

Picky hitch-hikers: vector choice leads to directed dispersal and fat-tailed kernels in a passively dispersing mite

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Abstract

Dispersal is a central life-history trait for most animals and plants: it allows to colonize new habitats, escape from competition or avoid inbreeding. Yet, not all species are mobile enough to perform sufficient dispersal. Such passive dispersers may use more mobile animals as dispersal vectors. If multiple potential vectors are available an active choice can allow to optimize the dispersal process and to determine the distribution of dispersal distances, i.e. an optimal dispersal kernel.

We explore dispersal and vector choice in the neotropical flower mite *Spadiseius calyptrogynae* using a dual approach which combines experiments and an individual-based simulation model. *S. calyptrogynae* is found in lowland rainforests in Costa Rica. It inhabits inflorescences of the understory palm *Calyptrogyne ghiesbreghtiana* and is phoretic on a number of flower visitors including bats, beetles and stingless bees. We hypothesised that the mites should optimise their dispersal kernel by actively choosing a specific mix of potential phoretic vectors.

In a simple olfactometer setup we showed that the flower mites do indeed discriminate between potential vectors. Subsequently we used an individual-based model to analyse the evolutionary forces responsible for the observed patterns of vector choice. The mites combine vectors exhibiting long-distance dispersal with those allowing for more localized dispersal. This results in a fat-tailed dispersal kernel that guarantees the occasional colonization of new host plant patches (long distance) while optimizing the exploitation of clumped resources (local dispersal). Additionally, kin competition results in a preference for small vectors that transport only few individuals at a time. At the same time, these vectors lead to directed dispersal towards suitable habitat, which increases the stability of this very specialized interaction. Our findings can be applied to other phoretic systems but also to vector-based seed dispersal, for example.

Keywords: dispersal, phoresy, flower mites, *Spadiseius calyptrogynae*, cuticular components, volatiles, kin competition, information use, fat-tail, long-distance dispersal, kernel mixing, directed dispersal

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Introduction

Dispersal is a central life-history trait for all animal and plant species: emigration and immigration are the only processes besides birth and death events that influence population dynamics. Many of the evolutionary forces driving emigration are quite well understood, at least from a theoretical point of view (for reviews see Bowler and Benton 2005; Ronce 2007). On the one hand, the avoidance of kin competition, for example, is an important factor selecting for dispersal (Hamilton and May 1977). Besides this, habitat variability in space and time (McPeck and Holt 1992), demographic fluctuations (Travis and Dytham 1998; Cadet et al. 2003) and local extinctions (Comins et al. 1980; Roff 1994) also favour increased dispersal rates. On the other hand, dispersal may be a very costly behaviour: in addition to increased predation risk during transition and physiological costs (i.e. energy spent during dispersal, investment in movement and flight apparatus; see e.g. Zera and Mole 1994) dispersers may not find suitable habitats and perish (Cody and Overton 1996). Dispersing individuals may also pay opportunity costs which are, for example, due to maladaptation to new habitat conditions or loss of social rank (for a recent review see Bonte et al. 2012). As a consequence, these factors select against dispersal.

Particularly for species that inhabit ephemeral habitats, such as small ponds, river banks prone to flooding, dung pats, carcasses or — as in this study — flowers, dispersal is necessary to guarantee the (long-term) persistence of the lineage. Individuals have to leave their habitat and disperse to new resources before the habitat completely degenerates and the local populations goes extinct. The resulting evolutionary dynamics of dispersal may be highly complex (see e.g. Travis and Dytham 1999). If such systems show high degrees of specialization — as in this study — successful dispersal may become an important challenge. Depending on the system of interest, dispersal may happen through space or through time by dormant stages. Since our study species, *Spadiseius calyptrogynae*, does not exhibit any dormant stages, we will focus on dispersal through space.

As dispersal is vital for species living in ephemeral habitats it is surprising to find highly non-mobile species specialized to such environments, such as — among many other examples — mites living in patchily distributed flowers (Colwell 1973; Tschapka and Cunningham 2004; Guerra et al. 2012), nematodes living in tropical figs (Krishnan et al. 2010) or annelids and ostracods found in bromeliads (Lopez et al. 2005). Individuals of such non-mobile species have evolved to use other more mobile taxa as means of transportation. This behaviour, known as phoresy, allows non-mobile species to persist in unstable spatially structured populations (Colwell 1985; Houck and OConnor 1991; Soroker et al. 2003; Niogret et al. 2006).

In such harsh but predictable environments — and especially if the individuals have to rely on other species for dispersal — one can assume that the use of information is highly adaptive since it may confer a substantial evolutionary advantage over a random strategy (Ronce 2007). This is especially relevant if the focal species is specialized to a specific habitat, i.e. plant species. It has for example been shown that mites inhabiting dung pats (Niogret et al. 2004, 2006), broad mites (Soroker et al. 2003) and fig nematodes (Krishnan et al. 2010) use chemical signals to locate potential phoretic hosts and to discriminate between alternatives.

Here, we will analyse dispersal and vector choice by the neotropical bat flower mite *Spadiseius calyptrogynae* (Acari: Mesostigmata; Lindquist and Moraza 2008). This species is particularly interesting because it shows highly specialized habitat requirements and is only found on a single understory palm species (*Calyptrogyne ghiesbreghtiana*) in the tropical lowland rainforest of Costa Rica (Tschapka and Cunningham 2004). The palm flowers year round and often occurs in swamps. Since these occur in patches the palm shows a clumped distribution. Inflorescences are protandrous, i.e. they first develop male flowers that are followed by females flowers, over an inflorescence lifespan of ca. 9–11 days. Only one inflorescence flowers at any given time per palm (Cunningham 1995), which forces the flower mites to change their habitat at least once and possibly up to 2–3 times during their lifetime. For detailed studies on the biology of *Calyptrogyne ghiesbreghtiana* see Cunningham (1995, 1996, 1997a,b, 2000).

The flower visitors are on the contrary not specialized to the palm species. The inflorescences are visited by bats (*Artibeus watsoni/phaeotis*), one stingless bee species (*Trigona fulviventris*) and two beetles (*Chasmodia collaris* — Scarabeidae, *Cholus curialis* — Curculionidae). The bats are frugivorous (Lopez and Vaughan 2007) and the stingless bee is a generalist and visits a large number of flowering plants (Janzen 1983). Very little is known about the coleopterans and we thus cannot completely exclude that these are specialized on *Calptrogynae ghiesbreghtiana* although personal observations indicate a more generalist behaviour (Sperr pers. obs.).

In addition to variation in the quality of their interaction with the host palm (mutualistic pollination to floral herbivory), these four flower visitors differ markedly in terms of (1) visitation pattern, (2) size, i.e. transportation capacity and (3) mobility, i.e. the dispersal kernel. We will now detail these differences (for a summary see table 1) and forward some hypotheses how these may influence the quality of the dispersal vectors from the point of view of phoretic mites. The following paragraphs allow the reader to become more familiar with the system under study. Note that the data referred to in the following paragraphs are taken from Sperr and Tschapka (in prep.) if not indicated otherwise.

(1) The most frequent visitors to the palm are the stringless bees (*Trigona fulviventris*) with approximately 30–35 visits per day (the numbers were corrected for duration since too short visits do not allow a mite to climb onto a potential phoretic vector). The second most common visitors are bats (*Artibeus* spp.; the data come from video recordings and thus the two visiting species *A. watsoni* and *A. phaeotis* cannot be distinguished; even in the field this is problematic; see Timm and LaVal 1998) with ca. 2–3 visits per night. Finally, the coleopterans are rare visitors with respectively 1 and less than 1 visit per day for *Cholus curialis* (Curculionidae) and *Chasmodia collaris* (Scarabaeidae). In addition *Trigona fulviventris* and *Cholus curialis* show a marked preference for male flowers, as they feed on pollen.

(2) In terms of transportation capacity, the bat species, *Artibeus* spp., may carry a large number of mites on their wings (up to 360 individuals) while the scarabid beetle, *Chasmodia collaris*, has a slightly lower transportation capacity, the weevil *Cholus curialis* was found to carry no more than 50 mites and the maximal mite load for *Trigona fulviventris* was 7 mites.

(3) The dispersal distances covered by *Artibeus* spp. can be estimated from their home range area that covers between 3 and 4 hectares (Chaverri et al. 2007). This is comparable in size to the territory of a *Trigona fulviventris* colony (ca. 180 m in diameter; see Janzen 1983). *Cholus curialis* were found to be very philopatric and leave a *Calyptrogyna* stand only very rarely while *Chasmodia collaris* exhibits long-distance movement of up to 800 m in a few days.

From this short overview of the system’s natural history we forward the following hypotheses: (1) As dispersal is obligate and very frequent, the mites should either rely on very frequent visitors — such as *Trigona fulviventris* and *Artibeus* spp. — or not discriminate between phoretic hosts at all. (2) Mites should rely on small vectors — such as *Trigona fulviventris* or *Cholus curialis* — in order to avoid inbreeding (Bengtsson 1978; Ravigné et al. 2006) and minimize kin competition (Hamilton and May 1977; Poethke et al. 2007). Of course, group dispersal may be advantageous to overcome Allee effects (for a summary see Courchamp et al. 2008) and mites could avoid kin competition and inbreeding by disembarking on different subsequently visited palms. Yet, depending on the revisitation probability, such a behaviour could be extremely costly. (3) Directed dispersal towards early stage inflorescences should be evolutionarily advantageous. Since dispersal is costly (Bonte et al. 2012) the phoretic mites should be selected to minimize the number of dispersal events which would favour *Trigona fulviventris* and *Cholus curialis*. These vectors visit inflorescences early after the onset of flowering, i.e. during the male flowering phase (*Calyptrogyna ghiesbreghtiana* is protandrous). Even if females lay eggs multiple times on different inflorescences, an early stage inflorescence facilitates the successful development of its offspring. (4) In terms of dispersal distances we hypothesise that the phoretic mites should show a preference for vectors with intermediate dispersal distances — such as *Artibeus* spp. — which would allow the mites to disperse within host plant patches but also to occasionally colonize new patches.

We investigate the preferences exhibited by *Spadiseius calyptrogynae* in dual-choice and cafeteria olfactometer setups. In addition, we develop an individual-based model that includes the necessary system-specific features (for other approaches combining theoretical and empirical work see e.g. Ronce et al. 1998; Baiser et al. 2013). This allows us to revisit our hypotheses, to test whether we have included all critical assumptions that lead to the system-specific behaviour and to analyse the effects of these assumptions. This study is the first to analyse insect cuticular components and volatiles isolated from bat fur as potential cues which enable informed phoretic dispersal decisions in flower mites and to combine this with a formal individual-based model to explore evolutionarily stable phoretic dispersal strategies.

In more general terms this study allows us to test whether theory developed for more classical active and passive dispersal modes can also be applied to phoretic dispersal. Phoretic systems are by far more complex and selective pressures less clear since emigration decisions define the subsequent dispersal phases, i.e. transition and immigration.

Material and Methods

Study site

The study was conducted from March to April 2012 at La Selva Biological Station, a nature reserve located at the confluence of the rivers Puerto Viejo and Sarapiquí in the north-eastern Caribbean lowland rainforest of Costa Rica (10°26' N, 83°59' W). The station receives roughly 4000 mm of precipitation per year with on average more than 100 mm per month. Seasonality is not very pronounced, a period of less rainfall occurs from February to April (Sanford et al. 1994).

To guarantee the most natural environmental conditions while keeping a controlled experimental setting, the experiments were performed in the ambient laboratory of the field station between 19:00 h and 06:00 h. This time frame was chosen based on the study species' and its phoretic vectors' natural activity peaks.

Organisms

Spadiseius calyptrogynae were kept on collected *Calyptrogynae ghiesbreghtiana* inflorescences in the ambient laboratory. Experimental individuals were randomly collected from the inflorescence.

For extraction of cuticular components and other scent cues *Chasmodia collaris* (two individuals), *Cholus curialis* (four individuals) and *Trigona fulviventris* (10 individuals) were caught directly on *C. ghiesbreghtiana* inflorescences using an insect net. Bats (*Artibeus watsoni* or *A. phaeotis*, two individuals; *Glossophaga* sp., probably *G. commissarisi*, one individual) were captured with mist nets (mesh size 16 mm, 6 m x 2.5 m, Vohwinkel, Germany) set in front of flowering *C. ghiesbreghtiana*. Species were identified using the key by Timm and LaVal (1998).

Experiments

All choice tests followed the same design. Glass Petri dishes (diameter: 50 mm) were divided into four sectors of equal size. Identical scent extracts (treatments) were applied to diagonally opposite sectors. Experiments always started 15 min. after extract application in order to guarantee a solvent-free surface. Single mites were placed in the center of the Petri dish using a fine artist brush. The time a mite spent in a specific sector was recorded for 180 sec. or until it left the experimental arena. Petri dishes and tweezers were cleaned with acetone, hexane and 90% ethanol before use. Every 10 consecutive tests the Petri dish was cleaned and new extracts were used. Previous experiments indicate that the results are not biased by this protocol. We did not record any evidence that scents decay during this time or that mites produce scent tracks.

Scent collection and dual-choice tests

In order to determine whether *S. calyptrogynae* use olfactory cues during phoretic vector choice, extracts of two flower visitors were tested in the above described experimental setup against each other. Individual of *C. collaris*, *T. fulviventris* and *C. curialis* were extracted in 2 ml of hexane for 20 sec. after having been frozen (-20°C for 3 days Niogret et al. 2006). Before extraction we made sure to remove all traces of pollen, mites or other particles from the insects. In addition, ca. 10 mg of fur (2 cm² from the back of the animals with clean scissors) was collected from *Artibeus* sp. and *Glossophaga* sp. as a control and extracted for 48 h (room temperature, darkness) in 2 ml hexane (Ghanem 2008). Extracts were stored at -20°C until used.

Glossophaga sp. fur extract is used as a control. Individuals of this species do visit *C. ghiesbreghtiana* (Tschapka 2003), yet their hovering flight style (these bats are actually nectarivorous) prevents prolonged body contact with the inflorescences which does not allow mites to use this species as a phoretic vector (Tschapka and Cunningham 2004).

In order to make the volatile concentration in extracts comparable to each other, the concentrations were normalized to the surface of the vectors (mean values from all sampled individuals; surface estimated as an ellipsoid; *Chasmodia collaris*: 5.9 cm², *Cholus curialis*: 1.0 cm², *Trigona fulviventris*: 0.4 cm², bats: 2 cm² from the back of the animals). We tested the effect of this normalization by running additional cafeteria experiments (see below) with a two-fold increased concentration of *Artibeus* sp. extract and found no qualitative influence on our results (results not shown).

30 μl of each normalized extract was directly applied to opposing Petri dish sectors and tested against the same amount of extract from an other vector (or control). As described above, the time each mite (for all dual-choice experiments: $N = 50$ mites; except when explicitly indicated otherwise) spent in a specific sector was recorded for 3 min. or until it left the experimental arena.

Cafeteria experiment

These dual-choice experiments were supplemented by cafeteria experiments in which normalized extracts of all four vectors (*Chasmodia collaris*, *Cholus curialis*, *Trigona fulviventris* and *Artibeus* sp.) were tested simultaneously against each other, which mimics a more complex environment. The experiments were performed as described above with $N = 100$ mites.

Statistical methods

The statistical analysis for all choice experiments (dual-choice and cafeteria) was performed using generalized linear mixed models (GLMM; “glmmPQL” function of package “MASS” version 7.3-19; R 2.15.1). For the dual-choice tests the time a mite spent in sectors containing the same extract (of the 4 sectors 2 contained the same extract) was added. We implemented the extract and mite instar (categories: larvae, protonymphs, deutonymphs, males or females; see Lindquist and Moraza 2008) as fixed effects and the individuals as random effects in order to account for the two (four) values obtained per mite in the dual-choice (cafeteria) experiments. If necessary the data were transformed to allow a Gaussian error distribution. If this was not possible we chose a “Tweedie” GLMM (package “tweedie” version 2.1.1; R 2.15.1; see also Smyth and Verbyla 1999). This error distribution is a compound Poisson distribution and allows a mass of values at zero and continuous non-negative real numbers, as is the case for our time measurements. For the cafeteria experiment we ran an additional Tukey post-hoc test (function “glht” of the package “multcomp” version 1.2-12).

Individual-based simulation model

In order to derive evolutionarily stable phoretic dispersal strategies for the system under investigation we use a well established individual-based simulation approach (see e.g. Travis and Dytham 1999; Poethke and Hovestadt 2002; Fronhofer et al. 2011, 2012). Such models can be reasonably well applied to a large number of arthropod species. Note that individual-based simulations include the effects of kin competition by default (Poethke et al. 2007). Of course, some system-specific features were introduced and will be described in detail below (for a summary of parameters see table 1).

Our spatially explicit model is grid-based and uses a fractal landscape (generated in R with package “ecomodtools” version 0.1-1; see Chipperfield et al. 2011) which allows us to control the autocorrelation (Hurst index; standard $H = 0.25$; here and in the following we will indicate standard parameter values in brackets). To test the influence of these specific parameter values we ran a sensitivity analysis; see Appendix table 3) and the proportion of suitable habitat (standard: $p_H = 0.5$). Decreasing Hurst indices indicate more fragmented landscapes. The grid (1024 cells) is wrapped around a torus in order to simulate an infinite world.

One cell represents ca. 10 x 10 m of tropical lowland rainforest. For simplicity we assume that such a cell, if suitable, contains one flowering individual of the palm *Calypstrogyne ghiesbreghtiana* at any time. Note that this will not always be the same individual, but subsequently different palms. One grid cell thus hosts one local population of the flower mites *Spadiseius calyptrrogynae*. We assume a local carrying capacity of $K = 100$ mites and a maximal patch age of $t_{max} = 3$ generations after which the local population goes extinct deterministically. This is a realistic parametrisation if we assume a generation time of 3–4 days (pers. obs.). The patch may be recolonized in the next time step.

Our model is semi-continuous which means that we assume discrete, non-overlapping generations, while iterating the dispersal step which approximates continuous time. This allows us to balance technical constraints (e.g. simulation time) while analysing the process of interest, i.e. phoretic dispersal, in detail (see below). For simplicity we implement a clonal model and assume logistic population growth in local populations (Beverton and Holt 1957). The mean number of offspring a female mite produces per generation is calculated as:

$$\lambda = \lambda_0 \cdot \frac{1}{1 + aN_t} \quad (1)$$

Table 1: System summary (data from Sperr and Tschapka in prep.) and model parameters.

phoretic vector	visitation rate (per day)	dispersal distance (mean, cells)	dispersal mortality	vector capacity	patch preference	
<i>Artibeus</i> sp.	high	intermediate	intermediate	very high	75	none
<i>T. fulviventris</i>	very high	intermediate	intermediate	very low	5	early
<i>C. collaris</i>	low	high	low	high	50	none
<i>C. curialis</i>	intermediate	low	high	low	10	early

with $\lambda_0 = 4$ as fecundity, N_t as the actual population size and the susceptibility to crowding $a = (\lambda_0 - 1)/K$. The realized number of offspring is then drawn from a Poisson distribution with mean λ . Every offspring inherits from its parent a vector-valued trait which codes for the genetically fixed preferences for the four phoretic vectors, i.e. bats (*Artibeus* spp.), bees (*Trigona fulviventris*), and the two coleopterans (*Chasmodia collaris* and *Cholus curialis*). These four preferences (real numbers between 0 and 1) are subject to evolution and we therefore assume that these preferences may mutate. Mutations occur rarely (mutation rate $m = 0.001$). If such a mutation occurs the preference values inherited are changed by adding a random number drawn from a uniform distribution ($0 \pm \Delta m$, with $\Delta m = 0.2$). Since the values are limited between zero and 1 we assume reflecting boundary conditions.

For the sake of simplicity, and because exact information about the life-history of the flower mite *Spadiseius calyptrogynae* is still lacking, we assume natal dispersal, i.e. only one dispersal event before reproduction. As stated above, the dispersal step is simulated in continuous time (see e.g. Allen and Dytham 2009). The dispersal procedure is event-based with 150 iterations per patch and generation. An event is a visitation by a certain flower visitor and happens for every suitable habitat patch (inflorescence) according to visitation probabilities estimated from flower visitation data ($p(\textit{Artibeus}) = 0.07$; $p(\textit{Chasmodia}) = 0.02$; $p(\textit{Cholus}) = 0.04$; $p(\textit{Trigona}) = 0.7$; these values are calculated from table 1 and take into account the number of iterations and generation time). After the visitation event has been determined all mites may decide to use this phoretic vector or not, according to their individual preferences (see above). If the number of potential dispersers is greater than the phoretic vector's capacity ($K(\textit{Artibeus}) = 75$; $K(\textit{Chasmodia}) = 50$; $K(\textit{Cholus}) = 10$; $K(\textit{Trigona}) = 5$) a subset of dispersers is chosen randomly.

For every phoretic vector a dispersal distance is drawn from a skewed dispersal kernel with probability density $P(d) = \alpha^2 d e^{-\alpha d}$ and mean $M = 2/\alpha$ following Gros et al. (2006). Note that we tested other kernel shapes (e.g. negative-exponential) and found that our results were not altered qualitatively. Every vector is characterized by a specific mean dispersal distance which reflects data from field observations (see Introduction and table 1) relative to the underlying landscape ($M(\textit{Artibeus}) = 5$; $M(\textit{Chasmodia}) = 10$; $M(\textit{Cholus}) = 1$; $M(\textit{Trigona}) = 4$). As we have to fit the resulting dispersal distances to the underlying grid, we assume area-to-area dispersal.

In order to incorporate the characteristic preference for early stage inflorescences (i.e. male, depletion of pollen) by *Cholus curialis* and *Trigona fulviventris* we implemented a second, informed dispersal step. After arriving in the target patch defined by the dispersal kernel, vectors may relocate to one of the 8 nearest neighbours of the target cell. In order to avoid strong artefacts all vectors prefer suitable over non-suitable patches, i.e. *Calyptrogynae* over non-*Calyptrogynae* patches. Yet, *Cholus curialis* and *Trigona fulviventris* will relocate deterministically to the youngest patch (equivalent to male flowering phase) if suitable cells are encountered. If more than one patch has the same age, the target is chosen randomly amongst those.

In addition, phoretic vectors may not revisit any conspecific plant, which corresponds e.g. to a return to the bat roost or bee colony or to some other activity which does not include visiting a new plant. This results in an additional mortality term for the phoretic mites ($\mu(\textit{Artibeus}) = 0.5$; $\mu(\textit{Chasmodia}) = 0.4$; $\mu(\textit{Cholus}) = 0.6$; $\mu(\textit{Trigona}) = 0.5$). These parameters are the only ones that we cannot directly estimate from field data. Since *Artibeus* spp. and *Trigona fulviventris* are not specialized pollinators to *C. ghiesbreghtiana* (although the bats are the main pollinators; see e.g. Tschapka 2003) we assume that the revisitation probabilities are low and thus the mortality term is high. Visitation patterns of *Chasmodia collaris* and *Cholus curialis* remain unknown. From personal observations (Sperr and Fronhofer pers. obs.) we estimate *Chasmodia collaris* to revisit *Calyptrogynae ghiesbreghtiana* more often than *Cholus curialis*. The influence of changing these values is analysed in the Appendix (sensitivity analysis; table 3). Note that this mortality term greatly influences the variance of a phoretic dispersal event, since all phoretic mites on a vector are prone to die simultaneously.

Simulations were run for 3000 generations in order to allow the system to reach equilibrium. The results presented below are mean values over 25 replicate simulation runs. For the sensitivity analysis we used 10 replicates for every tested parameter combination.

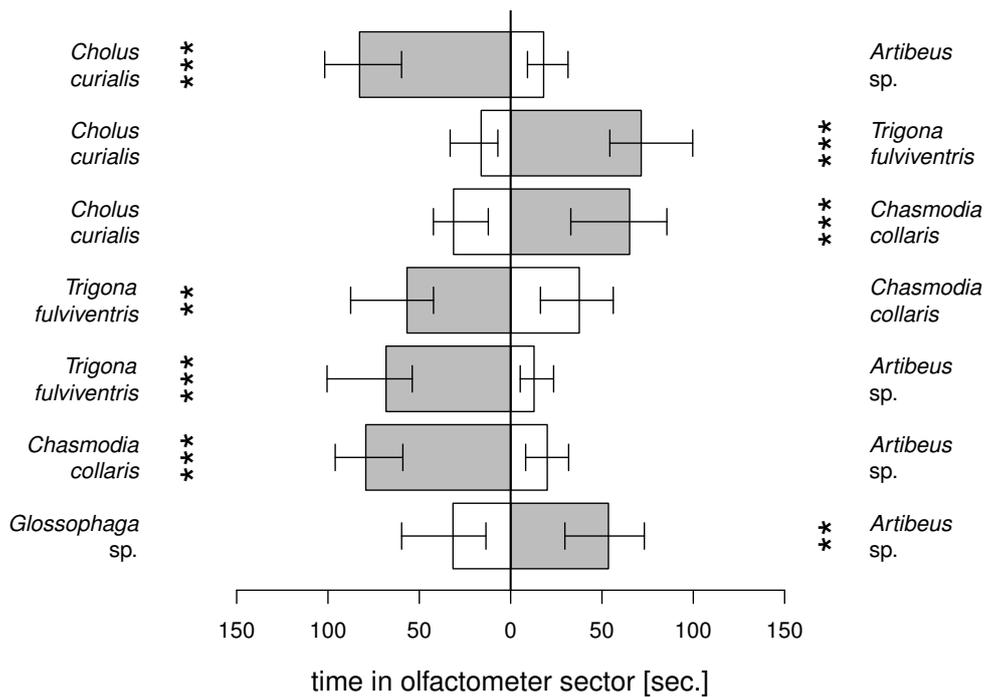


Figure 1: Dual-choice tests. Vector extracts (see plot margins) were tested in a basic olfactometer setup against each other. Bars show the time mites spent in the corresponding sectors (median, 25% and 75% percentiles for $N = 50$ mites in each experiment). See text for the statistical analysis (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

Results

Dual-choice tests

The results of our olfactometer dual-choice experiments show that *Spadiseius calyptrogynae* does indeed discriminate between phoretic vectors using olfactory cues (figure 1). *Artibeus sp.* scent was preferred over fur extract of the bat *Glossophaga sp.* (GLMM: $N = 50$; $t = -2.98$; $p = 0.0045$). In all experiments mite instar was found to have no significant effect (results not shown). *Cholus curialis* cuticular extract was significantly preferred over *Artibeus sp.* (GLMM: $N = 50$; $t = 11.94$; $p < 0.001$). *Chasmodia collaris* cuticular extract was significantly preferred over *Artibeus sp.* (GLMM: $N = 50$; $t = 12.7$; $p < 0.001$) and over *Cholus curialis* (GLMM: $N = 50$; $t = -4.53$; $p < 0.001$), but not over *Trigona fulviventris* (GLMM: $N = 50$; $t = 3.01$; $p = 0.004$). *Trigona fulviventris* cuticular extract was significantly preferred over all other tested extracts, i.e. *Artibeus sp.* (GLMM: $N = 50$; $t = 8.3$; $p < 0.001$) and *Cholus curialis* (GLMM: $N = 50$; $t = 9.33$; $p < 0.001$).

Cafeteria experiment

We found the same pattern in our cafeteria experiment (figure 2 A) indicating that cuticular extracts of *Trigona fulviventris* are preferred over all other choices (Tukey's test; *T. fulviventris* vs. *Artibeus sp.*: $z = 7.74$; $p < 0.001$; *T. fulviventris* vs. *C. collaris*: $z = 3.27$; $p = 0.005$; *T. fulviventris* vs. *C. curialis*: $z = 6.97$; $p < 0.001$) while *Chasmodia collaris* fares better than the two remaining extracts (Tukey's test; *C. collaris* vs. *Artibeus sp.*: $z = 5.14$; $p < 0.001$; *C. collaris* vs. *C. curialis*: $z = -4.13$; $p < 0.001$). In the cafeteria experiment the mites did not differ significantly in their choice of extracts of *Artibeus sp.* and *Cholus curialis* (Tukey's test: $z = 1.19$; $p = 0.63$).

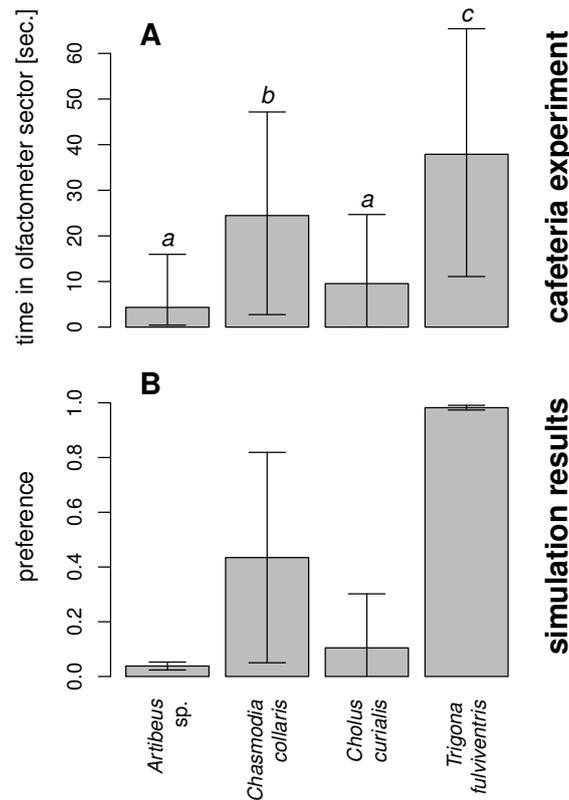


Figure 2: Cafeteria experiment and simulation model results. Figure A shows the results of the cafeteria experiment which is analogous to the dual-choice test with the difference that four vector extracts are tested against each other simultaneously ($N = 100$ mites). The letters indicate significantly different values (Tukey's test after GLMM; see text for results). Bars represent the median with the 25% and 75% percentiles as error bars. Figure B shows results from the individual-based simulation. The values depicted are mean preferences ($\pm s.d.$) for the different vectors. Note the corresponding variances between figures A and B.

Individual-based simulation model

The individual-based model described above and parametrized as detailed (table 1) fits the empirical data remarkably well (compare figures 2 A and 2 B). Figure 2 B shows the evolutionarily stable phoretic vector preferences. In general, all individuals have a pronounced preference for *Trigona fulviventris* as a phoretic vector. Some mites also show a lower but still substantial preference for *Chasmodia collaris* and *Cholus curialis*. A remarkable pattern is the important variance exhibited in the preferences for *Chasmodia collaris* and *Cholus curialis*. Upon closer investigation (figure 3) we found that the preferences were distributed multimodally. Note that this occurs across simulations and not within. Figure 3 shows two axes of phenotype space. The two remaining axes can be ignored since all individuals exhibit uniformly low preferences for *Artibeus sp.* and high preferences for *Trigona fulviventris*. While some individuals rely completely on the *Trigona* bees for dispersal (individuals in the lower left part of figure 3) others rely on both *Trigona fulviventris* and *Chasmodia collaris* (individuals in the lower right part of figure 3), while a third group does not discriminate between these two vectors and *Cholus curialis*.

This multimodality can also be found in the empirically collected data (figure 4 and table 2). Note that since the data gained from the dual-choice test are paired (one time measure for each of the two extracts per tested individual) we show the differences in figure 4. Table 2 indicates that the bimodality can be found for preferences of *Chasmodia collaris* and *Cholus curialis*, as our individual-based simulation model suggests (figure 3).

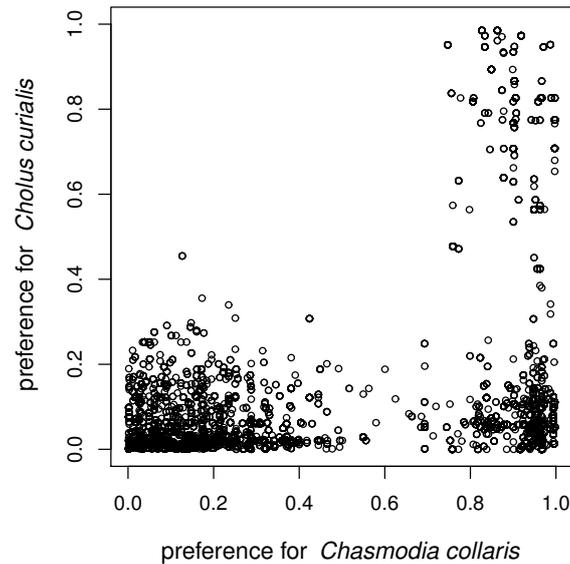


Figure 3: Simulation model results: phenotype space. This figure shows the same results as figure 2 B, yet here every individual is represented by a dot. Phenotype space has four dimensions (the four dispersal vectors), yet since preference for *Artibeus* sp. is constantly low and preference for *Trigona fulviventris* is constantly high (see figure 2 B) we have omitted these two dimensions for clarity. Note the three distinct dispersal strategies (lower left: preference for *Trigona fulviventris* only; lower right: preference for *Trigona fulviventris* and *Chasmodia collaris*; upper right: preference for *Trigona fulviventris*, *Chasmodia collaris* and *Cholus curialis*). The multimodality occurs across and not within simulation runs. The figure shows 10000 randomly drawn individuals from 25 simulation repeats.

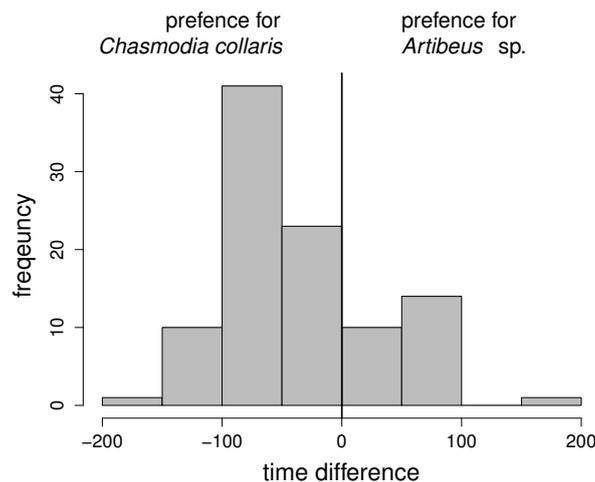


Figure 4: Preference distribution. Distribution of the time differences for a new repeat of the dual-choice test *Chasmodia collaris* vs. *Artibeus* sp. ($N = 100$ mites). We chose to show the distribution of the differences since the time a mite spend in one sector and in the other is not independent (“paired”). The histogram shows a clear bimodality.

Discussion

In summary, since *Spadiseius* mites live in an ephemeral habitat dispersal is obligatory. As the mites are not mobile enough they have to rely on phoresy. A number of flower visitors are potentially available as vectors. These differ in a large number of attributes. Our empirical work indicates that the mites are able to discriminate between these flower visitors using olfactory cues isolated from cuticles and fur. Our simulation results confirm that discrimination between these vectors is evolutionarily advantageous as the patterns obtained from the simulations are in good accordance with the empirical results. Especially in such possibly very stochastic and specialized systems information use is crucial for population viability. Kin competition is a major driving force for the evolution of dispersal and responsible for the choice of small vectors. The autocorrelated occurrence of the host plant selects for fat-tailed dispersal kernels which is achieved by mixing short- and long-distance dispersal vectors. In addition, vector choice does not only influence emigration and transition, but also immigration into new patches (directed dispersal). We will now discuss each of these point in more detail.

Dispersers use chemical cues for vector choice

Our results indicate that the phoretic bat-flower mites of the species *Spadiseius calyptrogynae* use chemical cues present on flower visitors to make informed decisions for phoretic dispersal. In accordance with our first hypothesis these flower mites are quite choosy in terms of phoretic vectors (figures 1 and 2). Our individual-based simulation model confirms that the exhibited informed dispersal strategy is evolutionarily stable and thus fares better than (random) other strategies.

Our results are consistent, regardless of the exact experimental set-up: the dual-choice and cafeteria experiments yield comparable results (figures 1 and 2). It is particularly interesting that the mites have apparently evolved to use insect cuticular hydrocarbons — which are known to be important in a large number of ecological contexts for recognition (for reviews see Howard and Blomquist 2005; Blomquist and Bagnères 2010) — but also scent cues from mammalian vectors. In addition, the latter cues used by the mites seem to be vector specific and not generally mammalian since the mites were able to discriminate between vector and non-vector bat species (*Artibeus* sp. vs. *Glossophaga* sp.; figure 1). This might also be relevant for discriminating between visits by perching bats and rare visits by mouse opossums (Sperr et al. 2009).

Our empirical data indicate that mite instar has no influence on vector choice, although it is assumed that adult females are the main dispersers (Lindquist and Moraza 2008). Yet, larvae, nymphs and males do have to disperse when their inflorescence withers and these individuals may have the same sensory capacities and preferences as females do. We suggest that all stages may at least potentially use information from vector scent cues to determine an appropriate vector. Note that phoresy by all stages has been observed in other flower mite species (see Lindquist and Moraza 2008, and literature cited therein).

Kin competition influences vector choice

The empirically collected data (figure 1, 4 and 2 A, table 2) and the simulation results (figure 2 B and 3) suggest that, as predicted by our second hypothesis, most mites exclusively use individuals of the stingless bee species *Trigona fulviventris* as phoretic vectors. This vector has multiple advantages (see also table 1): it is quite reliable since visitation rate is high. In addition, using *Trigona fulviventris* as a dispersal vector is the best option for avoiding kin competition (Hamilton and May 1977). Kin competition has repeatedly been shown to be a very important factor influencing dispersal evolution (e.g. Poethke et al. 2007).

Additional simulations show that the low preference for *Artibeus* is mainly due to its large size. If both vectors are implemented as completely identical except for their carrying capacity the evolutionarily stable preference is always for the smaller vector.

Vector choice leads to directed dispersal

Regardless of other possible disadvantages (e.g. low revisitation frequency) *Trigona fulviventris* prefers early stage inflorescences as the bees collect pollen. As suggested by our third hypothesis, this allows an optimal exploitation of such a short lived habitat as a flower since it maximises the time between arrival and patch extinction. This reduces dispersal mortality over subsequent generations and allows eggs to

hatch.

The most important pollinator of *C. ghiesbreghtiana* — *Artibeus* spp. (Tschapka 2003) — is not a preferred vector. Of course, it may be critical to compare insect cuticular components to extracts from bat fur. As we have tested the effect of increasing (doubling) the concentration of *Artibeus* sp. extract in the cafeteria experiment we are confident that our results are not artefacts of simple concentration or intensity effects. Furthermore, the mites are faced with exactly the same choice in the field. The only difference is that we tested fur from the bats' backs (in order to avoid important contamination with pollen and other plant substances) and that mites only attach to the bats' wing membranes. Nevertheless, our empirical and simulation results both indicate that *Artibeus* spp. are not prime dispersal vectors. We think that different evolutionary forces are relevant for plants and mites: while the palms should rely on visitors that transfer pollen from male to female inflorescences, the phoretic mites on the contrary should favour vectors that revisit early stage inflorescences since this alleviates the pressure of immediate relocation and allows egg development. Our empirical results may further be influenced by the fact that we have conducted our field study during the 'dry' season (note that even during these months precipitation is not low; see Sanford et al. 1994) which implies a lower number of flowering *Calyptrogyne* palms. During this period *Artibeus* spp. may be especially poor phoretic vectors because of lowered revisitation probabilities since the bats have to rely on other food sources. If vector preference is a plastic trait higher densities of flowering *Calyptrogyne* individuals may have led to a higher preference for *Artibeus* spp. as a vector. Here again, we can use the results from the individual-based model to formulate an informed hypothesis. Even if we decrease fragmentation and increase habitat availability (see sensitivity analysis; Appendix table 3) our model does not indicate that *Artibeus* sp. may become more attractive. Due to these spatial effects we would hypothesise that long-distance dispersal with *Chasmodia collaris* becomes less important, as it is too costly. The stingless bees remain the most appropriate dispersal vectors.

Directed dispersal has recently been demonstrated in animal dispersed palms in Barro Colorado Island (Hirsch et al. 2012). These authors show that scatter-hoarding seed dispersers lead to seed dispersal away from areas with high conspecific densities and thus high competition and mortality. Our study demonstrates the importance of the same principle for phoretic animals in ephemeral habitats. Directed dispersal in our case leads to colonization of habitats that have just recently become suitable. This reduces intra-specific competition and allows the establishment of new local populations with maximal longevities.

In this study we have only analysed information use for emigration decisions, but of course immigration is just as important. We here suggest that emigration decisions are influenced by and determine immigration: the use of certain vectors, such as the stingless bees, leads to directed dispersal towards early stage inflorescences. Informed immigration may still be evolutionarily advantageous, especially in this bat-flower mite system since most of the phoretic vectors are not specialized on *Calyptrogyne ghiesbreghtiana*. This question will be dealt with in detail elsewhere.

Vector mixing leads to fat-tailed dispersal kernels

An important fraction of dispersers exhibit an equally pronounced preference for *Trigona fulviventris* and a comparatively rare dispersal vector: the scarab beetle *Chasmodia collaris* (figure 4, 2 and 3). This vector has one central advantage, which is its long-distance flights (table 1). As the host palm *Calyptrogyne ghiesbreghtiana* frequently occurs in swamps, which leads to a clustered distribution, long-distance dispersal events allow the (re-)colonization of new host plant clusters. Although this dispersal behaviour is very risky, i.e. bears an important mortality risk, the pay-off for colonizing distant, eventually empty patches seems to balance these costs.

Hovestadt et al. (2001) show that in autocorrelated landscapes 'fat-tailed' dispersal kernels evolve. This is due to the antagonistic effects of kin competition — which would select for a uniform distribution of individuals of a lineage throughout the landscape (Hamilton and May 1977) — and dispersal costs — which increase with distance due to the autocorrelation of the habitat. Long-distance dispersal and fat-tailed dispersal kernels are extensively being studied in plants (Nathan 2006; Nathan et al. 2008b) but observations of long-distance dispersal are limited (Gillespie et al. 2012). The host palm shows exactly such an autocorrelated distribution and our results suggest that mites achieve a heavily fat-tailed dispersal kernel by mixing a short-distance (*Trigona fulviventris*) and a long-distance dispersal kernel (*Chasmodia collaris*).

This interpretation leads immediately to the question why our results suggest that mites showing only

short-distance dispersal with *Trigona fulviventris* seem to coexist with the individuals using a mixed strategy. Additional simulations show that coexistence is actually not evolutionary stable. Since the long-distance vectors (*Chasmodia collaris*) are very rare and imply high levels of dispersal mortality selection acts very slowly. The high intrinsic stochasticity of the system under study may lead to the fixation of short-distance dispersers using exclusively the stingless bees. Further simulations indicate that populations monomorphic for the mixed strategy cannot be invaded by individuals showing a preference for short-distance dispersal only. Conversely, a population monomorphic for *Trigona fulviventris* can be (slowly) invaded by a strategy characterized by a mixed kernel.

Note that a third strategy, which is actually a minority (figure 3), seems to be rather unspecific and disperses additionally on *Cholus curialis* (see also figure 1 and 2). This vector has the advantage of most probably staying in the present *Calyptrigyne* stand but preferring, just as *Trigona fulviventris*, early stage inflorescences. The overall costs associated with this choice seem to be low enough for selection to act slowly.

Such patterns of short-distance movement and long-distance dispersal are not found in the closely related hummingbird-flower mites (e.g. Colwell 1973). As most hummingbird-flowers (e.g. *Heliconia* spp.) flower over longer periods of time and may have subsequently flowering inflorescences on one plant, these mites can often simply walk to the next flower as soon as the currently inhabited one withers. In flower mites inhabiting *C. ghiesbreghtiana* this is not possible — as only one inflorescence flowers at any given time — and the corresponding short-distance movements have to be effected by phoretic dispersal on appropriate vectors, e.g. *Trigona fulviventris* or *Cholus curialis*.

Although in the field other cues may also be used to determine the identity of a vector, such as body temperature or movement patterns, chemical cues seem to play a pivotal role. Chemical communication is wide spread (for a review see Steiger et al. 2011) although in this case ‘communication’ may be the wrong term since the vectors probably provide the cues that help to identify them unintentionally (‘chemical eavesdropping’). A number of other studies have analysed the importance of chemical cues for phoretic dispersal (Soroker et al. 2003; Niogret et al. 2004; Krishnan et al. 2010). Yet, none of these found evidence for non-random use of multiple vectors in order to combine short-distance movement with long-distance dispersal events.

Robustness of simulation results

To our knowledge our study is the first to combine chemo ecological experiments in the field with a simple individual-based model. This allows us to analyse in more detail the underlying eco-evolutionary dynamics that lead to the observed and measured patterns. Of course, our individual-based model is far from capturing all the complexities of the system we are analysing. For instance, we assume non-overlapping generations, clonal reproduction (i.e. we model only female mites) and the same specific dispersal kernel form (although the means are different) for all vectors. Of course, the landscape is highly artificial and the annual dynamics of *Calyptrigyne ghiesbreghtiana* are ignored. Yet, this is exactly the advantage of such a model (see e.g. Kokko 2005). In this modelling study we were interested in optimal phoretic dispersal strategies. Thus, although simplifying the life-history of animals and plants greatly we modelled the crucial dispersal step quasi continuously. And although or especially because all elements included in the model are greatly simplified the model stays tractable and the results are understandable. The model helped us interpret such abstract features as the variance exhibited by the behaviour of the mites in the dual-choice and cafeteria experiments as representing different dispersal strategies. The simulations show that the stingless bee *Trigona fulviventris* should be the preferred phoretic vector. Note that this pattern is consistent throughout the sensitivity analysis (see Appendix table 3) even when this vector is penalized by high mortality rates. Similarly clear is the result that *Artibeus* sp. is not an adaptive choice. *Chasmodia collaris* — the long-distance disperser — very rarely drops in attractivity below preferences of 0.2, except when high additional mortalities are assumed. This is not surprising since the mortality for a disperser on *Chasmodia collaris* is already very high in the standard scenario. The adaptive value of *Cholus curialis* depends somewhat more on the parameter combinations.

Concluding remarks

We have shown that the use of (chemical) information is highly adaptive for taking emigration decisions, because non-random emigration allows to influence the shape of the dispersal kernel and may lead to

directed dispersal. We have analysed our hypotheses using a dual approach and presented empirical results from chemo-ecological studies with tropical flower-dwelling mites and individual-based simulation results.

The evolutionary forces discussed above are relevant to any phoretic species. They are especially important for specialized interactions, as such systems can only be stable if the (more) mobile partner is able to reach its host. Our conclusions can also be applied to other systems, for example to animal dispersed seed plants as appropriate vectors are crucial for the realization of optimal dispersal kernels. ‘Vector choice’ in plants can be achieved by fruit morphology, for example (e.g. Flörchinger et al. 2010). In animal dispersed plants kin competition should also favour small vectors. In autocorrelated habitats vector mixing can be used to achieve fat-tailed dispersal kernels (Nathan et al. 2008a).

We hope that our results also show how helpful such dual approaches, combining experimental work *in situ* and *in silico*, can be for a better understanding of ecological and evolutionary dynamics and their feedback loops. Such studies are particularly important to bridge the gap between empirical and theoretical ecology (Restif et al. 2012).

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Appendix

Normality of data obtained by dual-choice test. Sensitivity analysis of the individual-based model.

Table 2: Distribution of the data from the dual-choice experiments. Since per tested mite two values (one for each extract) were collected the data are paired and we analyse the differences, as in a paired t-test for example. The distribution of these differences is tested for normality (Shapiro-Wilk test of normality). Significantly non-normally distributed differences indicate bimodality as in figure 4.

vectors	normality of difference distribution
<i>Artibeus</i> sp. vs. <i>Glossophaga</i> sp.	$W = 0.98, p = 0.68$
<i>Trigona fulviventris</i> vs. <i>Chasmodia collaris</i>	$W = 0.99, p = 0.99$
<i>Cholus curialis</i> vs. <i>Chasmodia collaris</i>	$W = 0.98, p = 0.67$
<i>Artibeus</i> sp. vs. <i>Trigona fulviventris</i>	$W = 0.97, p = 0.16$
<i>Cholus curialis</i> vs. <i>Trigona fulviventris</i>	$W = 0.98, p = 0.54$
<i>Artibeus</i> sp. vs. <i>Chasmodia collaris</i>	$W = 0.96, p = 0.004$
<i>Artibeus</i> sp. vs. <i>Cholus curialis</i>	$W = 0.93, p = 0.007$

Table 3: Individual-based simulation model: sensitivity analysis. The table basically shows the same results as figure 2 B (cafeteria experiment; simulation results). For every phoretic vector the mean and the standard deviation of the evolutionarily stable preference is shown ($mean \pm s.d.$). The first results row shows the standard run for comparison. The first column indicates which parameter was changed and the second column the corresponding tested value. The results are means from 10 simulation runs.

		<i>Artibeus</i> sp.	<i>C. collaris</i>	<i>C. curialis</i>	<i>T. fulviventris</i>
	standard	0.033 \pm 0.013	0.452 \pm 0.409	0.192 \pm 0.298	0.985 \pm 0.008
λ	3	0.035 \pm 0.019	0.208 \pm 0.271	0.362 \pm 0.347	0.986 \pm 0.003
	4	0.058 \pm 0.008	0.460 \pm 0.359	0.046 \pm 0.015	0.982 \pm 0.007
t_{max}	2	0.015 \pm 0.004	0.043 \pm 0.015	0.148 \pm 0.202	0.982 \pm 0.010
	4	0.130 \pm 0.048	0.867 \pm 0.302	0.072 \pm 0.062	0.879 \pm 0.306
H	0	0.041 \pm 0.014	0.585 \pm 0.372	0.088 \pm 0.126	0.982 \pm 0.009
	0.5	0.044 \pm 0.015	0.284 \pm 0.312	0.098 \pm 0.098	0.979 \pm 0.008
	0.3	0.031 \pm 0.011	0.319 \pm 0.346	0.691 \pm 0.337	0.981 \pm 0.009
p_H	0.4	0.023 \pm 0.009	0.294 \pm 0.307	0.440 \pm 0.402	0.977 \pm 0.010
	0.6	0.041 \pm 0.009	0.229 \pm 0.254	0.167 \pm 0.270	0.983 \pm 0.005
$M(\textit{Artibeus})$	6	0.034 \pm 0.011	0.266 \pm 0.258	0.044 \pm 0.018	0.984 \pm 0.006
	4	0.046 \pm 0.012	0.316 \pm 0.342	0.288 \pm 0.390	0.980 \pm 0.006
$M(\textit{Chasmodia})$	11	0.039 \pm 0.016	0.446 \pm 0.430	0.142 \pm 0.294	0.986 \pm 0.004
	9	0.036 \pm 0.014	0.550 \pm 0.420	0.147 \pm 0.281	0.980 \pm 0.010
$M(\textit{Cholus})$	2	0.033 \pm 0.006	0.250 \pm 0.250	0.122 \pm 0.227	0.977 \pm 0.005
$M(\textit{Trigona})$	5	0.045 \pm 0.020	0.739 \pm 0.357	0.249 \pm 0.333	0.980 \pm 0.011
	3	0.045 \pm 0.164	0.531 \pm 0.366	0.155 \pm 0.255	0.985 \pm 0.005
$\mu(\textit{Artibeus})$	0.4	0.218 \pm 0.044	0.402 \pm 0.384	0.059 \pm 0.023	0.986 \pm 0.008
	0.6	0.016 \pm 0.005	0.525 \pm 0.423	0.121 \pm 0.159	0.982 \pm 0.007
$\mu(\textit{Chasmodia})$	0.3	0.045 \pm 0.014	0.963 \pm 0.023	0.191 \pm 0.307	0.980 \pm 0.008
	0.5	0.031 \pm 0.009	0.063 \pm 0.030	0.247 \pm 0.357	0.982 \pm 0.008
$\mu(\textit{Cholus})$	0.5	0.032 \pm 0.008	0.235 \pm 0.249	0.936 \pm 0.043	0.981 \pm 0.010
	0.7	0.045 \pm 0.011	0.221 \pm 0.243	0.025 \pm 0.009	0.981 \pm 0.008
$\mu(\textit{Trigona})$	0.4	0.018 \pm 0.006	0.172 \pm 0.287	0.021 \pm 0.006	0.981 \pm 0.010
	0.6	0.118 \pm 0.061	0.526 \pm 0.322	0.803 \pm 0.270	0.880 \pm 0.306