

Persistent variation in spatial behavior affects the structure and function of interaction networks

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Abstract The function of a network is affected by its structure. For example, the presence of highly interactive individuals, or hubs, influences the extent and rate of information spread across a network. In a network of interactions, the duration over which individual variation in interactions persists may affect how the network operates. Individuals may persist in their behavior over time and across situations, often referred to as personality. Colonies of social insects are an example of a biological system in which the structure of the coordinated networks of interacting workers may greatly influence information flow within the colony, and therefore its collective behavior. Here I investigate the effects of persistence in walking patterns on interaction networks using computer simulations that are parameterized using observed behavior of harvester ants. I examine how the duration of persistence in spatial behavior influences network structure. Furthermore, I explore how spatial features of the environment affect the relationship between persistent behavior and network structure. I show that as persistence increases, the skewness of the weighted degree distribution of the interaction network increases. However, this relationship holds only when ants are confined in a space with boundaries, but not when physical barriers are absent. These findings suggest that the influence of animal personalities on network structure and function depends on the environment in which the animals reside [*Current Zoology* 61 (1): 98–106, 2015].

Keywords Agent based model, Collective behavior, Complex system, Self organization, Personality, Temperament

Complex systems such as the brain and social insect colonies operate as networks of interacting agents. The structure of interaction networks determines how one region of the network is connected to another and how far and rapidly information propagates across the network (Watts and Strogatz, 1998). Thus, network structure affects its response to changes in the environment such as disturbances (Callaway et al., 2000) or changes in food availability (Sendova-Franks et al., 2010). Individuals vary in number and rate of interactions (Hock et al., 2010) because of differences during development (McDonald, 2007) age, sex (Croft et al., 2005), and genetic relatedness (Pinter-Wollman et al., 2009). For example, in certain networks the distribution of interactions among individuals, i.e., the weighted degree (or strength) distribution (Barrat et al., 2004), may be skewed, with few highly connected individuals, often called ‘hubs’, and many individuals that experience only few interactions. In a network with highly connected individuals, these hubs have a greater effect on how fast information flows on the network than the other individuals in the network (Barabasi and Albert, 1999).

Natural selection acts on individual variation. There-

fore, it is important to understand the causes and consequences of variation among individuals in biological systems. In recent years, there has been a growing interest in understanding the tradeoffs caused by consistent behavioral variation among animals that persists across more than one situation and over time, termed personalities (Gosling, 2001), behavioral syndromes (Sih et al., 2004), or temperament (Reale et al., 2007). Network position is an example of a behavior that may persist, affecting the collective behavior and fitness of the group as a whole (Sih et al., 2009; Wilson et al., 2013; Pinter-Wollman et al., 2014). If an individual occupies a central position in the network for a long time, the loss of this central node may cause the network to break down (Lusseau and Newman, 2004; Flack et al., 2006). However, in some systems, other individuals may quickly take over the role of the removed group members (Robson and Traniello, 1999; Beverly et al., 2009; Pinter-Wollman et al., 2012). Here I investigate how the duration over which individual variation in behavior persists affects social network structure.

Social insects in which workers are sterile are unique

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in that natural selection acts on the colony as a whole instead of on individual workers. These sterile workers use local interactions to produce complex colony behaviors. Many social insect interaction networks are distributed and operate as an integrated system, like regulatory or engineered networks, in contrast with social networks, because unlike other social groups, selection is not acting on each sterile individual but on the group as a whole (Fewell, 2003; Waters and Fewell, 2012). Still, individual variation is prevalent in social insects (Jandt et al., 2014); workers vary in which tasks they perform and in how diligently they perform these tasks (Jaisson et al., 1988; Retana and Cerda, 1991; Gordon et al., 2005; Dornhaus, 2008; Pinter-Wollman et al., 2012), and such behavioral variation persists over time and across situations (Jandt et al., 2014). Individual workers also vary in how much they interact with one another (Pinter-Wollman et al., 2011; Jeanson, 2012; Waters and Fewell, 2012) enhancing how far and how quickly information, for example about a food resource, flows across the interaction network (Pinter-Wollman et al., 2011; Mersch et al., 2013).

The collective foraging behavior of harvester ant colonies is regulated through a network of interactions. Workers of the harvester ant *Pogonomyrmex barbatus* interact using brief antennal contacts (Gordon, 2010) during which they detect task-specific chemical cues (Greene and Gordon, 2003, 2007). Interaction rates with returning foragers in the nest chamber closest to the nest exit provide information about food availability and determine the rate of foraging activity (Schafer et al., 2006; Pinter-Wollman et al., 2011; Greene et al., 2013; Pinter-Wollman et al., 2013). On short timescales of minutes, interaction networks show a skewed weighted degree distribution, in which individual variation in interaction rate (Pinter-Wollman et al., 2011) is due to variation in spatial behavior (Pinter-Wollman et al., 2011; Pinter-Wollman et al., 2013). Networks with skewed weighted degree distributions and those with many interactions both facilitate widespread transfer of information across the entire interaction network (Bansal et al., 2007; Pinter-Wollman et al., 2011). Thus, variation among foragers in the rate of interaction may influence the regulation of colony foraging behavior overall. However, it is not known whether persistence in this variation in interaction rate may impact network structure and therefore foraging regulation.

The structure of a social insect colony's interaction network emerges from the walking patterns of the workers, which are affected by the spatial organization of

chambers or resources in their nest (Adler and Gordon, 1992; Gordon et al., 1993; Naug, 2008; Sendova-Franks et al., 2010; Pinter-Wollman et al., 2011; Jeanson, 2012; Mersch et al., 2013; Pinter-Wollman et al., 2013). When ants leave their nest, e.g., to forage or maintain the nest mound, they effectively no longer have physical barriers that constrain their walking paths. Pheromone trails may focus the walking paths of ants outside the nest (Traniello, 1989), but even such spatial guides do not physically restrain the ants in a certain space, only lead them along a preferable path. Thus, outside the nest there are effectively no barriers that restrict the walking patterns of ants and therefore they encounter each other at a lower frequency than inside the nest. Thus, it is possible that the effects of persistent individual variation in spatial behavior on network structure will differ in the presence or absence of barriers in the environment.

Here I investigate how persistence in the individual variation in spatial behavior among workers of harvester ants affects network structure and function. Using a computer simulation, I test the hypothesis that increasing the persistence of individual variation in walking patterns increases the skewness of a network's weighted degree distribution and the total number of interactions. I further examine whether the relationship between persistence in walking patterns and network structure is maintained when changing the spatial setting in which interactions occur, i.e., when removing spatial barriers.

1 Materials and Methods

To test the effect of persistence in walking patterns on the skewness of a network's weighted degree distribution and its total number of interactions, I constructed an agent-based, spatially explicit computer simulation (Fig. 1). I tested whether persistence in spatial activity would increase or decrease the skewness of the network's weighted degree distribution and the total number of interactions when physical boundaries are present and when they are absent. The rules and parameters of the model were set to simulate the observed individual variation and walking trajectories of harvester ants (Pinter-Wollman et al., 2011) and a local sensitivity analysis of the selected parameters is provided in the supplementary material along with the code for the simulations. The simulated ants' movement was modeled as a correlated random walk (Kareiva and Shigesada, 1983) with constant speed. An ant i moved in a direction $\theta_{i,t}$ during time step t . At each time step, the ant's direction was updated to: $\theta_{i,t+1} = \theta_{i,t} + d\theta$ where $d\theta$ was drawn from a normal distribution with an average of

zero and a standard deviation of σ_i as in Adler and Gordon (1992). To produce individual variation among ants in their turning angles, I varied σ_i , an ant-specific parameter that determines an ant's walking tortuosity, by drawing values of σ from an exponential distribution with an average of $\pi/8$. Variation among ants in walking tortuosity was observed empirically by Pinter-Wollman et al (2011). At the beginning of each simulation, each ant was assigned a value of σ_i . To simulate persistence in walking patterns I defined τ , a parameter that determines the frequency at which an ant changes its path tortuosity (σ_i). Every τ time steps, all ants were randomly assigned a new tortuosity parameter σ_i . So the larger the τ , the longer the ants persisted in their walking pattern. In each simulation there were 100 ants that walked according to the above rules for 1000 time steps. I ran 100 simulations for each of five τ values: 1 (change σ_i every time step), 10, 100, 500 (change σ_i every 10, 100, or 500 time steps), and infinity (implemented as 1001 in this case - no change in σ_i throughout the simulation) (Fig. 1A, B, supplementary movies 1, 2). I then constructed the interaction network among the simulated ants, with interactions defined as co-localization in time and space. An interaction was recorded if ants were at a distance of 5 steps from one another during a certain time point. If two ants remained interacting for longer than one time step, with up to 4 time steps separating consecutive interactions, these interactions were aggregated and considered as a single interaction event (see simulation code in the supplementary material). To measure the distribution of interactions among individuals I used the skewness, a measure of the asymmetry of a probability distribution, of the weighted degree distribution, i.e., the distribution of the total number of interactions each ant experienced (Barrat et

al., 2004). Networks in which interactions are homogeneously distributed among individuals have low skewness. Networks with high heterogeneity among individuals in interaction rate, e.g., with most individuals experiencing few interactions and few interaction hubs experiencing many interactions, have high skewness. I compared the skewness of the weighted degree distribution obtained from the 100 simulations of each of the five τ values using a one way ANOVA. To determine whether persistence also affected the total number of interactions experienced by all simulated ants, I summed the number of interactions in each simulation and compared results for the 100 simulations of each of the five τ -values using a one way ANOVA.

To simulate the effect of boundaries, the ants were placed either in a finite arena with boundaries, or were not confined (Fig. 1). In a finite arena of 100×100 ant lengths, when an ant reached the boundary, if its next step would have placed the ant outside the arena, the x or y coordinates of that next step (whichever one would have been outside the arena) were automatically modified to be back at the boundary. This rule effectively caused ants that reached the boundary to walk along it (Fig. 1A, supplementary movie 1), a behavior observed in several ant species (Gordon et al., 1993), including *P. barbatus* (personal observations). To simulate a large, infinite arena, I implemented a periodic boundary condition (PBC), i.e. ants that stepped outside a 100×100 ant-length screen, re-appeared at the opposite side (Fig. 1C, supplementary movie 3), as if they were walking on a torus or sphere (Gordon et al., 1993). Thus, effectively these ants did not encounter any boundaries, yet they did not randomly diffuse away from one another as they would have if I had simply increased the size of the arena. Finally, to determine the effect of boundaries on

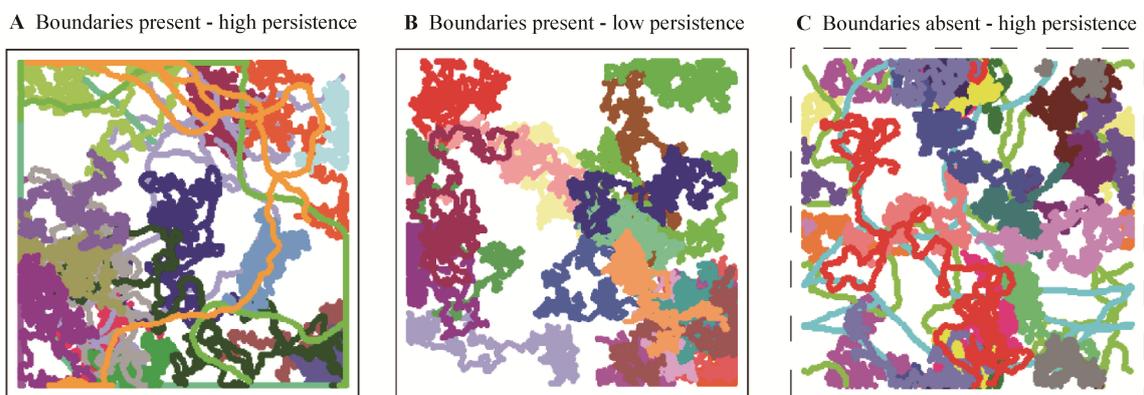


Fig. 1 Trajectories of simulated ants

A. Boundaries and high persistence ($\tau=1001$). **B.** Boundaries and low persistence ($\tau=1$). **C.** No boundaries (PBC) and high persistence ($\tau=1001$). Each ant is depicted in a different color and only 20 ants run for 700 time steps are shown for clarity.

the location of the interactions I examined for each simulation run the ratio between the number of interactions that occurred along the boundary, or edge of the screen, and the number of interactions that occurred in the remainder of the arena. The region near the boundary or edge of the screen was defined as the area along the boundary or screen edge that is the width of the distance two ants had to be from one another to be considered interacting, which was 5 ant lengths. The ratio between interactions at the edge and the remainder of the arena from the 100 simulations of each of the five τ values were compared using a one way ANOVA.

All simulations and analyses were conducted in R version 2.15.2. The code for the simulation can be found in the electronic supplementary material.

2 Results

When confined by boundaries, an increase in walking pattern persistence led to an increase in the skewness of the weighted degree distribution of the interaction network, i.e., an increase in the variability among individuals in their interactions (ANOVA: $F_{4,495} = 42$, P

< 0.0001 , Fig. 2). Furthermore, as persistence increased, so did the overall number of interactions (ANOVA: $F_{4,495} = 142$, $P < 0.0001$, Fig. 3A). The numerical results of the simulations with high persistence are similar to the results from the empirical networks that were reported by Pinter-Wollman et al. (2011) and were used to parameterize the simulation.

However, when there were no effective boundaries (i.e., PBC), persistent behavior did not affect network structure or total number of interactions. The weighted degree distribution did not change as persistence increased (ANOVA: $F_{4,495} = 1.6$, $P = 0.18$, Fig. 4) and neither did the overall number of interactions (ANOVA: $F_{4,495} = 0.2$, $P = 0.94$, Fig. 3B).

As persistence increased, the proportion of interactions along the arena edges increased when boundaries were present but not when they were effectively absent (PBC). In the simulations with arena boundaries, the ratio between interactions near the arena boundary and the remainder of the arena changed with persistence (ANOVA: $F_{4,495} = 409$, $P < 0.0001$, Fig. 5A). However, when barriers were absent, persistence in walking pat-

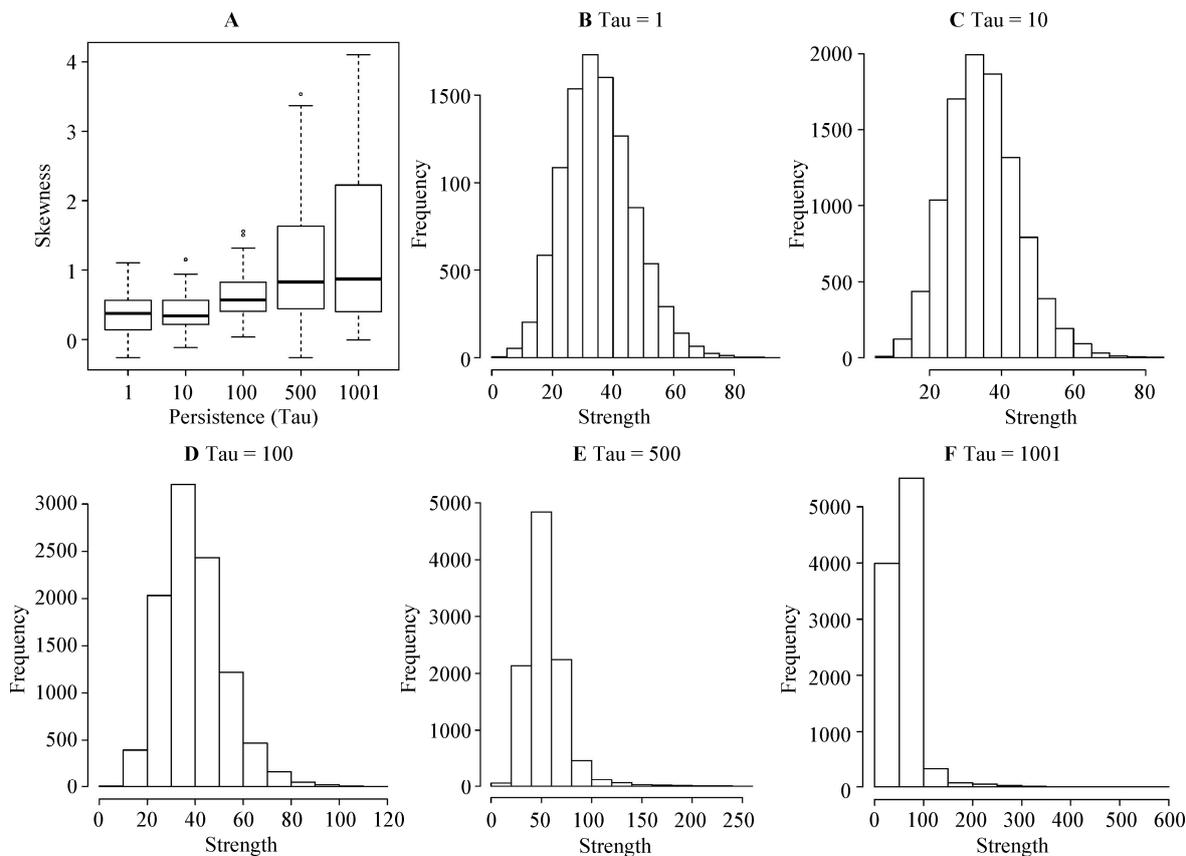


Fig. 2 When boundaries were present, as persistence increased, weighted degree distribution became more skewed

A. Boxplots of the skewness of 100 simulations for each persistence level. In all figures with boxplots the boxes indicate the lower and upper quartiles, horizontal lines within boxes indicate the median, whiskers extend to the 1.5 interquartile range from the box, and points indicate outliers. **B**–**F.** The weighted degree distribution of all simulations of each persistence level (τ).

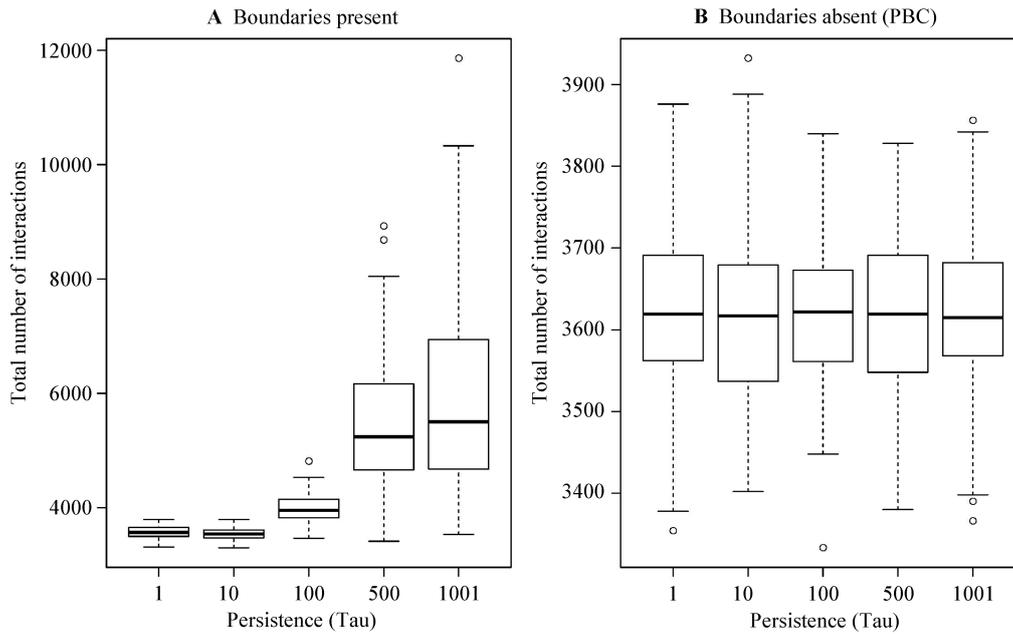


Fig. 3 Total number of interactions as a function of persistence (A) when boundaries were present and, (B) when boundaries were absent (PBC)

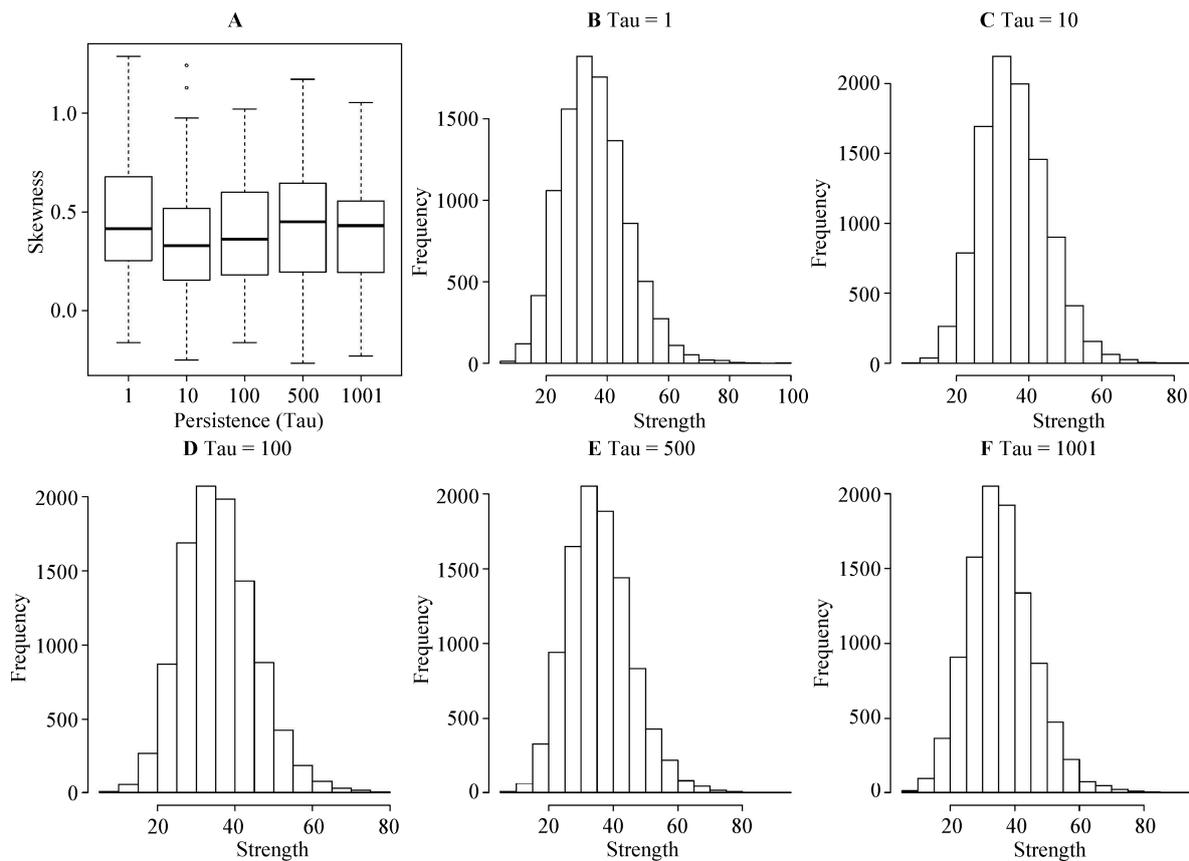


Fig. 4 When boundaries were effectively absent (PBC) there was no relationship between persistence and weighted degree distribution

A. Boxplots of the skewness of 100 simulations for each persistence level. B–F. The weighted degree distribution of all simulations of each persistence level (tau).

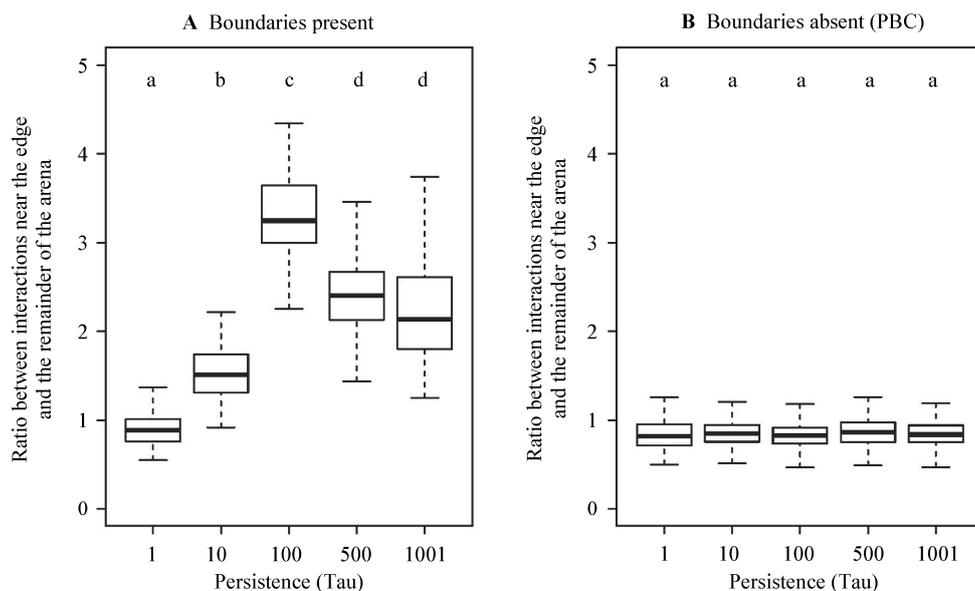


Fig. 5 Ratio between the number of interactions near the edge of the arena and elsewhere in the arena (A) when boundaries were present and, (B) when boundaries were effectively absent (PBC)

Different letters indicate statistically significant differences using a post hoc Tukey test.

terns did not affect the ratio between the number of interactions along the screen edge and the number of interactions elsewhere in the arena (ANOVA: $F_{4,495} = 0.7$, $P = 0.59$, Fig. 5B).

3 Discussion

The model presented here shows that persistence in the spatial behavior of ants may promote interaction networks with a skewed weighted degree distribution and many interactions. This relationship between the persistence in spatial behavior and network structure holds if ant movements are confined by boundaries but not if movements are not confined, i.e., in PBC. Skewed weighted degree distribution and increased interaction rate both facilitate the speed of information flow among ants (Pinter-Wollman et al., 2011). Thus, persistent spatial behavior may facilitate information flow inside the nest but not outside. This difference in the effect of persistence in walking pattern on network structure under different environmental conditions may explain how social insect colonies regulate their collective behavior to fit the various ecological constraints they face. Outside the nest, there are many more risks, such as predation (Munger, 1984) and desiccation (Lighton and Feener, 1989), than inside the nest. The organization of a colony's workforce takes these differences into account by allocating younger workers, who have a long life ahead of them, to brood care inside the nest and older workers, that are near the end of their lives, to handling the refuse pile (Gordon et al., 2005). Interac-

tion networks with skewed weighted degree distributions rely on few individuals with many interactions, i.e. hubs, to transmit information rapidly. If such hub individuals are lost, the flow of information on the network is greatly affected because the social structure is broken at an important link (Lusseau and Newman, 2004). Thus, having an interaction network that relies on one or few key individuals is not robust to risky conditions such as those outside the nest. However, in the safety of the nest, where the risk of losing workers is low, communication can rely on networks that enhance the speed of information flow, despite their low structural robustness. My simulations show that maintaining persistent behavioral variation among workers, i.e. having colonies comprised of workers with various personalities, provides the benefits of rapid information flow within the nest, without paying the potential costs of network breakdown outside the nest. Thus alleviating the potential constraints that emerge from animal personalities carrying over to inappropriate situations that have been suggested for other animal systems (Sih et al., 2004).

Another tradeoff that may be resolved by the effects of behavioral persistence on network structure is the tradeoff between information flow and the spread of disease on a network: when information flow is rapid, so is disease transmission. Workers in a colony perform various tasks, which are often spatially segregated (Sendova-Franks and Franks, 1995; Jandt and Dornhaus, 2009; Mersch et al., 2013). Thus, interactions among workers of different tasks might be less frequent than

interactions among workers of the same task, creating a modular interaction network (Fewell, 2003). Models of disease transmission on modular networks of social insects show a decrease in the rate of disease transmission as network modularity increases (Naug and Camazine, 2002). Indeed, in honey bees, segregation of interactions among age groups protects the youngest bees from contracting a disease brought into the nest by foragers (Feigenbaum and Naug, 2010). In contrast, when a starved colony of *T. albipennis* receives food, mixing among tasks increases substantially, facilitating rapid food distribution throughout the colony (Sendova-Franks et al., 2010). Furthermore, in the social wasp *Ropalidia marginata*, the degree distribution of the interaction network becomes more skewed as the colony increases in size (Naug, 2009), thus as a colony grows, its interaction network changes to facilitate faster information flow to all its constituents. Such complexity in a colony's interaction network allows it to balance fast information flow within a task, or when food is distributed, with slow disease spread among tasks. The model I presented suggests that frequent task switching, i.e. low behavioral persistence, could be another potential way to balance rapid information flow and disease transmission: it is possible that as workers switch tasks, they maintain their position within the interaction network of their new task, but because of factors (spatial or temporal) that separate task groups, this persistence no longer affects interactions with ants from its prior task. Examining the interplay between interactions among tasks and within tasks will further elucidate how a colony balances the tradeoffs between rapid information dissemination and disease transmission.

The difference in the relationship between persistent

behavior and network structure when boundaries are present and when they are effectively absent (PBC) may be explained by the location of interactions. When boundaries were present, the proportion of interactions along the boundary increased with persistence (Fig. 5A). Thus, when persistence in walking patterns was high, the few individuals with trajectories of low tortuosity, who are the ones that experience the most interactions (Pinter-Wollman et al., 2011), tended to remain along the arena boundary, once they reached it (Fig. 1A), and interacted with one another frequently along the edge (Fig. 6A), skewing the distribution of interactions among individuals. When persistence was low, path tortuosity changed more frequently and individuals did not necessarily remain at the boundary (Fig. 1B, 6B). When boundaries were effectively absent (PBC), there was no spatial 'sink' for ants with low path tortuosity (Fig. 1C) and so their likelihood of interacting with others did not change with persistence (Fig. 5B, 6C). It has been shown empirically that certain ant species tend to walk along arena edges to increase their interaction rate, and even when placed on a spherical arena, with no boundaries, certain ants will aggregate at particular locations on the sphere to increase their interaction rate (Gordon et al., 1993). Thus, it seems as though ants can regulate their spatial behavior to enhance the effect of persistent individual variation on the structure of the interaction network.

Because social insects vary in how their nests are structured and in their ecological needs, species may vary in how persistent behavioral variation influences network structure. In small lab nest chambers, *P. barbatus* ants vary in interaction rate over short periods of five minutes (Pinter-Wollman et al., 2011). Workers of

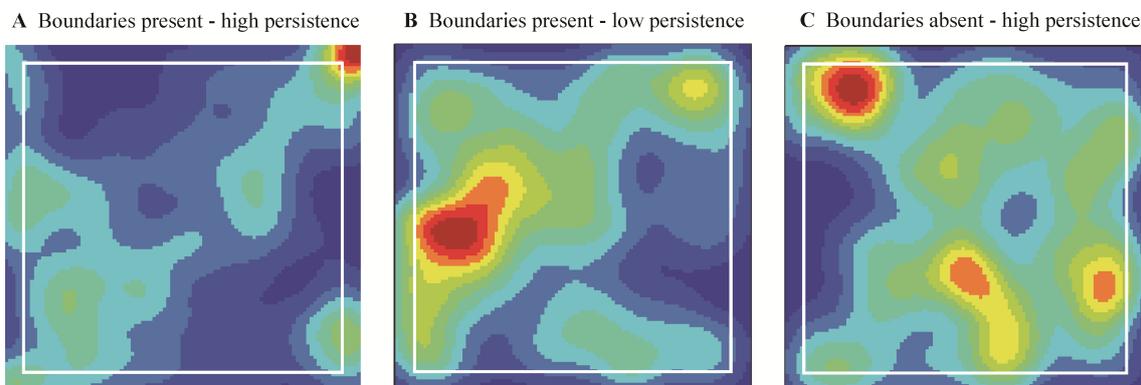


Fig. 6 Heatmap of interactions of three simulation runs with 100 ants each for 1,000 time points

A. with boundaries and high persistence ($\tau = 1,001$). B. with boundaries and low persistence ($\tau = 1$). C. When boundaries were effectively absent (PBC) and high persistence ($\tau = 1,001$). Red colors indicate many interactions and blue colors indicate few interactions. The white empty squares are drawn 5 ant lengths from the boundary or edge of the screen to indicate which interactions were considered along the edge (outside the square) and which interactions were considered to be in the remainder of the arena (inside the white square).

the ant *Odontomachus hastatus* exhibit both individual variation and persistence in interaction rate over a three week period (Jeanson, 2012). In contrast, workers of the ant *Temnothorax rugatulus* do not exhibit persistence in interaction rate (Blonder et al., 2012). *Temnothorax* ants form small colonies of 30–200 workers that live in small cavities (Franks et al., 1992) in which all individuals might be able to interact with one another frequently, reducing the need for an interaction network structure that facilitates fast information flow. However, *P. barbatus* ants form large colonies of up to 10,000 workers that live in complex nests (Tschinkel, 2004; Gordon, 2010), in which the likelihood is low that any worker will interact with most others. Thus, having interaction networks in which individuals persist in their behavior may facilitate the speed of information flow in such large colonies.

Persistent individual variation in spatial behavior may be caused by many factors. For example, temperature (Azcarate et al., 2007), gene expression (Whitfield et al., 2003; Ingram et al., 2005), age (Seeley, 1982), and the task a worker performs, which determines where the worker is located within the nest (Sendova-Franks and Franks, 1995; Jandt and Dornhaus, 2009) all influence a worker's spatial behavior. Further studies are needed to determine what produces individual differences among workers in spatial activity to better understand the temporal scale on which such variation persists and therefore the magnitude of its effect on the structure of the interaction network among workers in a colony. Understanding how the behavior of each individual agent in a network changes, and how this alters network function, can explain how complex biological systems regulate collective behavior in various environments.

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Electronic Suplumentry Material

Code of the simulation as it was run in the software R version 2.15.2

```
#####
# load libraries
library('igraph')
library('MASS')
library('moments')

# clear workspace
rm(list=ls()) # clean workspace
graphics.off() # close all figures

#####

# set model parameters

n=100 # number of ants
iter = 1000 # number of time steps
thresh=5 # distance two ants need to be during a certain time step to be considered interacting
sims=100 # number of simulation iterations
Tau=c(1,10,100,500,1001) # Tau values (1,10,100,500,1001)
geomtype=c(1,2) # what happens at the boundary? 1=stay at boundary, 2=appear on other side of screen
(walk on ball)
anglescale = pi/8 # the average of the exponential distribution that determines the standard
deviation of the normal distribution from which the change in turning angle is drawn at each time
step
bndsiz=100 # the size of a side of the square arena

# initiate arrays for storing simulation results
skews=array(NA, dim=c(sims,length(Tau), length(geomtype)))
WDdists=array(NA, dim=c(sims,n,length(Tau),length(geomtype)))
prop_edge_int=array(NA, dim=c(sims,length(Tau),length(geomtype)))

for (h in 1:length(geomtype)){
  bnd = c(0, bndsiz) # the size of the arena
  for (k in 1:length(Tau)){
    for (s in 1:sims){
      AntXY = matrix(runif(n*2, min=bndsiz/2-50, max=bndsiz/2+50),n,2) # in-
      itialize random ant position so that they start in a 100*100 square in the middle
      of the arena (if want to change their spread - need to change the 50)
      AntV = matrix(1,n,1) # current Ant velocity (Vx,Vy)
      AntTeta = runif(n,0,2*pi) # initialize first turning angle
      Tortuosity = rexp(n, anglescale) # trajectory persistence

      # initiate variables to fill in when simulation runs:
      AntHistoryX = matrix(NA, nrow=iter,ncol=n)
      AntHistoryY = matrix(NA, nrow=iter,ncol=n)

      # create a data frame to fill in association as the simulation runs (will
      remove this first row later):
      association=data.frame(t(c(x=1,y=1,t=1,ith=1,jth=1)))

## simulation:

for(i in 1:iter){
  if ((i %% Tau[k] )==0){
    Tortuosity = rexp(n, anglescale)
  }

  # random change in direction dVx,dVy
```

```

dTeta = rnorm(n,0,Tortuosity)
AntTeta = AntTeta+dTeta;

AntXY[,1] = AntXY[,1]+AntV*cos(AntTeta)
AntXY[,2] = AntXY[,2]+AntV*sin(AntTeta)

# deal with boundary:

# scenario 1: place ants that leave the arena at the boundary

if(geomtype[h]==1){
  for (j in 1:n){

    if (AntXY[j,1]<min(bnd)){AntXY[j,1]=min(bnd)}
    if (AntXY[j,1]>max(bnd)){AntXY[j,1]=max(bnd)}
    if (AntXY[j,2]<min(bnd)){AntXY[j,2]=min(bnd)}
    if (AntXY[j,2]>max(bnd)){AntXY[j,2]=max(bnd)}
  }
}

# Scenario 2: appear on other side of screen (walk on ball)
if(geomtype[h]==2){
  for (j in 1:n){

    if (AntXY[j,1]<min(bnd)){AntXY[j,1]=max(bnd)}
    if (AntXY[j,1]>max(bnd)){AntXY[j,1]=min(bnd)}
    if (AntXY[j,2]<min(bnd)){AntXY[j,2]=max(bnd)}
    if (AntXY[j,2]>max(bnd)){AntXY[j,2]=min(bnd)}
  }
}

# store location information for each time step
AntHistoryX[i,] = t(AntXY[,1])
AntHistoryY[i,] = t(AntXY[,2])

# get the interactions that happened during this time point and save
in a variable. (information about the interaction to keep: XYTij)
distance=dist(AntXY)
ij=which(distance<thresh, arr.ind=TRUE)
if(length(ij)>0){
  ij=which(as.matrix(distance)==distance[ij], arr.ind=TRUE)

  ## save in the dataframe of interactions:
  ith=ij[,1]
  jth=ij[,2]
  xs=cbind(AntXY[ij[,1],1],AntXY[ij[,2],1])
  x=apply(xs,1,mean)
  ys=cbind(AntXY[ij[,1],2],AntXY[ij[,2],2])
  y=apply(ys,1,mean)
  t=i
  xytij=cbind(x,y,t,ith,jth)

  if(length(xytij)>1){association=rbind(association,xytij)}
}
}

# remove the first row I inserted when creating the association data frame:
association=association[-1,]
association=association[order(association$ith,association$jth,association$t),]

```

```

association_agg=association

# aggregate interactions so that as long as two ants are interacting it counts as only one interaction
and not as many interactions (for each time frame), to be consistent with the analysis of the empirical
data in Pinter-Wollman et al 2011:
cnt=1
while(cnt<dim(association_agg)[1]){
  current_row=association_agg[cnt,]
  next_row=association_agg[cnt+1,]
  if(current_row$ith==next_row$ith&
      current_row$jth==next_row$jth&
      next_row$t-current_row$t<5){
    association_agg=association_agg[-cnt,]
  }else{
    cnt=cnt+1
  }
}

## set up network and get weighted degree (strength) data
for.net=as.matrix(association_agg[,c(4,5)])
net=graph.edgelist(for.net,directed=FALSE)
for_WD=get.adjacency(net)

# remove node '0' that was automatically added by igraph
if(dim(for_WD)[1]>n){for_WD=for_WD[-1,-1]}

# calculate strength and the skewness of its distribution
WD=apply(for_WD,2,sum )

      if(length(WD)<n){WD=c(WD,rep(0,(n-length(WD))))} # add 0 to the WD for ants
      that did not interact with anyone else

skns=skewness(WD)

# store for further analysis:
skews[s,k,h]=skns
WDdists[s,,k,h]=WD

  # calculate the ratio between interactions along the boundaries of the arena and
  the middle of the arena
edge=0
inside=0
for (i in 1:dim(association)[1]){
  if(association$x[i]>(bndsiz-thresh)|association$x[i]<thresh|asso
    ciation$y[i]>(bndsiz-thresh)|association$y[i]<thresh) # if an in-
    teraction happened within the threshold distance that defines an
    interaction from the boundary of the arena
    {edge=edge+1}
  else
    {inside=inside+1}
}

# normalize number of interactions by the area in which they happen
edge_area=(bndsiz*thresh)*2+(bndsiz-2*thresh)*thresh*2
edge_norm=edge/edge_area
inside_norm=inside/(bndsiz^2-edge_area)

# store for further analysis
prop_edge_int[s,k,h]=edge_norm/inside_norm

}
}
}

```