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A Game Theoretical Analysis of the Mating Sign Behavior in the Honey bee

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Abstract Queens of the honey bee, *Apis mellifera* (L.), exhibit extreme polyandry, mating with up to forty-five different males (drones). This increases the genetic diversity of their colonies and consequently their fitness. After copulation, drones leave a mating sign in the genital opening of the queen which has been shown to promote additional mating of the queen. On one hand, this signing behavior is beneficial for the drone because it increases the genetic diversity of the resulting colony. On the other hand, it decreases the proportion of the drone's personal offspring among colony members which is detrimental to the drone. We analyze the adaptiveness and evolutionary stability of this drone's behavior with a game-theoretical model. We find that theoretically both the strategy of leaving a mating sign and the strategy of not leaving a mating sign can be evolutionary stable, depending on natural parameters. However, for most scenarios, including all biologically plausible ones, based on empirical data the signing strategy is not favored. We conclude that leaving a sign is not in the interest of the drone unless it serves biological functions other than increasing subsequent queen mating chances.

Keywords Mating behavior · ESS · Game theory · Strategy

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1 Introduction

The mating patterns of animals are highly variable, and in many species one or both sexes mate with multiple partners. Polyandry, males mating with only one female but females mating with several males, is relatively rare among insects. However, some social insects, such as leaf cutter ants, army ants, harvester ants form notable exceptions [3, 27, 15]. Honey bees provide probably the most striking case because queens of several species in their genus *Apis* can mate with over forty different males (drones) during a very short time at the beginning of their lives [5, 26]. Honey bee queens and drones mature for about one week in their parental colony before they leave for mating flights [30, 22]. On these mating flights both sexes fly to mating arenas, called drone congregation areas (DCAs), where mate location and mating takes place [16]. Although, the mating behavior is therefore difficult to observe, tethered-queen studies have shown that the queens are usually located by vision and scent by drones, pursued by several drones, and mated consecutively by one of them in flight [13].

During copulation, the drone inserts his endophallus and transfers sperm into the oviduct. In the process, the male copulatory organs sever from the drone to be left in the genital opening of the queen as a so-called mating sign, while the drone dies shortly after copulation [31]. The sperm persists in the oviduct and migrates later to the spermatheca for long-term storage. The mating sign blocks the genital opening and thus needs to be removed by the next drone before mating. However, it has empirically been demonstrated that the mating sign increases the number of subsequent matings: in a choice test, drones mated more with queens with a mating sign than unsigned ones by a factor of 1.7 [11]. At the end of the mating flight, queens return to their hives with the last mating sign in place which is removed by the workers in the hive. Therefore, beekeepers can use the mating sign to identify queens that return successfully from mating flights.

The mating sign of the honey bee is an example of the more general phenomenon of males clogging the genital opening of their mate with a mating plug after copulation [8]. However, in contrast to the honey bee, in most species this leads to decreased subsequent copulation chances of the female. The mating plug can serve as a signal or as a physical barrier to prevent successful future mating [8]. This increases the plugging male's fitness by preventing sperm competition or complete removal of his sperm by any successor, thus maximizing his paternity among the female's offspring [8]. In contrast, mating plugs may disadvantage females by decreasing the overall genetic diversity among her offspring and the potential to select her offspring's paternity. For example, multiple mating confers a selective advantage to bumble bee (*Bombus terrestris*) queens due to lower pathogen loads among the descendent colony [1]. However, this species is usually singly-mated which is attributed to an efficient mating plug that increases drone fitness [2]. Thus, male and female interests diverge, resulting in an evolutionary arms race between the sexes [8].

In honey bees, the ancestral mating scenario may have resembled that of bumble bees but the finding that drone mating signs enhance the number of subsequent matings [11] radically alters the interpretation of this behavior. It is possible that the ancestral behavior persists because of evolutionary inertia and drones leave the mating sign because it used to be adaptive by preventing other drones from mating with the queen. An alternative explanation is that the mating sign fulfills important physiological roles in mating, such as retention of the sperm in the female genital tract during flight [29], or aiding the sperm migration into the spermatheca [28]. Finally, selection for multiple mating in honey bees may be sufficiently strong to select for cooperation among all concerned parties to facilitate female multiple mating, thus leading to a mating sign that enhances a queen's subsequent mating chance [14]. In this case, the increase in colony performing would have to outweigh not only the costs of multiple mating to the queen, but also the cost of the signing behavior to the drone, including the dilution of his sperm contribution to the next generation.

This study aims to analyze the adaptiveness and evolutionary stability of the drone's signing strategy in a game-theoretical framework. In this context, the fitness benefit for an individual drone to leave a mating sign or not is dependent on the population frequency of drones leaving a mating sign, the function connecting the number of matings and queen fitness, and other factors that determine average mating number of queens, such as the time a queen spends in the DCA (total mating time), the time it takes for a drone mate to find the queen, and the decrease in that time due to a mating sign. We analyze the fitness functions for the queen and each drone to determine conditions under which the strategy ”to sign“ or ”not to sign“ is an evolutionary stable strategy (ESS). An ESS is a strategy such that, if all the members of a population adopt it, no mutant strategy can invade [18].

In Section 2, we develop our model by introducing fitness functions for the queen and each drone and we analyze the fitness for the average drone. In Section 3 we state the conditions for different strategies to be ESSs. In Section 4, we state our main results. Finally, in Section 5, we provide the conclusion and discussion of our results.

2 Methods

2.1 Mathematical model of honey bee mating mating behavior

For modeling purposes, we consider the following idealization. A queen flies into the drone congregation area and remains there for time T. A drone mates with the queen in a negligible amount of time. After mating, the drone does or does not sign the queen. A drone that leaves a sign will be called a *Signer* and a drone that never leaves a sign will be called an *Unsigner* because he removes any potential previous mating sign without replacing it. Drones die after the mating but there is a large number of drones in the congregation area and we may thus assume that the density of drones remains constant over time. We assume that the time needed for a queen to be found (and mated) by a drone follow the exponential distribution with means σ^{-1} (for signed queen) and υ^{-1} (for unsigned queen). Leaving a sign increases the likelihood that a subsequent drone will find the queen, meaning

$$\upsilon < \sigma. \tag{1}$$

2.2 Queen fitness function and drone fitness function

The queen fitness, $F_q(n)$, is a function of the number of drones the queen mates with. Each drone is thought to contribute an equal amount of sperm to the queen [28] and thus has an equal share of the paternity of the brood. Therefore, the fitness function for a drone, given the queen mated n times, is

$$F_d(n) = \frac{F_q(n)}{n}. \tag{2}$$

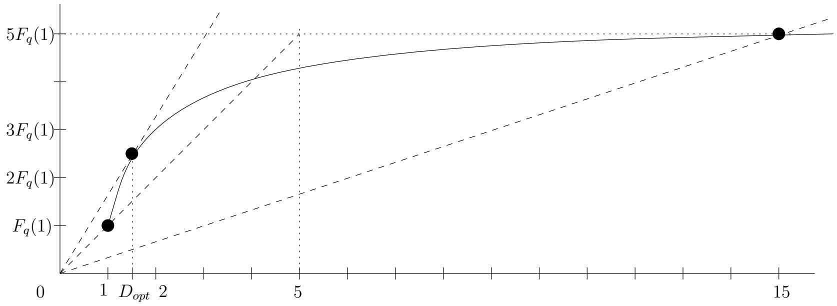

Fig. 1 An example of a queen fitness function and a demonstration that once $F_q(15) \approx 5F_q(1)$, the maximal drone fitness has to occur for less than 5 mates. Note that the drone fitness $F_d(x)$ corresponds to the slope of the line connecting the origin with the point $[x, F_q(x)]$. The function F_d attains its maximum at exactly one point D_{opt}.

There is empirical evidence that the queen fitness is generally an increasing function of n with diminishing returns [6,9]. Therefore, we may idealize the fitness function to be a smooth, positive, increasing and concave-down function $F_q(x)$ on $[1, \infty)$. Hence

$$F_d'(x) = \left(\frac{F_q(x)}{x}\right)' = \frac{F_q'(x)x - F_q(x)}{x^2} \tag{3}$$

and since

$$\left(F_q'(x)x - F_q(x)\right)' = F_q''(x)x < 0 \tag{4}$$

we get $F_d'(x) = 0$ for at most one value of x. Consequently, there is a unique $D_{opt} \in [1, \infty]$ such that

$$F_d \text{ is increasing on } (1, D_{opt}), \text{ and} \tag{5}$$

$$F_d \text{ decreasing on } (D_{opt}, \infty). \tag{6}$$

As we will see later, the above observation on D_{opt} plays a crucial role in the analysis of optimality of drone's behavior.

2.3 Estimating D_{opt}

The properties of F_q allow us to estimate D_{opt} even when we do not know the function F_q explicitly. Just knowing the approximate values of $F_q(1)$ and $F_q(k)$, for some (generally large) mating number k, such as those in [17], can give us a very useful estimate for D_{opt} (see Figure 1).

If $F_q(k) < kF_q(1)$, in other words, if $F_d(k) < F_d(1)$, then

$$D_{opt} \leq \frac{F_q(k)}{F_q(1)}. \tag{7}$$

Indeed, since $F_d(k) < F_d(1)$ there is $x_0 < k$ such that $F_d'(x_0) < 0$ and consequently, by (6), $F_d'(x) < 0$ for all $x > x_0$. Thus, $D_{opt} < x_0 < k$. If we assume, for the contrary, $D_{opt} > \frac{F_q(k)}{F_q(1)}$, then since F_q is increasing, we get

$$F_d(D_{opt}) \geq F_d(1) \tag{8}$$

$$F_q(D_{opt}) \geq \frac{F_q(1)}{1} \cdot D_{opt} > \frac{F_q(1)}{1} \cdot \frac{F_q(k)}{F_q(1)} = F_q(k) \tag{9}$$

$$D_{opt} > k, \tag{10}$$

a contradiction.

2.4 Approximating the expected drone's fitness

Let F_d^{xY} be the expected fitness of a drone using strategy x - s(signer) or u(unsigner) - if other drones in the population use a strategy Y - S(signer) or U(unsigner). Then

$$F_d^{xY} = \sum_{n=1}^{\infty} \pi_n^{xY} \frac{F(n)}{n} \tag{11}$$

where π_n^{xY} is the probability the queen mated n times during the time T given that she mated with the focal drone.

The probabilities π_n^{xY} and consequently F_d^{xY} can be calculated explicitly (see Appendix). However, the formulas did not allow us any further analytical progress. We therefore used the approximation

$$\sum_{n=1}^{\infty} \pi_n^{xY} \frac{F_q(n)}{n} \approx \frac{F_q\left(\sum_{n=1}^{\infty} n\pi_n^{xY}\right)}{\sum_{n=1}^{\infty} n\pi_n^{xY}} \tag{12}$$

which yields

$$F_d^{xY} \approx \frac{F_q\left(N^{xY}\right)}{N^{xY}} = F_d\left(N^{xY}\right) \tag{13}$$

where N^{xY} is the average number of drones the queen mates with during time T in the population of Y if she mates with the focal drone using strategy x. We can easily evaluate all values of N^{xY} (see Appendix).

In order to check the approximation (12) we run simulations based on Gillespie's algorithm [7]. In most cases, the results from the simulations were consistent with the approximations. This is a consequence of the function F_d being almost linear or even almost constant as long as it is considered only on $[1, D_{opt}]$ or on $[D_{opt}, \infty)$. The approximation were indeed worst when the expected number of mates was around D_{opt}, yet even then there was no more than 5% relative difference between simulated and approximated values.

3 Conditions on ESSs

A *signer* strategy is an ESS if the expected fitness for a single *unsigner* in a population of *signers* is lower than the expected fitness of an average drone in the population and vice-versa. Based on (13), a *signer* strategy is an ESS if

$$F_d(N^{sS}) > F_d(N^{uS}) \tag{14}$$

and similarly, an *unsigner* strategy is an ESS if

$$F_d(N^{uU}) > F_d(N^{sU}). \tag{15}$$

Since we can evaluate all of N^{xY} explicitly, we can formulate (14) and (15) in terms of σ, υ, T, and $F_d(x)$. We note that for most of the analysis, it is not the values N^{sS} and N^{uS}, but rather the difference $N^{sS} - N^{uS}$ that is important. It follows that

$$N^{sS} - N^{uS} = \left(\frac{\sigma}{\upsilon} - 1\right)\left(1 - \frac{1 - e^{-\upsilon T}}{\upsilon T}\right) > 0 \tag{16}$$

and thus, by (14), *signer* is ESS if and only if

$$N^{sS} < D^{signer}_{crit} \tag{17}$$

where D^{signer}_{crit} is the unique value such that

$$F_d(D^{signer}_{crit}) = F_d\left(D^{signer}_{crit} - \left(\frac{\sigma}{\upsilon} - 1\right)\left(1 - \frac{1 - e^{-\upsilon T}}{\upsilon T}\right)\right) \tag{18}$$

This is illustrated in Figure 2. A similar condition can be formulated for *unsigner* to be an ESS.

However, it is hard to practically evaluate D^{signer}_{crit} as it depends too much on the shape of the function $F_d(x) = F_q(x)/x$, which was never been empirically determined. Thus, we formulate sufficient conditions for *signer* and *unsigner* to be an ESS in terms of D_{opt} which we can estimate.

Since F_d is increasing on $[1, D_{opt}]$, a sufficient condition for a *signer* strategy to be an ESS is

$$N^{sS} < D_{opt}, \tag{19}$$

and, similarly, since F_d is decreasing on $[D_{opt}, \infty)$, a sufficient condition for an *unsigner* to be ESS is

$$N^{uU} > D_{opt}. \tag{20}$$

Conversely, a sufficient condition for a *signer* not to be an ESS is

$$N^{uS} > D_{opt} \tag{21}$$

as then $D_{opt} < N^{uS} < N^{sS}$ and thus $F_d(N^{uS}) > F_d(N^{sS})$, i.e. a single *unsigner* does better in the population of *signers* than the average *signer*. Note that, by (16), (21) holds if

$$N^{sS} > D_{opt} + \frac{\sigma}{\upsilon} - 1 \tag{22}$$

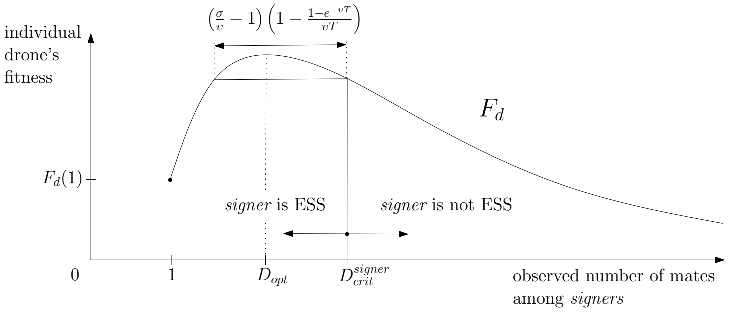

Fig. 2 Regions where *signer* is and is not ESS. If we know σ, υ, T, and mainly the function $F_d(x) = F_q(x)/x$, we can tell whether the drones behave optimally or not based on the observed number of mates.

4 Non-optimality of signing behavior

The inequalities (19) and (22) both contain only

- N^{sS}, an experimentally observable average number of mates,
- σ/υ which can be experimentally measured, and
- D_{opt}, that can be estimated, by (7), by experimentally measuring F_q at two sufficiently distinct values.

Note that we do not really need an estimate for T. This is favorable because such estimates are available but highly variable [28,30,24,12,10]. Thus, we can now use our analysis and available data to test whether drones behave optimally.

Empirical data suggest that a queen mates with 12 drones on average [25], and thus

$$N^{sS} \approx 12. \tag{23}$$

Using data from [17], we get $F_q(1) \approx 19$ and $F_q(15) \approx 72$; the numbers correspond to colony growth in terms of the number of thousands of bees in colonies (at the end of the study) whose queen mated with 1 and 15 drones respectively. We consider this measure to be proportional to the queen fitness. Thus, by (7), we may estimate

$$D_{opt} < \frac{F_q(15)}{F_q(1)} = \frac{72}{19} \approx 3.8. \tag{24}$$

Even if the estimates from [17] were to change by 25% in any direction, we still get as an upper estimate

$$D_{opt} < \frac{1.25 F_q(15)}{0.75 F_q(1)} < 6.4. \tag{25}$$

Moreover, as can be seen from Figure 1, the estimate for D_{opt} is usually inflated and thus, D_{opt} is likely significantly smaller than 6. Also, by [11],

$$\sigma/\upsilon \approx 1.73 < 2. \tag{26}$$

We thus have

$$N^{sS} > D_{opt} + \frac{\sigma}{\upsilon} - 1, \tag{27}$$

which, by (22), means that *signer* is not ESS. In this biologically plausible scenario, drones do not gain any fitness from leaving the mating sign to increase subsequent mating chances. Note that we have enough room for making N^{sS} smaller and σ/υ bigger and still not violating (22) which means that *signer* is not ESS even if the experimental data used here were not nearly exact.

5 Conclusion and discussion

In contrast to the general functions of mating plugs [7], the honey bee mating sign has been shown to promote additional matings by the female [11]. While this may be a case for male-female cooperation to promote their common long-term fitness interests through a genetically diverse colony [14] the signing behavior results in immediate death of the male drone [31] and thus bears a fitness cost. This cost may be small if the chances of another mating opportunity are negligible [2] but promoting future matings also dilutes the focal drone's contribution to the queen's offspring, reducing his fitness. Through our game theoretical analysis, enabled by parameter values from empirical studies, we show that the signing behavior is not an ESS [29] and in fact maladaptive for a broad range of parameter values. Thus, we conclude that the function to promote additional matings by the queen can not explain the evolutionary maintenance of honey bee mating signs.

Several non-mutually exclusive alternative explanations exists for the prevalence of mating signs in *Apis mellifera* and several other species in this genus [20]. Foremost, the mating signs may present a physical barrier that aids sperm retention in the oviduct by preventing back flow out of the queen after mating is completed in full flight [14]. Second, the mating process itself requires an effective, physical coupling mechanism, which may be best provided by the drone copulatory organs that remain in the queen, separating from the drone. In addition, the male accessory gland products may play other important roles in aiding sperm migration to the spermatheca and surviving the queen physiological environment, include her immune system [8].

Another important potential explanation for the occurrence of honey bee mating signs despite their potentially non-adaptive nature for drones is the hypothesis that the queens realize their fitness interest of mating many times despite the drones' effort to prevent future matings. In this line of argument, our argument that drone signing behavior to increase subsequent mating chances is non-adaptive could be inverted: drone signing behavior to decrease subsequent mating chances may be adaptive for a drone but runs against the queen's interest. In contrast to mating plugs in the closely related bumble bee, honey bee mating signs are easily removed [2] and our results suggest that the question of why honey bee drones are not more effective at hindering subsequent mating of the queen is as valid as the question whether the mating sign has evolved to increase subsequent mating chances of the queen. The system has the potential for an evolutionary arms race between queens and drones because their fitness interests diverge: the fitness of the average drone is $1/n$ times the respective queen fitness (2). For a queen, an optimum number of mating is high, given multiple benefits and relatively low mating costs [23,10] (and references therein), yet the optimum for drones is at a much lower mating number. Consequently, adaptations, such as male mating plugs, and counter-adaptations, such as mechanisms to render plugs ineffective, are to be expected. The third party in this evolutionary game are the other, unmated drones and their fitness interests coincide with that of the queen for additional matings.

However, our game theoretical model was designed for simplicity to focus on the signing behavior without considering changes in the other players' strategies.

Even this relatively simple analysis proved to be mathematically involved and dependent on empirical biological values that were difficult to extract from the literature. Based on current literature, we populated our analysis with the available data and evaluated the robustness of our conclusions with regard to variation in variables whose values we had the least confidence in. We found conditions under which signing might be beneficial. However, for most of the parameter space and the biologically most plausible scenarios, we found a consistent and strong disadvantage for drones to increase subsequent mating chances for the queen. Thus, we consider "signing" not an ESS in the analyzed mating game. This result was robust to a wide variation in mating times and the shape of queen fitness functions (Figure 1).

Mathematically, the question whether drone signing behavior represents an ESS or not represents a simple game theoretical problem with the essential twist of the finite total amount of time available for mating. A more detailed analysis reveals that there is not a strong selection pressure for *unsigners* to emerge in the population of *signers*. Since $\sigma/\upsilon < 2$, by (26), an *unsigner* would do better, but not much better than *signers*. Indeed, $N^{uS} > N^{sS} - 1$, and thus the queen will mate with almost the same number of drones. Since the slope of F_d around N^{sS} is really low (see Figure 2), we get $F_d(N^{uS}) - F_d(N^{sS})$ positive, yet generally very small.

In conclusion, we corroborate through mathematical analysis the view that the honey bee mating sign cannot be explained by its function to increase subsequent mating. Despite a lack of detailed biological data, this conclusion is robust and should hold for most conceivable evolutionary scenarios.

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6 Appendix

6.1 Exact calculations of F_d^{xY}

To calculate

$$F_d^{xY} = \sum_{n=1}^{\infty} \pi_n^{xY} \frac{F(n)}{n} \tag{28}$$

we evaluate $p_n(\mu, \nu, \tau)$, the probability a queen mated n times during time τ provided the queen is initially being found with speed μ and then, after the first and any subsequent mating, with speed ν.

Since if the queen does not mate at all in time τ, the first drone is expected to arrive after the time τ; and since the probability to mate $n+1$ times is superposition of all cases when the queen mates for the first time at time t and then mates n times in the remaining time $\tau - t$, it follows that

$$p_0(\mu,\nu,\tau) = \int_\tau^\infty \mu e^{-\mu t}\ \mathrm{d}t = e^{-\mu\tau} \tag{29}$$

$$p_{n+1}(\mu,\nu,\tau) = \int_0^\tau \mu e^{-\mu t} p_n(\nu,\nu,\tau - t)\ \mathrm{d}t \tag{30}$$

By the induction,

$$p_n(\mu,\mu,\tau) = \frac{(\mu\tau)^n}{n!} e^{-\mu\tau} \tag{31}$$

Consequently, for $\nu \neq \mu$, the integration by parts yields

$$p_n(\mu,\nu,\tau) = \mu\nu^{n-1} e^{-\nu\tau} \left(\frac{e^{(\nu-\mu)\tau}}{(\nu-\mu)^n} - \sum_{j=0}^{n-1} \frac{\tau^{n-1-j}}{(\nu-\mu)^{j+1}(n-1-j)!} \right) \tag{32}$$

Now we calculate π_n^{uU}. If the queen mated with a focal drone within time t, it then had to mate i times (for $i = 0, \dots, n-1$) before this drone and $n-1-i$ times after this drone. We thus have

$$\begin{aligned}
\pi_n^{uU} &= \frac{1}{T}\int_0^T \sum_{i=0}^{n-1} p_i(\upsilon,\upsilon,t) p_{n-1-i}(\upsilon,\upsilon,T-t)\ \mathrm{d}t && (33)\\
&= \frac{1}{T}\int_0^T \sum_{i=0}^{n-1} \frac{(\upsilon t)^i}{i!} e^{-\upsilon t} \frac{(\upsilon(T-t))^{n-1-i}}{(n-1-i)!} e^{-\upsilon(T-t)}\ \mathrm{d}t \\
&= \frac{1}{T} e^{-\upsilon T} \upsilon^{n-1} \int_0^T \sum_{i=0}^{n-1} \frac{t^i}{i!} \frac{(T-t)^{n-1-i}}{(n-1-i)!}\ \mathrm{d}t \\
&= \frac{1}{T} e^{-\upsilon T} \upsilon^{n-1} \int_0^T \frac{T^{n-1}}{(n-1)!}\ \mathrm{d}t \\
&= e^{-\upsilon T} \frac{(\upsilon T)^{n-1}}{(n-1)!} && (34)
\end{aligned}$$

Notice that the expected number of mates for a queen is

$$N^{uU} = \sum_{n=1}^\infty n\pi_n^{uU} = \upsilon T + 1 \tag{35}$$

One would expect, on average, υT drones during the time T. However, N^{uU} is the average number of mates for a queen given the focal drone mated with the queen. Since we assume the mating is happening instantaneously, the queen has still time T to mate with other drones which yields to $\upsilon T + 1$ mates in total. Calculating other probabilities is similar to (33)

$$\pi_n^{sU} = \frac{1}{T}\int_0^T \sum_{i=0}^{n-1} p_i(\upsilon,\upsilon,t) p_{n-1-i}(\sigma,\upsilon,T-t)\ \mathrm{d}t \tag{36}$$

$$\pi_n^{sS} = \frac{1}{T}\int_0^T \sum_{i=0}^{n-1} p_i(\upsilon,\sigma,t) p_{n-1-i}(\sigma,\sigma,T-t)\ \mathrm{d}t \tag{37}$$

$$\pi_n^{uS} = \frac{1}{T}\int_0^T \sum_{i=0}^{n-1} p_i(\upsilon,\sigma,t) p_{n-1-i}(\upsilon,\sigma,T-t)\ \mathrm{d}t \tag{38}$$

6.2 Exact calculations of N^{xY}

Let us first calculate an auxiliary function, $Q(\mu, \nu, \tau)$, the average number of mates during time τ provided the queen is initially being found with speed μ and then, after the first and any subsequent mating, with speed ν.

If drones are searching at speed μ then the expected time for a queen to be found is μ^{-1} and thus $Q(\mu, \mu, \tau) = \mu\tau$. To calculate $Q(\mu, \nu, \tau)$, we observe that if a queen is found at time $t \leq \tau$ with probability $\mu e^{-\mu t}$ dt then after mating with the focal drone, she mates, on average, with $Q(\nu, \nu, (\tau - t))$ mates in the remaining time. Hence

$$\begin{aligned} Q(\mu, \nu, \tau) &= \int_0^\tau \mu e^{-\mu t}(1 + \nu(\tau - t))\ \mathrm{d}t \\ &= \nu\tau + \left(1 - \frac{\nu}{\mu}\right)\left(1 - e^{-\mu\tau}\right). \end{aligned} \tag{39}$$

Now, consider a population of drones playing only the *unsigner* strategy. Then the focal drone finds the queen at time t with probability T^{-1} dt. Before being found by the focal drone at time t, the queen mated with other $Q(\upsilon, \upsilon, t)$ drones. Since the focal drone is *unsigner* the queen will mate with $Q(\upsilon, \upsilon, T - t)$ drones in the remaining time. Hence

$$\begin{aligned} N^{uU} &= \frac{1}{T}\int_0^T \left[Q(\upsilon, \upsilon, t) + 1 + Q(\upsilon, \upsilon, T - t)\right]\ \mathrm{d}t \\ &= \upsilon T + 1 \end{aligned} \tag{40}$$

Similarly,

$$\begin{aligned} N^{sU} &= \frac{1}{T}\int_0^T Q(\upsilon, \upsilon, t) + 1 + Q(\sigma, \upsilon, T - t)\ \mathrm{d}t \\ &= \upsilon T + 1 + \left(1 - \frac{\upsilon}{\sigma}\right)\left(1 - \frac{1 - e^{-\sigma T}}{\sigma T}\right) \end{aligned} \tag{41}$$

$$\begin{aligned} N^{uS} &= \frac{1}{T}\int_0^T Q(\upsilon, \sigma, t) + 1 + Q(\upsilon, \sigma, T - t)\ \mathrm{d}t \\ &= \sigma T + 1 - 2\left(\frac{\sigma}{\upsilon} - 1\right)\left(1 - \frac{1 - e^{-\upsilon T}}{\upsilon T}\right) \end{aligned} \tag{42}$$

$$\begin{aligned} N^{sS} &= \frac{1}{T}\int_0^T Q(\upsilon, \sigma, t) + 1 + Q(\sigma, \sigma, T - t)\ \mathrm{d}t \\ &= \sigma T + 1 - \left(\frac{\sigma}{\upsilon} - 1\right)\left(1 - \frac{1 - e^{-\upsilon T}}{\upsilon T}\right) \end{aligned} \tag{43}$$