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RESEARCH PAPER

Collective Migration in House Dust Mites

Anne-Catherine Mailleux*, Aina Astudillo Fernandez†, Gilles S. Martin*, Claire Detrain† & Jean-Louis Deneubourg†

* Unit of Ecology and Biogeography, Catholic University of Louvain, Louvain-la-Neuve, Belgium

† Service d'Ecologie Sociale, Université libre de Bruxelles, CP231, Brussels, Belgium

Correspondence

Anne-Catherine Mailleux, Unit of Ecology and Biogeography, Catholic University of Louvain, Croix du Sud 4-5 (Carnoy), 1348, Louvain-la-Neuve, Belgium.

E-mail: anne-catherine.mailleux@uclouvain.be

Abstract

House dust mites (*Dermatophagoides pteronyssinus*) are widespread in the furniture and mattresses of homes throughout Eurasia. Because human occupation induces wide diurnal fluctuations in temperature and relative humidity, the most favourable locations for mites change constantly and they must migrate repeatedly. Here, we triggered and studied mites migration movements to a new area. Mites migrated from a starting arena to a second arena through a diamond-shaped corridor offering a choice between two branches of equal length. In this article, we show that local air dryness and a distant water source were both necessary to trigger collective migration. Males and nymphs had a higher probability of migration than larvae and females. When migrating, although both branches initially appeared to be chosen equally, most mites eventually ended up choosing one particular branch. When about 50 or more mites had passed, there was an obvious choice of branch. We used a modelling approach to show that these data support the hypothesis that mites lay an attractive trail that is reinforced by followers. Consequently, the consistency of the collective choice is higher as the number of migrants grows. This article is the first to observe dust mite migration as a collective phenomenon.

Introduction

Collective migrations occur in a wide range of taxa throughout the animal kingdom. Among the most studied examples are the social insects, such as ants during foraging (Hölldobler & Wilson 1990), fish (Sumpter 2009), birds (Bajec & Heppner 2009) and other vertebrates (Couzin & Krauze 2003). Collective migration is also observable in groups with a simpler social structure, such as earthworms (Zirbes et al. 2010). Animals migrate during their nomadic phase (Gotwald 1995), when they search for a new suitable shelter (Hölldobler & Wilson 1990; Mallon et al. 2001), when their resting place become overcrowded (Seeley & Buhrman 1999; Visscher & Camazine 1999) and during swarming (Seeley & Buhrman 1999; Visscher & Camazine 1999; Seeley & Visscher 2004).

One crucial question is how individuals in the group move as an integrated social unit (Dyer 2000). The mechanisms underlying collective migration have been poorly studied. It is sometimes thought that collective migration is organized by a sophisticated system of communication among individuals belonging to highly organized societies such as ants and termites (Hölldobler & Wilson 1990). By contrast, previous studies have shown that collective migration does not necessary rely on a complex organization (Deneubourg & Goss 1989; Bonabeau et al. 1997) and can simply be achieved through amplification processes that result from simple interactions between individuals (Bonabeau et al. 1997; Camazine et al. 2001; Deneubourg & Goss 1989; Jeanson et al. 2004). Migrating individuals can start a coordinated migration by following simple rules that induce positive feedback loops. These rules

are similar for subsocial or eusocial species and may lead to similarities in their patterns of migration (Buhl et al. 2006; Costa 2006) regardless of their degree of social organization. An example of an amplification process leading to coordinated migration is *Anelosimus eximius*, a social spider that produces silk threads that is followed by nestmates during displacement (Furey 1998). This silk-laying behaviour leads to the formation of silk 'highways' that ensure group cohesion as well as collective decision-making processes during swarming (Lubin & Robinson 1982; Avilès & Tufino 1998; Saffre et al. 1999a,b; Mailleux et al. 2008). Other examples of collective migration based on silk following can be found in species with a simpler social organization such as caterpillars (Fitzgerald 1995) and solitary spiders (Jeanson et al. 2004). The underlying dynamics could easily be compared with those involved in collective nest moving in ants (Hölldobler & Wilson 1990; Verhaeghe et al. 1992; Morgan 2008), which are based on, among other things, a trail pheromone-following behaviour. Indeed, in the same way as silk is used by spiders, spider mites (Yano 2008) and caterpillars, trail pheromones might lead to amplification processes and collective decisions, as shown in ants and other subsocial species such as lepidopteran larvae (Roessingh 1990; Fitzgerald 2003).

Here, we focused on the group of migration of *Dermatophagoides pteronyssinus* (Trouessart 1897), a house dust mite species distributed throughout Eurasia that causes allergic symptoms (for a review on house dust mites, see Colloff 2009). Despite their medical and economic importance, the migratory behaviour of this species has been poorly studied (Crowther et al. 2001). This mite feeds on human skin scale and is found in the locations where this scale collects, such as in bedding, carpets and padded furniture (Murray et al. 1985). The dust mite is not limited by food supply: we shed dead skin at a daily rate of about 1.0 g per person, a sufficient amount for several thousand mites to survive on for months (Crowther et al. 2000). Considering its size, it is no more limited by space: a mattress offers a considerable volume of space to populations of mites. (Crowther et al. 2000, 2001; Colloff 2009); therefore, the biological traits of house dust mite populations are unusual in that they are relatively free of the normal constraints of food supply, space and predators.

The dust mite population size is mainly influenced by the physical factors of temperature and humidity, which are known to affect both reproduction and development rates (Arlian 1992; Crowther et al. 2001). In mattresses, humidity and temperature show large daily variations related to human occupation (Arlian 1992; Crowther et al. 2001). Consequently, the most favourable locations for mites constantly shift. Previous articles suggest that mites move away from dry conditions up a humidity gradient (Crowther et al. 2000, 2001). At bedtime, dust mites migrate towards humans to absorb water from breathing and perspiration before taking refuge and aggregating in the depth of the mattress when humans get up in the morning. There is evidence for the migration of mites between microhabitats within the home (Mollet & Robinson 1995; Mollet 1996) but nothing is known about migrating dust mite populations (Colloff 2009) that have been poorly studied, although migration must be a crucial phase for the survival of dust mites (Glass et al. 1998).

In this study, we triggered migration movements to investigate the behavioural mechanisms involved when these arthropods migrate to a new area. In the first part of this study, we studied the migration of mites to four different hygrometric conditions. The stage, sex and speed of migrating and non-migrating individuals were analysed. In the second part of this study, we analysed and quantified dust mite social behaviour, leading to group cohesion in experimentally induced migrations. In our article, we called social behaviour any behaviour that results from an interaction between individuals, which is the opposite to non-social behaviour, which results from an interaction between an individual and its environment (Sokolowski 2010). Theoretical approaches were used to analyse our data.

Materials and Methods

Experimental Set-Up

Mites were reared in Petri dishes and fed with human skin flakes (skin and whiskers obtained by cleaning electric shavers) and fish food (Tetra Goldfish crips). All mites were reared together under similar conditions (20°C and 75% relative humidity). The experiments took place in a room kept at 20°C and 40% relative humidity.

The experimental set-up consisted of a starting arena connected to a second arena (called the arrival arena) by two corridors (Fig. 1). The floor and roof were made of glass; the middle layer was made of Plexiglas. This set-up offered an opportunity for mites to move along two branches of equal length (4 cm). We compared the migration dynamics of the mites with (W) and without (D) a water source
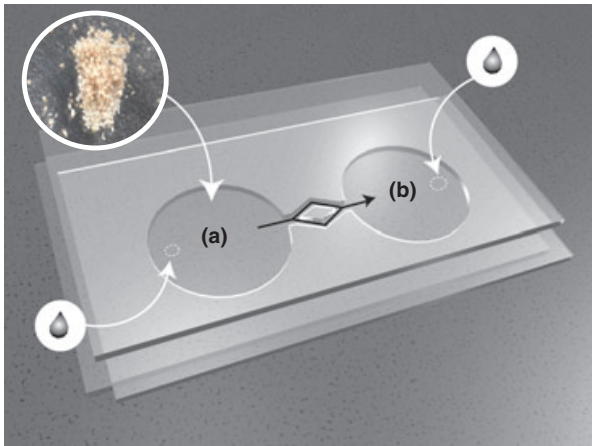
Fig. 1: The experimental set-up consisted of an initial arena A connected to a second arena B by two corridors (diameter of the arenas = 8 cm, figure 1). The floor and roof were in glass, the middle layer was in Plexiglas. This set-up offered the opportunity for mites to move along two branches of equal length (4 cm). We compared the migration dynamics of the mites (see the photo of an initial group of aggregated mites) with or without a water source (a small dish containing 0.3 ml of water, represented by droplet) placed in the starting arena and/or in the arrival arena.

(a small dish containing 0.3 ml of water) placed in the starting arena and/or in the arrival arena. Therefore, the behaviour of dust mites was tested under four hygrometric conditions: (1) starting arena D (Dry arena) to the arrival arena W (arena with a source of Water), (2) W → D, (3) D → D, and (4) W → W. We placed a group of mites in the starting arena at the beginning of each experiment. These mites either migrated to the arrival arena or they did not. Traffic on the two branches (number of individuals) was recorded by a video camera (×10) for 2 h. From this video recording, we identified the sex and stage of development and we also measured the walking speed of individuals. After each experiment, the sex (male, female) and stage (nymph, larvae) were identified using the following procedure. Migrant and non-migrant mites were placed in separate Petri dishes containing ethanol 95% for 1 wk. Afterwards, they were dried for 1 d and placed in lactic acid for 1 wk (Colloff 2009). Then, the mites were extracted under a stereo binocular microscope. This method accentuated the chitin structure of mites and facilitated the identification of the development stage and sex of the mites. The experimental situation was tested ten times for every situation (except with D → W, which was tested 12 times, but the composition of the two supplementary observations was not studied). The starting groups of mites

were composed of 302, 243–338 individuals (median, first and third quartile) and were similar for the four hygrometric conditions (N total = 11 761, Kruskal–Wallis test, KW = 5.47, p = 0.14).

The local surroundings of the set-up were homogenous to prevent any cues such as lights or temperature affecting the movement. The experimental set-ups were cleaned (with hexane, then ethanol) and carefully rinsed after each migration.

Statistical Analysis

The effect of environmental conditions and development stage/sex on the proportion of migrating individuals
Concerning the first part of this study (the analysis of the migration of mites under four different hygrometric conditions): Some experimental data (number of migrants) were analysed using GraphPad Instat version 3.05 for Win95/NT (GraphPad Software 1998, Inc., San Diego, CA, USA). As the numbers of migrants were not normally distributed, we used nonparametric statistical tests (Kruskal–Wallis). The other experimental data (proportions of migrants, proportions of developmental stages and sexes, and walking speeds) were analysed with generalized linear mixed modelling (generalized linear model – GLM).

First, we used GLM with a binomial distribution to estimate how migration was influenced by the hygrometric treatments in the starting and arrival arenas while taking into account the sex and development stage. We used the proportions of migrating individuals in each stage and sex category as the dependent variables. Three fixed effect explanatory variables were included in the model: starting arena treatment (Wet or Dry), arrival arena treatment (Wet or Dry) and the development stage (Male, Female, Larva, Nymph). Second and third level interactions were also included in the model. The experiment number was used as a random variable to consider the non-independence of the migration values for the four stages within each experiment. We used type II (Fox 2002) likelihood ratio tests (LRT) to test the significance of each explanatory variable. We respected the marginality rules, as models without one main effect are compared with the full model without the higher level interactions containing this main effect.

Second, we used a similar approach to estimate the differences of speed between sexes and developmental stages. The dependent variable was the mite speed expressed in micrometers/second and we used a linear mixed model with normal error distribution. The fixed and random explanatory variables were the same as the binomial model. The analysis was

performed in the language R (R Development Core Team 2009) with the package lme4 (Bates & Sarkar 2008).

The collective choice of a path

Concerning the second part of this study (analysis of the mechanisms leading to group cohesion), Monte Carlo simulations and tests used to compare them with the experimental data were coded with Matlab. The expected choice dynamics were calculated for the two situations. In the first one, we tested the hypothesis that mites choose their path at random (binomial situation). In the second one, we tested the hypothesis that mites influence each other choices (trail model situation). Monte Carlo simulations used in the calculations for both situations were essentially the same and only differed in their probabilities p_L and p_R of choosing respectively the left and the right branch. In the case of the binomial choice, they were taken to be equal to 0.5, in the trail model they were given in Eq. (1).

One simulation consisted of 12 experiments *in silico*. We took into account only the first 82 mites, as at least 82 individuals migrated in the 12 experiments observed *in vivo*. For each virtual experiment, 82 mites were successively given the choice between two branches: the comparison between a randomly generated number and the probabilities p_L and p_R determined the choice of each mite. After each passing mite, the percentage of mites that had chosen the winner branch was counted. The branch walked by most mites (>50%) will hereafter called the winner branch. The average of the 12 virtual experiments was calculated. Computing this simulation 10 000 times allowed us to establish the most likely choice dynamics (average of the 10 000 simulations) as well as the confidence interval (95%) around it.

Results

Effects of Hygrometric Conditions and Developmental Stage/Sex on the Proportion of Migrating Individuals

The likelihood ratio tests are shown in Table 1. The random component of the experiment was 0.66 for a residual variance taken to be 1. The model was slightly overdispersed (overdispersion parameter based on Pearson residuals = 4.3). However, we considered that this deviation from the binomial model was negligible relative to the very low p-values obtained with the likelihood ratio tests (Table 1). These tests showed that the third level interaction

Table 1: Likelihood ratio tests (Type II, Fox 2002) for the proportion of migrating individual model. This model is a binomial mixed model of the proportion of migrating individuals (dependent variable) vs. hygrometric treatment in the starting arena, hygrometric treatment in the arrival arena and the stage. The experiment is used as random variable

	Likelihood ratio	df	p
Stage	303.816381	3	0.0000
Starting	34.043682	1	0.0000
Arrival	18.162306	1	0.0000
Stage: starting	3.803532	3	0.2835
Stage: arrival	2.037230	3	0.5647
Starting: arrival	3.676385	1	0.0000
Stage: starting: arrival	31.414925	3	0.0000

was highly significant (LRT = 31.41, df = 3, p < 0.0001). We then concluded that the treatment in the starting arena had an effect on the proportion of migrating individuals, and that the effect of this treatment depended on the treatment in the arrival arena (or *vice versa*), and that this synergistic effect (second level interaction) is different between sexes and developmental stages (third level interaction).

Effects of hygrometric conditions on the proportion of migrating individuals

Dry conditions in the starting arena and wet conditions in the arrival arena seemed to enhance migration. The probability of leaving the starting arena (estimated by the model) was 0.175 with the 'wet' treatment and only 0.023 with the 'dry' treatment after controlling for sex, developmental stage and arrival treatment. The probability of migrating was 0.036 for a dry treatment in the arrival arena and 0.119 for a wet treatment in the arrival arena, independently of all other effects. However, the probability of migrating for a given starting treatment strongly depended on the arrival treatment (second level interaction – Fig. 2a). For a dry starting treatment, the probability of migrating was 0.367 – independently of the sex and stage – if the arrival arena received a wet treatment, while it was only 0.071 for a dry treatment in the arrival arena. For wet conditions in the starting arena, the probability of leaving was low for both treatments in the arrival arena (wet: 0.031; dry: 0.018).

Effects of stage and sex on the proportion of migrating individuals

There were clear-cut differences in the proportion of migrating individuals between sexes and stages,

Fig. 2: Probability estimates (with SE) derived from a mixed GLM with binomial distribution for the proportion of migrating individuals (dependent variable) with as explanatory variables a) the combination of hygrometric treatments in the starting and arrival arenas after controlling for sex and stage b) the different stages and sexes after controlling for hygrometric treatments in the starting and arrival arenas.
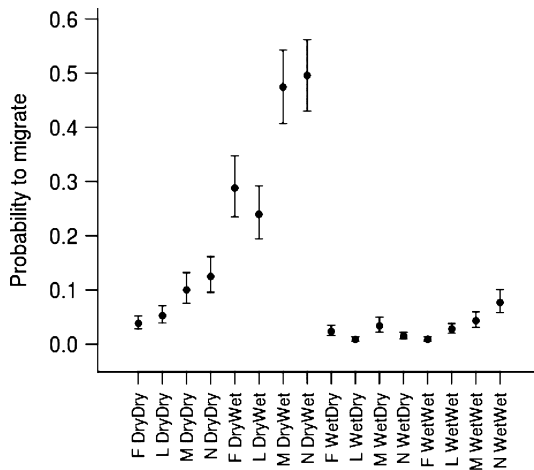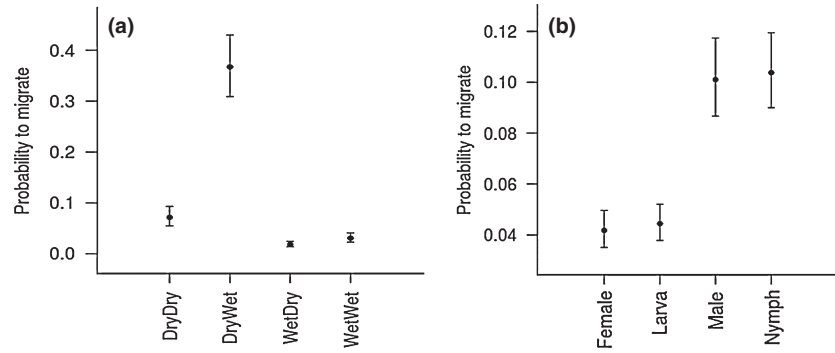

Fig. 3: Probability estimates (with SE) derived from a mixed GLM with binomial distribution for the proportion of migrating individuals (dependent variable) with as explanatory variables the stage (F for female, L for larva, M for male and N for nymph), the hygrometric treatment in the starting arena (wet or dry) and the hygrometric treatment in the arrival arena (wet or dry).
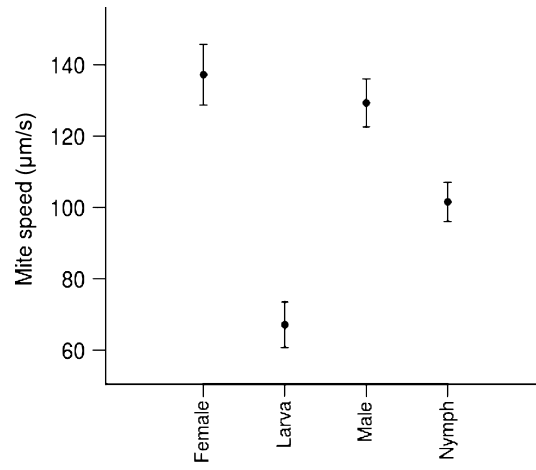

Fig. 4: Mite speed estimates (with SE) derived from a mixed GLM with normal distribution with as explanatory variables the different stages and sexes after controlling for hygrometric treatments in the starting and arrival arenas.

independently of the hygrometric conditions (Fig. 3): The males and nymphs had a much higher probability (0.101–0.104, respectively) to migrate than the females and larvae (0.042–0.044, respectively).

However, these differences between sexes and stages were stronger in some hygrometric conditions (third level interaction – Fig. 4). For a 'wet to dry treatment', the differences between stages and sexes were very low, all probability values being close to 0. In 'dry to dry' and 'wet to wet' conditions, the males and nymphs migrated just slightly more than the females and larvae. In 'dry to wet' conditions, although females and larvae were more prone to migrate than in the other conditions, a stronger migration was observed for the males and nymphs.

Effects of stages and sex on migration speed

The likelihood ratio test results are given in Table 2. According to these tests, the models including interactions were not significantly better than the models without interactions. There were clear differences between developmental stages (LRT = 220.7, df = 3, p < 0.0001) and there was also an influence of the arrival arena treatment (LRT = 12.3, df = 1, p = 0.0004). After controlling for the hygrometric treatments, the males and females had similar speed estimates (129.4 and 137.3 μm/s, respectively – Fig. 4). The larvae moved themselves at quite lower (67.1 μm/s) and the nymphs showed intermediate speed values (101.6 μm/s).

The Collective Choice of a Path

A central question in this study was how dust mites chose their path and what influences their collective

	Likelihood ratio	df	p
Stage	220.6698050	3	0.0000
Starting	2.1962857	1	0.1383
Arrival	12.3380118	1	0.0004
Stage: starting	0.5294007	3	0.9124
Stage: arrival	4.7205838	3	0.1934
Starting: arrival	1.4705195	1	0.2253
Stage: starting: arrival	2.8362549	3	0.4176

choice. For this question, we focused on the twelve experiments of condition D>W that triggered the highest number of migrants. In these experiments, the mites faced a choice between two identical options (the two branches of the diamond-shaped set-up). If the mites had chosen at random, with an equal probability of taking the right or left branch, independently from each other, the expected number of mites on either side would have presented a binomial distribution. However, the binomial tests (Fig. 5) showed that the experimental results clearly differed from a binomial distribution in 9 cases out of 12: one of the branches was clearly preferentially selected by the mites.

This asymmetric distribution between the two presumably identical branches could have resulted from one of two possible deviations from the binomial situation. Either the branches were not identical (the probabilities of taking either side were different), or the mites did not choose independently from each

other. The former possibility could be ruled out because the mites did not show a preference for one of the branches: overall the left and the right branch were taken at comparable frequencies (1007 and 1082 times, respectively).

The remaining possibility was that the mites influenced each others' choices. The question then became one of *how* they influenced one another. A first clue was found in the dynamics of the choice. By the dynamics of the choice, we meant how the average proportion of mites on the winner branch varied with time or, more precisely, with the number of mites that have already migrated towards the arrival arena. This average proportion was only calculated for the first 82 mites that was the minimal number of mites observed in all the experiments. At first, the mites seemed to choose indiscriminately between the two sides. For that matter, the choice dynamics of the first 82 or so mites did not differ from what would have been expected in a binomial situation (Fig. 6a). The selection of a branch came progressively and was amplified as more mites migrated to the arrival arena. This amplification suggested a mechanism analogous to trail laying/trail following in ants. Mites would leave an attractive trail as they passed through a branch. The probability of taking that branch for the following mites would increase, thereby reinforcing the trail and launching a positive feedback loop that would result in an asymmetrical distribution.

To test this hypothesis, we formulated a model derived from a choice function previously used to explain trail formation in ants (Deneubourg et al.
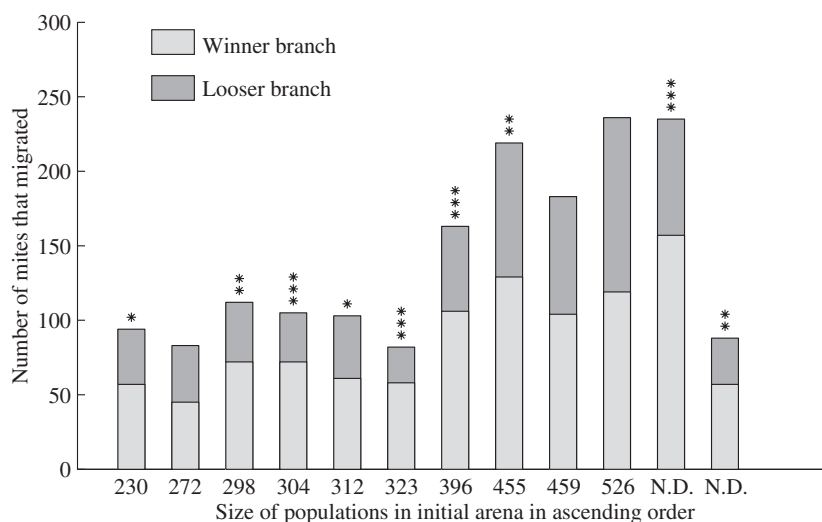

Fig. 5: Results of the binomial tests for the 12 experiments ordered by the size of the initial populations (x axis). The height of the bars represents the total number of mites that migrated. The dark and light greys represent the fraction that chose the loser and the winner branch, respectively. Nine experiments out of twelve significantly differed from the binomial distribution. (*: P < 0.05, **: P < 0.01, ***: P < 0.001).
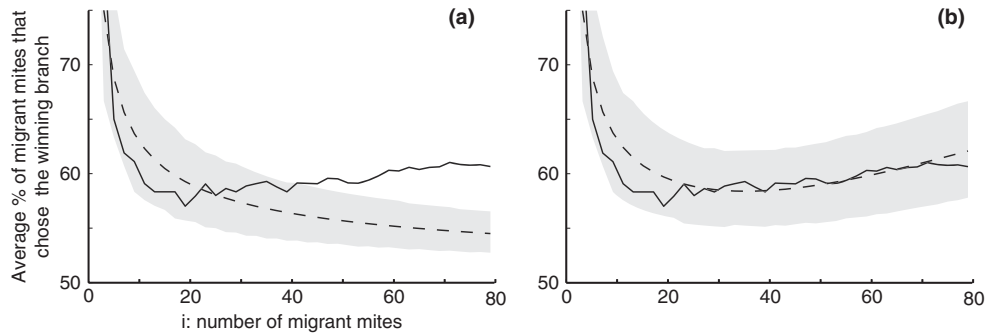
Fig. 6: Experimental vs. expected results under the null hypothesis of a) the binomial model and b) the trail model. The expected means of 12 experiments (dashed line), surrounded by its 95% confidence interval (grey area), were calculated with Monte Carlo simulations (N = 105). The experimental data (solid line) can be predicted by the trail model, but not by the binomial model.

1990). According to our model, each individual chooses the left or the right branch with the following probabilities:

$$\mathrm{p}_L = \frac{\kappa^\varepsilon + L^\varepsilon}{2\kappa^\varepsilon + L^\varepsilon + R^\varepsilon} \quad \text{and} \quad \mathrm{p}_R = \frac{\kappa^\varepsilon + R^\varepsilon}{2\kappa^\varepsilon + L^\varepsilon + R^\varepsilon}, \quad (1)$$

where L and R are the numbers of preceding mites that chose the left and right branches, respectively. Parameter κ represented the inherent attractiveness of the branches, independently of any trail. The exponent ε was the degree of nonlinearity of the response.

The choice dynamics predicted by this model greatly depended on the values of κ and ε. For very large values of κ, the influence of the trail on each branch (L^ε and R^ε) was negligible, so the probability of choosing either branch was approx. 0.5, and the dynamics approximated the dynamics expected in a binomial situation. The exponent ε has a decisive effect on the dynamics of the choice. If $\varepsilon = 1$, there is no amplification process and the distribution between left and right becomes more symmetrical as more mites pass. However, if $\varepsilon > 1$, the positive feedback is such that the asymmetry is amplified with each passing mite, and results in the selection of one of the branches.

We calculated the expected choice dynamics under the assumptions of our model with Monte Carlo simulations (explained in detail in Appendix A). We tested values of κ ranging from 0 to 200 and ε from 1 to 4. We found that our model's predictions fit the experimental results very closely (Fig. 6b). The best correspondence was found for $\kappa = 26$ and $\varepsilon = 2.8$. To evaluate the agreement between our experiments and our predictions, we calculated the average number of mites on the winner branch as a function of the number of passing mites, both for the experiments and for the simulations. We checked for a linear correlation between the experimental and the theoretical results. We found the highest correlation coefficient ($R^2 = 0.9994$) for the parameter set in Fig. 6. The slope was not different from one [$s = 0.9994$ (0.994, 1.005)] and the y intercept was not different from zero [$y_0 = -0.03463$ (−0.1881, 0.1188)].

Discussion

Dust mite migration is a crucial phase for their survival (Glass et al. 1998; Crowther et al. 2000; Colloff 2009). In this study, we identified some determinants of their migratory behaviour. First, the triggering factor for migration is a humidity gradient. Second, the tendency to migrate depends on developmental stage and sex. Finally, once on the move, the direction taken by a mite is influenced by the behaviour of its conspecifics.

Our experiments showed that local dryness strongly influences migration dynamics, especially when a distant water source can be perceived. Although this migration is collective there is not always unanimity in the individual responses: some individuals may decide to stay or to migrate to an arena even the hygrometry is unfavourable at this location. This might be attributed to differences in the individual response thresholds to environmental conditions. In our experiments, no matter what the hygrometric conditions were, nymphs and males were more inclined to migrate than to stay in the initial arena (also, these were always more numerous). On the other hand, females and larvae had a lower tendency to migrate. These differences between the proportion of migrating males and females were not linked to their respective walking

speeds that are similar. Arlian et al. (1998) showed that females are more resilient at a low relative humidity than males and are therefore more likely to survive a reduced relative humidity. This could be attributed to their bigger body size and hence their lower surface/volume ratio that makes them less vulnerable to dehydration than males. The fact that females tended to migrate less than males could be explained by a higher tolerance of the females to local dryness. The larvae walked slowly but the length of the experience was long enough for them to reach the arrival arena. Therefore, their low walking speed did not explain their low migration rate. Is this stage more sedentary? Are they influenced by the presence of females? These questions call for new experiments.

Individual variability in the tendency to migrate can be explained by qualitative and quantitative variations in individual responsiveness (Beshers & Fewell 2001). Responsiveness of an individual is regulated by internal factors such as genetic predisposition, physiology, developmental stage, sex and age (Robinson 1992; Page et al. 1997). The responsiveness of an individual can also depend on several external factors, such as the relative humidity and light intensity in the laboratory. Here, we identified three factors that modulated individual responsiveness in house dust mites: an environmental factor (relative humidity), and two internal factors (sex and developmental stage). Concerning the differences observed in the responsiveness, we made the assumption that dust mites possess a spectrum of migration and invasion mechanisms that include both individual and collective strategies. Our hypothesis was that the interplay between the distribution of individual responsiveness in the group and the environmental conditions determines the proportion of mites that migrate and lay a trail leading to an amplification process. Therefore, individual and collective migration modes might represent temporary states that can interchange depending on this interplay. During our experiments, the four stages: female, males, larvae and nymphs might have had a different responsiveness to the presence of the other mites, for instance, via an aggregative pheromone. This might rule their tendency to migrate or stay in a non-migrant group.

Mite migration is commonly understood as the solitary movement of individuals, triggered by and directed towards environmental gradients. Here, we showed that dust mites do indeed move towards a humidity gradient, but also that they have the capability to migrate collectively and that the mechanism involved in this social behaviour is partially decoded. The good agreement between the model and the experimental data strongly suggests that the mites were able to perceive the branch that was taken by most previous mites. This perception increases their probability of taking that branch. This created a positive feedback loop (or an amplification process) that resulted in the selection of one branch. We evidenced and quantified this part of the amplifying process but the underlying biological trait remains to be investigated. The likeliest possibility is the laying and following of a chemical trail. As mites move, it is likely that they passively lay chemicals on the substrate that then guide the followers (as observed on spiders by Jeanson & Deneubourg 2006a,b). Another possibility is that the presence of mites raises the local humidity and/or CO_2 concentration. Identifying the chemical cues (trail pheromones, H_2O, CO_2) involved in the emergence of collective choices could be another interesting step of this study.

We cannot state that the collective behaviour seen in our laboratory experiments directly translates to that observed in the field, although it would be interesting to verify this point. However, one can assume that the maintenance of cohesion while migrating may be advantageous to house dust mites. Indeed, collective migration behaviour might be linked to the advantages of individuals remaining in groups (Rivault et al. 1998; Ame et al. 2004; Prokopy & Roitberg 2005; Le Goff et al. 2009). The two main species of dust mites, *D. pteronyssinus* and *Dermatophagoides farinae*, are highly aggregative and this behaviour might significantly reduce individual water loss (Glass et al. 1998). We hypothesized that collective migration offers them the possibility of forming aggregates to protect them from dehydration (Wharton et al. 1979). In general, forming such aggregates has many advantages for both the individual and the group because it provides easier access to food and mates as well as protection against predators (Ranta et al. 1993; Wertheim 2005). It also presents disadvantages since forming aggregates means sharing food, mates and living space, and can result in inter-individual conflicts (Ranta et al. 1993; Wertheim et al. 2004; Prokopy & Roitberg 2005; Wertheim 2005). Although group formation is of critical importance for many species, few reports have studied the parameters modulating spatial distribution, especially in non-eusocial arthropods such as *Tetranychus urticae* (Millar 1993; Strong et al. 1997).

In biology, the study of social organization has mainly focused on species characterized by a high level of sociality (Hölldobler & Wilson 1990; Seeley

1996). Species characterized by a simpler social organization have been poorly studied (Costa 2006; Sokolowski 2010). In European house dust mites (*D. pteronyssinus*), social behaviours have not yet been explored because this species is widely supposed to be solitary. It is seen as an animal that only aggregates in response to attractive cues in its environment. Acari present the basic features required for the emergence of coherent migration and collective decision making, such as mutual conspecific attraction, spatial proximity and spatio-temporal overlap of generations. Despite these prerequisites, in Acari there is little evidence of social behaviours apart from aggregative behaviours and they are mainly found in spider mites building silk nests (Kotaro & Saito 2004). Nevertheless, social interactions in organisms with simple social structures, such as Acari, share common themes with decision making in more complex organisms, which makes them a relevant and useful subject of study. In the case of dust mites, this relevance is reinforced by their importance for health issues.

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