the ‘plug’ position was significantly lower in females that had cohabited with males compared to the other two treatments ($F_{2,55} = 4.02$; $p = 0.023$), although there was no relationship between plug position and any of the measured traits of males or intersexual interactions ($p > 0.5$ for male size, male condition, courtship duration, and copulation duration). This study suggests that females may respond to cues indicating the availability of males (cohabitation) and adjust the likelihood of monopolization of paternity by their first mate (see predictions in Sect. 2.2.2).

2.4 Conclusions

In this chapter, we sought to highlight the potential of spiders in the genus *Latrodectus* for the study of CFC. Our current understanding of the biology and evolutionary ecology of these spiders as it relates to paternity is rudimentary. Nevertheless, the available information suggests future studies in this genus may yield interesting insights into the contexts in which CFC evolves, and how female-mediated effects on sperm use compare to those arising from SC or SAC. We argue that *Latrodectus* females may benefit from choice, but employ cryptic methods to bias paternity toward favored males, rather than rejecting potential males outright because of a significant risk of remaining unmated in nature. The few studies currently available suggest larger, more vigorous males are favored, but even less-preferred males often mate successfully. We predict that cryptic mechanisms of adjusting paternity may be more likely, or be employed more frequently, in species where spatiotemporal variation in the availability of males generates groups of females likely to encounter few males, or in contexts where the first male encountered is frequently of a non-preferred phenotype. We suggest cryptic choice may operate via female physiological responses to mating males that adjust the likelihood of sperm storage or effective sperm plug placement by males. This predicts evolutionary links between the risk of remaining unmated and the frequency with which ‘successful’ versus ‘failed’ plugs are found in field-caught females. More commonly, however, paternity biases may be introduced by female-determined variation in the number of copulations ceded to first compared

to subsequent mates and variation in the duration of those copulations. Although these ideas are intriguing and *Latrodectus* could be an important model for understanding CFC, our ability to make general inferences is hampered since only 7 species have been the subject of formal study of reproductive behaviors or ecology. This chapter suggests some targeted behavioral, physiological, and comparative studies that, if conducted on a range of species, may leverage the fascinating variation in this group to enrich our understanding of the evolution of CFC and interactive effects of CFC and other post-copulatory processes.

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