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MINI REVIEW

Ecology of female mating failure/lifelong virginity: a review of causal mechanisms in insects and arachnids

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Abstract

Sexual reproduction implies binary outcomes of competitive interactions for access to male gametes: lifelong virgin females with null fitness vs. mated females with variable (generally nonzero) fitness. Female mating failure has long remained a dormant concept in sexual selection theory in part because it is acutely maladaptive (lifelong virgins that do not reproduce are strongly selected against) and also due to widespread acceptance of the Bateman–Trivers paradigm (anisogamy and correlated sex roles). Based on recent scientific output on lifelong virginity across multiple taxonomic groups in insects (Coleoptera, Diptera, Hemiptera, Lepidoptera, Odonata, Orthoptera, Strepsiptera), female mating failure has become a mainstay of sexual selection over the last decade. Lifelong virginity and senescence (death) are intertwined processes; old virgin females compensate for increased risk of lifelong virginity by becoming less choosy and increasing investment in mating-related activities. Low rates of female lifelong virginity (<5%) in most natural populations of insects indicate that sex generally 'works' due to selective pressures acting on both males and females to enhance lifetime fitness. Mating failures are most common in insects with female flightlessness; these pressures may lead in evolutionary time to transitionary pathways from sexual reproduction to parthenogenesis. Female mating probability is affected by nonlinear density-dependent processes dependent upon the scale of observation (mate-encounter Allee effect at large spatial scales, mating interferences between females at small scales). Mate choice and sex role reversal (females being the active sexual partner) are ubiquitous in insects and arachnids with significant paternal investment, but consequences in terms of female lifelong virginity remain unknown. Logistically, conceptual development of female mating failure in insects is most limited by the lack of broadly applicable methods to assess rates of lifetime virginity among flighted females.

Problem at hand

Obligatory sexual reproduction entails the union of male and female gametes for production of viable offspring. For both males and females, outcomes of competitive interactions for access to gametes can be two-way: lifelong virgins with null fitness vs. mated individuals with variable (generally nonzero) fitness. The fitness of females often increases with the number of copulations or the quality of the male partner (Puurtinen & Fromhage, 2017; Suzaki et al., 2018). Nevertheless, the fitness increments of first (virginal) mating generally outweigh increments of subsequent (polyandrous) copulations (Kokko & Mappes, 2005; Larranaga et al., 2018). Due to predominance of anisogamy and asymmetric reproductive investment (Bateman–Trivers paradigm: promiscuous males with cheap sperm vs. coy females carrying costly eggs), rates of lifelong virginity are typically higher in males than in females (Janicke & Morrow, 2018). Although males are generally the competitive and promiscuous sex in insects and arachnids, counterexamples of male mate choice and paternal reproductive investment are known (Bonduriansky, 2001). Such sex role reversal poses an evolutionary puzzle in relation to female lifelong virginity, as discussed below.

Widespread validity and support of the Bateman–Trivers paradigm had two unintended negative consequences:

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(1) suppression of research on female sex roles, as indicated by severe male bias in sexual selection theory, and (2) a misleading assumption that all females mate at least once in their life (Wing, 1991; West-Eberhard, 2005; Kokko et al., 2012). In demographic terms, instances of female lifelong virginity have measurable consequences (net reproductive loss; Greenbank, 1963) because the egg stage interlocks parental and offspring generations and provides a proxy of abundance for population studies; in comparison, lifelong virginity in males has limited heuristic value as a demographic descriptor. This literature review focuses on the prevalence of lifelong virginity in diplo-diploid female insects and arachnids. Haplo-diploid Hymenoptera are not included because virgin females lay fertile eggs, i.e., female mating failure (FMF) is not linked with zero fitness. Historically, the term 'female mating failure' was coined half a century ago for females that do not mate as adults (Greenbank, 1963); it is synonymous with lifelong virginity, and the two terms are used interchangeably. Sexual selection processes that may affect female fitness after mating (such as cryptic female choice, postzygotic failure, or interspecific mating interference) are outside the scope of the review.

The review has two objectives: provide a synopsis of FMF as a concept and update recent literature on causal factors associated with lifelong virginity: (1) senescence (death) as the ultimate cause of FMF; (2) low risk of FMF as an emergent property of male/female adaptive behavioral syndromes; (3) mating cost of female restricted motility; (4) temporal patterns of FMF and reproductive asynchrony; (5) density-dependent processes and the plausibility of mate-encounter Allee effect; (6) natural mating disruption as an example of intraspecific mating interference; and (7) carryover effects linking host-plant quality with risk of FMF.

FMF as an overlooked outcome of sexual reproduction

Female mating failure has long remained a dormant concept in sexual selection theory due to its maladaptive nature, i.e., lifelong virgins that do not reproduce are strongly selected against (Arnqvist & Henriksson, 1997; Kokko & Mappes, 2005; Faust & Forrest, 2017). The first formal attempt to conceptualize FMF linked lifelong virginity with runaway selection caused by strong female preference for male characters, in which contests low-quality females ('wallflowers') often remain unmated (de Jong & Sabelis, 1991; Allison & Cardé, 2016). As expected, virgins are less choosy than mated females due to the risk of encountering/rejecting a single male before death (Kokko & Mappes, 2005; Ghislandi, 2017). Polyandry (multiple male partners) can thus be viewed as a byproduct of low threshold for mate acceptance that evolved primarily to prevent lifelong virginity (Gowaty & Hubbell, 2013; Kokko & Mappes, 2013; Greenfield, 2016). Empirical observations in insect populations reveal relatively high levels of FMF among small females, females with long prereproductive maturation, young females (still sexually receptive), species with flightless females, and populations with female-biased sex ratio or reproductive asynchrony (Calabrese et al., 2008; Rhainds, 2010).

Mating status of individual females is most often determined based on the presence/absence of spermatophore in the bursa copulatrix; extent of FMF can be assessed at the population level with sentinel, tethered, or feral females (Rhainds, 2010; Nielsen et al., 2017). Females in natural populations can be collected using an array of sampling procedures (resident females on host plants, in-flight females captured with light traps or malaise traps, migrant females collected in the airspace, and females collected postmortem on drop trays; Rhainds, 2013, 2015). Studies that report mating probabilities for multiple sampling procedures are useful to contrast behavioral processes among virgin and mated females (Wada et al., 1980; Rhainds, 2013; Cheng et al., 2016; Nielsen et al., 2017). Sampling tools that target live individuals (resident, in-flight, migrant females) provide punctual assessments of lifelong virginity at the time of sampling; punctual virginity may underestimate demographic rate of FMF because some females would have eventually mated in their hypothetical (post sampling) life. Unequivocal measures of FMF rely on day-to-day meticulous observations (Wing, 1991; Cordero, 1992; del Castillo & Núñez-Farfán, 2002) or postmortem assessment of mating status (Rhainds et al., 2009; Tobin et al., 2013).

Female insects are usually small and mobile, and thus hard to track individually for lifetime assessment of mating success. Empirical observations of lifetime (day-to-day) mating probability of individual virgin females in natural populations are rare and hard to gather. Lack of broadly applicable methods to assess rates of lifelong virginity among large samples of flighted females remains the strongest impediment to basic understanding of FMF in insects.

Senescence as the ultimate cause of FMF

Lifelong virginity and senescence (death) are intertwined processes. Virgin females may fail to mate as adults either because they never encounter males or all their mating attempts are rejected by males. The two scenarios are difficult to distinguish in nature unless females are individually followed day to day throughout their entire lifetime. If sex is prerequisite to reproduction, it is assumed that females prioritize mate-seeking roles until at least one fertile copulation is secured. In that context, risk of FMF due to females rejecting a viable copulation early in life without encountering another mate is deemed low, not only due to the obviously maladaptive nature of such behavior but also because virgins are considerable less choosy than mated females (Kokko et al., 2012). On the other hand, rejection of 'toxic' males with negative impacts on female fitness is adaptive under all circumstances (Priklopil et al., 2015).

The unusual mating system of wolf spiders (Araneae: Lycosidae) illustrates the pitfalls of females rejecting mating opportunities early in life and subsequently dying as virgins. Precopulatory cannibalism of males by females is inherently fraught with a high risk of FMF due to consumption of males/rejection of copulation by virgin cannibals (Newman & Elgar, 1991; Arnqvist & Henriksson, 1997). High rates of precopulatory cannibalism are obviously maladaptive for males, and also for females because they induce male-biased sex ratios by consuming receptive mating partners without accessing their sperm. Strong selection against precopulatory cannibalism is expected to reduce its incidence in nature (Gavín-Centol et al., 2017; Fisher et al., 2018).

Learning (decision to accept or reject mating opportunities based on past experience) is adaptive if (and only if) virgin females have precise (near perfect) cognition of both future rates of mate encounter (e.g., by sensing ambient conspecific pheromone) and frequency distribution of male genotypes (Roitberg et al., 1993; Priklopil et al., 2015). In fruit fly adults (Diptera: Tephritidae), low mating probabilities and long latency periods of females paired with single males relative to larger groups (three males and one female, or one male and three females; Barry et al., 2003) illustrate linkages between learning and mate choice. Learning and rejection of mating opportunities early in life are most prevalent in long-lived females with prolonged reproductive maturation and high rates of mate encounter (Wilgers & Hebets, 2012; Henshaw, 2018). As expected, mating early in life has limited impact on fecundity of long-lived females (Lentini et al., 2018; Roets et al., 2018).

In contrast, mating early in life is optimal in short-lived females that do not feed as adults (capital breeding), because aging/starvation generally leads to functional senescence (accruing risk of virginity due to declining sexual attractiveness) and actuarial senescence (declining day-to-day survival) (Richerson et al., 1976; Boggs, 2009; Kartsev, 2014). Random mate selection by females (accept first male encountered) is the optimal rule to avoid FMF (Roitberg et al., 1993; Priklopil et al., 2015). The nutritional or physiological condition of females interacts with age to influence mating decisions (Wilgers & Hebets, 2012; Toft & Albo, 2015). Old virgin females compensate for ever-accruing risk of FMF with age by either becoming less choosy (Priklopil et al., 2015; Henshaw, 2018), or by increasing investment in mate signaling (de Cock et al., 2014; Simmons, 2015; Umbers et al., 2015). In some cases, physiological age (days before death) has a stronger influence on mating decisions than chronological age (days since emergence) (Ligout et al., 2012). In short-lived insects, delayed mating reduces lifetime fecundity of females due to metabolic cost of survival during the latency period combined with reduced duration of post mating oviposition period (Mori & Evenden, 2013; Gerken & Campbell, 2018). In purely monandrous species, mated females do not seek additional copulations unless they copulated with a poor-quality male (Elzinga et al., 2011; Forbes, 2014).

Prereproductive death, which relates to instances where females die prematurely before mating (e.g., due to predation or dispersal mortality; Lakovic et al., 2017), is closely related to but distinct from FMF, where females are assumed to die from senescence (aging process) (Boggs, 2009; Hassall et al., 2015). However, the distinction between FMF and prereproductive mortality is somehow irrelevant because females in nature generally die before reaching physiological senescence (Hassall et al., 2015; Reichard, 2016; Lemaniski & Fefferman, 2018). In insects with obligatory dispersal of virgin females from the natal patch (i.e., Noctuidae tracking ephemeral resources), high levels of prereproductive death are expected due to dispersal losses or low mate encounters among post dispersing females at sink patches (Lakovic et al., 2017; Kusaka & Matsuura, 2018).

Low risk of FMF as an emergent property of male–female adaptive behavioral syndromes

Sexual reproduction can be considered an evolutionary consequence of strong selective pressures acting on both males and females to enhance lifetime mating success. Females have evolved multiple behavioral adaptations to circumvent FMF (Rhainds, 2010; Lehtonen et al., 2012), most notably indiscriminate behavior of virgin females (low rate of mate rejection, independent of male attributes) relative to mated females (whom are more likely to be choosy and reject male mating attempts) (Kokko & Mappes, 2005). Conversely, aging virgins increase investment in mating activities (signaling or foraging) to counterbalance the ever-increasing risk of lifelong virginity (Lehtonen et al., 2012; de Cock et al., 2014; Simmons, 2015; Umbers et al., 2015). Other adaptations to mitigate FMF include selection of microhabitats most suitable for mate attraction (Rhainds, 2010, 2015), plasticity in sex role reversal (virgin females becoming the active partner when perceived abundance of males is low) (Lewis & Wang, 1991; Wing, 1991; Gwynne & Lorch, 2013; Westermann et al., 2014; Fritzsche et al., 2016), and agonistic interactions between virgin females for access to males (Rillich et al., 2009; Papadopoulos et al., 2009).

Adaptive behavior of 'selfish' males, who strive to increase lifetime fitness by optimizing both the number and quality of female partners, also reduces the extent of FMF in nature. Attributes of females that correlate with fitness (body size, age, mating status) influence the mating decision of males (Bonduriansky, 2001). In particular, males exhibit near universal preference for virgin over mated females in insects and arachnids (Thomas, 2011; Kelly, 2018). In extreme cases, males may be deterred by mated females (Xu et al., 2014) or prefer parasitized virgins over old (otherwise healthy) mated females (Fortin et al., 2018). Preference of males for virgin females is beneficial as it minimizes sperm competition and enhances reproductive output as residual fecundity of virgin females is usually higher than that of previously mated females.

Mate choice in males and rejection of potential female partners are most common in species with sex role reversal and significant male parental investment (Bonduriansky, 2001). Unfortunately, consequences of mate choice and sex role reversal have rarely been investigated in terms of FMF (Gwynne & Lorch, 2013). For example, we cannot yet distinguish between two opposite theoretical predictions: (1) high paternal investment in reproduction induces mate rejection of at least some females, which may enhance risk of FMF, or (2) active mate-seeking virgin females are more likely to encounter suitable males during their life than females who passively attract males.

Risk of FMF is also affected by abiotic factors as insects respond strongly to the environment (van Baaren & Candolin, 2018), such as ambient temperature (Westerman & Monteiro, 2016; Conrad et al., 2017), rainfall patterns (Ng et al., 2017), atmospheric pressure changes (Pellegrino et al., 2013), and anthropogenic light pollution (Altermatt & Ebert, 2016).

The role of immobility in FMF

Limited motility of females per se elevates the risk of FMF (Denno, 1994; Muniz et al., 2018) by restricting broad-range foraging for males when mating encounters are low, in particular due to generally short longevity of flightless females. In species with neotenic females (retention of juvenile traits at emergence), sexual selection tends to be further relaxed because female flightlessness is evolutionarily correlated with low mating capacity and short longevity of males, all of which exacerbate the risk of FMF (West-Eberhard, 2005). These trends generally hold true in three taxonomic groups with female neoteny and similar reproductive biology: fireflies (Coleoptera: Lampyridae) (South et al., 2011; de Cock et al., 2014), bagworms (Lepidoptera: Psychidae) (Rhainds et al., 2009), and twisted wings parasites (Strepsiptera) (Hrabar et al., 2014; Kathirithamby et al., 2015). Neoteny is also common in scale insects (Hemiptera: Pseudococcidae) (da Silva et al., 2009; Normark, 2003) although adults are often long-lived (>30 days) (Dogar et al., 2018; Lentini et al., 2018).

In addition to female neoteny, the four taxonomic groups above share other life-history traits, such as limited dispersal of larval progeny and high levels of inbred copulations, which over multiple generations lead to increasing genetic isolation between populations (West-Eberhard, 2005; Kartsev, 2014). In this context, selection against FMF may be weak at the individual level and rather operate at sib-group levels, i.e., the unit of natural/sexual selection is not an individual but rather a group of genetically related females at a given patch (kin selection) (West-Eberhard, 2005; Elzinga et al., 2011; Rhainds, 2015, 2018).

Parthenogenesis may have evolved as an escape route from maintenance of sex (males), i.e., development of eggs without fertilization and female-only populations (Schwander et al., 2010; Elzinga et al., 2011; Perotti et al., 2016). In evolutionary time, mating costs that limit female fitness influence the evolution of mating systems, in particular the transition from sexual to asexual reproduction (Gerber & Kokko, 2016; Burke & Bonduriansky, 2017). In the context of FMF in ecological time, however, the cost of first (virginal) copulation is deemed insignificant relative to null fitness of lifelong virginity (Roitberg, 1989; Wexler et al., 2017).

Hermaphroditism (monoecy) has repeatedly evolved in animals to circumvent FMF (Ghiselin, 1969) but is conspicuously rare in insects (Lehtonen et al., 2012) with the exception of few scale species (Hemiptera: Sternorrhyncha) (Normark, 2003). Why hermaphroditism is virtually absent in insects remains unclear, but its occurrence in scale insects is not entirely surprising given strong links between neoteny and FMF. In self-fertilizing hermaphrodites, the problem of FMF would be circumvented, but not so in hermaphrodites that depend on cross-fertilization.

Indirect evidence of mating cost related to female immobility is provided in *Heliconius* species with facultative pupal–adult mating; pupal–adult mating is characterized by males being attracted to the scent of female pupae shortly before emergence, such that males copulate when females are still partly enclosed in their pupal case. Sentinel individuals released as larva and allowed to mate as pupa largely failed to do so (two of 11 mated females, or 18.2%); in contrast, all females released as mobile adults mated at least once (Thurman et al., 2018). Low mating success of tethered females relative to feral females in field experiments is also consistent with a mating cost associated with restricted mobility (Rhainds, 2013). Under some climate-change scenarios, increasing wing load of adults (small wings relative to body size) implies reduced motility of females and increased risk of FMF (McCauley et al., 2018).

Effects of emergence time on mating failure

Theoretical models predicting outcomes of mating interactions relative to emergence time (Morbey & Ydenberg, 2001) have met diverse empirical observations: female mating probability may be higher in early, middle, or late phases of emergence cycles. In many instances, low female mating probability on a given day coincides with rarity of males (Calabrese & Fagan, 2004; Franco et al., 2004; Calabrese et al., 2008; Rhainds, 2010; Fauvergue, 2013; Faust & Forrest, 2017; Sciarretta et al., 2018). These studies support widely held views of female-biased sex ratios and/or acute shortage of males ('male vacuum') as triggers of FMF (Wing, 1991; Mendel et al., 2012; Fritzsche et al., 2016). As expected, the level of female choosiness declines as the sex ratio becomes female biased (Monier et al., 2018).

Synchronized emergence of males and females may limit reproductive asynchrony and reduce FMF (Junker et al., 2010; Osváth-Ferencz et al., 2017; Ehl et al., 2018). In contrast, short diel periodicity of mating activities and lack of congruence in emergence of males and females may lead to strong day-to-day variation in FMF (Wing, 1991; da Silva et al., 2009; Hrabar et al., 2014; Kathirithamby et al., 2015).

As ectotherms, insects undergo seasonal shifts in phenology because larval development and timing of adult emergence depend on temperature (Forrest, 2016; Chuine & Régnière, 2017). Protogyny (early emergence of females relative to males) is rare in insects relative to protandry (Morbey & Ydenberg, 2001), thus climate-induced protogyny is often presumed to increase FMF (Uyi et al., 2014; Bonal et al., 2015; McCauley et al., 2018; Ehl et al., 2018). However, protogyny is correlated with extended longevity of females (which counterbalances the risk of FMF; Degen et al., 2015, 2017) and may in fact enhance mating success of early emergent females by reducing late-season signal competition among conspecifics (Rhainds, 2018). Sex-specific pupation behavior of male and female larvae may affect emergence time and maintain protandry independent of environmental conditions: in fireflies, for example, pupation of male late instars on light-exposed substrates as opposed to females pupating in shaded locations is sufficient in itself to maintain protandry (Gentry, 2003; Mendel et al., 2012).

Density-dependent processes and mate-encounter Allee effect

The concept of FMF was first proposed as a demographic component in life tables of spruce budworm (Lepidoptera: Tortricidae); females that failed to mate were categorized as a reproductive mortality factor (Greenbank, 1963). The existence of mate-encounter Allee effect (logistic increment in mating probability with population density) in spruce budworm has vast ramifications for population dynamics and the implementation of large-scale management programs (Régnière et al., 2013).

The reality of mate-encounter Allee effect in insects is hard to dispute: density-dependent mating probabilities are mechanistically similar to concentration-dependent rates of collisions/reactions between particles (Moismann, 1957). Until recently, limited empirical support weakened the argument that mate-encounter Allee effects do matter in insects (Gascoigne et al., 2009). However, recent studies combined with rediscovery of old case studies (Fauvergue, 2013) have confirmed (or strongly implied) mate-encounter Allee effect across a broad taxonomic range (seven insect orders: Coleoptera, Collembola, Hemiptera, Isoptera, Odonata, Phasmotodea, and eight species of Lepidoptera; Table 1). The studies encompass broad demographic consequences in terms of geographic spread of invasive/native insects (Tobin et al., 2013; Lynch et al., 2014; Rhainds et al., 2015), life-history syndrome of color polymorphism (Cordero, 1992), transition from asexual to sexual reproduction (Schwander et al., 2010), and post dispersal establishment in breeding habitats (Kusaka & Matsuura, 2018).

The multiple studies documenting positive relationships between density and female mating probability (Table 1) reaffirm mate-encounter Allee effect as a natural phenomenon. Caution is still warranted as to its universality in insect populations, as the following four points illustrate. (1) Several field studies explicitly designed to demonstrate mate-encounter Allee effect failed to do so (Rhainds, 2010; Fauvergue, 2013). (2) Sampling constraints yielding imprecise estimates at low densities often prevent assessments of FMF in sparse populations, a problem circumvented by using captures of males at pheromone traps as a proxy for density. In such instances, the two variables are not statistically independent: pheromone traps reflect the abundance of mate-seeking males and are thus autocorrelated with

Table 1 Summary of field studies demonstrating or implying positive relationships between population density and female mating probability (mate-encounter Allee effect). Punctual mating probability refers to assessment of mating success among live virgin females, as opposed to lifetime virginity of dead females

Order	Family	Species	♀ mating probability	Density estimate	Reference
Coleoptera	Cerambycidae	*Tetropium fuscum*	Punctual	Distance from focal site	Rhainds et al. (2015)
Collembola		*Tomocerus minor*, *Orchesella cincta*	No. fertile eggs/ spermatophore	Periodical aggregations of adults	Verhoef & Nagelkerke (1977)
Hemiptera	Pseudococcidae	*Planococcus citri*	Punctual	♂/pheromone trap	Franco et al. (2004)
Isoptera	Rhinotermitidae	*Reticulitermes speratus*	Punctual	Mating pairs/patch	Kusaka & Matsuura (2018)
Lepidoptera	Lasiocampidae	*Malacosoma disstria*	P (♀ attract ♂)	Pupae/unit of foliage	Evenden et al. (2015)
	Lymantridae	*Lymantria dispar*	Lifetime (tethered ♀)	♂/pheromone trap	Tobin et al. (2013)
	Noctuidae	*Spodoptera litura*	Punctual	♂/♀/cage	Otake & Oyama (1973)
	Notodontidae	*Thaumetopoea pityocampa*	Inferred (not measured)	Aggregation of adults on host plants	Pimentel et al. (2017)
	Nymphalidae	*Melitaea cinxia*	Punctual	Local population of adults	Kuussaari et al. (1998)
	Papilionidae	*Parnassius smintheus*	Punctual	Local population of adults	Matter & Roland (2013)
	Psychidae	*Thyridopteryx ephemeraeformis*	Lifetime (feral ♀)	% infested plants	Lynch et al. (2014)
	Tortricidae	*Choristoneura fumiferana*	Lifetime (tethered ♀)	♂/pheromone trap	Régnière et al. (2013)
Odonata	Coenagrionidae	*Ischnura graellsii*	Marked – recaptured ♀	Local density of adults	Cordero (1992)
Phasmatodea	Timematidae	*Timema* species	Virgin reproduction	Adults in sweep net/min	Schwander et al. (2010)

female mating probability. In fact, some studies even use attraction of males to pheromone sources as a proxy for mating probability (Fauvergue, 2013). (3) Due to logistic constraints, many studies rely on punctual virginity of live females collected in the field at one point in time, as opposed to lifelong rates of virginity. The approach is valid in principle, unless apparent mate-encounter Allee effect is confounded by factors that mask or amplify the real effect of density (young age of punctual virgins sampled in early season when rates of FMF are high; Kuussaari et al., 1998). (4) The gypsy moth (Lepidoptera: Lymantridae) provides by far the most exhaustive support for density-dependent mating probabilities in any insect; consequently, it has come to dominate the literature to an extent that generates a presumption that mate-encounter Allee effect is near universal in nature (halo effect; Fauvergue, 2013).

Signal interference and natural mating disruption

The probability of FMF in insects has long been on the mind of applied entomologists who developed what became wonders of human ingenuity: population management programs against insect pests based on interference with normal mating behavior through olfactory-based mating disruption (Miller et al., 2006; Mori & Evenden, 2013). These studies frequently report mating status of females in control (untreated) plots, which provides valuable metadata on FMF rates.

In its literal sense, the prediction of ever-increasing female mating probability with population density is biologically implausible. Crowded conditions are expected to suppress mating directly through small body size and low attractiveness of emerging females, signal interference, and/or overaggregation of mate-seeking females (Cocroft & Rodriguez, 2005; Greenfield, 2016; Čokl et al., 2017; Rhainds, 2018). Opposite impacts of population density at different spatial scales typify ecological scaling inversion (Turner et al., 1989): (1) large-scale processes operating at the population level lead to positive relationships between density and mating probability (mate-encounter Allee effect), and (2) fine-scale processes operating, for example, at the host-plant level lead to mating overaggregations or signal jamming. Interestingly, these two processes cooccur at comparable scales in forest tent caterpillar (Lepidoptera: Lasiocampidae) (Evenden et al., 2015).

In moths, proximity of calling females has been hypothesized to enhance the mating success of both attractive and unattractive females (van Wijk et al., 2017). However, empirical observations suggest the reverse: at a small scale, mating probability of females tends to decline with the number of conspecifics (Shiga, 1977; references in Rhainds, 2010), suggestive of intrasexual competition among females for access to males.

Natural mating disruption (high rates of FMF on crowded host plants) can arise due to: (1) males being unable to discriminate receptive females from conspecific males or non receptive females (Richerson et al., 1976; Takeuchi, 2017; Sales et al., 2018), (2) passive olfactory signals of post reproductive conspecifics interfering with mate location (Gwynne & Lorch, 2013; Rhainds, 2018), or (3) adsorption of pheromone onto the foliage of host plants (Noldus et al., 1991). Testing these hypotheses requires small-scale mapping of female mating probability among georeferenced plants (van Wijk et al., 2017; Muniz et al., 2018; Sciarretta et al., 2018).

Carryover host-plant effects on FMF

Carryover effects, defined as consequences of larval host-plant quality on reproductive output of adult females, are more important in capital breeders, which rely exclusively on larval accumulated resources, than in income breeders, which feed as adults or receive male nutrients while in copula (Jervis et al., 2005). In capital breeders, carryover effects of plant quality translate into large size of females at pupation/adult emergence, which correlate positively with fitness components, including fecundity (Rhainds, 2015; Davis et al., 2016), lifespan (Holm et al., 2016; Meister et al., 2018), mating contest outcomes (Bath et al., 2015; Joel et al., 2017), and mating success (Rhainds, 2010; Gwynne & Lorch, 2013; de Cock et al., 2014).

Host plants directly affect outcomes of competitive interactions for access to males either as a physical substrate of vibration sexual signals (Cocroft & Rodríguez, 2005; Laumann et al., 2018), as resource in mating aggregations (Papadopoulos et al., 2009; Xu et al., 2017), or as sources of volatiles that synergize attraction of males to female-produced sex pheromone (Dekker & Barrozo, 2016). In pupal mating butterflies (Lepidoptera: Nymphalidae), foraging males locate sessile female pupae using cues associated with previous defoliation caused by feeding larvae (Estrada & Gilbert, 2010), highlighting a behavioral carryover effect of pupation site (Gentry, 2003; Mendel et al., 2012). In insects with neotenic females, female late instars seek pupation sites that alleviate the risk of FMF among emergent adults: mating probability often increases with the height position of females on host plants, illustrating behavioral adaptation of larval females with fitness consequences across developmental stages (Rhainds et al., 2009).

Floral deception in orchid-pollinator systems is linked to FMF in opposite ways across trophic levels. High numbers of males attracted to mimetic pheromone sources released by orchids may lead to FMF among wingless conspecific females that rely on pheromone for mate attraction (Wong & Schiestl, 2002; Schiestl, 2005). In contrast, low attractiveness of deceptive orchid flowers to pollinating males causes 100% fruit-set failure (Peakall, 1990).

Table 2 Factors correlated with high vs. low incidence of female mating failure in insect populations

Factor		Rate of lifelong virginity	
		Low	High
Female attributes	1. Mobility	Flighted females	Flightless/neoteny
	2. Prereproductive maturation	Short period	Long period
	3. Longevity	Long lived	Short lived
	4. Mating threshold	Indiscriminate	Choosy
	5. Body size	Large females	Small females
	6. Age of virgin	Young	Old
	7. Physical location on host plant	High	Low
Demographic variables	8. Emergence time	Reproductive synchrony	Reproductive asynchrony
	9. Operational sex ratio	Male biased	Female biased
	10. Population density (large scale)	High density	Low density (Allee effect)
	11. Population density (fine scale)	Low density	High density (signal jamming)

Based on Table 3 in Rhainds (2010). See also for 2: Bath et al. (2015); 3: Wilgers & Hebets (2012), Henshaw (2018); 4: Kokko & Mappes (2005); 8, 9: Calabrese & Fagan (2004), Calabrese et al. (2008); 10: Gascoigne et al. (2009), Fauvergue (2013); 11: Rhainds (2018).

Classic studies of tri-trophic interactions among defoliating caterpillars, induced plant volatiles, and parasitoids illustrate the influence of FMF as an emergent concept. Original hypotheses for behavioral response of parasitic wasps to defoliator-induced plant odors emphasized benefits from the emitter perspective ('plants cry for help') (Xu et al., 2017). Given that it may be equally (if not more) difficult to locate mating partners than suitable hosts, plant-induced volatiles may primarily mediate mating interactions among adult parasitoids (Kaplan, 2017; Xu et al., 2017).

Conclusion

The literature on FMF has blossomed over the last decade across a broad range of perspectives: adaptations furthering female mating success in evolutionary contexts, physiological basis of aging and mating failure, transition pathways between sexual–asexual reproduction in insects with neotenic females, mathematical models linking multiple factors to forecast FMF (reproductive asynchrony), mate-encounter Allee effect as an influent demographic process, host-plant developmental carry-over effects, experimental evidence for increased investment in mate signaling in environments when mating probability is low, and growing evidence for intraspecific interference between mate-seeking females (natural mating disruption).

Attributes of females associated with a relatively high risk of FMF include low mobility, small body size, old age, short lifespan, long prereproductive maturation, physical location, and discriminatory mating behavior (Table 2). Demographic variables linked with a high risk of FMF include emergence time (reproductive asynchrony, male-biased sex ratio, and both very low and high population densities (Table 2).

Research endeavors that are deemed critical to further our understanding of lifelong virginity include: (1) consolidating metadata on FMF from the literature on mating disruption trials; (2) investigating variation in female mating probability at both small and large spatial scales, using georeferenced locations and individual host plants; (3) elucidating the evolutionary puzzle of male mate choice and paternal reproductive investment in terms of FMF; and (4) comparing the incidence and causality of FMF across a broad taxonomic range including, but not restricted to, insects and arachnids.

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