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The Mathematics of Female Pheromone Signaling: Strategies for Aging Virgins

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ABSTRACT: Although females rarely experience strong mate limitation, delays or lifelong problems of mate acquisition are detrimental to female fitness. In systems where males search for females via pheromone plumes, it is often difficult to assess whether female signaling is costly. Direct costs include the energetics of pheromone production and attention from unwanted eavesdroppers, such as parasites, parasitoids, and predators. Suboptimal outcomes are also possible from too many or too few mating events or near-simultaneous arrival of males who make unwanted mating attempts (even if successfully thwarted). We show that, in theory, even small costs can lead to a scenario where young females signal less intensely (lower pheromone concentration and/or shorter time spent signaling) and increase signaling effort only as they age and gather evidence (while still virgin) on whether sperm limitation threatens their reproductive success. Our synthesis of the empirical data available on Lepidoptera supports this prediction for one frequently reported component of signaling—time spent calling (often reported as the time of onset of calling at night)—but not for another, pheromone titer. This difference is explicable under the plausible but currently untested assumption that signaling earlier than other females each night is a more reliable way of increasing the probability of acquiring at least one mate than producing a more concentrated pheromone plume.

Keywords: sperm limitation, sexual signaling, moth, Lepidoptera, sex pheromone, female mate choice, lifetime reproductive investment.

Introduction

Although finding a mate is paramount for all sexually reproducing organisms, effort spent searching for a mate is often markedly different between the sexes (Barnes 1982; Kasumovic and Andrade 2004; Kasumovic et al. 2007; Ambrogi et al. 2008). In most taxa, males perform the majority

of mate searching (Barnes 1982; Kasumovic and Andrade 2004; Kasumovic et al. 2007; Ambrogi et al. 2008), and females are more likely than males to encounter more mates than required for optimal fitness (Kokko and Wong 2007). Encountering too many mates can be costly rather than merely superfluous (Arnqvist and Nilsson 2000; Kawagoe et al. 2001). Nevertheless, an alternative—perhaps underappreciated—risk is that female fitness can suffer if male search effort does not guarantee all females are found. This can lead to delayed breeding (Mori and Evenden 2012), suboptimal sex ratios of progeny (Boivin 2012; Harpur et al. 2012), or complete failure to reproduce. Given that female mating failures are well documented (Calabrese et al. 2008; Rhainds 2010), there are circumstances under which females should actively search for mates.

Female mate acquisition effort may incur a range of costs, including (1) attracting parasites, parasitoids, or predators (Jones et al. 2002); (2) attracting males that are undesirable as mates, so energetic effort must be spent rejecting their mating attempts; (3) attracting males that are unwanted but able to overcome female mating resistance, leading to genital damage or physiological costs of multiple mating (Kawagoe et al. 2001; Hosken and Stockley 2004; Cordero and Miller 2012); and (4) spending resources on greater than adequate, costly signal production (Gavrilets et al. 2001; Kotiaho 2001; Johansson and Jones 2007; Harari et al. 2011).

In moths (Lepidoptera), mobility-related mate acquisition costs are paid by males, while females produce pheromones that increase detectability. Pheromones are emitted in minute quantities and can be detected by males over long distances (Regnier and Law 1968; Greenfield 1981; Angioy et al. 2003). Potential costs of chemical signaling include synthesis, storage, production, and the potential

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for predators, parasites, or parasitoids to eavesdrop (Dicke and Sabelis 1992). Finding empirical evidence for costs has proven difficult (Johansson and Jones 2007); it is assumed that the costs of pheromone production are low (Cardé and Baker 1984). Recent evidence suggests that pheromone producers pay both fitness and physiological costs (Foster and Johnson 2011; Harari et al. 2011). The general lack of evidence for pheromone production costs may reflect methodological difficulties (studies on concentrations of released pheromone are uncommon), or the scarcity of documented cases may match the theoretical prediction that females should expend minimal energy on pheromone production (Kokko and Wong 2007).

Theory predicts that costs of pheromone signaling should be low, and the literature reports very little data on such costs. However, the absence of published reports of such costs is unsatisfactory support for this theory. Here, we aim to overcome limitations of existing data by presenting an indirect way to test for costs of pheromonal signaling. We relate female pheromone emission to the chance of encountering one or more mates. If there are very low costs to pheromone production and it is similarly not particularly costly to deal with the consequences of copious pheromone production, then a female whose fitness is enhanced by mating should always call as much as possible to minimize the time spent unmated. If, on the other hand, producing higher concentrations of pheromone or producing pheromone for too long is costly—for any of the reasons listed above—then we expect an age-dependent pattern of pheromone production, where ageing virgin females gradually increase their signaling effort. We derive this prediction mathematically and present a synthesis of the empirical literature to reveal patterns in published data. We also comment on the multidimensional nature of pheromonal signaling in this context.

A Theoretical Approach to Adaptive Variation in Female Pheromone Production

The Rationale

To quantify signaling in female moths, empiricists have measured time spent calling and/or concentration of pheromone released (note that calling refers to pheromone release). The physiological costs of pheromone production are only beginning to become clear (Harari et al. 2011; Harari and Steinitz 2013). Even less attention has been paid to the spatial distribution of females (McNeil 1991), how developmental environment affects calling, and how calling neighbors affect a female's calling behavior (Stelinski et al. 2006). It is also unclear as to the relative transition between effects of long-range and short-range mate searching, because once males locate females, short-

range pheromones and acoustic cues may influence whether mating occurs (Birch et al. 1990; Conner 1999). Further, obviously all of these factors can be strongly influenced by the weather and climate (McNeil 1991; Pellegrino et al. 2013), and mate-searching males are known to navigate pheromone plumes of rather complex filamentous structure (e.g., Liu and Haynes 1992).

Females can simply modify male arrival rates by choosing not to call (e.g., after mating; Webster and Cardé 1984). Here we do not focus on the postmating response, since it may be influenced by either male manipulation of female receptivity or the females' choices. Instead, we focus on changes in virgin female signaling effort until their first mating.

Virgin females are unlikely to have precise information about the likelihood of encounters with potential mates, which tends to vary spatially (Robinet et al. 2008; Contarini et al. 2009) and temporally (Calabrese and Fagan 2004; Rhainds 2012). Even if male density were constant, there is inherent unpredictability in whether male flight paths cross female pheromone plumes. We therefore consider the key concept of mate arrival rate, by which we mean the rate (per unit time) at which males find a signaling female. Here males should be interpreted as a discrete sample from a Poisson process: if, for example, a signaling female attracts a male once every 2 h on average, and she calls for 1 h, then the total number of arriving males is Poisson distributed with parameter 1/2. Thus, there is ~61% probability that no male arrives (the value of the Poisson distribution at 0 with parameter 1/2 is 0.6065), 30% probability that one male arrives, ~8% probability that two males arrive, and ~1% probability that three or more males arrive.

All else being equal, an environment with larger average distances between females and males (low-density population) should lead to a lower mate arrival rate as the same pheromone plumes, when spaced wider apart, will be entered by males less often. This increases the risk that any given calling duration fails to attract a mate. Every night of such failure is costly, when incorporating the risk that a female may die before mating. We therefore expect females to adjust their signaling effort to male availability. However, if virgin moths can perceive only males that have already found them, they have to make decisions based on very incomplete information on local male densities. Therefore, we asked, if the only information that a virgin female has is how long she has signaled without having been found by a suitable mate, how should she adjust her signaling effort as she gets older? We end our analysis at first mating, since there are both female-specific and male-specific reasons why subsequent signaling effort changes thereafter (e.g., Andersson et al. 2000).

The Model

On any given night over her lifetime, a virgin female moth may be in a state where she requires a mate (either she is a virgin or sperm limited—the most common scenario and the one we focus on here—or she has completed a bout of reproduction and no longer has sperm available; Foster and Ayers 1996). By modifying her calling, she can adjust the arrival rate of males (see Poisson distribution explanation above). There is also a chance that she may die before she gets the chance to mate. If we assume that the daily mortality of females is m , this creates an iterative relationship between a female's expected fitness on night t and her expected fitness on night $t + 1$:

$$w_t = g_t + (1 - m)w_{t+1}, \quad (1)$$

where g_t is her fitness gain on night t (which we will derive below; $g_t = 0$ if she does not mate that night); m is mortality, measured on a daily basis such that the female survives with probability $1 - m$ to begin another night; and w_{t+1} is her expected fitness gain from night $t + 1$ onward (conditional on being alive).

Variable g_t is a function of the female's signaling effort on night t , which we denote S_t . Signaling effort may in some cases refer to the duration of calling, usually measured as earlier onset of calling, resulting in a longer period of calling each night (e.g., Delisle and McNeil 1987; Gemenio and Haynes 2000). An increase in pheromone concentration is an alternative mechanism to increase signaling effort (e.g., Foster et al. 1995), assuming that pheromonal cues are not at such high concentrations that they swamp male sensory receptors and arrest response; Baker and Haynes 1989; Vickers 2000).

We present two versions of our model, with different reasons as to why a female might not always maximize her signaling effort. In the first model, overly strong signals lead to suboptimally high arrival rates of males (energetic costs of above-optimal mating rate or mate rejection). In the second model, strong signaling effort is assumed physiologically or behaviorally costly, including costs of predators or parasitoids eavesdropping on the signal.

Optimizing Male Arrival Rate

Here we assume that attracting one male in one night is beneficial while the arrival of additional males is detrimental. A female's fitness gain during one night is zero if she does not attract any males, but she may survive (probability $1 - m$) to try again the following night. Because multiple males can find the same plume (Campion et al. 1974), our assumption that pheromone emission ceases subsequent to mating does not necessarily prevent near-simultaneous arrival of multiple males. We therefore spec-

ify the fitness consequences of attracting n males on night t for all values of $n \geq 0$. We do this by assuming that the fitness gain is $g_t = k^{n-1}$ for $n \geq 1$ (and $g_t = 0$ for $n = 0$, as stated above). Here $k < 1$ is a parameter that specifies the decline in female fitness if too many males find her (if $n = 1$, her fitness gain becomes 1 because $k^0 = 1$ for any k). Obviously, there are also circumstances with females benefitting from attracting more than one male. Such cases can be modeled as $k \geq 1$, and we explore them below (in the section "Balancing Mate Arrival Rate with Increasing Costs of Calling").

In a Poisson process, the arrival of one male is independent of any other male, but arrival rates depend on a female's signaling effort (S). The number of males that find the focal female on a given night is described by a function $\lambda(S)$ (the time-dependent notation is dropped to emphasize that we assume males are equally available each night). The number of males that find a female ($\lambda(S)$) increases with signaling effort (S) and also depends on how many males are searching for females in the area. We assume that the rate at which males find females is proportional to the number of males per area (fig. 1b) but that the relationship between the numbers of males that find a female ($\lambda(S)$) and female signaling effort (S) is nonlinear. Increases in female signaling effort (S) of a given magnitude have the largest impact if the female was not already using high signaling effort (fig. 1b).

Consider a female for whom the male arrival rate depends on signaling effort (S) according to the function $\lambda(S)$. Her fitness gain on night i , $g(i)$, is as a sum where the fitness consequence of each possible number of male arrivals is multiplied by the probability that signaling with effort (S) leads to this number of males arriving; this probability is Poisson:

$$g_i(S) = \sum_{n=1}^{\infty} k^{n-1} \frac{\lambda(S)^n e^{-\lambda(S)}}{n!}. \quad (2)$$

The best signaling effort is found by numerical maximization of $g_i(S)$.

However, equation (2) is not valid for situations where females cannot be certain about local male density. While females possess evolutionary knowledge regarding typical male densities, circumstances will often deviate from the average (Kokko and Mappes 2005), and females should adjust their signaling effort over time if previous efforts have not led to a desirable male arrival rate. Consider the female in a habitat patch where signaling leads to a low arrival rate, described by $\lambda_L(S) = 5(1 - \exp(-S))$, or in a patch where higher arrival rates can be expected, $\lambda_H(S) = 10(1 - \exp(-S))$ (depicted in fig. 1b). If the female survived for n nights and her calling sequence S_1, S_2, \dots, S_n has not yet attracted a male, it is possible to work

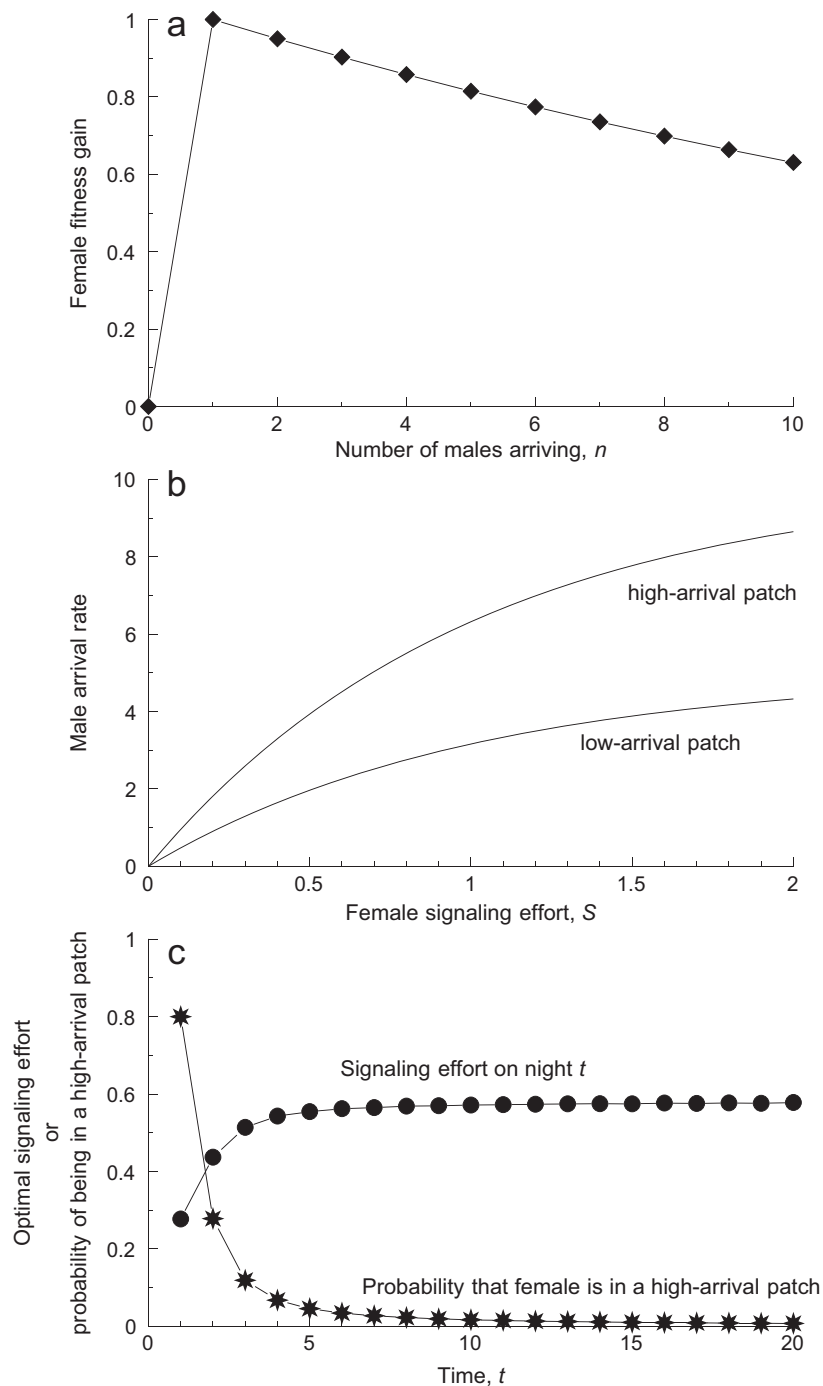


Figure 1: *a*, Fitness gain of a female depends on the number of males attracted per night. In this example, one male is optimal, and there is a slow decline with superfluous male attention (parameter k is set at 0.95; mortality is $m = 0.25$ per night). *b*, Depending on the type of habitat (or point in time over the season) in which a female finds herself, signaling effort may increase male arrival rates more or less steeply: $\lambda_H(S) = 5(1 - \exp(-S))$ or $\lambda_H(S) = 10(1 - \exp(-S))$. *c*, Optimal signaling career for a female who has by a particular point in time (t , nights since eclosion) not yet attracted any males. She starts out with calling effort of $S_1 = 0.28$ on the basis of the prior probability, which we set to $p = 0.8$ in this example; if she does not mate, she updates her knowledge of the probability that she is in a situation with low mate availability to $p_2 = 0.27$ and increases her signaling on the second night to $S_2 = 0.44$. If she still attracts no mates, she updates to $p_2 = 0.12$, and her third night is spent signaling with effort $S_3 = 0.51$, which is already close to her maximal effort 0.58, which is spent if p_i drops to close to 0 as a result of many mateless nights. For visual clarity, we show only the first 20 nights.

out the probability she is in either type of patch. On day 1, the probability p_1 that she is in a high-density patch is simply equal to the prior expectation, denoted p , of her residing in this type of patch; this is evolutionarily acquired knowledge.

Note that $p > 0.5$ is a likely prior (on the basis of evolutionary knowledge) because if patches mostly differ in overall density rather than sex ratio, then patches that have more females are also likely to have more males. For the same sex ratio, smaller average distances between individuals mean higher encounter rates between males and female pheromone plumes. Taken together, these facts mean that a randomly chosen female is more likely to live in a patch with relatively high than relatively low mate arrival rates. However, competition with other females may complicate this, as may the fact that low-arrival areas could be larger (such that a female may be unlikely to live in a high-arrival area). In general, we therefore do not preclude any particular value for the prior probability p .

In general, the probability of being in a high-arrival patch p_t can be derived from p_{t-1} using Bayes' theorem,

$$p_t = \frac{p_{t-1}P(0|\text{high-arrival patch})}{p_{t-1}P(0|\text{low-arrival patch}) + (1 - p_{t-1})P(0|\text{high-arrival patch})} \tag{3}$$

Here, updating female knowledge is based on the probabilities of no males arriving during one night, if the patch type is known (e.g., 5 or 10, using the example above) and the female's signaling effort was S_t . From Poisson-distributed male arrival distribution, it follows that

$$P(0|\text{low-arrival patch}) = e^{-\lambda_L(S_t)} \tag{4a}$$

$$P(0|\text{high-arrival patch}) = e^{-\lambda_H(S_t)} \tag{4b}$$

Using equations (3) and (4), it is possible to work out the entire sequence p_1, p_2, \dots, p_n , where n denotes the age beyond which a female is very unlikely to live. In practice, we used 10^{-6} as a cut-off probability; that is, we used the smallest useful value of n that produces $(1 - m)^n < 10^{-6}$ as the maximum age of a female. For example, $m = 0.5$ means that very few females live past 20 nights, while if $m = 0.1$, we considered fitness consequences for a total of 132 nights. We thus include potential life spans of excessive length (note that the average life span with $m = 0.1$ is 10 nights) to avoid situations where the longest-lived fraction of the population has its life span artificially truncated. For any value of m and n , we are thus assuming that the fate of $<0.0001\%$ of females (those who live for longer than n nights) does not have strong selective consequences. This is justifiable because, in practice, signaling

effort stabilized to a constant value long before the females reached age n .

Note that the sequence p_1, p_2, \dots, p_n depends on S_1, S_2, \dots, S_n . These signaling effort values are not necessarily optimal. It is not feasible to find all optimal values simultaneously, because while the current night's fitness gain (g_t) depends only on current signaling effort, the female's expected fitness (w_t) depends on all future signaling effort (S_t) values. We therefore adopted an iterative approach to determine the fitness-maximizing sequence of signaling efforts, using dynamic optimization methodology: best options are derived starting from the last time step and progressing toward the beginning. However, our system necessitates a more complex algorithm than working once from maximum age n backward to 1, because knowledge of all S_t values are required to derive the sequence p_t and knowledge of p_t is required to start the dynamic optimization procedure. We therefore started the algorithm with a randomly chosen sequence of S_t values (each S_t an independently uniformly distributed random number between 0 and 1) and proceeded as follows.

First, we derive the sequence of p_1, \dots, p_n on the basis of equations (3) and (4). Thereafter, the fitness of females of the oldest age class is given as

$$w_n(S_n) = g_n(S_n) = p_n \sum_{i=1}^{\infty} k^{i-1} \frac{\lambda_H(S_n)^i e^{-\lambda_H(S_n)}}{i!} + (1 - p_n) \sum_{i=1}^{\infty} k^{i-1} \frac{\lambda_L(S_n)^i e^{-\lambda_L(S_n)}}{i!} \tag{5}$$

Progressing from $t = n - 1$ backward toward $t = 1$, we obtain the fitness of each female age class as

$$w_t(S_t) = g_t(S_t) + (1 - m)w_{t+1}(S_{t+1}), \tag{6a}$$

where

$$g_t(S_t) = p_t \sum_{i=1}^{\infty} k^{i-1} \frac{\lambda_H(S_t)^i e^{-\lambda_H(S_t)}}{i!} + (1 - p_t) \sum_{i=1}^{\infty} k^{i-1} \frac{\lambda_L(S_t)^i e^{-\lambda_L(S_t)}}{i!} \tag{6b}$$

Thereafter, we sought the maximum value of expected female fitness (w_t) (with respect to signaling effort (S_t)) numerically for each female age t . We obtained the next iteration of the sequence of S_t values by adopting the updating rule $S'_t = (1 - \delta)S_t + \delta\hat{S}_t$, where S'_t is the new value of S_t , δ is a constant that regulates the speed of convergence toward the optimal values (we used $\delta = 0.25$, which led to good convergence), S_t is the old value (in the first iteration this is a random variable), and \hat{S}_t is the value that maximizes fitness given the current sequence of p_t

values. This completes one round of the iteration. The next round begins with recalculating the p_i sequence. The iteration was stopped once S_i and \hat{S}_i no longer differed by more than a predefined small value (0.001).

The emerging prediction is that the longer a female has remained virgin, the greater her signaling effort (fig. 1c). Optimal signaling effort (S_i) thus increases with the number of nights spent unmated if there is spatiotemporal variation in male availability that the female cannot estimate directly, but the female can get updated estimates of the situation if she fails to attract mates despite signaling.

These results generalize the following: a numerical examination of 11 equally spaced values of mortality (m) (from 0.1 to 0.99) combined with 10 different, equally spaced values of k (from 0.5 to 0.99) led—in every of the 110 computed cases—to a much lower signaling effort on the first night than the eventual maximum signaling effort (among the examined cases spanning the entire range of what is feasible for moth life histories, the maximum effort was minimally 1.20-fold and maximally 2.39-fold compared with the effort of the first night). The precise value of mortality (m) proved surprisingly unimportant for the general pattern, since relatively mild and relatively stark increases with time spent mateless were found at either low or high mortality ($m = 0.1$: increases were between 1.7-fold and 2.1-fold; $m = 0.99$: increases were between 1.2-fold and 2.3-fold). Thus, while the precise daily increase in signaling effort does not always strictly follow figure 1c, the general pattern is very robust. Our results also generalize beyond the particular number of males that find a female ($\lambda(S)$ functions in the example of fig. 1), because the scenario “no male arrivals for a given signaling effort” is generally more likely when males are scarce, and this is all that is needed for the estimate of p_i to increase over time. Also note that competition between females is implicitly included in the model: if other females’ mating efforts decrease local male availability for a focal female, this simply makes her more likely to experience a low-arrival situation $\lambda_L(S)$ than the higher $\lambda_H(S)$.

Balancing Mate Arrival Rate with Increasing Costs of Calling

The previous section was based on the idea that a female needs to adjust likely male arrival rates to a value that is neither too low (as this increases the probability that no mate arrives) nor too high (assumed to be costly; see above). It is also conceivable that a high number of males arriving per night is better for the female, for example, because of direct benefits of multiple mating or mate sampling. In such cases, an intermediate rather than maximal signaling effort can still be selected for, if high signaling effort is costly. Such costs can be difficult to detect precisely

because females are not typically expected to evolve highly costly mate acquisition traits (Kokko and Wong 2007), but it is noteworthy that (1) costs can shape mating systems even if they are small or (2) sometimes sperm limitation can make females evolve costly mate acquisition traits (for insect data, see Charlat et al. 2007; Calabrese et al. 2008; Rhainds 2010; for data from spatially varying situations, see Contarini et al. 2009; Rhainds 2012).

Accordingly, we now assume that multiple male arrivals are not costly (we modify the above model to have $k \geq 1$) and include direct costs of pheromone production. The latter modification is achieved by including a factor $(1 - c(S))$ in fitness $w_i(S_i)$ from equation (6a), describing a fractional loss of fitness of magnitude $c(S)$:

$$w_i(S_i) = (1 - c(S))g_i(S_i) + (1 - m)w_i \quad (7)$$

Hereafter, the model analysis proceeds as in “Optimizing Male Arrival Rate.” This version of the model essentially replicates the findings: costs can select for an intermediate signaling effort as well as a pattern where, if the female has incomplete information on male density, signaling effort will increase with the number of nights the female has remained mateless (fig. 2). It is notable that very small magnitudes of the cost (barely perceptible in fig. 2b) select for modulations in signaling effort.

As in “Optimizing Male Arrival Rate,” we investigated the generality of the pattern with 11 choices for mortality, m (as above), and with 10 equally spaced choices for the cost parameter c (between 0.1 and 0.9). Every case yielded a qualitative pattern similar to figure 2c, with maximal signaling effort ranging between 1.18-fold and 1.73-fold of the first night’s effort. Given the relatively small range of these values, it appears that knowing the precise value of mortality, m , is here even less important than in “The Model” to derive the general prediction that signaling will first increase and then plateau as the female ages.

Empirical Evidence on Female Signaling Effort

We reviewed the empirical evidence on age-related changes in virgin female moth signaling. We defined four types of relationship between age and signaling effort (fig. 3). Signaling effort may (1) remain unchanged as the female ages (e.g., Coffelt et al. 1979; Dong and Du 2001), (2) increase over time (e.g., Almeida et al. 2008), (3) decrease over time (e.g., Del Mazo-Cancino et al. 2004), or (4) be greatest in the middle of life (e.g., Corbitt et al. 1996). While other shapes are conceivable, we found no evidence for them in the literature.

Signaling effort in moths has been measured over different timescales. Studies tend to focus on diel fluctuations, lifetime signaling effort, or both (Babilis and Mazomenos 1992; Tang et al. 1992; Kamimura and Tatsuki 1993). To

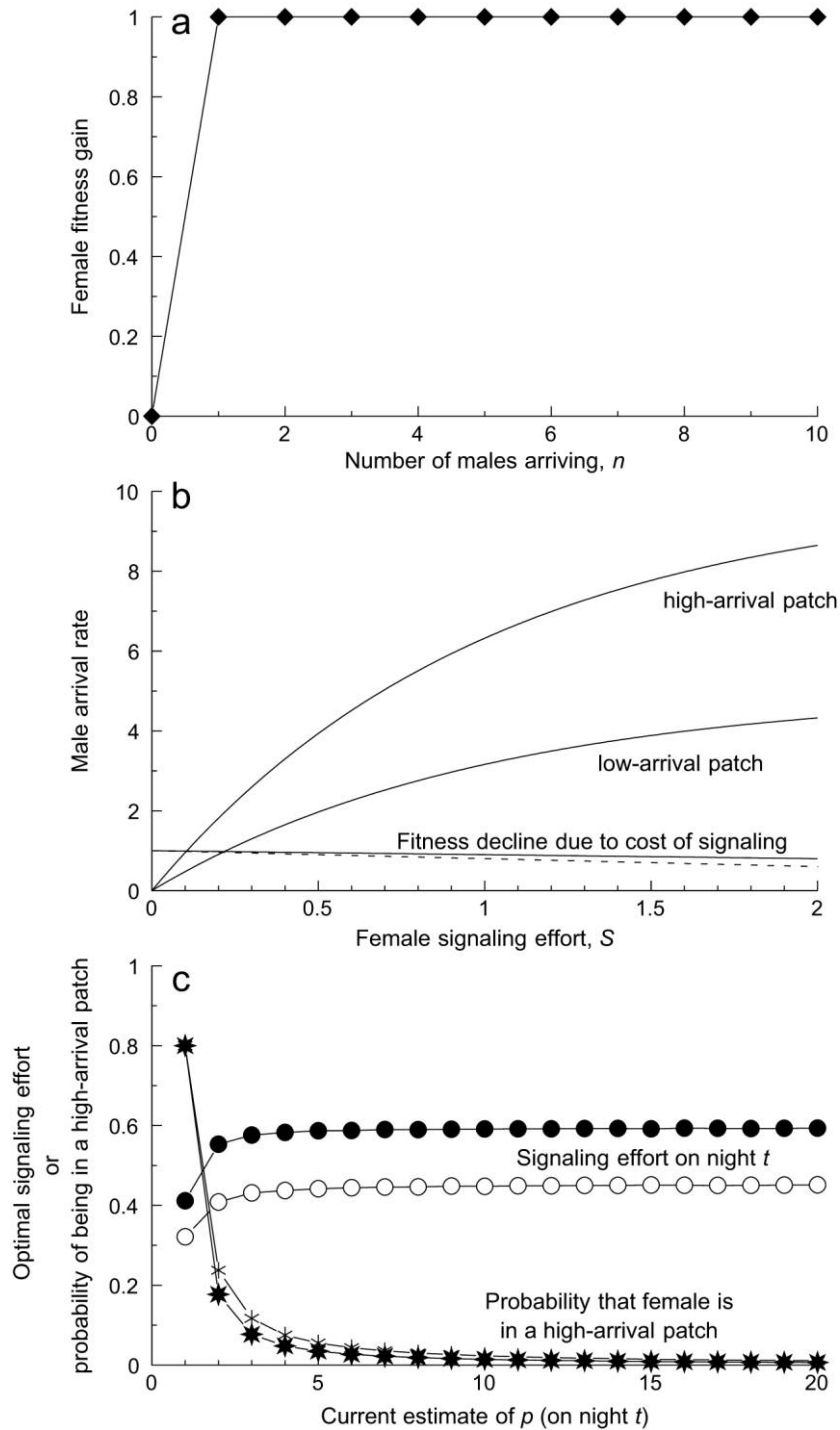


Figure 2: Same model as figure 1 but now $k = 1.0$ (a); also costs of signaling are now indicated as a decline in fitness with increased signaling effort, exemplified by $c(S_t) = \min\{1, cS_t\}$, which ensures that fitness becomes 0 (rather than negative) if $cS_t > 1$ (b). This leads to a solution that is qualitatively similar to figure 1, though with a more rapid approach of the maximal signaling effort over time (c). Two cases are shown: $c = 0.1$ (solid line in b and filled symbols in c) and $c = 0.2$ (dashed line in b and open symbols and thin star shapes in c). In both cases, $m = 0.25$.

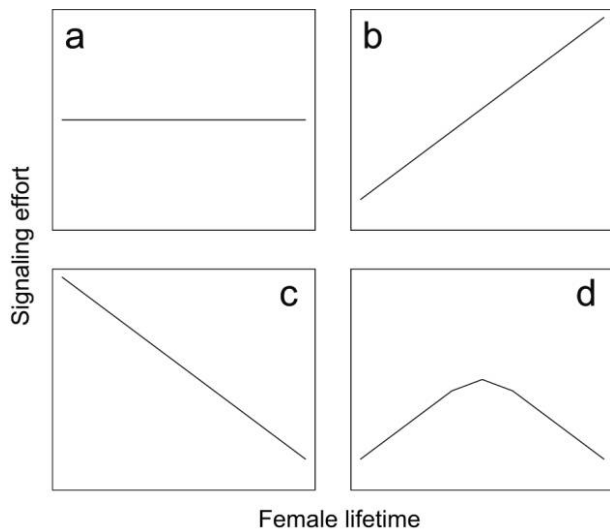


Figure 3: Schematic showing the four trends of signaling effort reported in the literature as it changes with age: no change with age (a), increase with age (b), decrease with age (c), peak in middle of life (d).

address our question of how virgin female signaling effort changes each night she remains unmated, we included only studies that measured signaling effort and how it changed as virgins aged. We found 52 studies that report age-dependent changes in virgin female moth signaling effort in 44 species (table 1). Unfortunately, most studies did not state whether signaling was quantified over the entire life span of the female or the length of the natural life span of these species (possibly related to feeding requirements). Consequently, we cannot rule out the possibility that some studies may misclassify cases with peak midlife signaling effort (option 4) as increased signaling effort over time (option 2) because of a failure to observe the decline phase.

Signaling effort (S) may refer to the duration of calling or to the concentration of the pheromone that the female produces. Empirical studies measure S in several different ways. Since direct measurement of pheromone plumes is difficult, many studies report pheromone concentration within the gland (table 1). Others report the proportion of females calling (Hendrikse 1979) or how early calling begins each night (Delisle and McNeil 1987; Kou and Chow 1987; Delisle 1992). Several studies report changes in calling bout number and bout length (Howlader and Gerber 1986; Jacas and Peña 2002; Mazor and Dunkelblum 2005; Ming et al. 2007), with calling bout defined as a period of time over which a female is observed in the characteristic position of raising her abdomen and periodically everting her ovipositor.

We excluded studies that reported only measures of the

proportion of females calling, since this provides no information on individual age-dependent changes. Likewise, we excluded studies reporting only the number or length of bouts, since the relationship to total calling effort remains unclear. This left 33 studies that measured time spent calling and 32 studies reporting pheromone titer, with 13 studies (on 12 species) that measured both (table 1). As females age, they often start calling earlier in scotophase (night). In our data set, time spent calling refers to an earlier onset of calling, which allows for an overall increase in time spent calling each night. Our titer data set includes 29 studies that measured pheromone concentration in the excised gland and five studies that measured pheromones released from the gland, which includes two studies that measured both: one on *Holomelina lamae* (Schal et al. 1987) and one on *Diaphania nitidalis* (Valles et al. 1992; table 1).

Increasing Calling Duration with Age Is the Dominant Pattern

The majority of studies (~70%) reported that virgin females spent a longer time calling as they aged (fig. 4). For some species, multiple studies reported changes in time spent calling with age. For three species (*Helicoverpa armigera*, *Agrotis ipsilon*, and *Pseudaletia unipunctata*), each study reported the same pattern of time spent calling with age (increase over time; table 1). For *Helicoverpa assulta*, however, one study reported an increase over 7 days (Kamimura and Tatsuki 1993), while another reported peak calling time in the middle of females' lives over 6 days (Ming et al. 2007; table 1).

Age-Dependent Changes of Pheromone Titer Show an Ambiguous Pattern

Approximately 40% of studies reported that titer concentration was highest in the middle of a female's life, and 34% reported that pheromone titer concentration decreases with age (fig. 4). Only 16% of studies reported an increase with age. For two species (*Lymantria dispar* and *H. assulta*), two studies each reported changes in titer with age. While the two studies on *H. assulta* were comparable and congruent, the two studies on *L. dispar* differed in their classification. One showed titer increasing with age over 3 days (Tang et al. 1992), while the other showed that titer was highest in the middle of the female's life over 7 days (Giebultowicz et al. 1990). When taking into account the different timescales of the studies, the data suggest that female *L. dispar* may produce highest concentrations in the middle of their lives, but this needs experimental confirmation.

Table 1: Summary of studies of virgin female calling effort in relation to age for 44 species of Lepidoptera

Species	Reference	Measure of calling effort studied	Measurement of pheromone titer	Change in calling effort with age	
				Pheromone titer	Time spent calling
<i>Agrotis ipsilon</i>	Gemeno and Haynes 2000	Time spent calling, pheromone titer	Amount in gland	Decreases	Increases
<i>A. ipsilon</i>	Swier et al. 1977	Time spent calling			Increases
<i>Amyelois transitella</i>	Coffelt et al. 1979	Time spent calling, pheromone titer	Amount released	No change	No change
<i>Autographa gamma</i>	Mazor and Dunkelblum 2005	Time spent calling, pheromone titer	Amount in gland	Peaks midlife	Increases
<i>Brachmia macroscopa</i>	Hirano and Muramoto 1976	Time spent calling			Increases
<i>Chilo suppressalis</i>	Kanno 1979	Time spent calling			Increases
<i>Choristoneura fumiferana</i>	Delisle et al. 2000	Pheromone titer	Amount in gland	Decreases	
<i>Choristoneura rosaceana</i>	Delisle et al. 2000	Pheromone titer	Amount in gland	Decreases	
<i>C. rosaceana</i>	Delisle 1992	Time spent calling			Increases
<i>Cnaphalocrocis medinalis</i>	Kawazu and Tatsuki 2002	Time spent calling, pheromone titer	Amount in gland	Peaks midlife	Increases
<i>Condylorrhiza vestigialis</i>	Ambrogi et al. 2008	Time spent calling			Increases
<i>Copitarsia consueta</i>	Rojas and Cibrián-Tovar 1994	Time spent calling			Increases
<i>Cornutiplusia circumflexa</i>	Mazor and Dunkelblum 2005	Time spent calling, pheromone titer	Amount in gland	Peaks midlife	Increases
<i>Ctenopseustis herana</i>	Foster et al. 1995	Pheromone titer	Amount in gland	Increases	
<i>Ctenopseustis obliquana</i>	Foster et al. 1995	Pheromone titer	Amount in gland	Peaks midlife	
<i>Diaphania nitidalis</i>	Valles et al. 1992	Pheromone titer	Both	Peaks midlife	
<i>Epiphyas postvittana</i>	Foster et al. 1995	Pheromone titer	Amount in gland	Increases	
<i>Estigmene acrea</i>	Del Mazo-Cancino et al. 2004	Time spent calling, pheromone titer	Amount in gland	Decreases	Increases
<i>Helicoverpa armigera</i>	Kou and Chow 1987	Time spent calling			Increases
<i>H. armigera</i>	Hou and Sheng 2000	Time spent calling			Increases
<i>H. armigera</i>	Ming et al. 2007	Time spent calling, pheromone titer	Amount in gland	Decreases	Increases
<i>Helicoverpa assulta</i>	Kamimura and Tatsuki 1993	Time spent calling, pheromone titer	Amount in gland	Decreases	Increases
<i>H. assulta</i>	Ming et al. 2007	Time spent calling, pheromone titer	Amount released	Decreases	Peaks midlife
<i>Helicoverpa virescens</i>	Foster and Johnson 2011	Pheromone titer	Amount in gland	Decreases	
<i>Helicoverpa zea</i>	Raina et al. 1986	Pheromone titer	Amount in gland	Peaks midlife	
<i>Heliothis peltigera</i>	Dunkelblum and Kehat 1992	Pheromone titer	Amount in gland	Increases	
<i>Holomelina lamae</i>	Schal et al. 1987	Pheromone titer	Both	No change	
<i>Homoeosoma electellum</i>	McNeil and Delisle 1989	Time spent calling			Increases
<i>Hydracacia micacea</i>	West et al. 1984	Time spent calling			Increases
<i>Keiferia lycopersicella</i>	McLaughlin et al. 1979	Time spent calling			Peaks midlife
<i>Lacanobia oleracea</i>	Corbitt et al. 1996	Pheromone titer	Amount in gland	Peaks midlife	
<i>Lymantria dispar</i>	Tang et al. 1992	Pheromone titer	Amount in gland	Increases	
<i>L. dispar</i>	Giebultowicz et al. 1990	Pheromone titer	Amount in gland	Peaks midlife	
<i>Mamestra configurata</i>	Howlader and Gerber 1986	Time spent calling			Increases
<i>Mythimna convecta</i>	Del Socorro and Gregg 1991	Time spent calling			Peaks midlife
<i>Nephoterix</i> sp.	Witethom 1992	Time spent calling			Peaks midlife
<i>Ostrinia furnacalis</i>	Boo and Park 1998	Pheromone titer	Amount in gland	Peaks midlife	
<i>Palpita unionalis</i>	Mazomenos et al. 2002	Time spent calling, pheromone titer	Amount in gland	Peaks midlife	Decreases
<i>Phthorimaea operculella</i>	Ono et al. 1990	Pheromone titer	Amount in gland	Decreases	
<i>Phyllocnistis citrella</i>	Jacas and Peña 2002	Time spent calling			No change
<i>Planotortrix octo</i>	Foster et al. 1995	Pheromone titer	Amount in gland	Peaks midlife	
<i>Platynota stultana</i>	Webster and Carde 1982	Pheromone titer	Amount in gland	Decreases	
<i>Plusia chalcites</i>	Snir et al. 1986	Pheromone titer	Amount in gland	Peaks midlife	
<i>Pseudaletia sequax</i>	Almeida et al. 2008	Time spent calling			Increases
<i>Pseudaletia unipuncta</i>	Cusson and McNeil 1989	Pheromone titer	Amount in gland	Peaks midlife	
<i>P. unipuncta</i>	Delisle and McNeil 1987	Time spent calling			Increases
<i>P. unipuncta</i>	Turgeon and McNeil 1982	Time spent calling			Increases
<i>Sesamia calamistis</i>	Fiaboe et al. 2003	Time spent calling			Decreases
<i>Sesamia nonagrioides</i>	Babilis and Mazamenos 1992	Time spent calling			Increases
<i>Spodoptera exigua</i>	Dong and Du 2001	Time spent calling, pheromone titer	Amount in gland	No change	Increases
<i>Spodoptera littoralis</i>	Dunkelblum et al. 1987	Time spent calling, pheromone titer	Amount in gland	Decreases	Peaks midlife
<i>Trichoplusia ni</i>	Bjostad et al. 1980	Time spent calling, pheromone titer	Amount released	Increases	Decreases

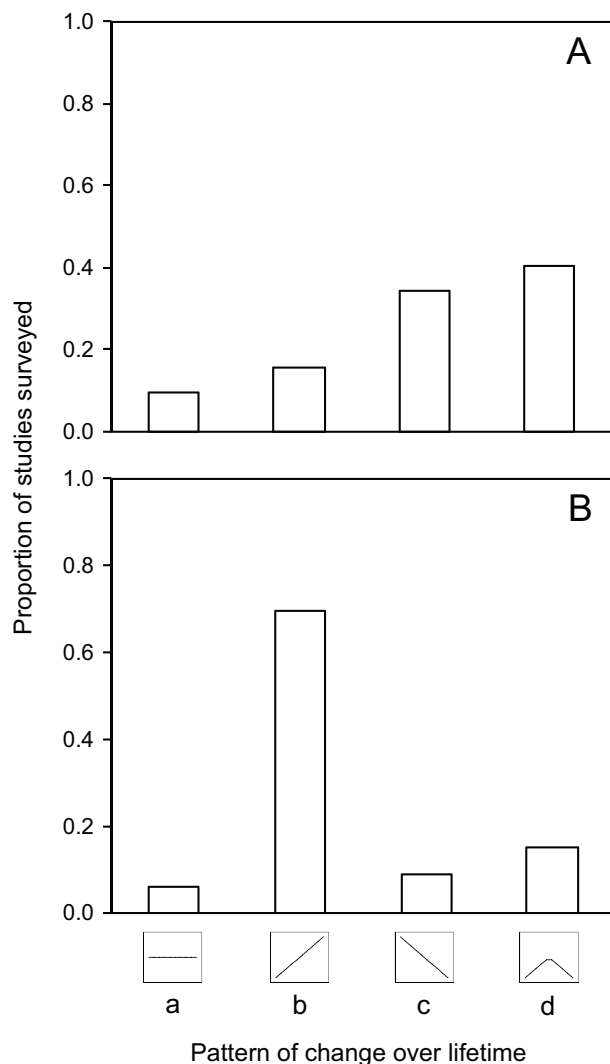


Figure 4: Proportion of studies that report one of the four patterns of signaling effort from literature for pheromone titer (A) and time spent calling (B).

Interpretation of Empirical and Theoretical Evidence

Our prediction of increased signaling by virgin females as they age was better supported when signaling effort is measured as time spent calling than when it is measured as pheromone titer. This interesting result highlights gaps in our current understanding of the consequences of these two components of signaling effort with respect to mate acquisition, and we investigated this matter with further modeling (appendix, available online). To sum up these supplementary theoretical advances, they suggest that the predicted age-dependent changes in signaling effort are more likely to be found in the timing of signaling rather than pheromone concentrations. Our empirical data set

matched these predictions because females generally did not increase the amount of pheromone they produce with age, despite remaining unmated. Most studies reported a decline in pheromone titer with increasing age, either immediately after eclosion or after a peak in titer in midlife (Foster et al. 1995; Foster and Greenwood 1997).

There are several potential explanations for why pheromone titer should decline with age, each worthy of further study. Many measures of pheromone titer are taken from within the gland, which may be a poor proxy for concentration in the plume. Over a short timescale, the correlation could be negative if a female who has emitted a lot of pheromone has less left in the gland (Schal et al. 1987). More data are needed to verify that the concentrations are a useful proxy for each other (e.g., Valles et al. 1992).

There could be ontogenetic constraints to pheromone production if slow maturation meets senescence at the midlife peak. Typically, declines in pheromone titer have been attributed to senescence, and there is evidence for internal hormonal suppression of pheromone biosynthesis in older virgin females (Teal et al. 1990; Delisle and Simard 2003) as well as reduction over time in the capability of synthesizing pheromone components (Foster and Greenwood 1997; Delisle and Simard 2003; Bober et al. 2010).

Interestingly, it might be simply incorrect to assume that plumes with higher pheromone concentration result in a linear increase in the number of males attracted (see appendix). It is often assumed that the number of males that respond to a female is a direct indicator of the amount of pheromone that she is producing (Cardé and Hagaman 1984; Delisle and Royer 1994). However, supporting the view that the matter is likely to be complex (appendix), studies of male responses to varying concentrations of synthetic pheromones indicate a nonlinear pattern. Typically, male numbers increase up to a certain concentration but with no additional increase—and sometimes a reduction—at higher concentrations (Baker et al. 1985; Mafra-Neto and Cardé 1995; Vickers 2000). While single moths might not be capable of producing such high concentrations, multiple females signaling in close proximity to each other could create a similar, cumulative effect. This could create an indirect cost if females select for males that can detect minute amounts of pheromone (Lloyd 1979; Greenfield 1981).

Given that both empirical and theoretical arguments point to a convoluted relationship between titer and male response, it is easy to understand why our models perform much better when the trait in question is more clearly related to male arrival rates (time spent calling) than when it is not (pheromone titers). The increase with age in female signaling effort—in the form of greater amount of time spent calling—appears a robust prediction. However,

the amount of empirical data currently available is limited. While studies investigating the relationship between female mating success and age have been conducted in moths (Delisle 1995; Evenden et al. 2006), we are unaware of any study that has directly investigated the relationship between calling effort and male response. Such studies would provide important data, especially if they investigated both time spent calling and pheromone titer. Typically, the times of night when females call coincide with the times when the number of males flying is near its peak, which in turn correspond to abiotic factors, such as suitable temperature and humidity (Castroville and Cardé 1979; Gemeno and Haynes 2000). Studies aiming to estimate likely male arrival rates will have to control for such factors also.

Contrasting patterns in pheromone titer and time spent calling over a female moth's life also suggest that these two traits might trade off. Increasing calling rate with age may be a behavioral strategy for older females to cope with a physiologically driven decline in pheromone production (Webster and Cardé 1982; Delisle and Royer 1994; Mazor and Dunkelblum 2005). Unfortunately, data for both traits together exist for only 12 species in 13 studies (table 1). Although this precludes strong conclusions, it is interesting to note that eight out of the 12 species showed an increase in time spent calling accompanied by (1) an immediate decline ($n = 4$: *Estigmene acrea*, *Agrotis ipsilon*, *Helicoverpa armigera*, and *Helicoverpa assulta*), (2) eventual decline ($n = 3$: *Cornutiplusia circumflexa*, *Autographa gamma*, and *Cnaphalocrocis medinalis*), or (3) no change over time ($n = 1$: *Spodoptera exigua*) in pheromone titer (table 1). No species has been reported to increase both time spent calling and pheromone titer with age.

For two species (*H. assulta* and *Spodoptera littoralis*), time spent calling was longest in the middle of their lives, while their pheromone titer declined as they aged. The two studies on the Oriental tobacco budworm (*H. assulta*) both report that pheromone titer decreased with age, but time spent calling was reported either to increase with age or to peak at midlife. This discrepancy perhaps suggests that strategies in different populations vary and/or that experimental repetition is needed to reveal a generalized strategy per species. Two species with apparently unusual strategies are the cabbage looper (*Trichoplusia ni*) and the jasmine moth (*Palpita unionalis*): pheromone titer increases with age, accompanied by an immediate (*T. ni*) or eventual (*P. unionalis*) decrease in calling time (table 1). This suggests that any trade-off between the two aspects of signaling effort may be operating in reverse in these species.

Discussion

Mate searching in moths offers great opportunities to examine whether mate acquisition is a challenge for females

and, if so, how this challenge shapes female life histories. Our model makes a clear, intuitive prediction: a virgin female's signaling effort should increase with days they remain virgin. Linking this prediction to existing empirical data proved partially successful. Females appear to adjust one measure of signaling effort (time spent calling) but not the other (pheromone concentration). Our supplementary models suggest that adjusting timing is probably a more efficient way to manipulate male arrival rates, but the opposite patterns were found to be possible in principle. We predicted the latter case only in cases where males remained stationary until a plume reached them. Given that even the simplest of plume models—which lack much known detail (Vickers 2000; Cardé and Willis 2008; Riffell et al. 2008)—could produce such a diverse set of outcomes when male behavior alone was varied, it appears robust to caution against any expectations of greatly increased arrival rates with increases of pheromone output.

Very few empirical studies report both measures of time spent calling and of pheromone titer. With respect to pheromone titer, studies usually report either the concentration of pheromone present in the excised ovipositor gland or the concentration of pheromone emitted. This approach is problematic because the relationship between these two measures has not been thoroughly investigated; thus, their relative importance is unclear (Schal et al. 1987; Valles et al. 1992). Time spent calling (producing pheromone) has been measured in many different ways. The most common measures are the number or length of calling bouts and the onset of calling (how early in the night females begin to call). We found good correspondence to model predictions when using the onset of calling, but the tendency of studies to report only one or two of the above list of traits precludes drawing more than observational conclusions about potential trade-offs.

Moths show great potential for examining female mate acquisition. Even if males perform most of the search, the risk of remaining unmated can select for the less mobile sex (females) to perform costly behaviors. However, if mate availability varies, the best early-life strategy is to initially avoid these costs. This is the rationale behind the increasing signaling effort with age. We have identified three prominent gaps in existing knowledge that, once filled, would aid in quantifying how signaling effort translates into mating success.

First, in empirical work, the outcome of female signaling effort is rarely quantified in a way that is relevant to real-life scenarios. To examine the validity of theory, it would be extremely valuable to examine how males arrive at artificial pheromone sites combining data on pheromone release duration with how much pheromone is present. Many studies have compiled data on the latter (i.e., effect of artificial pheromone concentration on number of males

trapped and its modeling; e.g., Guichard et al. 2012) but not in combination with the former. This is unfortunate, since females appear to mainly increase their signaling effort by beginning to call earlier rather than louder.

Second, to understand female strategy and lifetime investment, it is critical to measure the natural life spans of females in the field. This measure and how it relates to the possibly artificially lengthened life in laboratory conditions could then be confidently compared with signaling effort. Studies that have considered both field and laboratory populations have arrived at different results (West et al. 1984).

Finally, there are understudied aspects of moth signaling systems that apply both to our theoretical developments and to empirical research. In our model, we assumed that a female's mate encounter rate depends on the environment and her own signaling effort, but we did not explicitly examine feedback between fitness and other females' signaling effort. If neighboring females interfere with a focal female's mating efforts, selection toward earlier calling can intensify in a manner analogous to earlier arrival of migratory organisms when the number of competitors increases (Kokko et al. 2006). Although many empirical studies have measured the percentage of females calling (e.g., Webster and Cardé 1982; Babilis and Mazomenos 1992; Kamimura and Tatsuki 1993; Ming et al. 2007), more information on their spatial arrangement could prove useful. Females can potentially use cues other than their own mating status to adjust signaling effort: if females can perceive the signals of competing females, there is potential for more complex signaling strategies than the ones modeled by us (Harari et al. 2011). Experimental manipulation of juvenile environments can also prove informative (Gibbs et al. 2004).

Theory predicts that pheromonal communication can make the two sexes pay asymmetric costs, with females paying much less than males (Kokko and Wong 2007). It is consequently no surprise that Lepidoptera-dominated research into pheromonal communication has found it difficult to identify costs of this modality of signaling (Johansson and Jones 2007; Symonds and Elgar 2008). Our results suggest that these costs exist and that, despite being potentially small, they influence the life-history scheduling of females. More generally, by providing a formal framework in which future studies of female signaling behavior can be accommodated, our model identifies questions such as "How do pheromone concentration and time spent calling interact?" and "How does a multicomponent signal influence the mate encounter frequency?" These questions need to be addressed to improve our understanding of female mate search efforts that can appear subtle but reflect dramatic fitness consequences.

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