Whether to walk or take the bus: effects of dispersal strategies on hummingbird mite distribution

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Abstract: The spatial distribution of species that use other organisms as vectors is driven by the behavior of their vector as well as by their own dispersal capabilities. The mite *Proctolaelaps kirmsei* lives in *Hamelia patens* flowers, and travels on hummingbirds that visit these flowers. We studied the demographic patterns of *P. kirmsei* at four spatial scales: between hummingbird territories, between trees, between inflorescences, and between flowers. There was high variation in mites/flower among inflorescences within trees (46% of the total variation). Variance among clumps of trees also appeared to be meaningful (32%) but was non-significant. Trees within clumps, and flowers within inflorescences, were quite homogenous. Variation among inflorescences was not attributable to age of inflorescence. Other possible causes for mite variation include resource differences, hummingbird visitation rates, and differences between immigration and emigration. Similar spatial patterns in mite abundance may be common in other hummingbird-mite systems that involve territorial hummingbirds and plants with long-lived inflorescences.

Key Words: Ascidae, commensalism, Hamelia patens, *inflorescence, nectar, La Selva, parasitism,* Proctolaelaps kirmsei

Introduction

Species that use other organisms for transportation between hosts (phoresy) are often limited in distribution and dispersal by the movement patterns of their vectors. For example, human parasites like malaria, sleeping sickness, and botflies can only exist with mosquitoes and are limited to the mammals that mosquitoes bite. Mites (Mesostigmata: Ascidae) often use other organisms to move between resources and are frequently parasitic. Mite distribution could be determined both by their individual movement patterns as well as those of their vectors.

The mite *Proctolaelaps kirmsei* feeds on the nectar and pollen of the hummingbird-pollinated *Hamelia patens* (Rubiaceae). The mites are common on this host plant, which flowers year-round. It produces from one to several dozen inflorescences at a time, consisting of up to five flowers each of which lasts for ~24 hours. Hummingbirds act as mite vectors, transporting *P. kirmsei* in their nares from flower to flower (Colwell 1985). Mites are not dependent on hummingbirds to move between flowers within an inflorescence (Wolfenbarger 1990) and may be capable of inter-inflorescence movement as well. Patterns in mite demography could be affected by both independent movement of mites and movement via hummingbirds. Mites must continually immigrate to and emigrate from flowers to survive, so mite populations at every spatial scale depend on movements of some kind to remain viable.

We compared the amount of variation in mite abundance between flowers, inflorescences, trees, and clumps of trees to study how hummingbird foraging patterns and independent mite movement affect mite distribution. If hummingbirds frequently transport mites, we would expect to see most variation in mite abundance between hummingbird territories and little variation within a territory. If hummingbird transportation is rare we would expect to see high variation between trees.

The frequency of independent mite movements should also affect their distribution. If mites are capable of extensive independent movement within trees, we would expect mite abundance to be similar between inflorescences within a tree as well as between flowers. However, if they are not able to move

well without the hummingbird vectors, mite abundance should vary between inflorescences. Variation among inflorescences could also be a result of differential population growth over time, in which case, we would expect to find more mites in older inflorescences that had already permitted multiple mite generations.

Methods

On 15 February 2002 we sampled mite populations in 48 flowers of *H. patens* at La Estación Biológica La Selva, Costa Rica. Flowers were located on 8 trees near the research buildings and cabins. Trees were partitioned into clumps of putative hummingbird territories (~0.16 ha). We sampled flowers from 2 trees in every clump and from 2 new and 1 old inflorescence on every tree. New inflorescences were defined as having fewer past fruits than unopened flower buds, while old inflorescences had more fruits than unopened flowers. Within each inflorescence we sampled 2 individual flowers that were open that day. All inflorescences had at least 2 open flowers on the day of sampling, and were no more than 3 m above the ground. Both flowers and inflorescences were chosen randomly within these constraints.

For each inflorescence, we recorded the number of opened flowers, unopened flowers, and fruits. For each sampled flower, we counted the mite population with a microscope, removing mites as we counted. We used a nested ANOVA to partition the hierarchical variance in mite abundance; old inflorescences were excluded from this analysis. We used a two-way ANOVA to compare number of mites per inflorescence in old and young inflorescences. Mite abundance was transformed as $\log_{10}(x+1)$ to improve normality.

Results

We found a total of 197 mites in the 48 flowers. The nested ANOVA of 32 young inflorescences indicated high variance among inflorescences within trees (46%) and among clumps of trees (32%, but not significant; Table 1). In contrast, there was little variation among trees within territories (3%) or among flowers within inflorescences (19%).

There was no difference in mites/flower between old and young flowers ($F_{1,16} = 0.66$, $P = 0.74$), nor in mites/inflorescence between old and young flowers.

Discussion

Homogeneity of mite populations among nearby trees (within tree clumps) suggests that individual hummingbirds distribute mites among trees within their territories. They do not seem to distribute mites as evenly between tree clumps, presumably because individual hummingbirds move less frequently between clumps. If so, variance among clumps would become statistically significant with a larger sample size of clumps; as it was, this was the least robust statistical test in the nested ANOVA. The rufous-tailed

TABLE 1. Nested ANOVA results showing the amount of variation in mite abundance explained at each of four levels; between tree clumps, between trees, between inflorescences and between replicate flowers.

Source	Df	MS	F	P	Estimated standard deviation	% Total Variance
Tree clumps	3	0.683	3.02	0.16	0.24	32
Trees (clumps)	4	0.226	1.12	0.41	0.08	3
Inflor (trees, clumps)	8	0.202	5.91	0.0013	0.29	46
Flowers (inflor, trees, clumps)	16	0.034	-	-	0.18	19

hummingbird (*Amazilia tzacatl*) is the most common pollinator of *H. patens* (Bulova 1990) at La Selva, and its territorial behavior may produce spatial patterns in mite distribution that correspond to territory sizes. Trees that differ in hummingbird visitation rates (e.g., those that fall in the center of territories vs. between territories) could be hypothesized to differ in mite abundance. Alternatively, variation in mite abundance among clumps of trees could be due to differences in flowering patterns that influence the resource base for mites.

The high variation in mite populations between inflorescences could result from either frequent or infrequent movement within a tree. If mites are able to travel within trees, they may aggregate in areas of high resource density and leave an inflorescence when its resources decline. If mites do not travel between inflorescences without hummingbirds, inflorescence differences (e.g. visitation rates, age, or resource quantity) could affect the mite populations within them. Initial colonization of inflorescences could be affected by hummingbird preference for certain flowers. For example, hummingbirds may preferentially visit certain tree heights; Gabel et al. (1996 - 97) found mites to be more abundant near the top of trees. Aggregations of inflorescences and nectar differences between flowers may also influence hummingbird visitation patterns, with consequences for mite populations.

Contrary to our expectation that older inflorescences would accumulate larger mite populations, mite abundance was independent of inflorescence. Homogeneity between young and old inflorescences is best explained by frequent emigration and immigration of mites between inflorescences within a tree. A tendency for population accumulation in older inflorescences could also be offset by higher emigration or lower immigration on hummingbirds.

According to Colwell (1995) mites travel daily to new flowers within an inflorescence. This high mobility within inflorescences is reflected by our results, since mite population varied little at this level.

The attributes of this system that seem to affect the distribution of mites may similarly affect other systems of hummingbird mites. Mite demographics on the scale of trees or tree clumps seem to vary according to hummingbird behaviors such as territoriality, flower preferences, and specialization on certain plant species. If host trees allocate resources unequally between inflorescences, or have aggregated inflorescences, there could be consequences for mite distribution patterns that depend on the mobility of mites and how they respond to small-scale differences in habitat. Understanding these dynamic factors could allow reasonable predictions of mite demographic patterns in this and other systems.

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