GLADYS JULIETH CASTIBLANCO QUIROGA

ON THE SYNERGETIC INTERACTIONS BETWEEN TERMITE SOLDIERS AND WORKERS

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-graduação em Entomologia, para obtenção do título de *Magister Scientiae*.

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APROVADA: 22 de Fevereiro de 2016

Leticia Ribeiro de Paiva
(Coorientadora)

Ricardo Ribeiro de Castro Solar

Og Francisco Fonseca de Souza
Orientador

Aos meus pais, Gladys Quiroga e Hugo Castiblanco,
por serem essas pessoas tão maravilhosas...

A esses seres... pequenos mas enormes, frágeis mas fortes, ocultos mas visíveis,
simples mas complexos,
por ter me inspirado uma curiosidade inesgotável...

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Resumo

CASTIBLANCO QUIROGA, Gladys Julieth, M.Sc., Universidade Federal de Viçosa, Fevereiro de 2016. **On the synergetic interactions between termite soldiers and workers** Orientador: Og Francisco Fonseca de Souza. Co-orientadores: Leticia Riveiro de Paiva e Paulo Fellipe Cristaldo.

Uma resposta comum de animais sociais à pressão de predação é alocar alguns indivíduos para a função de defesa. Em cupins, a evolução da casta de soldados, parece ter ocorrido como uma resposta extrema a predação, uma vez que são morfofisiologicamente adaptados à defesa, estéreis e incapazes de se alimentarem sozinhos. No entanto, Vários estudos têm mostrado a participação ativa da casta de soldados em tarefas de exploração do espaço como forrageio. Ditas observações são relevantes pois a alta contribuição dos operários em defesa sugere que os soldados tem um grau de redundância nas colônias de cupins. Tal redundância parece ocorrer em *Cornitermes cumulans*, no qual os operários são mais participativos que os soldados na defesa do ninho. Aqui nós hipotetizamos que uma forma de diminuir o custo da casta de soldados é que eles sejam capazes de fazer mais do que só defender. Especificamente, prevemos que tal contribuição deve ser otimizar estratégias de busca. No experimento de caminhamento com *C. cumulans* encontramos que a velocidade média de deslocamento dos operários cresce não-linearmente com a presença de soldados. Esse resultado e a presença de padrões de movimento altamente coerentes com vôo de Lévy sugerem que os soldados reforçam a capacidade exploratória dos operários em *C. cumulans*. A eficiência na exploração do espaço na presença de soldados pode estar contribuindo na entrada de recursos na colônia e na diminuição

da mortalidade. Assim, nossos resultados mostram uma vantagem intrínseca de ter soldados na colônia, o que pode diminuir o custo dos soldados nas colônias de cupins.

Abstract

CASTIBLANCO QUIROGA, Gladys Julieth, M.Sc., Universidade Federal de Viçosa, February of 2016. **On the synergetic interactions between termite soldiers and workers** Adviser: Og Francisco Fonseca de Souza. Co-advisers: Leticia Ribeiro de Paiva and Paulo Fellipe Cristaldo.

A common response to predation pressure in social animals has been to allocate some individuals to defence tasks. In termites, the evolution of soldier caste was the most extreme anti-predatory response, because they are highly specialized in defence, sterile and incapable of perform self-maintenance. However, many studies have shown the active role of soldiers in tasks of space exploration like foraging. Such observations are important because the high contribution of workers in defence suggest some redundancy rate of soldier caste in termite colonies. The redundancy seems occurs in *Cornitermes cumulans*, where the workers being more responsive to threats than soldiers. Here we hypothesized that one way to diminish the cost of soldiers is that they are capable to do more than only defence. Specifically, we anticipate that soldiers are capable to optimize the search strategy of the workers. In the walking experiment with *C. cumulans* we find that the mean speed of the workers increases nonlinear with the number of soldiers. This result and the presence of patterns highly coherent with Lévy flight motion suggests that the soldiers strengthen the exploratory capacity of workers in *C. cumulans*. In doing so, soldiers are expected to provide significant contributions to the intake of resources and to decreasing mortality in the colony. Then, our results propose an intrinsic advantage

of have soldiers in the colony, and this may diminish the cost of soldiers in termite colonies.

1 Introduction

In animals living in group, escape from predators has been a key issue in order to protect their brood and valuable resources (Rivera-Marchand et al., 2008). A common response for predation in social animals has been to allocate some individuals to the guard task. This occurs from social mammals, such as meerkats (Bateman et al., 2012) and banded mongoose (Cant, 2003), to eusocial groups as flatworms (Hechinger et al., 2011), shrimps (Duffy & Macdonald, 2010), aphids (Braendle & Foster, 2004), thrips (Perry et al., 2004), bees (Breed et al., 1992), ants (Wilson, 1984) and termites (Prestwich, 1984). In termites, the evolution of soldier caste was the most extreme anti-predator strategy. Soldiers were the first caste completely sterile (Thorne et al., 2003), highly specialized for defence and very expensive for colonies in production and maintenance (Tian & Zhou, 2014). Despite the high investment to soldier production, in termites colonies, the defensive function of workers seem to be as important as that of soldiers (Deligne et al., 1981). In fact, Roux & Korb (2004) showed in *Cryptotermes secundus* (Kalotermitidae) that the presence of soldiers does not enhance the survival and growth of colonies. Then, in the light of current knowledge the soldiers have some redundant rate in their role in termite colonies. Here, we given evidence that soldiers have not redundant role at leats in space exploration task in laboratory conditions. On the contrary, they strengthen solutions in space exploration performed by workers.

A common misconception about termite biology is that, as consequence of the high specialization of soldiers, the defensive functions of the colony are taken only by this caste. However, is well-known that workers take part in key process of defence, such as build and nest repairing, block openings (Deligne et al., 1981), patrolling (Traniello, 1981), alarm (Šobotník et al., 2010), and various defensive behaviours such as threatening postures (Ishikawa & Miura, 2012), counterattack with bite (Eisner et al., 1976) and suicidal tactics (Šobotník et al., 2012). Also, the loss of soldier caste in all species of Neotropical Apicotermitineae, may indicate that to keep a caste only for defensive purposes is unnecessary. In fact, in Apicotermitineae the defensive functions are efficiently taken by workers with weapons as advanced as those of soldiers, such as the rupture of body wall (Costa-Leonardo, 2004), defecation on enemy with a highly mobile abdomen (Coaton, 1971) and even possible defensive secretions from frontal gland (Šobotník et al., 2010).

The supposed redundancy rate of soldiers is a problem in terms of resource allocation in termite nests. If soldiers are expensive and their role can be performed by workers, can soldiers contribute beyond of defense in termites colonies? This question seems specially suitable for *Cornitermes cumulans* (Termitidae: Syntermitinae). In this termite specie, soldiers contingent is as low as 5% (Haverty, 1977) of the whole nest population, the nest structure is very robust (Cosarinsky, 2011) presenting walls capable of resist enemies (Cristaldo, 2010) and the workers are far more responsive to nest disturbance than are the soldiers (Cristaldo, 2010). In addition, workers of *C. cumulans* promptly attack enemies, even in the presence of soldiers, at least in petri dishes (Fig.1).

Figura 1: **Helping behaviour of workers of *Cornitermes cumulans*.** Ant biting by workers of *C. cumulans* in a controlled assay in petri dish. The proportion of workers and soldiers of the group shown in the figure correspond with the natural proportion of castes.

A plausible hypothesis of the way by which soldiers increase the benefits of the colony is that they can be able to exert more than only defence. In fact, soldiers were already observed helping with foraging activities in a range of species (Traniello, 1981; Heidecker & Leuthold, 1984; Haifig et al., 2015). In addition to defending the workers, soldiers can also explore new areas and recruit workers to newly discovered resources. Workers, in their turn, may also defend territory in addition to collecting and processing food. While denouncing full integration between soldiers and workers, theses tasks bear an underlying, frequently overlooked, basis: Efficient space exploration. That is, either to defend conquered territories or to explore new areas, soldiers and workers must latter patrolling skills to spot intruders and to locate resources, and they seem to do so in a highly concerted way. It is then plausible to suspect this to be the "extra function" of soldiers: to integrate with workers in optimal exploration of space, and this will be our working hypothesis.

An alternative hypothesis is that termite soldiers would be redundant indeed, in the sense that they would be backup elements in the colony functioning simply as "alleviators" of the working load of workers. However, this hypothesis lacks support for two reasons: first, soldiers are expensive in production and maintenance, so that this high investment would not be justified; second, as result of being highly specialized they could not fully fill the role of the workers.

In the present study, we analysed the role of soldiers of *Cornitermes cumulans* in modifying space exploration by workers in controlled lab assays. To this end we designed a walking assay in which we evaluated the effect of numbers soldiers on the exploratory behavior of workers in 75 experimental termite groups from 13 wild nests collected in grasslands in South-eastern Brazil. Our rationale was that the kinetics of workers should be a function of the amount of soldiers in the group. Such a variation can be inferred from the physical properties of walking trajectories of workers confined with soldiers in groups composed of varying proportions of such castes. As null hypothesis, we consider that if soldiers have a minor role in space exploration the exploratory behaviour of workers should no change with the presence of soldiers. In brief, here we argue that soldiers can perform more that merely defend, e.g. optimizing the searching behaviour of workers.

2 Materials and Methods

2.1 Rationale

In order to know the effect of number of soldiers on the exploratory behaviour of workers, a walking assay was design using as biological model *Cornitermes cumulans* (Kollar) (Blattaria: Isoptera: Termitidae: Syntermitinae). Density is known as an important modulator of interactions and phase transitions in collective responses of termites (Miramontes & DeSouza, 2008). As collective behaviours, among them space exploration, depend on of social interactions it was necessary to include density as a control parameter in our trials. To do so, we manipulated the number of soldiers and workers in three different densities and measured their effect on kinetics of one focal worker in each experimental group. Here, density means the total area occupied by individuals divided by the total petri dish area (Miramontes & DeSouza, 1996).

2.2 Ethics Statment

No specific permissions were required for the field collect or experimental activities reported in this manuscript. ODS holds a permanent permission from IBAMA (The Brazilian Institute for the Environment and Renewable Natural Resources). Tacit approval from the Brazilian Federal Government is implied by hiring ODS and LRP as Scientific Researches, by awarding research grants to PCF and GJC, and by awarding ODS with a Fellowship from CNPq (The Brazilian Council for Research). No protected species were sampled.

2.3 Model species

Cornitermes spp. are Neotropical termites occurring in several habitats, including savannas ("Cerrado" in Brazil), grasslands, forest and human modified landscapes as crop areas and pastures (Cancello, 1989). *Cornitermes cumulans* build epigeal nests, and is naturally distributed in Brazil (Central and Southern regions), Paraguay and Argentina (Araujo, 1970).

2.4 Sampling

Nests of *C. cumulans* were sampled in the Brazilian Atlantic Forest biome, on pastureland in the municipality of Viçosa (S20°45′, W42°52′), Minas Gerais State, Southeastern Brazil. Termite workers and soldiers of *C. cumulans* were collected from 13 colonies with no sign of damage (See Appendix A, Table 4) from 23rd July 2014 to 26th September 2014 and from 3rd February 2015 to 3rd June 2015. In Köppen system, the study area corresponds to Cfb climate (subtropical climate, without dry season and temperate summer) (Alvares et al., 2013). The maximum and minimum temperature registered for the 2014 period was 16.9°C - 20.1°C, and for the 2015 period was 18.3°C - 23.1°C; the precipitation during the two study periods, ranged from 0.0 mm to 12.2 mm and from 0.0 mm to 110.4mm, respectively (Instituto Nacional de Meterología, 2015).

2.5 Movement recordings: Walking experiment

Controlled walking behaviour bioassays were performed with groups (n= 75) composed by different number of soldiers and workers in three distinct densities (see Table 1). The area ratio between soldiers and workers is 1:2, that is the area occupied by one soldier is proportional to area occupied by two workers. Bioassays consisted to track continuously the movement of one focal worker confined in an experimental arena with no obstacle, food or water up to 6 hours. Arenas consisted of a glass petri dish (ø=53 mm) placed down over a sand-blasted flat glass. To allow the optimal contrast for detection, the focal worker was painted with nontoxic mixture composed of white glue:dye as described by Marins et al. (prep).

Trajectories of the focal individuals were systematically collected at a sample rate of one Cartesian position every 0.5 s with a video-tracking software EthovisionXT (Version 8.5.614, Noldus Information Technology) coupled with a video camera (Panasonic WV-BP334) hence producing series of 10 to 50 thousand Cartesian points. Each data series was plotted to check the recording quality of the trajectory (See Appendix B). A total of 22 experimental treatments were conducted. Each treatment was composed of a specific soldier-workers number in a particular group density (see Table 1) for the reasons explained above.

Table 1: **Number of *Cornitermes cumulans* termite soldiers and workers confined together in experimental arenas, from which the movement of an arbitrary worker was tracked for 6 hours**. Number of individuals have been chosen as to provide distinct group densities. Each row corresponds to a given treatment. Each termite colony provided to each of one of every treatment. Replicates and colony identity are provided in Table 4, Appendix A.

	Number of individuals per caste	
Density	Soldiers	Workers
Low (0.08-0.09)	0	10
	1	8
	2	6
	3	4
	4	2
	5	1
Optimal (0.12-0.13)	0	14
	1	12
	3	8
	2	10
	4	6
	5	4
	6	2
	7	1
High (0.20)	0	24
	1	22
	2	20
	4	16
	5	14
	6	12
	7	10
	11	2

2.6 Exploratory behavior of termite workers

The kinetics of free-walking behavior of termite workers was analyzed in terms of (*i*) search strategy and (*ii*) the mean speed of displacement. Mean speed of displacement and search strategy are complementary parameters of walking behavior. While the speed of displacement characterizes the quickness used by worker to do the task exploration, the search strategy describes how efficiently the worker visits regions in the walking area.

2.6.1 Search strategy

The search strategy comprises the spatial rules used by the workers to solve the search problem. There are two general strategies to solve the search problem, systematic and random search (Bartumeus et al., 2005). In systematic searches, the walker explores the given area following an organized plan, that is, the search is essentially a deterministic process. This strategy is extremely efficient in terms of finding a target, but it is energetically very expensive because it implies an exhaustive revision of the entire search area. The systematic search is useful when the individual knows relevant information about the target position, like what occurs with the isopod *Hemilepistus reaumuri* searching for the entrance of its burrow (Hoffmann, 1983).

In random searches, the walker explores the area not using any organized plan, thereby, the displacement is stochastic and the walker may return many times to the same previous place (Bénichou et al., 2005). Under these conditions, finding the target is uncertain, but energetic costs are low because the walker does not inspect the entire search area. In random processes, finding targets depends on their density, then the random searcher is efficient when targets are abundant in the search area. For example, marine predators, like blue sharks, perform random searches when the prey is abundant (Humphries et al., 2010).

A special class of random search, named Lévy flight or Lévy walk, mixes the advantages of both systematic and random searches, that is, the efficient use of energy and the high performance to find the target. The success of the Lévy strategy to find the target is due to its two movement phases (Bénichou et al., 2005). In the first phase the walker does an exhaustive search in the vicinity of a given point, and in the second phase it moves to new search areas through a fast movement. Such phases of exhaustive search and fast movements are described by short and long steps, respectively. Then, the Lévy flight strategy is a saltatory process that permits to find the target without high investment of energy, because it does not imply searching in the entire area. Its efficiency comes from the fact that the repeating pattern of short and long steps induces fractal properties to Lévy flights.

We described the search strategy in terms of alpha value (α), that is, the scale exponent of the slope of the curve that describes increments in the mean squared displacement (MSD) as a function of the time scale (i.e., the time interval τ). The MSD is a measure of the average distance that a particle travels in a given time interval. In our case, the "particle" is a termite confined in a petri dish.

In a two-dimensional space, the mean displacement of a particle can be estimated by the squared hypotenuse of the triangle whose catets are the distance travelled in x and y axes (hence "mean squared displacement" MSD). Under random displacement, the particle (or the termite, in our case) tends to not deviate a lot from its initial position, after a given time elapse; step lengths are normally distributed around the point of origin of the path. Because step lengths do not vary a lot, if we change the time interval in which displacements are measured, the MSD (which is ultimately the average of step lengths over a given time interval) increases proportionately to the length of time interval. That is, rather than measuring distance travelled from time 1 to time 2 and so on each time-step, we can measure distance travelled from time 1 to time 3, and hence successively each 2 time-steps. Repeating this process each 3, 4, etc time-steps allows plotting MSD versus time-step lengths (also called "Tau" τ). Since in this case MSD is proportional to τ, we would obtain a line with slope $\alpha = 1$ in the plot.

If, however the termite is travelling using Lévy-walks, its step lengths will follow a Power-law, or Pareto-Lévy, distribution, rather than the Gaussian distribution typical of Brownian (i.e., random) motion. This is because it will explore the space performing a lot of short steps combined with occasional very long trips. In doing so, as time elapses the termite will tend to get far from its original position, and the curve MSD versus Tau will have alpha between 1 and 2 ($\alpha > 1$). This is an important topic, because it implies that the individual can explore more space in the same time interval when compared with a random movement. In this sense, the walker makes a more efficient use of time and energy.

Finally, if the relation between the displacement and time interval yields $\alpha < 1$, the movement is called "subdiffusion" and means that the searcher walks less and less as time elapses. The subdiffusion movement occurs in proteins that perform active transportation processes in cells (Weiss et al., 2003).

2.6.2 Mean speed of the displacement

The speed of the displacement is directly related to the search time. The search time is a limiting factor in the context of searching for a randomly located object, like a hint of a nearby predator or food. In this context, the survival of the colony may depend on optimized search time to detect a potential threat or resources. Thus, other factors held constant a more efficient search should be one that spends less search time, that is, one that increases the speed of displacement .
The mean speed of displacement of focal termite workers was obtained calculating the average of the instantaneous speed of each time interval (τ).

2.7 Data analysis

In order to check the effect of the number of soldiers on the walking behaviour of workers, we analysed the data using a Generalized Linear Modelling (GLM) under normal error distribution. The full statistical model included the alpha value or the mean speed of the displacement, according to case, as the response variables; and the number of soldiers, the number of workers and density as predictor variables. We included all the simple terms plus all interactions between the explanatory variables. The models were systematically ranked by Akaike Information Criterion (AIC) to select the best fitted model. The AIC criterion favours the fit and simplicity of models that involves more than one possible predictor (Symonds & Moussalli, 2011). Here, the best model was one with the lower AIC index, that is the minimum distance between the theoretical truth model and the observed phenomenon. All the analyses were carried out in R (R Core Team, 2013).

3 Results

We found a non-linear correlation between the kinetics of workers and the social context as represented by different number of termite workers and soldiers confined together in the experimental arena.

3.1 Search strategy

The scaling exponent (α) of MSD curve was consistent with search strategy of Lévy flight (α>1), both, in the presence or absence of soldiers (See Fig.2). Accordingly the step lengths distribution in the shape a power law (Fig.3) and the scale invariance (Fig.4) of the trajectories of walkers were congruent with the Lévy flight strategy.

The number of soldiers in the Petri dish affected nonlinearly the walking pattern of the focal worker which was confined in there. Such an effect, however, was modulated by the density of the individuals and the number of workers confined together (AIC= -278.55, table 2). In arenas containing more than one worker, the scaling exponent alpha increases with increments in the soldier number, up to a peak, after which it decreases, thereby forming a parabola, or stabilizes at high alpha value (See Fig.5). In arenas containing a single worker, the alpha exponent increases nonlinearly with increasing soldier numbers, stabilizing at a high value.

There was a transition from positive to negative effects of the number of soldiers on the efficiency of the focal worker displacement: above a certain number, the presence of soldiers impaired the flow of the focal worker regardless the total number of workers therein confined. When there were no workers besides the focal worker in the arena, the number of soldiers tended to only affect positively the scaling exponent. There was also a transition from positive to negative effects of the number of workers on the scaling exponent of the focal worker displacement, but this did depend on the number of soldiers therein confined: the larger the number of workers, the higher the scaling exponent up to a certain point (when the number of soldiers = 7) where this trend was reversed.

The density of individuals (workers plus soldiers taken together) negatively effected the scaling exponent of MSD of focal worker, implying that displacement was less efficient as density increased.
The peaks of the scaling exponent of the MSD of the focal worker occurred at the same number of soldiers for a given amount of workers present in the arena, regardless the density of individuals in the arena. That is to say, the number of individuals per se (as opposed to their proportional numbers, i.e., density) could also affect the scaling exponent.

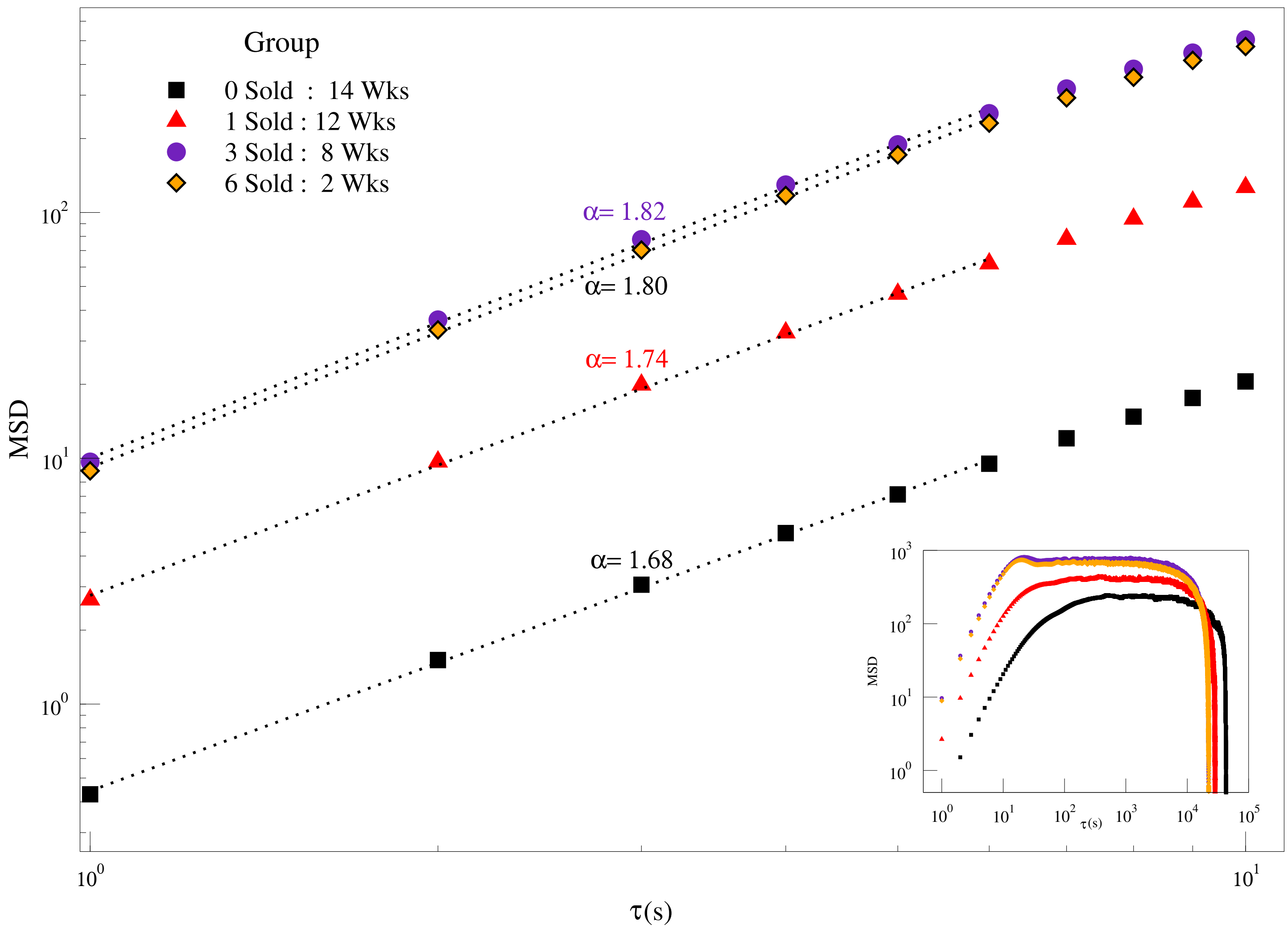


Figure 2: **Mean Squared Displacement (MSD) curves as function of the time interval τ.** *Main:* Zoom at unsatured area of MSD curves. *Inset:* Entire MSD curves. *Cornitermes cumulans* workers exhibited superdiffusion motion (α>1) consistent with the search strategy of Lévy flight. In both, with and without soldiers, all workers examined showed the best theoretical searching strategy. For simplicity, here we show only the curves for arenas under optimal density (0.12).

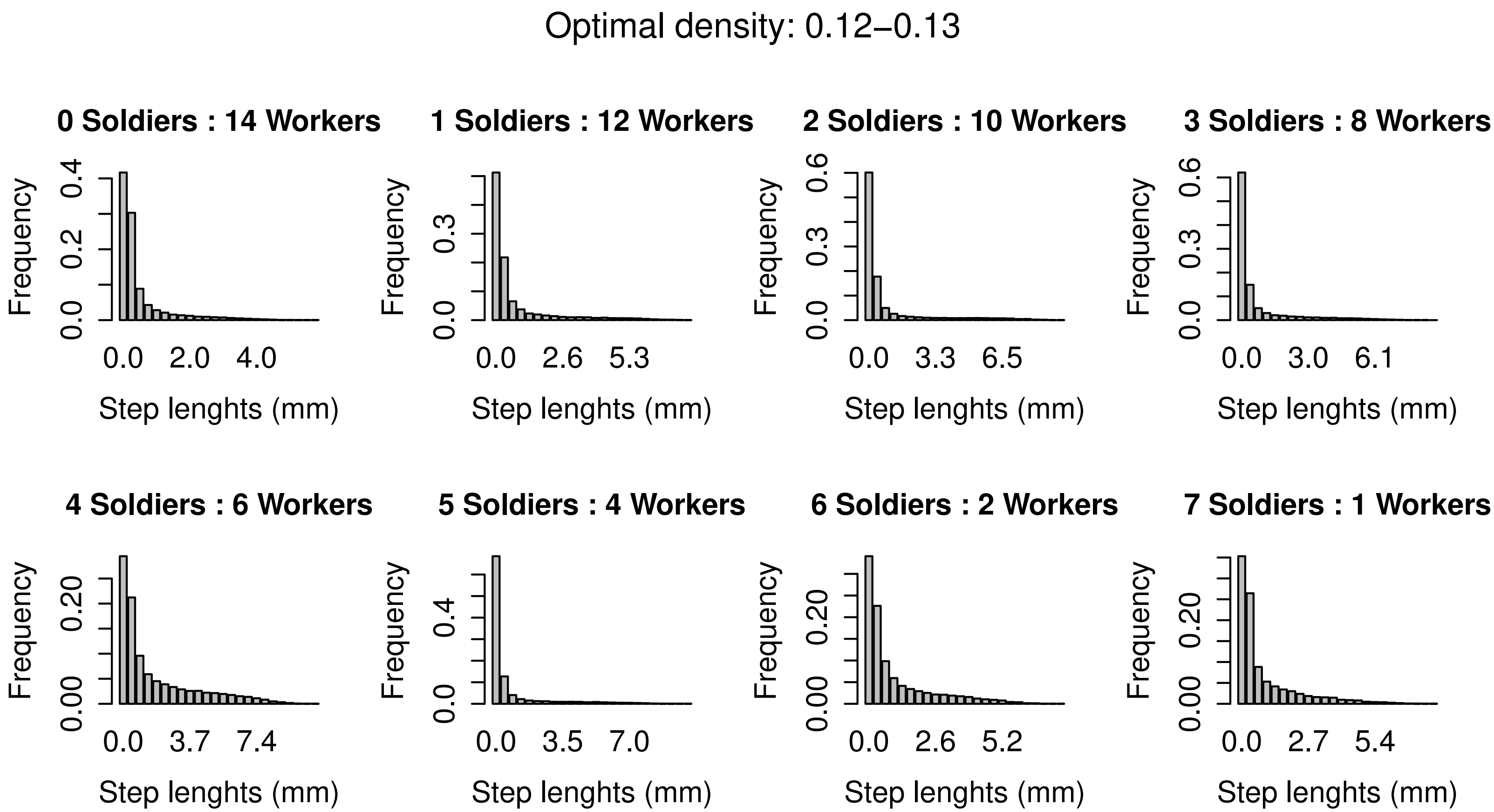


Figure 3: **Step lenght distribution.** Step length distribution for a focal termite worker (*Cornitermes cumulans*). Here, one example is shown for each treatment (number of soldiers and workers) in optimal density. Note the power-law shape for the step length distributions, consistent with the search strategy of Lévy flight.

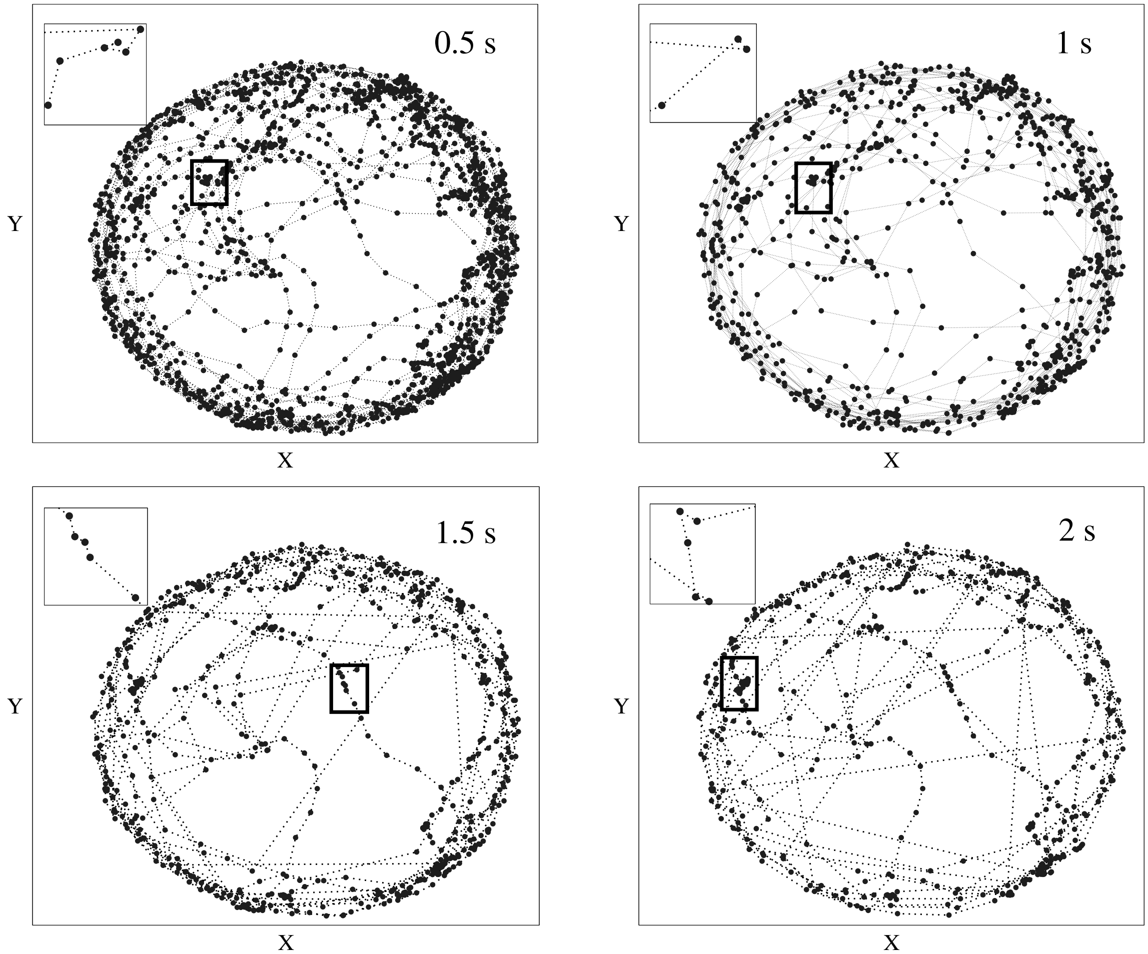


Figure 4: **Scale invariance property** Scale invariance property in the trajectory of a termite worker in *Cornitermes cumulans*. Here is shown a segment of the first 2000 steps of a data series for a focal worker. The series was cut into four timescales: 0.5, 1, 1.5 and 2 seconds (s). The pattern of short and long steps (inset) can be seen in every timescale and this is called "scale invariance".

Table 2: **Model selection by Akaike Information Criterion (AIC) of the scaling exponent (α).** The models were systematically ranked by Akaike Information Criterion (AIC) to select the best fitted model. The best model was one with the lower AIC index (final model item). More negative AIC means less loss of information, then a better model.

Initial Model:

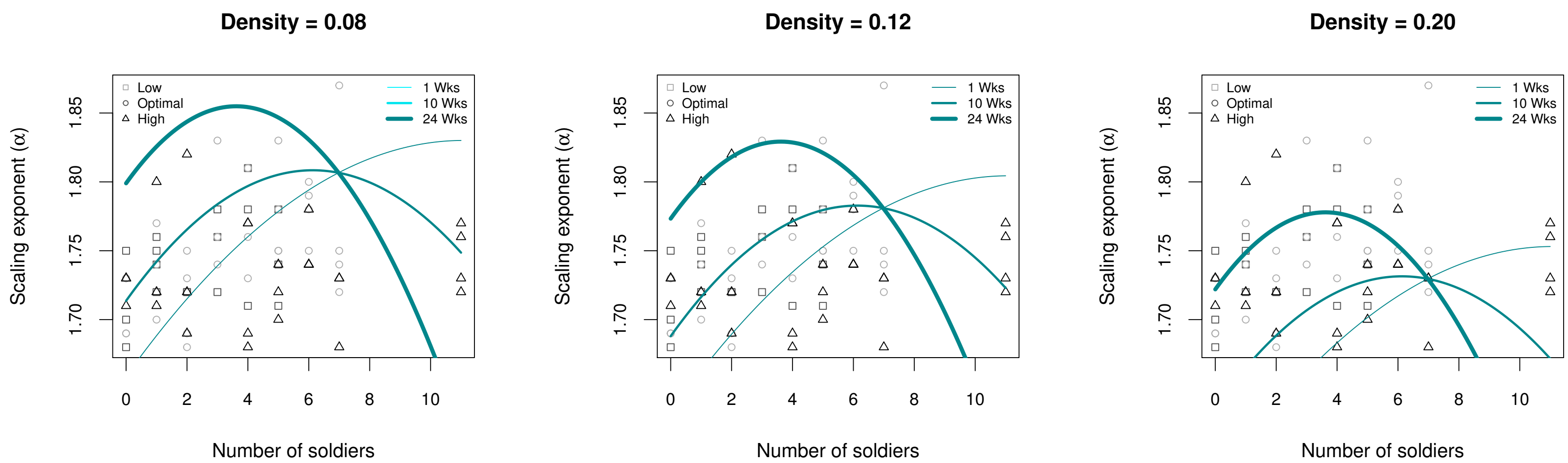
Alpha (I(Sold_Number^3) + I(Sold_Number^2) + Sold_Number + Density + Wk_Number)^2

Final Model:

Alpha I(Sold_Number^2) + Sold_Number + Density + Wk_Number + I(Sold_Number^2):Wk_Number

Step	Term removed	df	Deviance	Residual df.	Residual deviance	AIC
1	None			60	0.08371849	-264.9930
2	- I(Sold_Number^2):Sold_Number	0	0.000000e+00	60	0.08371849	-264.9930
3	- I(Sold_Number^3):Sold_Number	1	1.024414e-04	61	0.08382094	-266.9013
4	- Sold_Number:Wk_Number	1	9.854822e-06	62	0.08383079	-268.8924
5	- Sold_Number:Density	1	1.157877e-03	63	0.08498867	-269.8636
6	- I(Sold_Number^3):Density	1	1.190891e-03	64	0.08617956	-270.8200
7	- I(Sold_Number^2):Density	1	1.343130e-03	65	0.08752269	-271.6601
8	- I(Sold_Number^3):Wk_Number	1	4.453129e-04	66	0.08796800	-273.2795
9	-I(Sold_Number^3):I(Sold_Number^2)	1	4.114386e-04	67	0.08837944	-274.9295
10	- I(Sold_Number^3)	1	1.645174e-05	68	0.08839589	-276.9156
11	- Density:Wk_Number	1	4.330640e-04	69	0.08882896	-278.5490

Sold_Number: Number of soldiers, Wk_Number: Number of workers, df: degrees of freedom.



(a) Low (b) Optimal (c) High

Figure 5: **Scaling exponent (α) of the MSD of focal workers as function of the number of soldiers in *Cornitermes cumulans*.** Each point represents the focal worker of an experimental group. The scaling exponent (α) of exploratory behaviour in workers of *Cornitermes cumulans* change as a nonlinear function of the number of soldiers. Such an effect, also, was modulated by the density of individuals and the number of workers. Note that the pattern of the parabola is similar for all densities, however, higher overall values have been achieved at low density.
Low, Optimal and High mean the data series collected in low (0.08-0.09), optimal (0.12-0.13) and high (0.20) density of individuals, respectively; Wks: Workers, that is the number of workers.

3.2 Mean speed of displacement

The distribution of instantaneous speed of the workers displacement was consistent with the findings in the step length distribution because the shape is, also, a power law (See Fig. 6). As in the step length, the shape in the power law of the speed distribution supports the presence of processes highly similar of Lévy flight motion in the walking behaviour of the focal workers in *C. cumulans*.

The mean speed of the displacement in workers was regulated by both, the size of the group (density) and the social context (number of workers and soldiers). As happened with the search strategy, the mean speed of displacement of workers was affected nonlinearly by the number of soldiers confined together in the experimental arena (AIC= 225.10, see table 3).

The patterns described above are similar in all three densities, changing only in the values that defined the peak and the width of the curves.

There was a critical point above which the soldier numbers would negatively affect the focal worker speed. Such a transition point depended on the number of workers confined together, happening at lower soldier numbers for arenas containing less workers. This a transition point depended also on the density individuals confined together, again happening at lower soldier numbers for arenas with higher densities of individuals. Additionally, the focal worker experienced faster velocities when it was confined together with high numbers of workers than when confined with lower numbers.

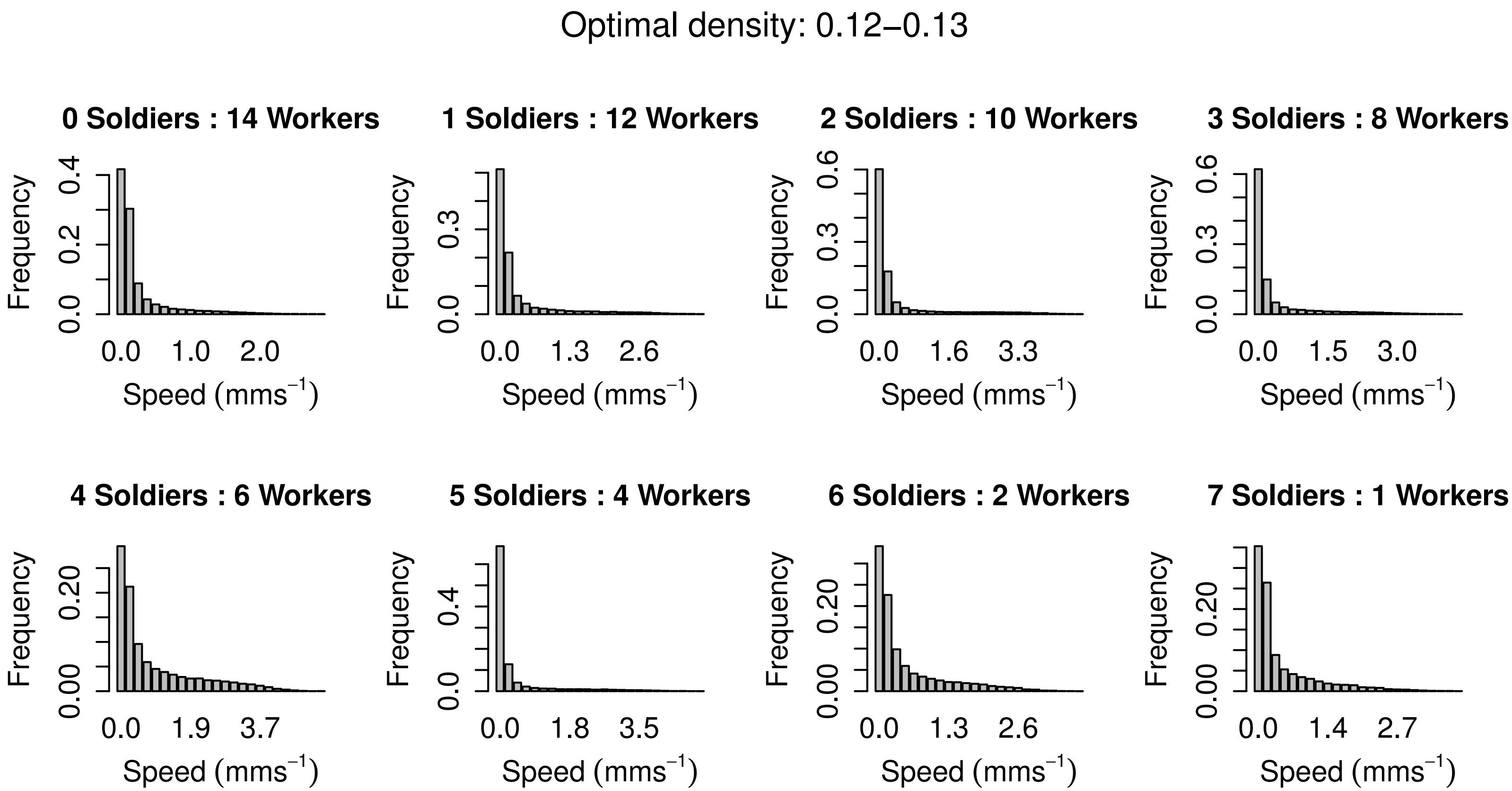


Figure 6: **Speed distribution.** Speed distribution of a displacement of focal termite worker (*Cornitermes cumulans*). Here, one example is shown for each treatment (number of soldiers and workers) in optimal density. Note the power-law shape for the speed distribution, consistent with the search strategy of Lévy flight.

Table 3: **Model selection by Akaike Information Criterion (AIC) of the mean speed of displacement.** The models were systematically ranked by Akaike Information Criterion (AIC) to select the best fitted model. The best model was one with the lower AIC index (final model item).

Initial Model:

Speed (I(Sold_Number^{3}) + I(Sold_Number^{2}) + Sold_Number +,Density + Wk_Number)^{2}

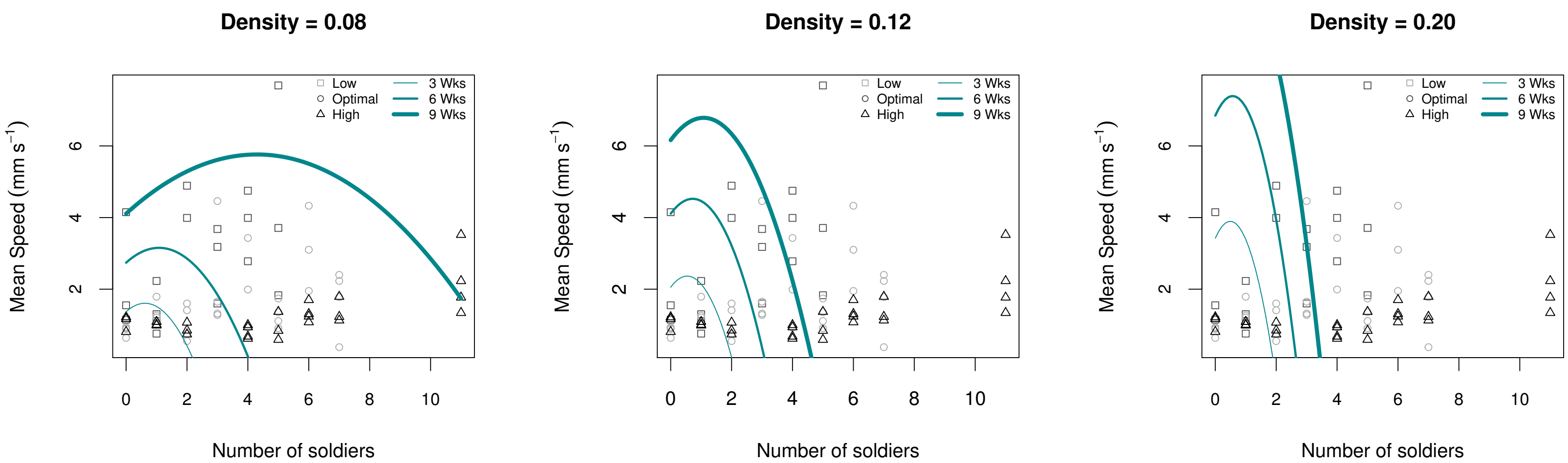
Final Model:

Speed I(Sold_Number^{3}) + I(Sold_Number^{2}) + Sold_Number +Density + Wk_Number +

I(Sold_Number^{2}):Density + I(Sold_Number^{2}):Wk_Number + Sold_Number:Density + Density:Wk_Number

Step	Term removed	df	Deviance	Residual df.	Residual deviance	AIC
1	None			60	62.20062	230.8065
2	- I(Sold_Number^{2}):Sold_Number	0	0.000000e+00	60	62.20062	230.8065
3	- I(Sold_Number^{3}):Density	1	0.0003503049	61	62.20097	228.8070
4	- I(Sold_Number^{3}):Op_Number	1	0.5830587998	62	62.78403	227.5067
5	- I(Sold_Number^{3}):Sold_Number	1	1.5893378154	63	64.37337	227.3817
6	- I(Sold_Number^{3}):I(Sold_Number^{2})	1	0.7375733470	64	65.11094	226.2361
7	- Sold_Number:Op_Number	1	0.7577405582	65	65.86868	225.1039

Sold_Number: Number of soldiers, Wk_Number: Number of workers, df: degrees of freedom.



(a) Low (b) Optimal (c) High

Figure 7: **Mean speed of displacement of the focal workers as function of the number of soldiers in *Cornitermes cumulans.*** Each point represents the focal worker of an experimental group. The mean speed of displacement of workers in *Cornitermes cumulans* change as a nonlinear function of the number of soldiers. However, note that the peaks of the mean speed change location according to the number of workers and density.
Low, Optimal and High mean the data series collected in low (0.08-0.09), optimal (0.12-0.13) and high (0.20) density of individuals, respectively; Wks: Workers, that is the number of workers.

4 Discussion

In termite colonies, the soldiers are highly specialized in defensive functions. However, the generalist caste of workers also take a important part in defence (Kriston et al., 1977; Prestwich, 1984; Noirot & Darlington, 2000b; Ishikawa & Miura, 2012). Specialized and generalist castes joining forces to perform key activities, like defence, is an interesting issue about cooperation in eusocial insects. Specifically for termites, where soldiers are an expensive, highly specialized caste, there seems to be no reason for such cooperation between castes. If workers can perform defence, how soldiers may contribute to the colony beyond of defence? Here we explore this problem, hypothesizing that soldiers, in addition to defence do take part in other crucial roles in the colony. Because of their known ability to explore new areas and recruit workers to newly discovered resources, soldiers may in fact integrate with workers optimizing space exploration thereby impacting positively the colony. We show that, the soldiers are capable of strengthening the performance of workers on their exploratory behaviour in laboratory conditions that finally should have a positive effect on the colony.

Our results showed that termite workers move in scale invariant patterns consistent with anomalous diffusion. These workers perform displacements following a pattern highly similar to Lévy flight movement. Beyon to the Lévy flight strategy, we showed that the scaling exponent of MSD curve changes in function of the social context, however the biological meaning remain for future study. Specifically, the scaling exponent of the workers movement was nonlinearly affected by the number of soldiers sharing such arenas, such an effect being also a function of the number of workers therein present.

Efficiency in space exploration was inferred from both, the presence of patterns highly similar to Lévy flight strategy and the increase in the mean speed of the focal workers displacement. In all three densities, the peak for the values of the mean speed was registered for the condition of few soldiers and many workers (see the curve with more workers in Fig.7). After the peak, the excess of soldiers had an adverse effect on the walking performance of workers. Then, our results suggest that soldiers and workers need an optimal proportion to attain the better condition for exploratory activities. This result made sense with the biology of termites, because despite the variability, in almost all species the soldiers are a minority in the colony. And, in the case of *C. cumulans*, soldiers represent only 5% (Haverty, 1977) of the individuals. A hence, possible cause of such low performance of workers, in non-natural proportions, may be a dynamic of negative feedback generated by the excess of soldiers.

The success of Lévy flight motion is based on the alternation of short and long steps phases. In short step phase, the motion of the walker is slow and the searcher explores at nearby location increasing the chance to detect the target. Long step phase, also called "jump" or "flight", represents the relocation stage in which the walker performs fast movements. Such fast movements increase the chance to visit new areas while optimizing the time spent. The global effect of these phases is to ensure the encounter of target in a short time. For this reason, foraging Lévy Flight hypothesis predict that when the target is sparsely, patchily distributed, difficult to detect or the foragers have limited sensorial skills, searchers use patterns of motion whose length travelled follow Pareto-Lévy distributions (Bénichou et al., 2005), that is, Lévy flight motion. Such distributions have been also found here the step length of the focal workers and the speed (Fig. 3 and 6)

Lévy flight pattern has been showed in many biological entities as animals (Viswanathan et al., 1996; Ramos-Fernández et al., 2004), T-cells (Harris et al., 2012), neurons (Rhodes & Turvey, 2007) and humans (Raichlen et al., 2014). And here, we report patterns highly similar to Lévy flight in workers of *C. cumulans* into collective conditions, this result is consistent with previous findings, where was shown that workers explores following the Lévy strategy, also, in a solitary condition. (Miramontes & DeSouza, 2008; Miramontes et al., 2014). However, our results showed by the first time, that the second phase of Lévy flight search -the speed- is modulated by the social context and, more specifically, to sinergistical interaction between soldiers and workers composing the social group. In this sense, we highlighted the plastic exploratory behaviour of workers in response to group composition.

The mean speed of displacement is a complementary parameter to describe walking behaviour. Specifically, increments in speed are related with the long step phase of the Lévy flight strategy, and consequently with the chance to visit new unexplored areas. In this sense, the nonlinear response of the mean speed of the displacement of workers as function of the number of soldiers can be modified the efficiency of the general pattern of Lévy flight. In all three densities the curve with more workers showed the most higher mean speed values when combined with low quantities of soldiers (i.e 4 soldiers). Our results of the patterns similar to Lévy flight searches and the nonlinear increases of the mean speed of the displacement of workers, suggest that the presence of soldiers strengthen the exploratory capacity of workers in *C. cumulans*.

Interestingly, the beneficial effect of soldiers suggests an unsuspected function of this caste: to strengthen collective responses, ultimately increasing the fitness of the colony. As a consequence of high morphological specialization, the soldiers are incapable of feeding and groom themselves, being hence completely dependent on the workers (Noirot & Noirot-Timothée, 1969). Soldiers are also incapable of perform other activities, as collect and distributed food, construct the nest or care for the brood (Noirot & Darlington, 2000a). For these reasons, termite soldiers are thought to present high costs for the colony (Tian & Zhou, 2014). However, our results with *C. cumulans* suggest that soldiers can perform more than only defence. Specifically, they contribute enhance efficiency of workers performing tasks whose success depends on efficient walking strategies, such as foraging, defence, repair the nest, escape from imminent threats and searching for suitable migration local. In fact, Termite Nests: Architecture & Defence (wel) showed that the natural soldier proportion (18.3%) in *Coptotermes formosanus* increases the number of workers traveling to more distant local when compared with the number of workers traveling on a condition of low soldier proportion (2.4%).

It is also possible that the efficiency achieved in presence of soldiers decreases the predation risk by reducing the time spent to find food or detecting threats. In any case our results evince that soldiers may indeed enhance the fitness of the colony not only by providing protection, but also by optimizing the walking capabilities of workers. Earlier, Oster and Wilson (1978) suggested that soldiers improve benefits in foraging tasks as they defend against predators in the foraging trail. More recently, Roux and Korb 2004 provided evidence for the intrinsic benefit hypothesis of soldiers (Noirot, 1990; Roisin, 1994, 1999), showing that soldier positively affected the production of primary reproductives and, hence, the fitness in colonies of *C. secundus*. Here, our results also propose an intrinsic advantage of soldiers in optimizing the performance of workers.

The exact mechanism by which termite soldiers triggered high efficiency in the exploratory behaviour of workers remains for future research. However, has been shown that collective behaviours in termites emerge nonlinearly from social facilitation processes (Grassé & Chauvin, 1944; Springhetti, 1990; Miramontes & DeSouza, 1996; DeSouza et al., 2001). Positive feedback arising from interactions between individuals is the key of such non-linear processes (DeSouza et al., 2001). Here we show nonlinear patterns which are reminiscent of positive and negative feedbacks arising from interindividual interactions. The number of soldiers provoked increments and then decrements in the mean speed, this pattern being dependent on the remaining workers in the arena and, moreover, on the density of individuals confined together. Then it is possible the social facilitation can be the general mechanism underlying the synergistic effect of soldiers on the exploratory behaviour of workers found here in *C. cumulans*.

This is also supported by the fact that nonlinear dynamics are typical results of multiplicative effects rather than additive process (Miramontes & DeSouza, 2008), and this demonstrates that the parts of the system are interdependent (Kello et al., 2010). Here, the synergistic output from interactions implies that soldiers and workers multiply forces, instead of having a summation or linear effect. This fact is important because it may have favoured the evolution of the low proportion of soldiers in termite colonies, as occurs in most species including *C. cumulans* where only 5% are soldiers and almost all Termitidae species (Haverty, 1977).

Here we measured for the first time the effect of termite soldiers on the exploratory behaviour of workers, and found non-redundant functions and synergistic effect. In evolutionary perspective, is possible that workers and soldiers have been positively selected as a consequence of the functional benefits of the synergistic effect of two castes with different abilities solving a common task, instead of having only workers. In brief, our results suggest the following conclusions: First, soldiers in *C. cumulans* can exert another relevant function in addition to defence: to strengthen the capabilities of workers in space exploration. Second, positive and negative effects of the number of soldiers on exploratory behaviour of workers (synergistic effect), can be evidence of the modulators in the castes proportions in *C. cumulans*.

APPENDIX

Appendix A

Table 4: **Sampling information**. Sampling information about the walking experiment using workers and soldiers of *Cornitermes cumulans*.
Group: short identification of the termite group sampled, *Serie full name:* full name of the data series with the Cartesian positions, *Nest:* nest sampled to collect the experimental groups, *Locality:* locality of the nest at Viçosa (Minas Gerais-Brazil), *Sampling date:* collects date of each experimental group, *Serie length:* number of Cartesian positions collected for each data series, *Density:* Total area occupied by individuals divided by the total petri dish area, *Soldiers:* Number of soldiers by experimental group, *Workers:* Number of workers by experimental group.

Group	Serie full name	Nest	Locality	Sampling date	Serie lenght	Density	Soldiers	Workers
S1	Cupim19FevTardeArena3	N02	Universidade Federal de Viçosa	2015-02-19	43155	0.08	0	10
S2	Cupim20AgoTardeArena2	N02	Universidade Federal de Viçosa	2014-08-20	43155	0.08	1	8
S3	Cupim19AgoTardeArena1	N02	Universidade Federal de Viçosa	2014-08-19	24253	0.08	3	4
S4	Cupim08AgoManhaArena1	N02	Universidade Federal de Viçosa	2014-08-08	43154	0.08	4	2
S5	Cupim20AgoTardeArena1	N02	Universidade Federal de Viçosa	2014-08-20	32576	0.09	5	1
S6	Cupim09FevTardeArena1	N01	Usina Alcool	2015-02-09	23214	0.08	1	8
S7	Cupim24AbrManhaArena3	N02	Usina Alcool	2015-04-24	23158	0.08	0	10
S8	Cupim25FevTardeArena2	N02	Usina Alcool	2015-02-25	43155	0.08	1	8
S9	Cupim18MarManhaArena3	N02	Usina Alcool	2015-03-18	42922	0.08	2	6
S10	Cupim25FevManhaArena2	N02	Usina Alcool	2015-02-25	37732	0.08	3	4
S11	Cupim16MarManhaArena1	N02	Usina Alcool	2015-03-16	23244	0.08	4	2

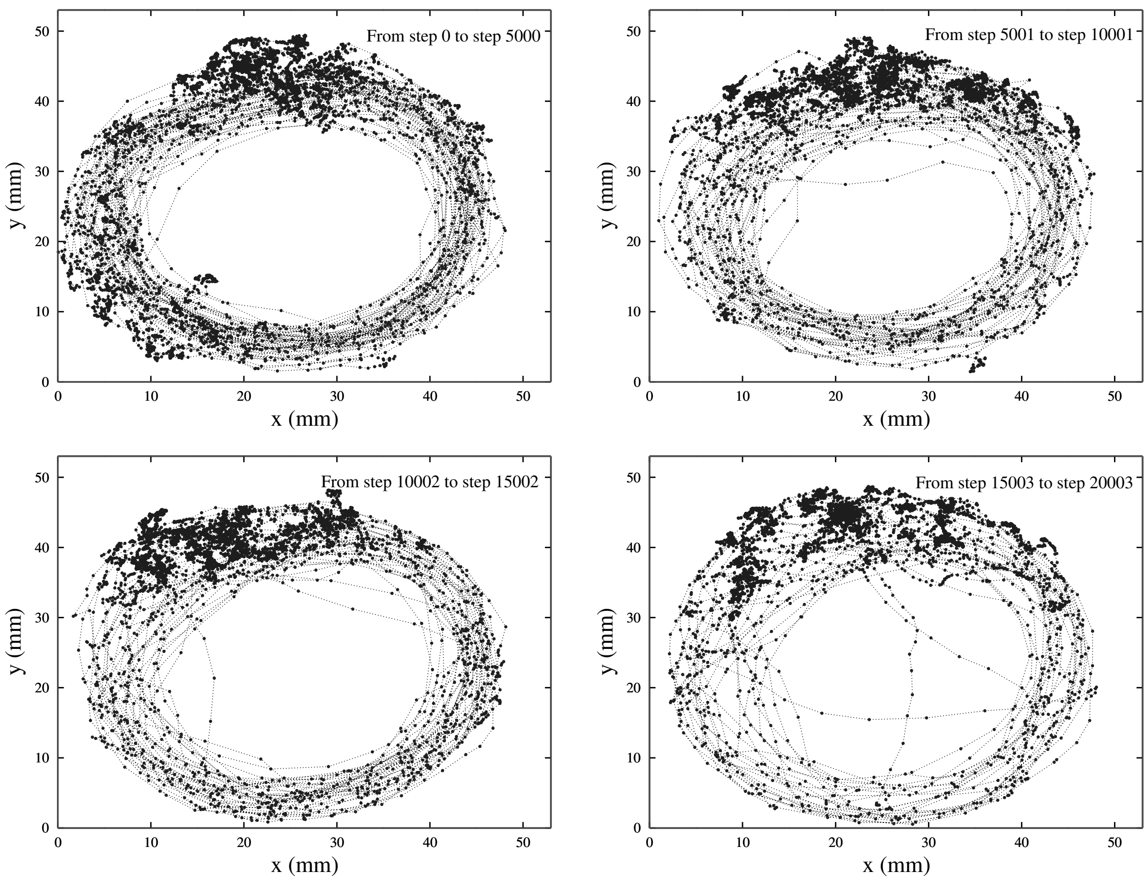
Group	Serie full name	Nest	Locality	Sampling date	Serie lenght	Density	Soldiers	Workers
S12	Cupim25FevManhaArena3	N02	Usina Alcool	2015-02-25	29494	0.09	5	1
S13	Cupim19MaManhaArena2	N04	Nobres-Porto Firme	2015-05-19	43155	0.08	0	10
S14	Cupim12MaNoiteArena2	N04	Nobres-Porto Firme	2015-05-12	30305	0.08	1	8
S15	Cupim19MaManhaArena3	N04	Nobres-Porto Firme	2015-05-19	24491	0.08	2	6
S16	Cupim19MaTardeArena2	N04	Nobres-Porto Firme	2015-05-19	43155	0.08	3	4
S17	Cupim19MaTardeArena1	N04	Nobres-Porto Firme	2015-05-19	21879	0.09	5	1
S18	Cupim02MarManhaArena3	N04	Universidade Federal de Viçosa	2015-03-02	27849	0.12	0	14
S19	Cupim02MarManhaArena1	N04	Universidade Federal de Viçosa	2015-03-02	33901	0.12	2	10
S20	Cupim12MaNoiteArena1	N04	Universidade Federal de Viçosa	2015-05-12	25651	0.12	3	8
S21	Cupim02SeptTardeArena3	N04	Universidade Federal de Viçosa	2014-09-02	22790	0.12	4	6
S22	Cupim02SetTardeArena1	N04	Universidade Federal de Viçosa	2014-09-02	29091	0.12	6	2
S23	Cupim02MarTardeArena3	N04	Universidade Federal de Viçosa	2015-03-02	20857	0.13	7	1
S24	Cupim22AgosTardeArena1	N01	Universidade Federal de Viçosa	2014-08-22	22217	0.12	3	8
S25	Cupim25JulTardeArena1	N01	Universidade Federal de Viçosa	2014-07-25	26461	0.12	5	4
S26	Cupim25JulTardeArena3	N01	Universidade Federal de Viçosa	2014-07-25	29667	0.13	7	1
S27	Cupim11MarManhaArena1	N03	Usina Alcool	2015-03-11	43155	0.12	0	14
S28	Cupim03MarTardeArena3	N03	Usina Alcool	2015-03-03	31586	0.12	2	10
S29	Cupim03MarTardeArena1	N03	Usina Alcool	2015-03-03	42384	0.12	3	8
S30	Cupim11MarTardeArena2	N03	Unsina Alcool	2015-03-11	21099	0.12	4	6
S31	Cupim11MarTardeArena1	N03	Usina Alcool	2015-03-11	23280	0.12	5	4
S32	Cupim11MarTardeArena3	N03	Usina Alcool	2015-03-11	21018	0.12	6	2
S33	Cupim11MarManhaArena3	N03	Usina Alcool	2015-03-11	20692	0.13	7	1
S34	Cupim08AbrTardeArena3	N04	Usina Reciclagem	2015-04-08	23913	0.12	0	14
S35	Cupim18MaNoiteArena2	N04	Usina Reciclagem	2015-05-18	34640	0.12	2	10
S36	Cupim30AbrManhaArena3	N04	Usina Reciclagem	2015-04-30	20435	0.12	4	6
S37	Cupim08AbrTardeArena1	N04	Usina Reciclagem	2015-04-08	23927	0.12	6	2
S38	Cupim31MarManhaArena4	N04	Usina Reciclagem	2015-03-31	22390	0.13	7	1

Group	Serie full name	Nest	Locality	Sampling date	Serie lenght	Density	Soldiers	Workers
S39	Cupim04MaManhaArena1	N02	Nobres-Porto Firme	2015-05-04	43155	0.12	0	14
S40	Cupim28AbrManhaArena3	N02	Nobres-Porto Firme	2015-04-28	28494	0.12	1	12
S41	Cupim22AbrTardeArena3	N02	Nobres-Porto Firme	2015-04-22	23367	0.12	2	10
S42	Cupim26MaTardeArena1	N02	Nobres-Porto Firme	2015-05-26	43155	0.12	3	8
S43	Cupim22AbrTardeArena2	N02	Nobres-Porto Firme	2015-04-22	23407	0.12	5	4
S44	Cupim26MaTardeArena2	N02	Nobres-Porto Firme	2015-05-26	22408	0.12	6	4
S45	Cupim30AgosTardeArena3	N03	Universidade Federal de Viçosa	2014-08-30	35095	0.20	1	22
S46	Cupim30AgosTardeArena2	N03	Universidade Federal de Viçosa	2014-08-30	25093	0.20	2	20
S47	Cupim10SeptTardeArena1	N03	Universidade Federal de Viçosa	2014-09-10	30930	0.20	4	16
S48	Cupim01SeptTardeArena1	N03	Universidade Federal de Viçosa	2014-09-01	26952	0.20	6	12
S49	Cupim01SeptTardeArena2	N03	Universidade Federal de Viçosa	2014-09-01	43154	0.20	7	10
S50	Cupim29MaNoiteArena1	N03	Universidade Federal de Viçosa	2015-05-29	35920	0.20	11	2
S51	Cupim18MarTardeArena1	N04	Usina Alcool	2015-03-18	43155	0.20	0	24
S52	Cupim17MarNoiteArena2	N04	Usina Alcool	2015-03-17	36057	0.20	4	16
S53	Cupim13MarTardeArena2	N04	Usina Alcool	2015-03-13	20841	0.20	5	4
S54	Cupim13MarTardeArena3	N04	Usina Alcool	2015-03-13	22038	0.20	6	12
S55	Cupim10AbrNoiteArena2	N04	Usina Alcool	2015-04-10	43155	0.20	7	10
S56	Cupim14MaiManhaArena1	N01	Usina Reciclagem	2015-05-14	25868	0.20	0	24
S57	Cupim30AbrNoiteArena3	N01	Usina Reciclagem	2015-04-30	43155	0.20	1	22
S58	Cupim14MaiNoiteArena3	N01	Usina Reciclagem	2015-05-14	43155	0.20	2	20
S59	Cupim14MaiNoiteArena2	N01	Usina Reciclagem	2015-05-14	43155	0.20	4	16
S60	Cupim31MarNoiteArena3	N01	Usina Reciclagem	2015-03-31	21441	0.20	5	14
S61	Cupim25MarTardeArena2	N01	Usina Reciclagem	2015-03-25	26415	0.20	6	12
S62	Cupim16AbrTardeArena1	N01	Usina Reciclagem	2015-04-16	43155	0.20	7	10
S63	Cupim30AbrNoiteArena1	N01	Usina Reciclagem	2015-04-30	38053	0.20	11	2
S64	Cupim06AbrTardeArena1	N01	Nobres-Porto Firme	2015-04-06	38729	0.20	0	24
S65	Cupim14AbrTardeArena2	N01	Nobres-Porto Firme	2015-04-14	25907	0.20	1	22

Group	Serie full name	Nest	Locality	Sampling date	Serie lenght	Density	Soldiers	Workers
S66	Cupim28AbrNoiteArena3	N01	Nobres-Porto Firme	2015-04-28	25774	0.20	2	20
S67	Cupim26MaNoiteArena1	N01	Nobres-Porto Firme	2015-05-26	24016	0.20	4	16
S68	Cupim28AbrNoiteArena1	N01	Nobres-Porto Firme	2015-04-28	20826	0.20	5	4
S69	Cupim26MaNoiteArena2	N01	Nobres-Porto Firme	2015-05-26	43155	0.20	6	12
S70	Cupim14AbrTardeArena1	N01	Nobres-Porto Firme	2015-04-14	36824	0.20	11	2
S71	Cupim19MaManhaArena1	N04	Nobres-Porto Firme	2015-05-19	17708	0.08	4	2
S72	Cupim10AbrTardeArena2	N03	Usina Alcool	2015-04-10	17120	0.12	1	12
S73	Cupim16AbrManhaArena2	N04	Usina Reciclagem	2015-04-16	18380	0.12	1	12
S74	Cupim18MaNoiteArena1	N04	Usina Reciclagem	2015-05-18	17076	0.12	5	4
S75	Cupim10AbrNoiteArena1	N04	Usina Alcool	2015-04-10	16937	0.20	11	2

Appendix B

Examples of trajectory plots of confined termite workers (*C. cumulans*) in the petri dish. The data series shown here were cut every 5000 steps to examine the quality of the data recordings.



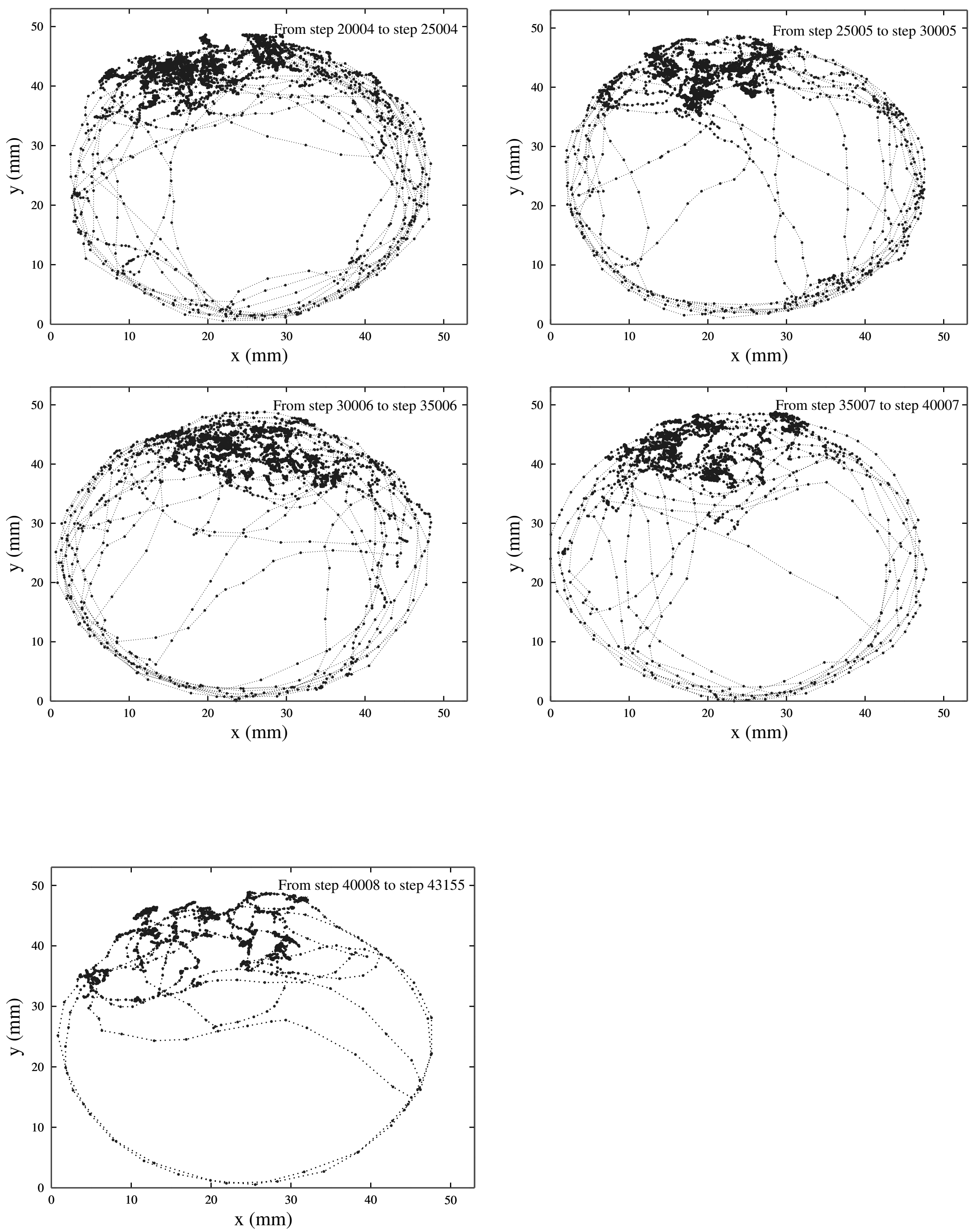


Figure 8: **Data serie S1 cut into segments of 5000 steps**. Each point on the curve represent the position of the focal worker in the petri dish.

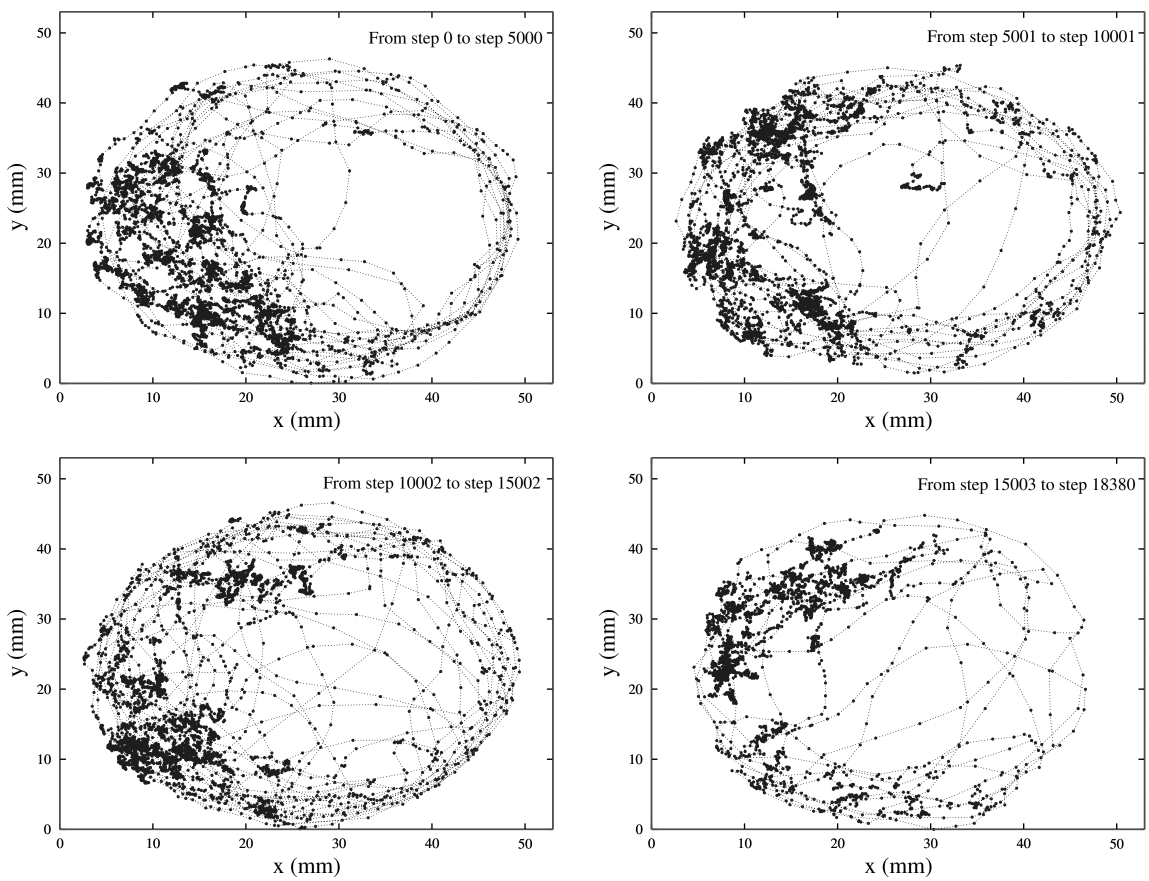
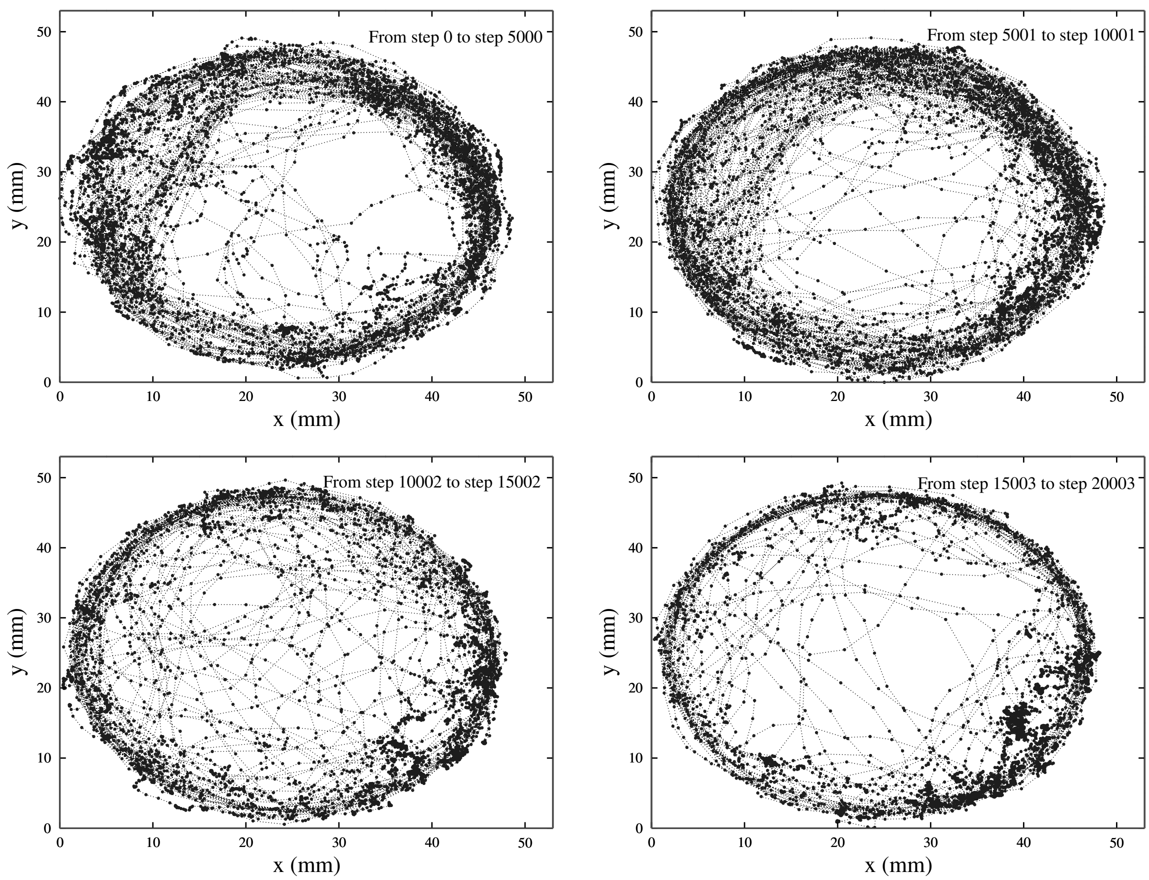


Figure 9: **Data serie S73 cut into segments of 5000 steps**. Each point on the curve represent the position of the focal worker in the petri dish.


From step 0 to step 5000
From step 5001 to step 10001
From step 10002 to step 15002
From step 15003 to step 20003
y (mm)
x (mm)
0
10
20
30
40
50

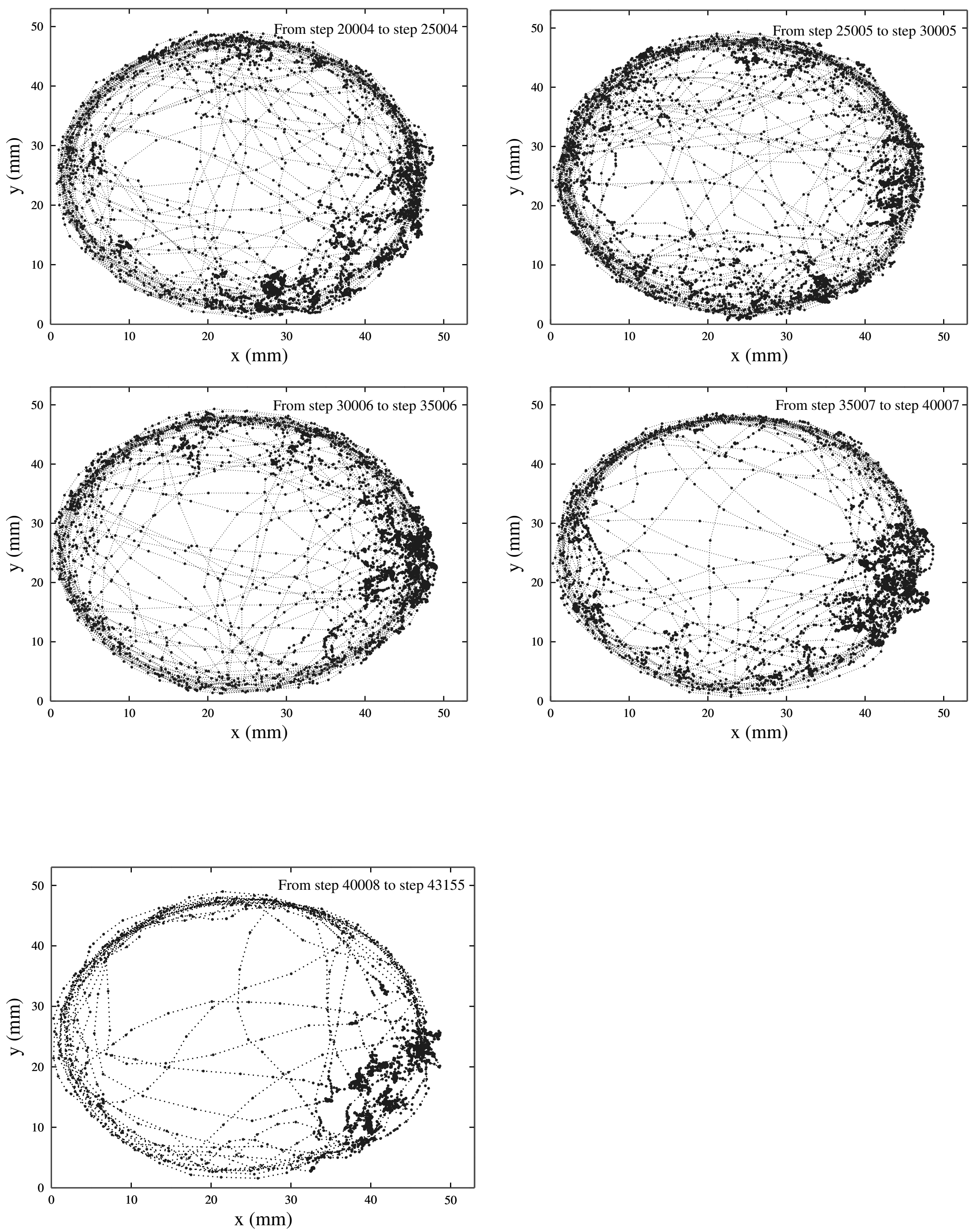


Figure 10: **Data serie S16 cut into segments of 5000 steps**. Each point on the curve represent the position of the focal worker in the petri dish.

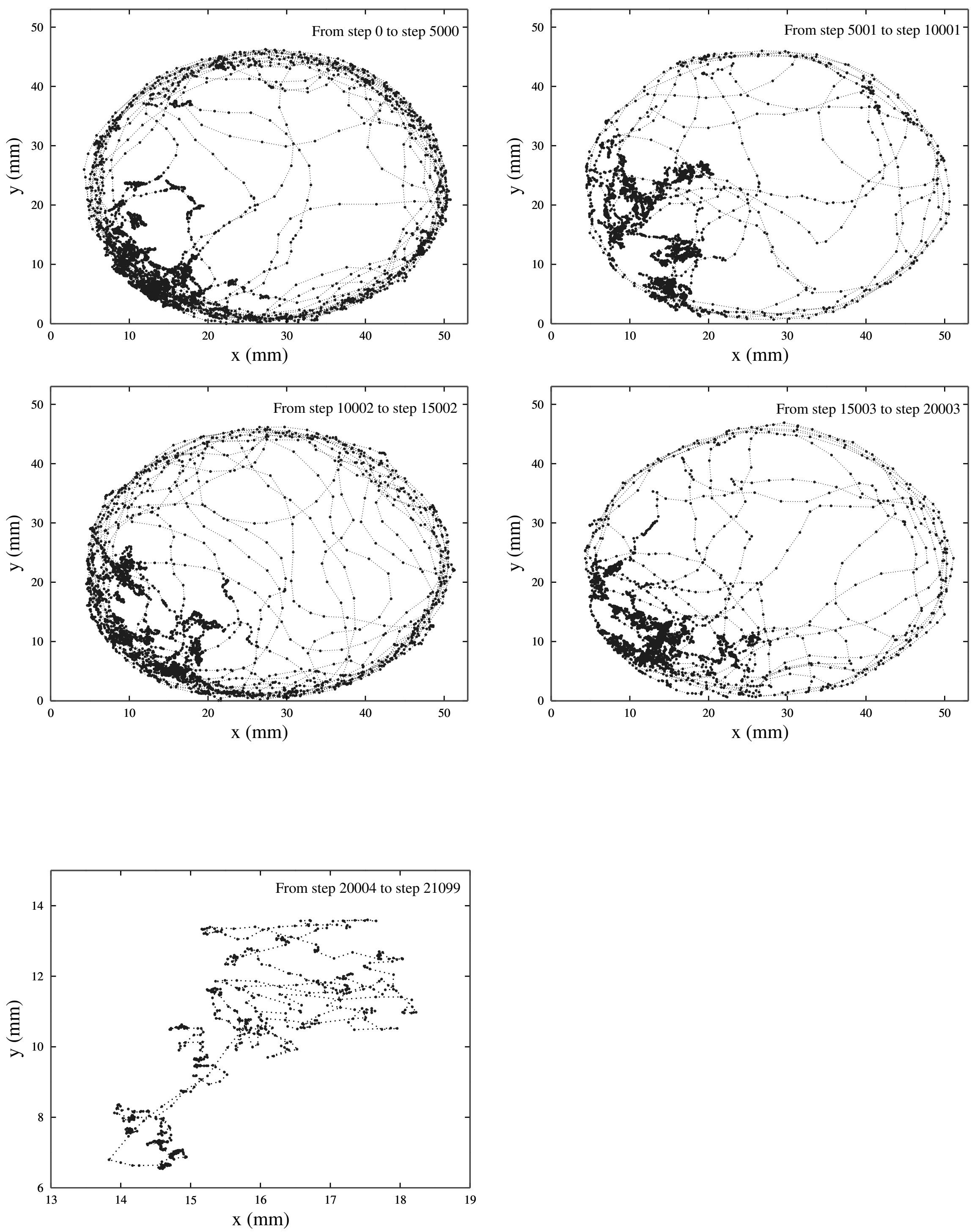


Figure 11: **Data serie S30 cut into segments of 5000 steps**. Each point on the curve represent the position of the focal worker in the petri dish.

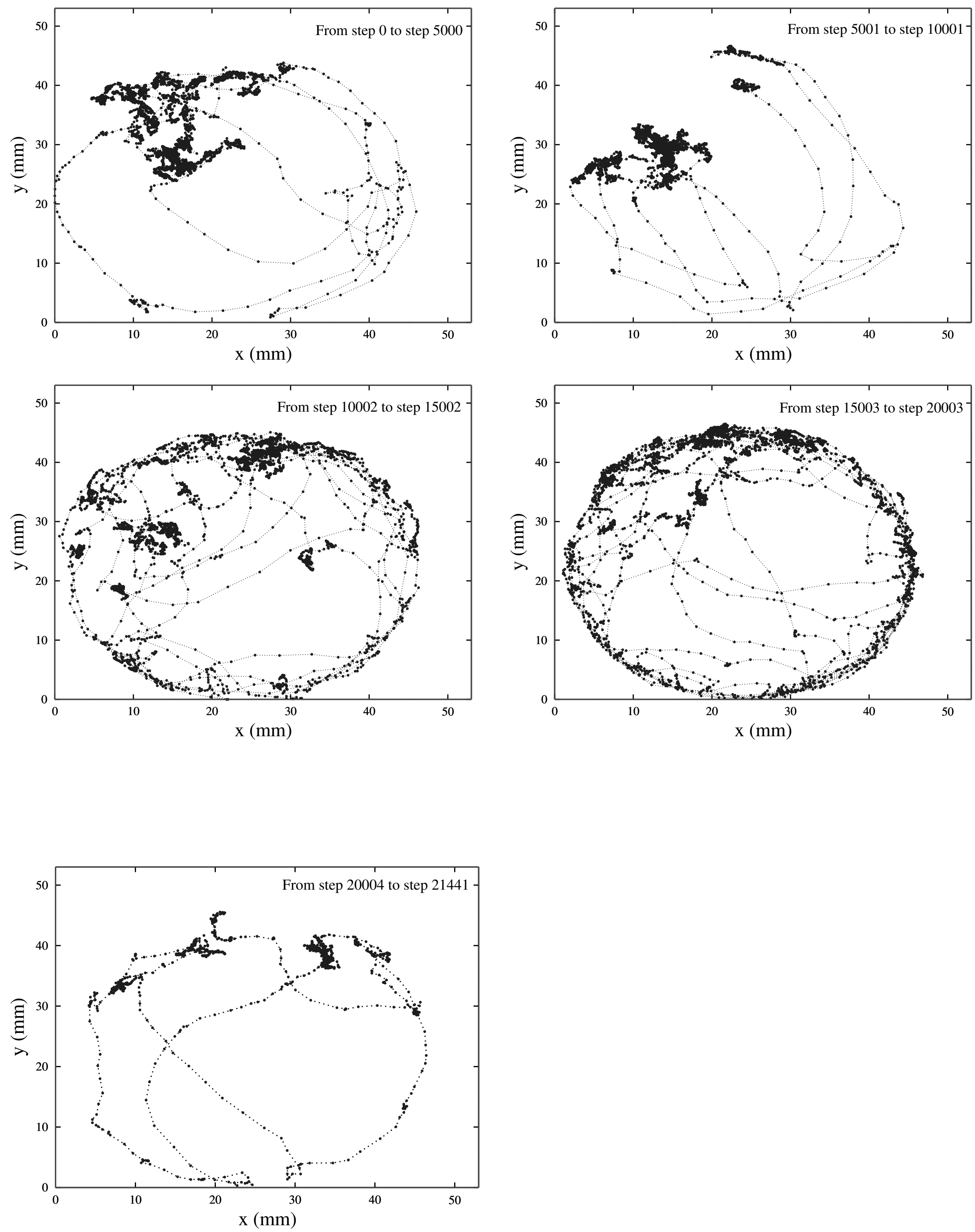


Figure 12: **Data serie S60 cut into segments of 5000 steps**. Each point on the curve represent the position of the focal worker in the petri dish.

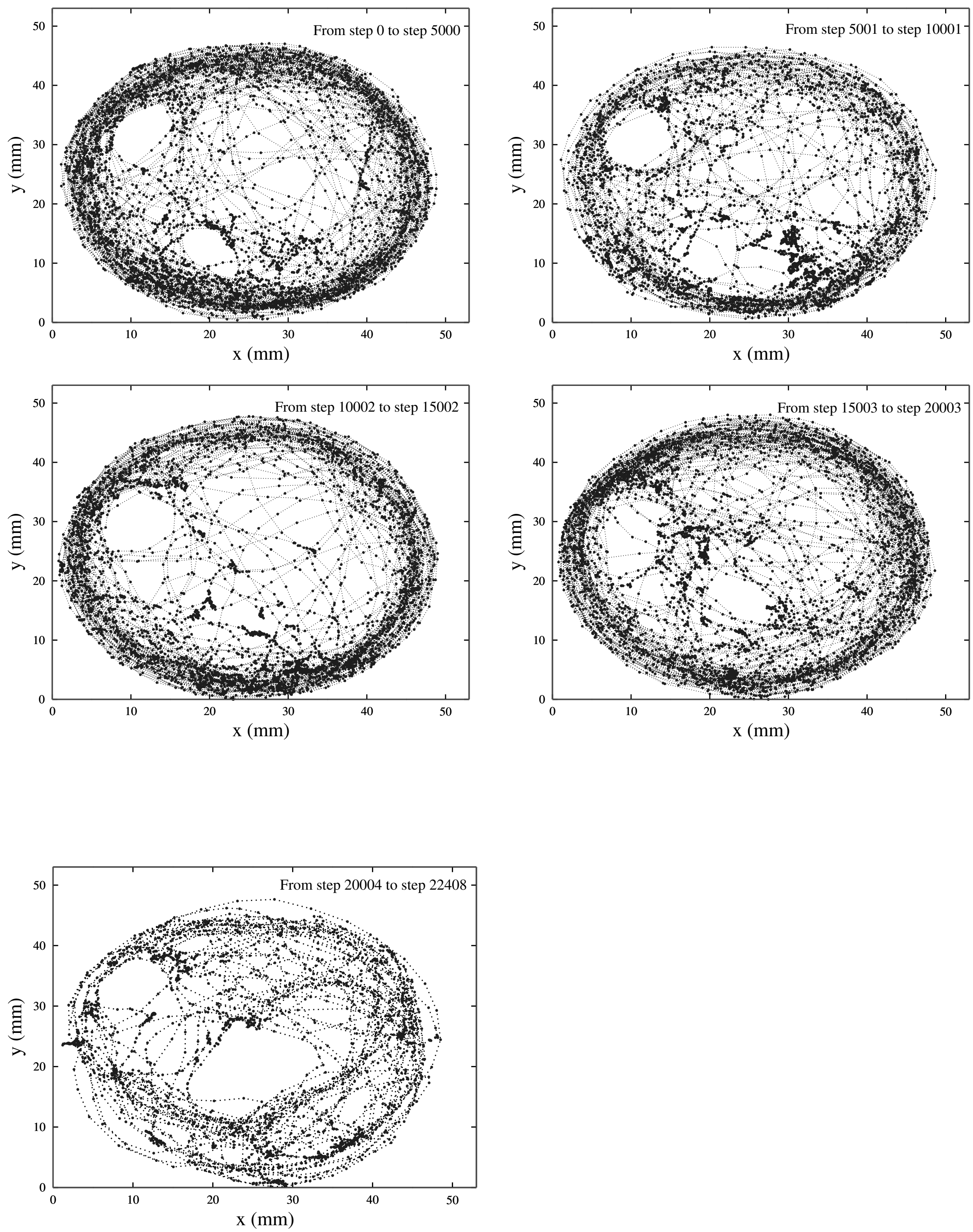
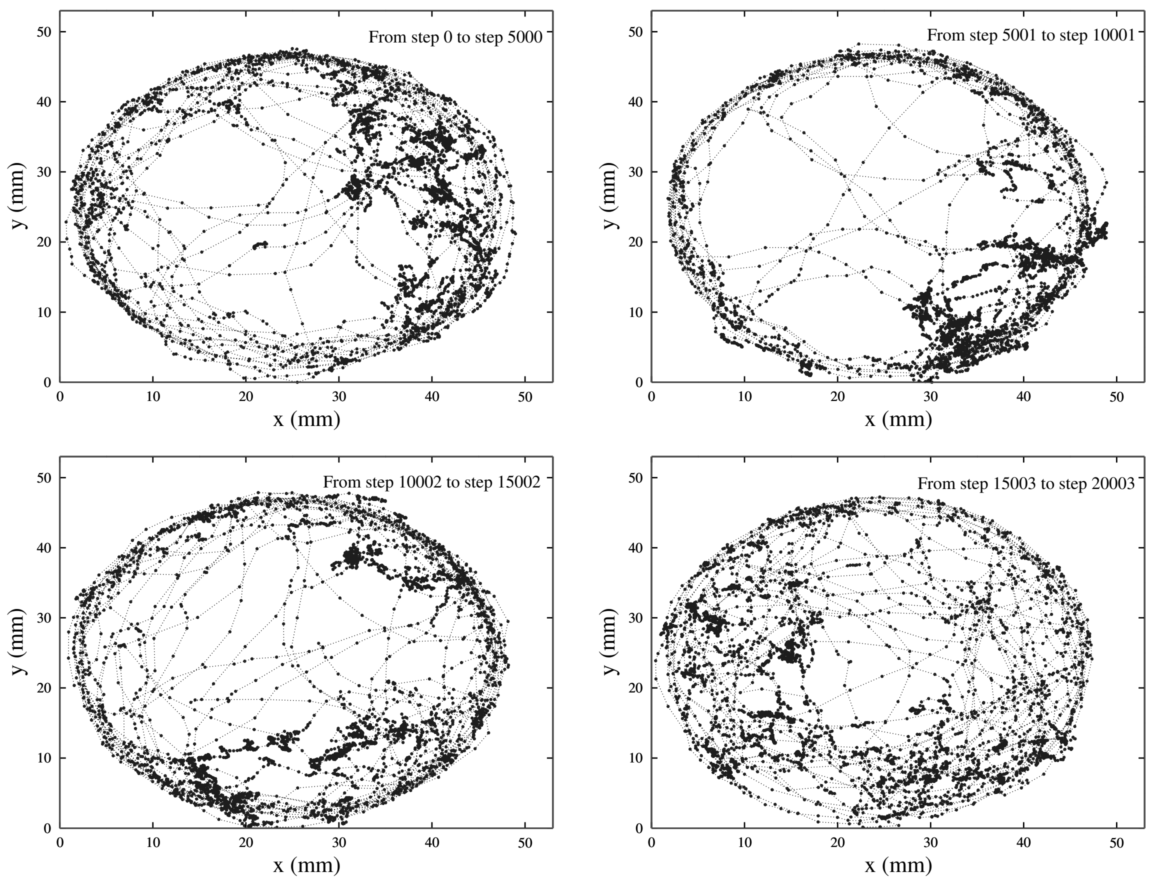


Figure 13: **Data serie S44 cut into segments of 5000 steps**. Each point on the curve represent the position of the focal worker in the petri dish.


From step 0 to step 5000
From step 5001 to step 10001
From step 10002 to step 15002
From step 15003 to step 20003
y (mm)
x (mm)

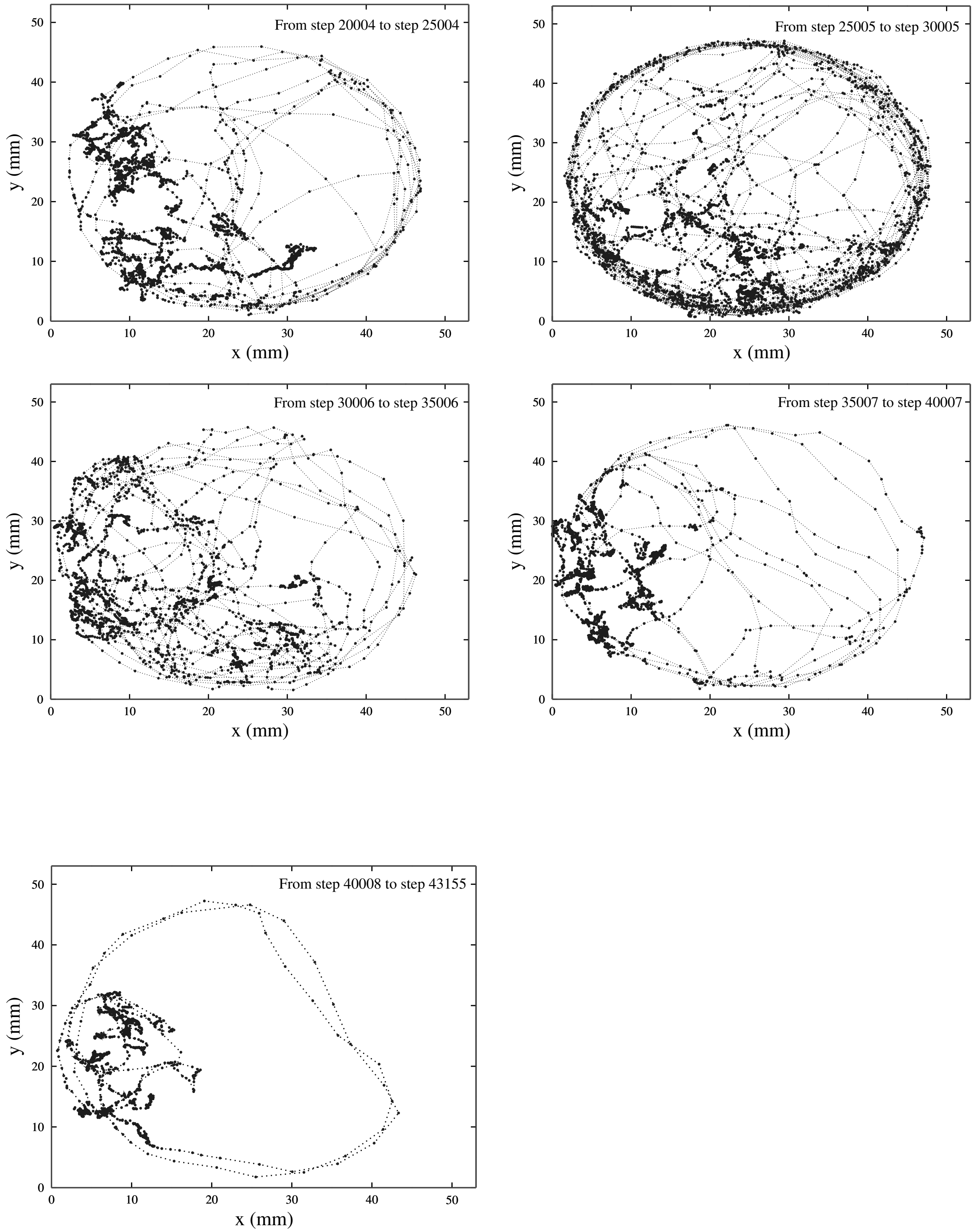
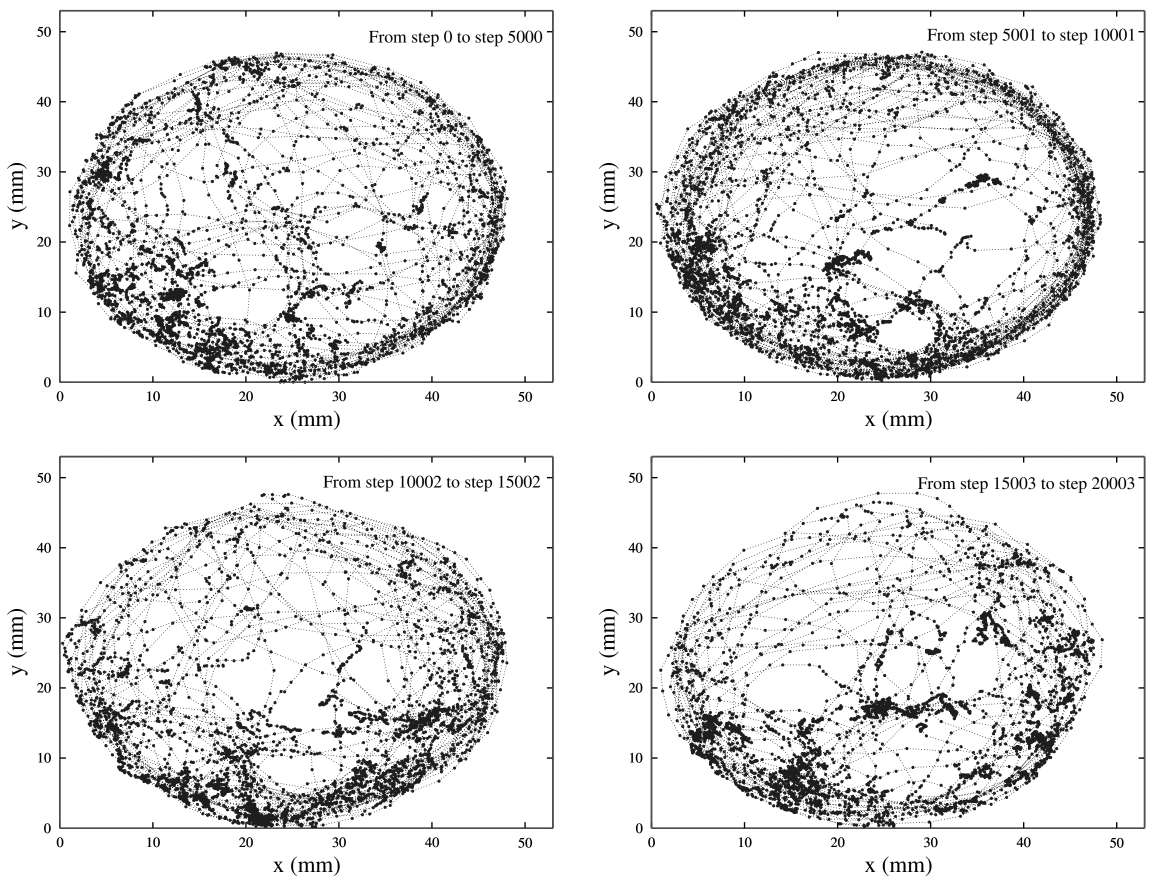


Figure 14: **Data serie S62 cut into segments of 5000 steps**. Each point on the curve represent the position of the focal worker in the petri dish.


From step 0 to step 5000
From step 5001 to step 10001
From step 10002 to step 15002
From step 15003 to step 20003
x (mm)
y (mm)
0
10
20
30
40
50

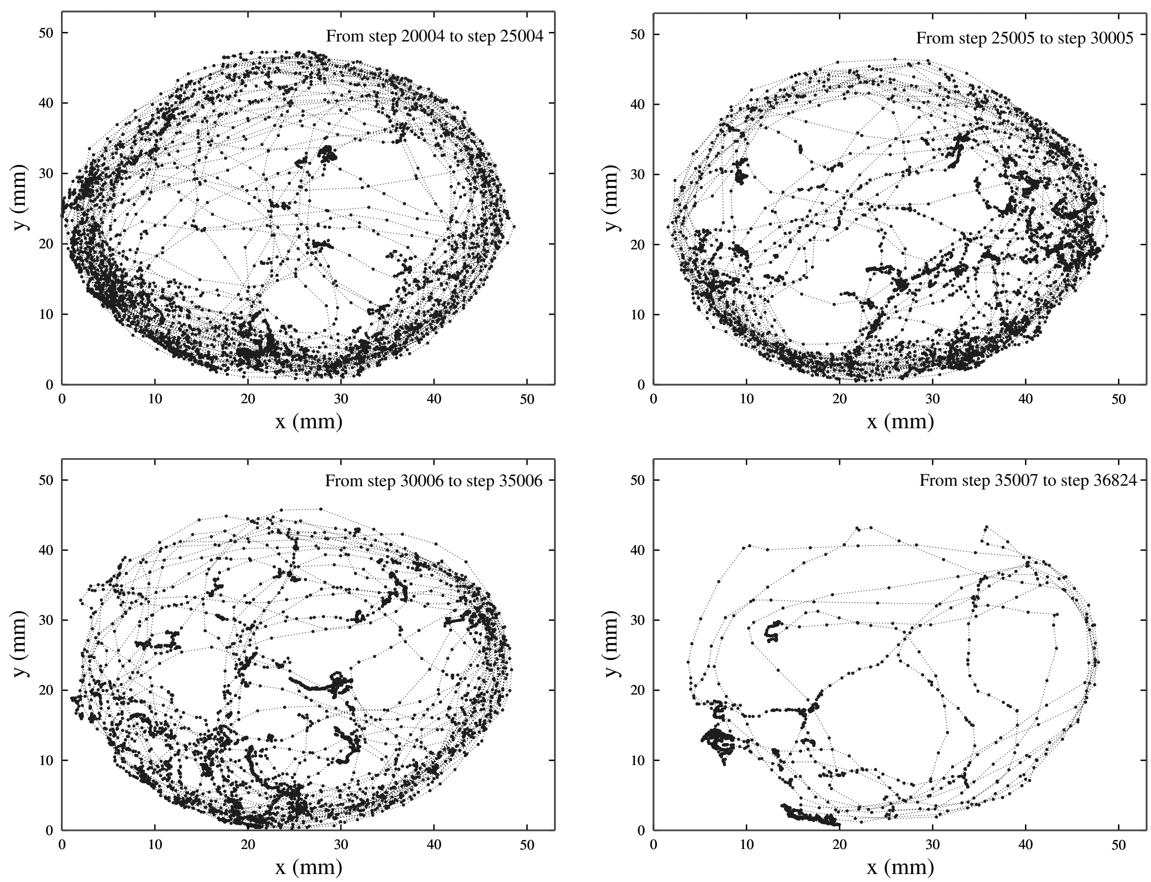


Figure 15: **Data serie S70 cut into segments of 5000 steps**. Each point on the curve represent the position of the focal worker in the petri dish.

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