

# More is Faster:

## Why Population Size Matters in Biological Search

Jannatul Ferdous,<sup>1</sup> G. Matthew Fricke,<sup>1,2</sup> Melanie E. Moses<sup>1,3,4\*</sup>

<sup>1</sup>*Department of Computer Science,* <sup>2</sup>*Center for Advanced Research Computing,*

<sup>3</sup>*Department of Biology, The University of New Mexico, Albuquerque, USA*

<sup>4</sup>*Santa Fe Institute, Santa Fe, USA*

*\*To whom correspondence should be addressed;*

*E-mail: melaniem@unm.edu.*

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**Abstract:** Many biological scenarios have multiple cooperating searchers, and the timing of the initial first contact between any one of those searchers and its target is critically important. However, we are unaware of biological models that predict how long it takes for the first of many searchers to discover a target. We present a novel mathematical model that predicts initial first contact times between searchers and targets distributed at random in a volume. We compare this model to the extreme first passage time approach in physics that assumes an infinite number of searchers all initially positioned at the same location. We explore how the number of searchers, the distribution of searchers and targets, and the initial distances between searchers and targets affect initial first contact times. Given a

constant density of uniformly distributed searchers and targets, the initial first contact time decreases linearly with both search volume and the number of searchers. However, given only a single target and searchers placed at the same starting location, the relationship between the initial first contact time and the number of searchers shifts from a linear decrease to a logarithmic decrease as the number of searchers grows very large. More generally, we show that initial first contact times can be dramatically faster than average first contact times and that initial first contact times decrease with the number of searchers while average search times are independent of the number of searchers. We suggest this is an underappreciated phenomenon in biology and other collective search problems.

## 1 Introduction

There are many biological examples of a large number of searchers attempting to find one or more targets. Sometimes, the first target discovered by the first lucky searcher is particularly important because it results in a cascade of downstream events. For example, in ant colonies, many ants forage for food; when the first one is successful, it may use pheromones to recruit other searchers. Thus, the time for the first ant to discover food may have a disproportionate impact on resource collection rates. Similarly, naïve T cells search for cognate antigen in lymph nodes. When T cells bind with target antigen they activate and replicate in an exponentially growing population of cells. Thus, the timing of the first contact by the first T cell that finds its target is particularly important in initiating the adaptive immune response. In these examples, the time it takes for the initial discovery of a target (what we call the initial first contact time) may be more important than the average time of all of the searchers to find their first targets. Here we develop and analyze mathematical models

and computer simulations to understand which factors affect initial first contact times.

In immune system models, it is common to consider the mean or median search time for a typical T cell to find its target, e.g., (Perelson and Wiegel, 2009; Wiegel and Perelson, 2004; Krummel et al., 2016; Celli et al., 2012). An analysis of initial first contact times in three-dimensional volumes has only recently been investigated in a series of publications (Lawley, 2020c,b; Lawley and Madrid, 2020), but these models do not apply to T cell search that motivated our work. The derivations in these other studies apply to searchers that start in a single location and search for a single target, and they rely on population sizes that approach infinity. We call the predictions of initial first contact times from such models  $t_\infty$ .

In this work we derive initial first contact time predictions for finite populations of searchers,  $t_{\text{fin}}$ . This model initially assumes a number of searchers and targets distributed at uniform random within a volume, and we predict how  $t_{\text{fin}}$  scales as the number of searchers increases. We then test different search scenarios, assess when assumptions made by the  $t_{\text{fin}}$  and  $t_\infty$  models hold, and compare simulated initial first contact times predicted by  $t_{\text{fin}}$  and  $t_\infty$ .

While we were motivated to develop  $t_{\text{fin}}$  to predict how quickly the first T cell would find its target antigen in a lymph node, we also examine whether  $t_{\text{fin}}$  can explain other search scenarios relevant for social insects and other collective foragers. Many studies have investigated how colony size affects social insect foraging, finding that larger colonies are more complex (Anderson and McShea, 2001), mass recruitment is more effective in larger ant colonies (Beekman et al., 2001), but waggle dances are not necessarily more effective in larger bee colonies (Dornhaus et al., 2006). (Popp and Dornhaus, 2023) found larger colonies searched an area faster and (Adler and Gordon, 1992) found larger colonies found more events. However, none of these studies modeled whether

the first event that triggered subsequent recruitment was found faster in larger colonies. Some studies suggest this may be the case. For example, a field study by (Donaldson-Matasci et al., 2013) found that larger honeybee colonies found resources faster, and as a result, overall foraging rates were better for larger colonies. Our previous field study(Flanagan et al., 2012) also found that larger seed harvester ant colonies found piles of seeds faster; however, neither of these studies had sufficiently detailed estimates of forager population size paired with and first discovery times to establish a quantitative relationship between the two. That is the focus of the models we build and analyze here.

Here we develop a model that predicts the initial first contact time for a finite number of searchers ( $t_{\text{fin}}$ ). We simulate search in different scenarios in order to validate conditions under which our theoretical assumptions do, and do not, hold. Our goal in this paper is not to test model predictions with biological data (which we leave to future work), but we parameterize our simulations to reflect the numbers of T cell searchers, antigen-carrying dendritic cell targets, and lymph node volumes across mammals. We show that  $t_{\text{fin}}$  depends on the number of searchers ( $N$ ). In scenarios where multiple searchers are involved, such as foraging ants, bees, or immune cells, a larger number of searchers can increase the likelihood of discovering a target quickly. We predict that more searchers exploring the environment increase the chances that one will stumble upon the target quickly, whether that target is a seed, a flower or an antigen. Our goal is to provide quantitative predictions and simulations that test this qualitative expectation given different numbers and placements of searchers and targets in different search volumes. In this paper we develop a general model of initial first contact times, considering various placements of searchers and targets, and we compare our analysis for finite  $N$  to physics models of initial first contact times that assume an infinite number of searchers all starting in the same location. This work is a step toward a more general biological theory of first contact

times. While we are unaware of quantitative models or data of initial first contact times, physicists have developed an extensive literature analyzing extreme first passage time ( $t_\infty$ ) (Redner, 2001; Lawley, 2020a; Basnayake et al., 2019; Weiss et al., 1983), an approach that predicts the time it takes for the fastest among an infinite number of searchers to find its target. However,  $t_\infty$  generally only considers search problems in which searchers all start at the same location and search for a single target, the number of searchers is assumed to approach infinity, and most work considers searchers on a one-dimensional line. To address these discrepancies from biological reality, we propose a mathematical model designed to predict first contacts in the immune system. Motivated by (Ferdous et al., 2024),  $t_{\text{fin}}$  is an idealized model of the initial first contact times between T cells and dendritic cells within the lymph node. This first contact is the critical step that initiates adaptive immunity and is a key factor in determining how long it takes T cells to control a viral infection. We consider a finite number of T cells as searchers and dendritic cells as targets, with both distributed uniformly in a bounded space representing the lymph node. We show in simulations that  $t_{\text{fin}}$  is proportional to the volume of the search space and inversely proportional to both the number of searchers and the targets. We investigate the influence of two factors that can reduce search time when there are more searchers: 1) the initial distance between the searchers and the targets and 2) the chance that a searcher happens to take a direct path to the target. We expect that both the shortest distance to a target and the most direct path to the target will decrease when there are more searchers because both of these fortuitous events are more likely to occur at least once when there are more searchers. The major contributions of this paper are that we 1) develop a model ( $t_{\text{fin}}$ ) that predicts initial first contact times for a finite number of randomly distributed searchers and targets, 2) compare  $t_{\text{fin}}$  to the  $t_\infty$  model that assumes an infinite number of searchers all starting in one location, 3) analyze the models in four

scenarios (cases 0-3) with varying searcher and target distributions in order to provide insights into the applicability of  $t_{\text{fin}}$  and  $t_{\infty}$  in different biologically relevant scenarios, and 4) simulate idealized versions of those scenarios to examine how well the analytical predictions correspond to those scenarios. We consider the following cases: In case 0, we consider a random distribution of multiple searchers and multiple targets. We test whether  $t_{\text{fin}}$  assumptions are met and whether simulations are consistent with  $t_{\text{fin}}$  predictions. We then compare  $t_{\text{fin}}$  to  $t_{\infty}$ , which assumes only a single target. Thus, for all other cases (1-3), we consider a single target located at the center of the search space ( $T = 1$ ), and all searchers start at the same fixed point at some specified distance from the target (See Figure 1). The different predictions of the  $t_{\infty}$  and  $t_{\text{fin}}$  approaches are summarized for each case in Table 1.

## 2 Predictions and Computational Methods

### 2.1 Summary of Scenarios

We show four scenarios in Figure 1. The  $t_{\text{fin}}$  and  $t_{\infty}$  predictions of initial first contact times differ because each approach rests on different assumptions. The predictions are summarized in Table 2.

- Case 0: For multiple searchers and multiple targets, both distributed at uniform random and with a constant density of searchers and targets,  $t_{\text{fin}}$  is expected to be inversely proportional to the volume of the search space and the number of searchers ( $N$ ), Equation (5). One of the primary assumptions for  $t_{\infty}$  is that all the searchers start from the same location; since that assumption does not hold in case 0,  $t_{\infty}$  does not make a prediction for case 0.
- Case 1: For a fixed initial distance between all the searchers and a single target,  $t_{\text{fin}}$  is expected to decrease linearly with the number of searchers,

according to Equation (7) (the same as case 0). In contrast,  $t_{\infty}$  predicts the initial first contact times to decrease logarithmically with  $N$  (Equation (13)).

- Case 2: For a fixed number of searchers,  $t_{\text{fin}}$  is expected to increase proportionally to the cube of the distance between all the searchers starting from the same location and the target according to Equation (8). Our analysis of  $t_{\infty}$  predicts that  $t_{\infty}$  scales quadratically with the distance in Equation (14).
- Case 3: If the density of searchers remains constant within a given volume, but all searchers initiate their search from a common starting point,  $t_{\text{fin}}$  is expected to be constant in Equation (9).  $t_{\infty}$  is expected to scale with length squared divided by  $N$  in Equation (15).

While  $t_{\text{fin}}$  and its underlying assumptions were originally formulated for Case 0, with multiple searchers and targets distributed randomly in a volume, we extend the examination of  $t_{\text{fin}}$  to cases 1-3 to assess whether it applies. Similarly,  $t_{\infty}$  and its assumptions were initially designed for Case 1 with the number of searchers approaching infinity. We explore how well the predictions of  $t_{\text{fin}}$  and  $t_{\infty}$  correspond to simulations given that the original assumptions may not hold in all cases. We note that our predictions for  $t_{\text{fin}}$  are based on an assumption that each searcher is independent, resulting in an exponential distribution of search times (Celli et al., 2012). We will show that the assumption holds in case 0 (the original scenario that  $t_{\text{fin}}$  was developed for), but it may not hold for other cases.

## 2.2 Analysis of $t_{\text{fin}}$

We initially developed  $t_{\text{fin}}$  to predict the initial first contact time given randomly distributed searchers and targets in a volume. We assume that the contact times between the searchers and targets are memoryless random processes,

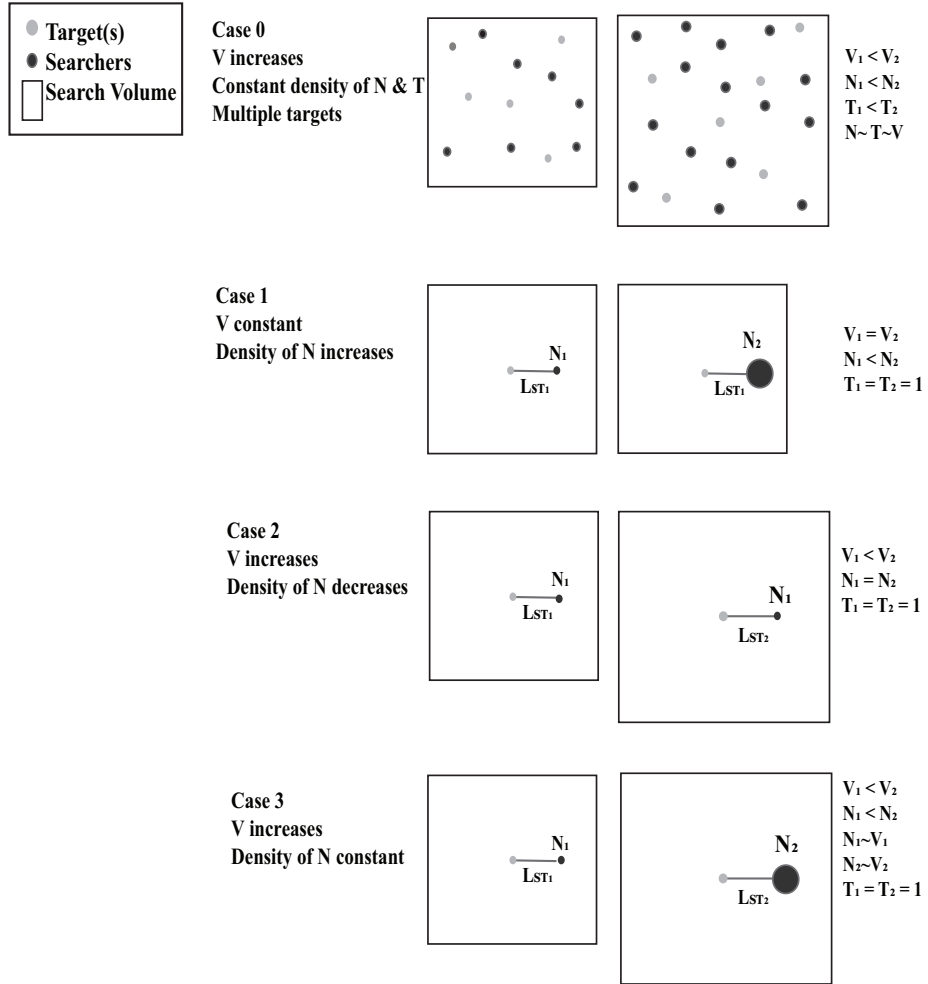


Figure 1: **Graphical Representation of the Simulated Cases.** In all cases there are multiple searchers ( $N$ ). Here,  $V$  is the search space,  $T$  is the number of searchers,  $N$  is the number of searchers,  $L_{ST}$  is the length of the distance from the searchers to the target. In case 0, there are multiple targets and the targets and searchers are distributed at uniform random in the volume, and their density is constant as the volume increases. In cases 1 - 3, there is a single target and the searchers are all located at the same place at distance  $L_{ST} = 0.25 L$  from the target so that searchers are equidistant from the target and the boundary. In case 1, the number of searchers  $N$  increases (indicated by the larger circle on the right) while  $L_{ST}$  and  $V$  are constant. In case 2,  $N$  is constant, and  $L_{ST}$  and  $V$  increase (indicated by the larger box on the right). In case 3,  $N$ ,  $L_{ST}$  and  $V$  all increase (indicated by the larger box size and larger circle on the right). We assume  $L_{ST}$  is proportional to  $V^{1/3}$ .



Table 1: **Comparison of  $t_{\infty}$  and  $t_{\text{fin}}$ .** We assumed an exponential distribution of search times and a finite number of searchers in our model of  $t_{\text{fin}}$ . In contrast,  $t_{\infty}$  assumes an infinite number of searchers and that the fastest searcher will follow the shortest (and therefore, most direct) path to the target.

Experimental variation in $N$ , $T$ and $V$	$t_{\infty}$ prediction	$t_{\text{fin}}$ prediction
Case 0 ( $N$ , $T$ and $V$ increase; multiple searchers and targets are distributed at uniform random)	no prediction	$E[t_{\text{fin}}] \propto N^{-1}$
Case 1 ( $N$ increases, $V$ is constant; searchers start at one location; single target)	$E[t_{\infty}] \propto \frac{1}{\ln(N)}$	$E[t_{\text{fin}}] \propto \frac{1}{N}$
Case 2 ( $N$ is constant, $V$ increases; searchers start at one location; single target)	$E[t_{\infty}] \propto L^2$	$E[t_{\text{fin}}] \propto L^3$
Case 3 ( $N$ and $V$ increase; searchers start at one location; single target)	$E[t_{\infty}] \propto \frac{L^2}{\ln N}$	$E[t_{\text{fin}}] \propto 1$

such that the first contact times of each searcher follow an exponential distribution. This is shown in case 0 as a bounded cube with  $N$  searchers looking for a number of targets ( $T$ ). If the probability that a searcher finds the target in time  $t$  is  $P(T_t)$ , then the probability  $P(T_t)$  that at least one searcher encounters a target between time 0 and time  $t$  can be modeled with an exponential distribution,

$$P(T < t) = \frac{NT}{\lambda} e^{-\frac{tNT}{\lambda}} \quad (1)$$

Here,  $\lambda$  is the mean contact time between a single searcher and a single target within a volume  $V$ . (Celli et al., 2012) showed that

$$\lambda \propto V \quad (2)$$

To obtain the expected encounter time, we integrate over all time,

$$E[t_{\text{fin}}] = \int_0^{\infty} \frac{tNT}{\lambda} e^{-\frac{tNT}{\lambda}} dt = \frac{\lambda}{NT} \quad (3)$$

By replacing  $\lambda$  with  $V$  from Equation (2) in Equation (3) we get,

$$E[t_{\text{fin}}] \propto \frac{V}{NT} \quad (4)$$

• **Case 0 (N, T, and L all increase, Multiple Targets):**

Here we assume there are multiple searchers and targets and the density of searchers and targets are constant,  $N \propto T \propto V$ , then from Equation (4) we get,

$$E[t_{\text{fin}}] \propto V^{-1} \propto N^{-1} \quad (5)$$

That is, given a constant density of searchers and targets, the time for the initial first contact between a searcher and a target is inversely proportional to the search volume and the number of searchers. In this scenario, the initial first contact predicted  $t_{\text{fin}}$  speeds up linearly with  $N$ .

In Figure 3 we show that simulations of case 0 generate exponentially distributed contact times among all of the searchers in a simulation, consistent with the primary assumption in  $t_{\text{fin}}$ . In (Figure 4) we show that the initial first contact times produced by the simulations are consistent with the ( $t_{\text{fin}}$ ) prediction. Next, in order to compare our  $t_{\text{fin}}$  prediction to the  $t_{\infty}$  prediction, we consider 3 other cases with searchers starting at the same location and searching for a single target. Thus we set the number of targets  $T = 1$ , simplifying Equation (4) to

$$E[t_{\text{fin}}] \propto \frac{V}{N} \quad (6)$$

In addition to allowing us to compare the predictions of the  $t_{\text{fin}}$  and  $t_{\infty}$  approaches, these scenarios also give us insights into the contribution of two factors that determine  $t_{\text{fin}}$ : (1) the initial distance between the lucky first searcher and the nearest target versus (2) the directness of the path of the lucky first searcher toward the target because in these scenarios we fix (1) the distance

between all searchers and the target.

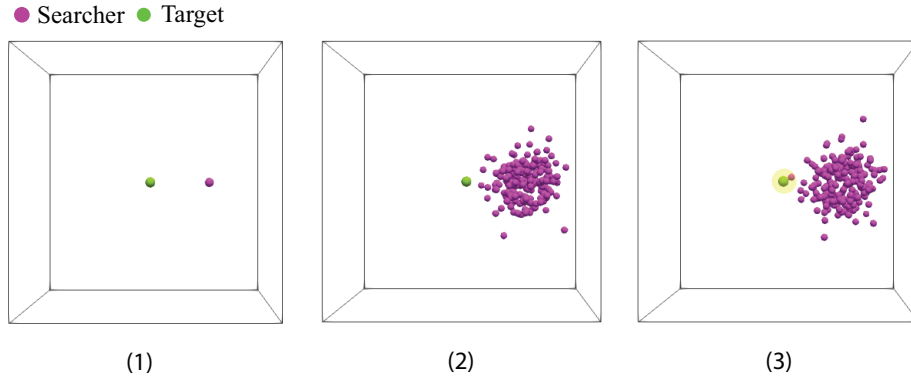


Figure 2: **Schematic Showing Simulations of Sases 1 - 3.** Multiple searchers (pink) looking for a target (green) in a confined cubic region, with the target placed at the center. The figure shows (A) the initial setup where all the searchers are in the same location with a fixed distance  $L_{ST} = 0.25L$  from the target at the center of a fixed volume (Case 1). (B) the search progress at the 250<sup>th</sup> step, with the searchers moving via Brownian motion and (C) the first contact between a searcher and the target (Highlighted in yellow). **In Case 1**, we fixed volume at  $8 \text{ mm}^3$  and systematically increased the number of searchers ( $N$ ) from 5 to 100 000. **In Case 2**, we increased  $V$  from 8 to 33 000  $\text{mm}^3$  ( $L$  from 2 to 32) with fixed  $N$ . **In Case 3**, we increased both  $V$  and  $N$  with the  $N$  ranging from 240 to 1 000 000 by scaling with the volume ( $N \propto V$ ). **In Case 0**, with randomly distributed searchers and multiple targets (not shown) we increased  $V$ ,  $T$  and  $N$  with the  $N$  ranging from 20 to 2000 ( $N \propto V$ ),  $T$  ranging from 80 to 8000, and  $V$  ranging from 8 to 790. Each simulation was replicated 30 times for each combination of parameters.

- **Case 1 (N increases, V is constant, Single Target):**

Since  $V$  is constant and  $N$  increases, Equation (6) is simplified to:

$$E[t_{\text{fin}}] \propto \frac{V}{N} \propto \frac{1}{N} \quad (7)$$

This case with a single target in a fixed volume gives the same prediction as case 0 for multiple randomly distributed searchers and targets in an increasing volume: as  $N$  increases, the expected initial first contact time decreases linearly.

- **Case 2 (N is constant, V increases, Single Target):**

Since  $V = L^3$  and  $N$  is constant, Equation (6) becomes,

$$E[t_{\text{fin}}] \propto \frac{V}{N} \propto L^3 \quad (8)$$

In this scenario, the expected initial first contact time increases linearly with the volume. As the search volume (and therefore  $L$ ) increase, it takes more time for the searchers to cover the increased space required to find the target.

- **Case 3 (N and V both increase, Single Target)** In this scenario we set  $N \propto V$ , so that Equation (6) predicts,

$$E[t_{\text{fin}}] \propto \frac{V}{N} \propto 1 \quad (9)$$

Thus if density is constant,  $t_{\text{fin}}$  is predicted to be constant across volumes.

### 2.3 Analysis of $t_\infty$

The  $t_\infty$  prediction was developed by physicists to describe the time for the first of an infinite number of searchers to find a target in an idealized search, originally on a one-dimensional line (Weiss et al., 1983; Redner, 2001). The theory has recently been expanded to more dimensions and more complex searches (Lawley, 2020a; Basnayake et al., 2019; Lawley, 2020c; Ro and Kim, 2017), but most formulations consider only very large  $N$  that approaches infinity.  $t_\infty$  predicts that,

$$E[t_\infty] \propto \frac{L_{ST}^2}{4D \ln(N)}, \quad N \rightarrow \infty \quad (10)$$

where  $N$  is the number of searchers,  $D$  is a diffusivity, and  $L_{ST}$  is the distance between the identical starting location of all searchers and the target. The model

assumes searchers move via a random walk. The time for the first searcher to reach the target is, in essence, the rate of spread of the furthest of the diffusing searchers. That diffusion creates a Gaussian distribution of distances from the start location. The logarithmic term in the denominator comes from determining the time it takes for the tail of the distribution to reach the target.

The full derivation of Equation (10) is in (Lawley, 2020c) (Equation 5-7, Section 2.1).  $t_\infty$  predicts that the distance traveled by the fastest searcher increases slowly. As the number of searchers increases, the time required for the first searcher to reach the target decreases as a slow logarithmic function of  $N$ . Note that this formulation of  $t_\infty$  doesn't specifically address how the volume of the search domain affects search time; it considers only the distance between searcher and target. This is because the approach assumes that the fastest searcher will be the one that has taken the most direct path from the start location to the target; any searcher that meandered through the full volume of the search space would not be the first searcher to arrive, and therefore would not be relevant to the initial first contact time. This argument only holds for large  $N$  that approaches infinity. However, many biological search processes have a finite number of searchers within a bounded volume, for example, immune cells search in the volume of a lymph node or an infected organ, and foraging animals search within a 2D or 3D territory. We consider only the 3D case here and set  $L_{ST}$  to scale with the side  $L$  of the volume  $V$  of the search domain such that ,

$$L_{ST} \propto L \propto V^{1/3} \tag{11}$$

For simplicity, we consider a constant rate of diffusivity ( $D$ ). By replacing  $L_{ST}$  with  $L$  and  $D$  with a constant, Equation (10) gives us a simplified expression

for  $t_\infty$  in a bounded volume of length  $L$ :

$$E[t_\infty] \propto \frac{L^2}{\ln(N)}, \quad N \rightarrow \infty \quad (12)$$

We consider three cases for Equation (12).

- **Case 1 (N increases, L is constant, Single Target):**

In this case, we assume that  $L_{ST}$  remains fixed. As the number of searchers  $N$  increases, we reformulate the equation Equation (12) by ignoring scaling constants to obtain a prediction from  $t_\infty$ ,

$$E[t_\infty] \propto \frac{L^2}{\ln(N)} \propto \frac{1}{\ln(N)} \quad N \rightarrow \infty \quad (13)$$

This equation predicts that as  $N$  grows, the expected time for finding the target decreases logarithmically with  $N$ . The diminishing returns of adding more searchers are evident, indicating that large groups of searchers only slightly reduce the search time compared to smaller groups when the distance ( $L$ ) is fixed.

- **Case 2 (N is constant, L increases, Single Target):**

In this case, we keep  $N$  constant while  $V$  (and therefore  $L_{ST}$ ) increase. Then, Equation (12) becomes,

$$E[t_\infty] \propto L^2 \quad (14)$$

In this scenario,  $t_\infty$  is predicted to increase with  $L^2$  while volume increases with  $L^3$ .

- **Case 3 (N and L increase, Single Target):** In this case,  $N$  increases

proportional to  $V$ , leading to:

$$E[t_\infty] \propto \frac{L^2}{\ln(N)}, \quad \text{where } N \propto V \propto L^3 \quad (15)$$

The different predictions from  $t_\infty$  and  $t_{\text{fin}}$  are summarized in Table 1.

## 2.4 Computational Experiments

In order to test the  $t_{\text{fin}}$  prediction for Case 0 and the competing predictions of  $t_{\text{fin}}$  and  $t_\infty$  for cases 1-3, we conduct a series of experiments using an agent-based model implemented in Biodynamo (Breitwieser et al., 2022). We consider that a contact happens when the centers of a searcher and a target are within  $10\ \mu\text{m}$  distance. Hence the physical sizes of searchers and targets do not affect search times. To simulate T cells searching for dendritic cells in the lymph node, we utilized a model of Brownian motion parameterized from empirical data of T cell movement in lymph nodes from (Fricke et al., 2016). Figure 2 illustrates the experimental setup of our simulations designed to test the predictions of the  $t_{\text{fin}}$  and  $t_\infty$  approaches to estimating the initial first contact times in the 4 cases shown in Figure 1.

The scarcity of empirical data presents a challenge in directly matching the numerical simulations to real biological systems. We acknowledge this limitation and took steps to align the simulation parameters in case 0 with available data from the immune system. We chose search volumes to match the range of sizes of mammalian lymph nodes and estimated numbers of searchers to match the number of T cells in each clonal line that search for antigen-bearing dendritic cells in each lymph node and also estimated the number of targets for case 0 to match the number of dendritic cells in lymph node carrying the same type of antigens. The purpose of the computational simulations is to establish a proof of principle showing how the initial first contact times vary with  $N$  and

various other specifications of the search problem. Our intent here is not to test our predictions with biological data, but rather to demonstrate through simulations how various mathematical assumptions and predictions hold given simple simulations using finite numbers of searchers, targets, and volumes that approximate different biological scenarios. Our simulations validate cases where different approaches ( $t_{\text{fin}}$  and  $t_{\infty}$ ) are (and are not) able to predict biologically relevant phenomena. All the data used in our analysis are summarized in an online dataset.<sup>1</sup>

## 2.5 Fitting Exponents Using the ABM

In order to fit model predictions to simulated data, we estimate the best-fit exponents that relate initial first contact times to the dependent variable in each scenario. We first consider the generic formula in Equation (4) as follows,

$$E[t_{\text{fin}}] \propto \frac{V^i}{N^j T^k} \quad (16)$$

For ease of presentation, we convert Equation (16) to base 10:

$$\begin{aligned} \log_{10}(E[t_{\text{fin}}]) &= \log_{10}\left(\frac{aV^i}{N^j T^k}\right) \\ &= \log_{10} a + i \log_{10}(V) - j \log_{10}(N) - k \log_{10}(T) \end{aligned} \quad (17)$$

If we set,  $C_1 = \log_{10} a$  then,

$$\log_{10}(E[t_{\text{fin}}]) = C_1 + i \log_{10}(V) - j \log_{10}(N) - k \log_{10}(T) \quad (18)$$

and exponentiating,

$$E[t_{\text{fin}}] = 10^{C_1 + i \log_{10}(V) - j \log_{10}(N) - k \log_{10}(T)} \quad (19)$$

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<sup>1</sup><https://docs.google.com/spreadsheets/d/1AiWJ2onZYN5F-42LNLv-14kUluWyQhGSD3JFk-mNT4Q/edit?usp=sharing>



For Case 0, where numbers of searchers and targets maintain a constant density as volume increase (i.e.,  $V \propto N$  and  $T \propto N$ ), we further simplify eq. (18) because  $N$ ,  $V$ , and  $T$  scale isometrically, thus we can substitute a single scaling exponent to reflect the scaling in terms of  $N$ :

$$\log_{10}(E[t_{\text{fin}}]) = C_1 + \mu \log_{10}(N)$$

We use linear regression on log-transformed simulation data to determine the value of the scaling exponent  $\mu$ . This provides the final scaling relationship between  $t_{\text{fin}}$  and  $N$  for case 0.

$$E[t_{\text{fin}}] = 10^{C_1 + \mu \log_{10}(N)}$$

We fit the scaling constant  $C_1$  to the simulated data.

Similarly, for Case 1 where there is a single target ( $\log_{10}(1) = 0$ ),  $N$  increases and  $V$  is constant ( $i \log_{10}(V) = C_2$ ), we simplify eq. (18) as,

$$\begin{aligned} \log_{10}(E[t_{\text{fin}}]) &= C_1 + C_2 - j \log_{10}(N) - 0 \\ &= C_{1'} - j \log_{10}(N) \end{aligned}$$

where  $C_{1'} = C_1 + C_2$ . We again use linear regression on log-transformed simulation data to determine the value of the scaling exponent  $j$ . We use the same procedure to estimate scaling exponents for cases 2 and 3 for  $t_{\text{fin}}$ ; and for  $t_{\infty}$  for Cases 1-3.

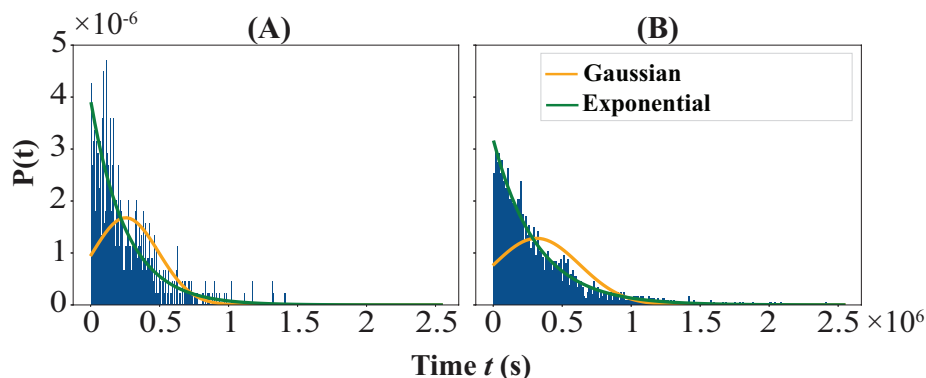


Figure 3: **Distribution of Contact Times of All Searchers within One Volume for Case 0.** We show the distribution of the first contact times in two (out of 30) simulations of case 0. Panel A shows the distribution of 629 first contacts for 629 searchers with 2533 targets in a  $921 \text{ mm}^3$  search volume. Panel B shows the distribution of 1989 first contact times for 1989 searchers with 8011 targets in a  $3640 \text{ mm}^3$  search volume. Data are plotted as a histogram of probabilities of the initial first contact time of each searcher on the y-axis for the contact time given on the x-axis. The theoretical probability density functions (PDF) of a Gaussian distribution and an exponential distribution for the same mean and standard deviation as the data are shown for comparison. The data are visually consistent with an exponential distribution. The result of the goodness of fit tests (SSE and AIC) in Table 2 are consistent with our assumption of the exponential distribution of the first contact times.

### 3 Results: Comparing model predictions to simulated data

The  $t_{\text{fin}}$  approach to estimating the initial first contact times was developed for case 0 in which a uniform random distribution of searchers and targets are placed in a volume with constant density so that  $N$  and  $T$  increase linearly with  $V$ . The key assumption in  $t_{\text{fin}}$  is that initial first contact times (the first time any one of the searchers comes into contact with a target) are exponentially distributed within each simulation. This allows us to predict that the first time the *first* searcher in a given simulation will contact a target is  $\frac{1}{N}$ . We found that in all case 0 simulations, an exponential distribution was a good fit. We

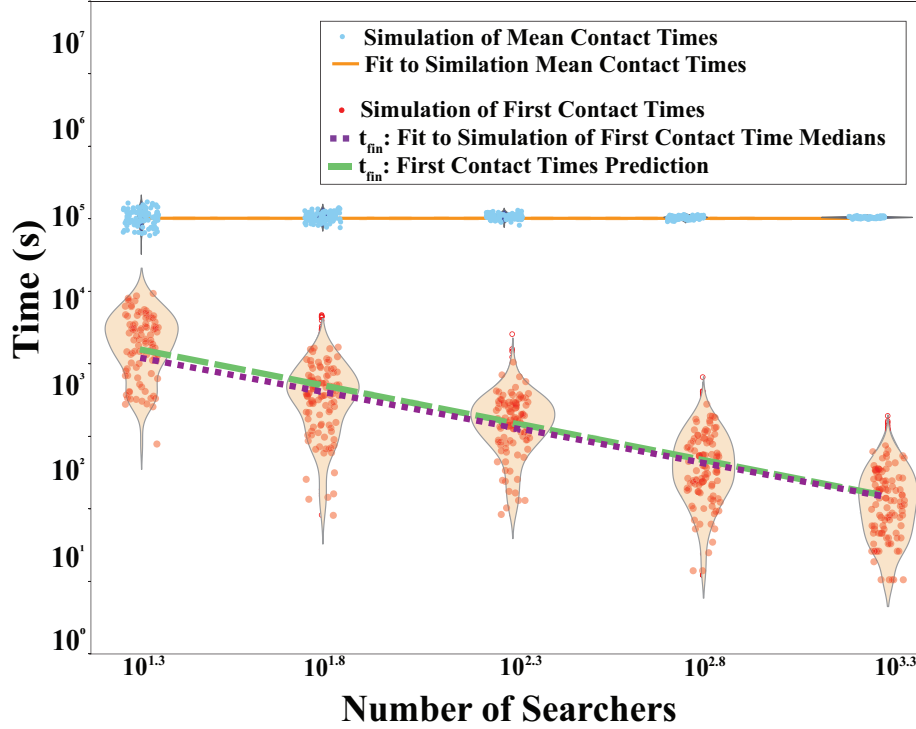


Figure 4:  $t_{\text{fin}}$  Predictions Compared to Simulations Corresponding to **Case 0: Constant Density, Multiple Targets**. Each red circle represents the time for the first searcher, in a population of  $N$  searchers, to contact its target, where  $N$  is varied along the x-axis. The initial first contact time for each replicated simulation is shown as red dots.  $t_{\text{fin}}$  is predicted to scale as  $N^{-1}$  (dashed green line, Equation (5)). The dotted purple line shows the regression through the simulated data:  $E[t_{\text{fin}}] \propto N^{-1.05}$  with a 95% CI  $[-1.1, -0.98]$  for the exponent, consistent with the exponent of -1 predicted by  $t_{\text{fin}}$ . Variance among the initial first contact times for a given  $N$  ranges from 0.25 to 0.36. In contrast, the mean search times (blue dot), averaged over all  $N$  searchers in each simulation, across the same values of  $N$ , are much larger and do not vary with  $N$ , and have extremely low variance, all less than 0.003. 100 replicates are used to calculate the mean first contact time and the initial first contact time for each value of  $N$ ; thus there are 100 blue and 100 red points for each value of  $N$ .

Table 2: Statistical comparisons of the Gaussian and exponential distribution fit to the initial first contact times for case 0. The exponential distribution has lower mean SSE and AIC values than the Gaussian distribution, indicating a better fit to the data. 100 simulations were replicated for each number of searchers. Numbers are given to two significant digits.

		Number of searchers				
		20	63	200	630	2000
Exponential	SSE	$8.1.2 \times 10^{-8}$	$4.6 \times 10^{-10}$	$4.6 \times 10^{-11}$	$4.6 \times 10^{-12}$	$7 \times 10^{-13}$
	AIC	2600	2800	3000	3200	3400
Gaussian	SSE	$1.3 \times 10^{-8}$	$6.7 \times 10^{-10}$	$1.2 \times 10^{-10}$	$3.7 \times 10^{-11}$	$1.9 \times 10^{-11}$
	AIC	2600	3000	3300	3900	4300

compare to a Gaussian to demonstrate the difference in sum of squares error (SSE) and Akaike information criteria (AIC) (Table 2). In Figure 3, we show example probability distributions from two sets of simulations. These and the other simulations show a close fit to an exponential distribution.

Given that the simulation validated the assumption that first contact times are exponentially distributed for case 0, we then test the prediction that  $t_{\text{fin}} \propto \frac{1}{N}$  from (Equation (5)). In figs. 4 to 7 we show model predictions compared to simple regressions through the data. We show only the predicted scaling relationship to  $N$  or  $V$  by fitting a constant to adjust the height of the line to fit the data. For  $t_{\text{fin}}$ , we chose a scaling constant to fit the height of the line to correspond to the smallest  $N$ , and for  $t_{\infty}$  we chose the scaling constant to fit the largest simulated  $N$ . Thus, the figures should be interpreted as demonstrating how simulations compares to model predictions for how initial first contact times change systematically with  $N$  or  $V$ . The fitting procedure is detailed in Section 2.5.

Figure 4 shows a very close correspondence between the  $t_{\text{fin}}$  prediction and the simulated data. We also show that initial first contact times are orders of magnitude faster than the mean first contact times. The mean search time is (unsurprisingly) unaffected by  $N$ , and it is far less variable. This demonstrates that our model for  $t_{\text{fin}}$  accurately predicts  $\frac{1}{N}$  scaling for its intended use case,

and that initial first contact times are substantially faster than mean contact times. We now test whether  $t_{\text{fin}}$  can be extended to 3 search scenarios with a

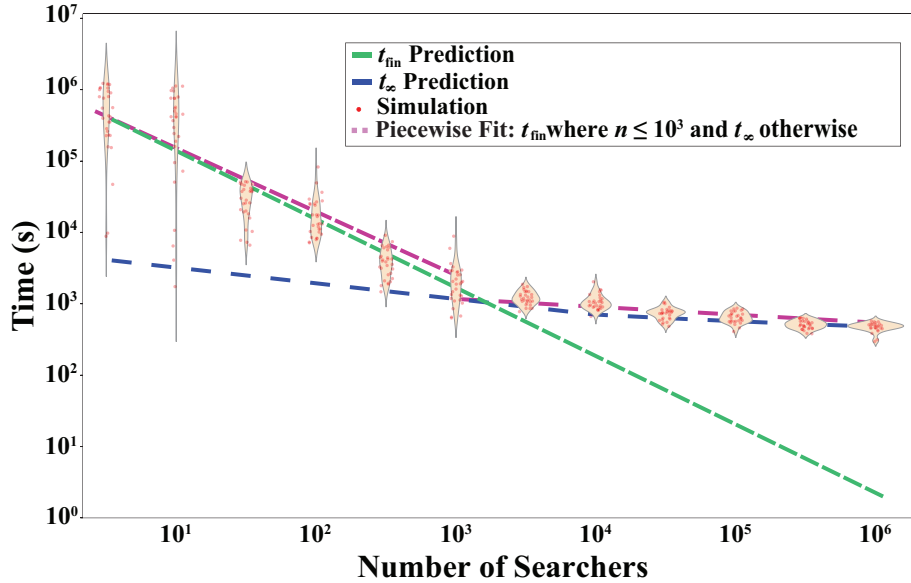


Figure 5:  $t_{\text{fin}}$  and  $t_{\infty}$  Predictions Compared to Simulations Corresponding to Case 1: Single Target, Constant Volume, Increasing  $N$ . Each red circle represents the time for the first searcher, in a population of  $N$  searchers, to contact its target, where  $N$  is varied along the x-axis. 30 simulations were run for each value of  $N$ , and the first contact in each simulation is shown. The pink dotted line connects the medians of the simulated data. The green line shows the  $t_{\text{fin}}$  prediction (Equation (7)) and the blue line shows the  $t_{\infty}$  prediction (Equation (13)), both fitted to the simulated data. The regression through the simulated first contact points  $N < 10^3$  is  $N^{-1.1}$  with 95% CI  $[-0.86, -1.3]$  consistent with the  $t_{\text{fin}}$  prediction for small  $N$ . The regression through data (pink line) where  $N \geq 10^3$  gives  $t_{\infty} \propto \log(N)^{-1.94}$  with a 95% CI  $[-2.1, -1.8]$  which is slightly steeper than the  $1/\log(N)$  prediction of  $t_{\infty}$ . Prediction lines are shown with scaling constants set to fit the median of either the smallest (for  $t_{\text{fin}}$ ) or largest (for  $t_{\infty}$ ) simulated data.

single target and all searchers placed at the same initial location. We compare  $t_{\text{fin}}$  predictions to  $t_{\infty}$  predictions that assume an infinite number of searchers. For case 1 we compare  $t_{\text{fin}}$  and  $t_{\infty}$  predictions given a single target in a constant search volume while increasing  $N$  across simulations. This was the scenario  $t_{\infty}$  was designed for, assuming  $N$  approaches infinity. Figure 5 shows that for

small  $N < 10^3$  initial first contact times decrease approximately linearly with  $N$ , consistent with our  $t_{\text{fin}}$  prediction that initial first contact times are proportional to  $\frac{1}{N}$ ; for large  $N \geq 10^3$ , simulations are approximately consistent with the  $t_{\infty}$  prediction, proportional to  $\frac{1}{\ln(N)}$  (Equation (13)). Thus, even in this search scenario that differs from the original scenario envisioned by the  $t_{\text{fin}}$  approach,  $t_{\text{fin}}$  approximates initial first contact times for biologically relevant numbers of searchers, while  $t_{\infty}$  better approximates initial first contact times for larger  $N$ .

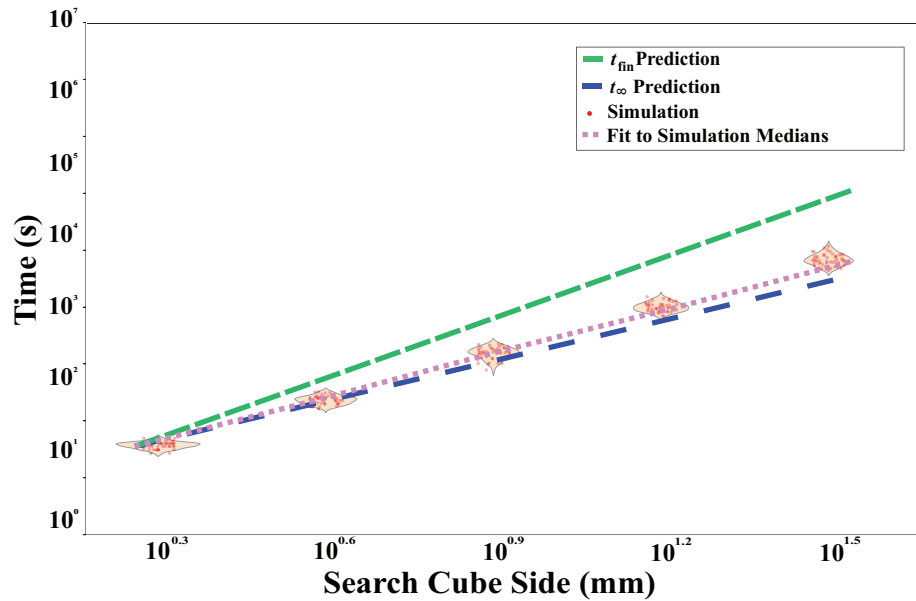


Figure 6:  $t_{\text{fin}}$  and  $t_{\infty}$  Predictions Compared to Simulations Corresponding to Case 2: Single Target, Increasing Volume, Constant  $N$ . Symbols are replicated from Figure 5. The green line shows the  $t_{\text{fin}} \propto L^3$  prediction and the blue line shows the  $t_{\infty} \propto L^2$  prediction. The regression through the simulated data is  $t \propto L^{2.17}$  with 95% CI [2.14, 2.2], close to the  $t_{\infty}$  prediction.

For case 2 we compare  $t_{\text{fin}}$  and  $t_{\infty}$  predictions to simulations where  $N$  is fixed and  $V$  increases. Figure 6 shows that the simulations are very close to the  $t_{\infty}$  prediction that time is proportional to  $L^2$ , and considerably less steep than

the  $t_{\text{fin}}$  prediction which is proportional to  $L^3$ . Similarly, the simulation tests of case 3 in which both  $N$  and  $V$  increase, are considerably closer to the  $t_{\infty}$  prediction ( $L^2/\ln(N)$ ) than the constant  $t_{\text{fin}}$  prediction.

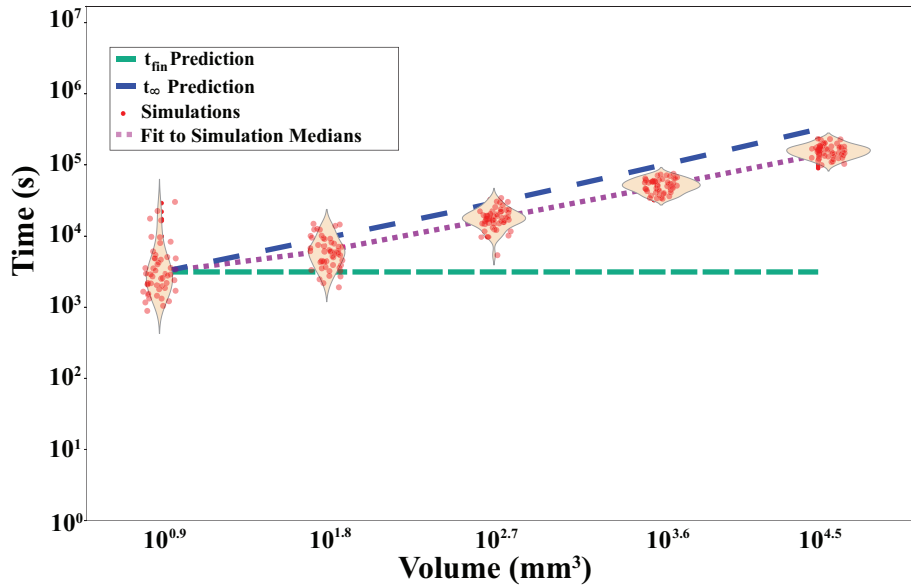


Figure 7:  $t_{\text{fin}}$  and  $t_{\infty}$  Predictions Compared to Simulations Corresponding to Case 3: Single Target, Increasing Volume, Increasing  $N$ . Symbols are replicated from Figure 5. The green line shows the  $t_{\text{fin}} \propto 1$  prediction and the blue line shows the  $t_{\infty} \propto L^2/\ln(N)$  prediction.

## 4 Discussion

### 4.1 Summary

We developed an analytical model,  $t_{\text{fin}}$ , designed to predict how quickly the first of many searchers finds its first target, given that searchers and targets are distributed randomly in a volume. Simulations validate the key  $t_{\text{fin}}$  assumption that search times are exponentially distributed (Figure 3) and the key prediction

that initial first contacts scale as  $\frac{1}{N}$  (Figure 4) for case 0 with a uniform random distribution of searchers and targets that are kept at constant density as volume increases. In order to compare  $t_{\text{fin}}$  to another model of initial first contact times ( $t_{\infty}$ ), we conduct a set of simulations where all searchers start at the same location and search for a single target. We find, for case 1 (where the distance between searchers and target is fixed), the  $t_{\text{fin}} \frac{1}{N}$  prediction is consistent with simulations for small  $N$ , and the  $t_{\infty} \frac{1}{\ln(N)}$  prediction is close to simulations for large  $N$  (Figure 5). In cases 2 and 3, we systematically increase the distance between the initial placement of searchers and the target. The initial first contact times are close to  $t_{\infty}$  predictions and quite far from  $t_{\text{fin}}$  predictions (Figure 6 and Figure 7). Our analysis of  $t_{\text{fin}}$  in case 0 suggests that the fastest searcher is one that is lucky in two respects: it happens to be placed near a target, and it takes a relatively direct path to the target. Because  $t_{\text{fin}}$  predictions do not hold in cases 2 and 3 when distance increases, this suggests that  $1/N$  scaling only holds when distances between searchers and targets are fixed. We suggest that the existence of lucky first searchers is an important benefit of collective search, particularly when the success of the first searcher causes important downstream events.

## 4.2 Interpretation of scenarios

In this paper we simulated idealized searches that correspond to the volume of lymph nodes across mammal sizes with estimates of the numbers of T cell searchers and dendritic cell targets within those lymph nodes, where the first T cell that find a dendritic cell presenting cognate antigen initiates the adaptive immune response motivated by ongoing work (Ferdous et al., 2024). However, we suggest that the initial first contact times are relevant to a broader range of biological phenomena.

To better characterize the circumstances under which  $t_{\text{fin}}$  makes valid pre-



dictions, we compare our analytical predictions, to the similar Extreme First Passage Time models developed by physicists to describe the time for a population of searchers to find a single target. That theory (that we call  $t_\infty$ ) employs the useful simplifying assumptions of an infinite number of searchers diffusing in one dimension to find a single target. Specifically, we compare the  $t_{\text{fin}}$  predictions to  $t_\infty$  predictions extended by Lawley (Lawley and Madrid, 2020) to predict the initial first contact times in three dimensions. While  $t_{\text{fin}}$  predicts that larger populations of searchers find their targets proportionally faster,  $t_\infty$  predicts a much slower logarithmic speedup in search times as  $N$  increases.

We compared  $t_\infty$  predictions to those of  $t_{\text{fin}}$  under three experimental cases. In case 1, when we hold the size of the search volume constant (and consequently the distance between the initial location of the searchers and the target are held constant), we find that simulated initial first contact times are consistent with the linear decrease with  $N$  predicted by  $t_{\text{fin}}$  when  $N$  is less than 1000; for  $N > 1000$  simulations are consistent with the  $t_\infty$  logarithmic prediction (Figure 5). This result suggests that when the only variation across experiments is  $N$ , the  $t_{\text{fin}}$  predictions are reasonable approximations for biologically relevant numbers of searchers. We note that in this case the key assumption holds that search times are exponentially distributed among the searchers within each simulation. However, there is a crossover, such that  $t_\infty$  applies when  $N$  approaches infinity. Once  $N$  is sufficiently large there is only a logarithmic benefit to increasing  $N$ . We expect that the values of  $N$  for which the  $\frac{1}{N}$  scaling regime holds depends on the details of how far apart the searchers are placed from the target, the behavior of searchers at the boundaries, and the dimension of the system (i.e. whether searchers are in 2D or 3D). Some of these issues are explored in (Ro and Kim, 2017) which also found a transition from  $\frac{1}{N}$  to  $\frac{1}{\ln(N)}$  scaling although the presented the transition in more general dimensionless terms rather than for a particular number of searchers. We leave additional analysis to future work

and suggest that interdisciplinary approaches among physicists, biologists, and computer scientists are needed to further understand which factors most influence initial first contact times in different scenarios with biologically relevant numbers of searchers.

In cases 2 and 3 when we simulate increasing distances between the target and initial searcher placements,  $t_{\text{fin}}$  predictions are not close to simulated results (Figure 6 and Figure 7). We predict that  $t_{\text{fin}}$  doesn't hold in these cases because the most important factor in these cases is that the distance between searchers and targets increases across simulations. This sheds light on an important feature of case 0, where searchers and targets are distributed at random and with constant density. In case 0, the distances between the initial placement of searchers and targets are determined by a random process, and therefore, when there are more searchers and targets in a larger volume, the *closest* distance between a searcher and the nearest target will decrease. Thus, the lucky first searcher will be one that happens to be very close to its target as well as one that happens to take a relatively direct path to that nearby target. The  $t_{\infty}$  predictions developed by physicists only consider the directness of the path because that approach assumes a fixed distance.

The  $\frac{1}{N}$  scaling of initial first contact times suggests a substantial and underappreciated advantage of collective search. Case 0 suggests that in a bigger lymph node with 100 times more T cell searchers and dendritic cell targets, T cell activation would occur 100 times faster. Case 1 suggests that a bee colony (or in 2D, an ant colony) with 100 more searchers starting in a single nest and foraging independently in a fixed-size territory, would find a single resource (e.g. a rare patch of flowers or food) 100 times faster. These advantages would not directly accrue to the average searcher, which would not find a target any faster if it continued to search independently. It is only the lucky first searcher that finds a target faster in a larger population. However, if there is any signal

(e.g., waggle dance or pheromone communication) or structural change (T cell replication or changes in influx and efflux to and from lymph nodes) following the first target discovery, then subsequent searchers could modify their search to take advantage of that information. This is consistent with findings from (Donaldson-Matasci et al., 2013) that larger bee colonies found resources faster and overall foraging rates were greater in larger colonies. Similarly, the first lucky mutation in a population or the lucky first receptor to bind in a cellular interaction, means that larger populations of individual agents have a lucky first encounter faster and the whole system can benefit from that lucky first encounter. Thus, the  $\frac{1}{N}$  initial first contact time confers a significant advantage to a large population size. However, we note a caveat that real biological systems may deviate in important ways from the simple simulations we used here. For example, the density of cognate T cells may not be constant in lymph nodes, and forager territory may scale non-linearly with the forager number. The transition from search times that scale as  $\frac{1}{N}$ , to search times that scale with  $\frac{1}{\ln(N)}$  is also important for analyzing the costs and benefits of increased population size. In many realistic scenarios, more searchers can lead to a proportionally faster search, but as size increases that benefit may diminish. This suggests that, combined with other tradeoffs, initial first contact times may contribute to an optimal colony size under different conditions. Our findings are relevant not only for understanding collective search in biology but also for engineering collective searchers in swarm robotics, a field that takes inspiration from collective search in biology (Dorigo et al., 2020; Lu et al., 2020; Fricke et al., 2013; Hecker and Moses, 2015; Talamali et al., 2021). Understanding the transition from linear to logarithmic dependence on the number of searchers and the shift from cubic to squared initial distance between the searchers and the target dependence with increasing search volume points to important constraints on scalability, a key concern in swarm robotics. We suggest that swarm robotic

systems can both benefit from an understanding of initial first contact times, and serve as real-world testbeds that can help to develop and refine biologically relevant theories about how initial first contact times depend on numbers, search areas, or volumes and the distribution of searchers and targets in space. Direct biological data to test the initial first contact time predictions are scarce. In other work (Ferdous et al., 2024) we show that  $t_{\text{fin}}$  predictions are consistent with the time to initiate adaptive immunity, but the details of how quickly each individual T cell finds its target are poorly understood. We hope that this paper will encourage biologists to report initial first contact times in empirical studies.

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## Author Contributions

JF wrote the software, performed computational experiments and created the figures under the supervision of GMF and MEM. JF, GMF, and MEM wrote the manuscript. MEM supervised JF on the selection of simulation parameters and place our results in context. JF derived the mathematical expressions under the supervision of GMF and MEM.

## Author Declaration

We declare we do not have any competing interests.

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