



## Aggregative group behavior in insect parasitic nematode dispersal



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### ABSTRACT

Movement behavior of foraging animals is critical to the determination of their spatial ecology and success in exploiting resources. Individuals sometimes gain advantages by foraging in groups to increase their efficiency in garnering these resources. Group movement behavior has been studied in various vertebrates. In this study we explored the propensity for innate group movement behavior among insect parasitic nematodes. Given that entomopathogenic nematodes benefit from group attack and infection, we hypothesized that the populations would tend to move in aggregate in the absence of extrinsic cues. Movement patterns of entomopathogenic nematodes in sand were investigated when nematodes were applied to a specific locus or when the nematodes emerged naturally from infected insect hosts; six nematode species in two genera were tested (*Heterorhabditis bacteriophora*, *Heterorhabditis indica*, *Steinernema carpocapsae*, *Steinernema feltiae*, *Steinernema glaseri* and *Steinernema riobrave*). Nematodes were applied in aqueous suspension via filter paper discs or in infected insect host cadavers (to mimic emergence in nature). We discovered that nematode dispersal resulted in an aggregated pattern rather than a random or uniform distribution; the only exception was *S. glaseri* when emerging directly from infected hosts. The group movement may have been continuous from the point of origin, or it may have been triggered by a propensity to aggregate after a short period of random movement. To our knowledge, this is the first report of group movement behavior in parasitic nematodes in the absence of external stimuli (e.g., without an insect or other apparent biotic or abiotic cue). These findings have implications for nematode spatial distribution and suggest that group behavior is involved in nematode foraging.

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### 1. Introduction

Behaviors involving movement are intimately tied to the spatial distribution and foraging success of most animals. When animals increase their individual fitness by exploiting resources in groups, the spatial distribution of their populations should be overdispersed. There are many examples of group foraging behavior, or cooperative behaviors, demonstrated by organisms of diverse trophic levels (Nøttestad et al., 2002; Fourcassie et al., 2010; Bonnell et al., 2013; Cook et al., 2013). Various biotic and abiotic factors can affect movement behavior (Perony and Townsend, 2013) such as group size (Bonnell et al., 2013), environmental spatial structure and resource availability (Patterson and Messier, 2001; Reeve and Cronin, 2010), and avoidance of predators (Srinivasan et al., 2010; De Vos and O'Riain, 2013). But if a mass-attack strategy is necessary for efficient garnering of resources, then we would hypothesize that even in the absence of these factors, populations should remain overdispersed, and thus their

movement should be en masse. In this study we investigated the group movement and aggregation behavior of insect parasitic nematodes in an arena that was environmentally homogeneous and devoid of resources.

Some species follow temporal patterns of random movement while foraging whereas others move in directed spatial patterns, alone or in aggregate (Bonnell et al., 2013). Here we are interested in how movement in groups relates to the behavior and fitness of the individual. For group behaviors to persist in any animal population there must be fitness gains for the individuals who form the group; the individuals within the group must win some advantage over individuals on their own (Clark and Mangel, 1986). This is especially true in groups composed of unrelated or distantly related individuals. These advantages potentially include increased probability of finding resources, better ability to overcome defensive actions of hosts or prey, or the mitigation of risk posed by engaging with the resource.

Entomopathogenic nematodes in the genera *Heterorhabditis* and *Steinernema* (the subjects of this study) are obligate parasites of insects. These nematodes are important natural regulators of insect populations and are also applied as biological control agents to suppress pest populations (Lacey and Shapiro-Ilan, 2008). The

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developmentally arrested infective juvenile nematodes (IJs), the only free-living stage, typically occupy soil habitats until they infect an insect, which they must do in order to resume development and reproduce. Generally, an insect host is infected by tens to hundreds of individual IJs, and a single IJ is seldom able to initiate a successful infection (Koppenhöfer et al., 2006; Nguyen et al., 2006), which confers a fitness advantage to individuals that invade hosts as part of a group. A few hours after the nematodes enter the host, the nematodes release symbiotic bacteria, which are the primary agents in killing the host (Kaya and Gaugler, 1993). Infected hosts generally die within 24–72 h, and the nematodes feed on the symbiotic bacteria and insect tissues, reproducing for one to three generations (Kaya and Gaugler, 1993). As food resources dwindle, a new cycle of IJs is produced and they emerge to seek new hosts. The number of IJs exiting a host can range from tens of thousands to hundreds of thousands (Shapiro-Ilan and Gaugler, 2002).

Foraging strategies among entomopathogenic nematode species vary along a continuum between ambushers, which generally sit and wait for a passing host, and cruisers that actively search for hosts (Lewis et al., 1992). Entomopathogenic nematodes can exhibit a combination of these behaviors to locate hosts and although some species exhibit primarily ambush-type behaviors and others are mainly cruisers, others are considered intermediate in their foraging behavior (Campbell and Kaya, 1999; Lewis, 2002). Foraging strategies may contribute to spatial distribution of entomopathogenic nematode populations in the environment.

Several studies indicate that the distribution of entomopathogenic nematode populations is aggregated in nature (Stuart and Gaugler, 1994; Campbell et al., 1996). The clumped distribution may largely be due to a sparse distribution of infection loci and subsequent mass emergence from host cadavers, thus creating nematode hot spots within the soil ecosystem (Campbell et al., 1996; Spiridonov et al., 2007). However, we suggest that aggregate distributions may also result from group nematode movement when dispersing from hosts or points of application. Group movement of entomopathogenic nematodes may have adaptive value, e.g., in maximising chances for successful host infection. Similar to some other predators and parasites, group attack is generally required by entomopathogenic nematodes to overcome host defenses (Li et al., 2007). Although entomopathogenic nematode dispersal has been studied in terms of biotic and abiotic factors that affect movement, or distance travelled within the soil profile (Stuart et al., 2006; Jabbour and Barbercheck, 2008; El-Borai et al., 2011), there is a dearth of knowledge on more general patterns of movement, especially when biotic and abiotic drivers of movement are not confounding results. Recently, Fushing et al. (2008) described mathematically the temporal aspects of group infection behavior in certain entomopathogenic nematode species. In a similar fashion, we hypothesise that entomopathogenic nematodes also display group movement behavior, even in the absence of hosts. In this study that hypothesis was tested with six species of entomopathogenic nematodes.

## 2. Materials and methods

### 2.1. Experimental approach

All nematodes were cultured *in vivo* at 25 °C in commercially obtained final instar *Galleria mellonella* according to procedures described in Kaya and Stock (1997). Nematode species included *Heterorhabditis bacteriophora* (Oswego strain), *Heterorhabditis indica* (HOM1 strain), *Steinernema carpocapsae* (All strain), *Steinernema feltiae* (SN strain), *Steinernema glaseri* (NJ43 strain) and *Steinernema riobrave* (355 strain). The nematodes were stored in culture flasks at 13 °C for less than 2 weeks prior to experimentation.

Nematodes were applied to experimental arenas using two approaches: application in infected host cadavers or in aqueous suspension. The cadaver approach was intended to represent natural emergence from the host, whereas the aqueous suspension method was intended to mimic artificial introduction of nematodes to the environment for purposes of biological pest control. Experimental arenas consisted of polypropylene boxes (20.5 × 20.5 cm, 9 cm deep) containing sand filled to a depth of 2.5 cm. In all arenas, the final total moisture level in sand was at approximate field capacity (10%). For the cadaver application approach, three nematode-infected hosts (at 3 days p.i.) were placed in the center of each arena. The cadavers were observed daily for the initiation of nematode emergence. The number of IJs that emerged per cadaver was estimated based on separate yield assessments (Kaya and Stock, 1997) conducted on 10 replicate insects each. The results indicated average (±S.E.M.) IJ production by the species as follows: *H. bacteriophora* produced 244,390 ± 28,419.1 IJs; *H. indica* produced 112,210 ± 11,183.9 IJs; *S. carpocapsae* produced 178,300 ± 15,507.9 IJs; *S. feltiae* produced 153,700 ± 14,272 IJs; *S. glaseri* produced 76,650 ± 5,299.9 IJs; *S. riobrave* produced 126,080 ± 10,788.9 IJs. For application of aqueous suspensions, 200,000 IJs from culture flasks (except 300,000 IJs were used for *S. riobrave*) were vacuum filtered onto filter paper (60 mm, Whatman No. 1); the filter paper was then placed upside down in the center of a sand arena. Arenas were stored inside plastic bags at 25 °C until nematode movement was assessed. The plastic bags contained moist paper towels to ensure that high levels of relative humidity (approximately 100%) were maintained. There were four replicate arenas for each species and application approach. Experiments addressing movement of each nematode species were conducted separately, and all experiments were repeated once in time (i.e., run two times in total) using different batches of nematodes and insects.

In arenas with host cadavers, the results of nematode movement were assessed 3 days after IJ emergence began. In arenas receiving aqueous nematode applications, resulting nematode movements were assessed 3 days post-treatment. At the time of assessment, cadavers and filter papers were removed and soil cores measuring 2 cm diameter and 2.5 cm depth were taken at four points that were 4.5 cm from the center of the arena (diagonally and equidistant from each other). The sand from each core was then placed in 100 ml of tap water in a 250 ml beaker, and the number of nematodes in the core was determined by dilution counts under a stereomicroscope (Shapiro-Ilan et al., 2006). For the aqueous suspension approach, the total number of IJs entering sand was also estimated by washing any remaining IJs from the filter paper and subtracting that number from the number originally applied.

### 2.2. Analysis of movement patterns

Our goal was to determine whether there is evidence that the post-emergence or post-application distribution of nematodes indicate aggregated movement patterns. The null hypothesis was that the nematodes move independently versus the alternate hypothesis that they tend to aggregate. Two different approaches to the analysis were taken.

#### 2.2.1. First approach: Index of Dispersion

If the null hypothesis is further specified to be that the nematodes undergo independent diffusive movement, then the number of IJs that is found in a core of a fixed size should follow a Poisson distribution with a mean proportional to the area of the core. The data for each trial consisted of the four cores of equal size that were equidistant from the center. Thus, under the null hypothesis each core follows a Poisson distribution with the same mean.

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