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Rita de Cássia Guimarães Mesquita and **Carlos Henrique Franciscon**

Projeto Dinâmica Biológica de Fragmentos Florestais
Depto. Ecologia—INPA
Cx. P. 478
Manaus, Amazonas 69083
Brazil

Pollen Consumption by the Hummingbird Flower Mite *Proctolaelaps kirmsei* and Possible Fitness Effects on *Hamelia patens*[1]

HUMMINGBIRD FLOWER MITES LIVE IN THE FLOWERS of a variety of plant species and can disperse between inflorescences via the hummingbird pollinators of these plants. The interaction between hummingbirds, hummingbird flower mites, and the host plants of the mites has been studied extensively (Colwell 1973, 1979, 1985, 1986a, b; Dobkin 1984, 1985, 1987, 1990; Heyneman *et al.* 1991). How these mites affect their host plants, however, has yet to be determined, although the impact was considered to be minimal (Dobkin 1984, Colwell 1985). Dobkin (1984, 1987, 1990) has also suggested that some hummingbird flower mites may act as secondary pollinators. Mites from the genus *Proctolaelaps* (Gamasina: Ascidae) consume floral nectar (Colwell 1973, 1995; Dobkin 1984; Heyneman *et al.* 1991) and pollen (Dobkin 1990, Colwell & Naeem 1994), either of which could reduce the fitness of the host plant. Here, we report that the hummingbird flower mite *Proctolaelaps kirmsei* consumes whole pollen grains of its host plant *Hamelia patens* (Rubiaceae). We also present the first estimates of the amount of pollen consumed by hummingbird flower mites, and its effect on male fitness of the host plant.

Hamelia patens, a hummingbird-pollinated treelet that flowers year round, is common in light gaps at La Selva Biological Station in the Atlantic tropical lowland rainforest in Costa Rica (Hartshorn 1983).
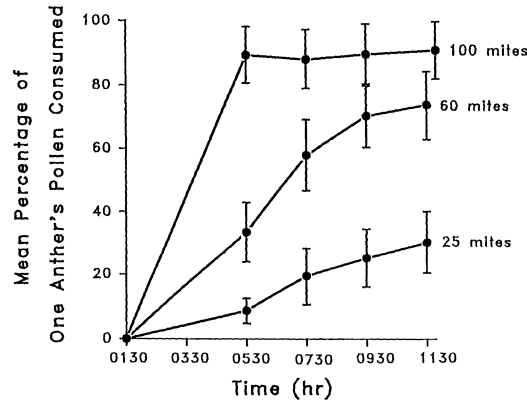
FIGURE 1.   Mean percentages (±1 SE) of one anther's pollen consumption over time for three mite population densities. There were nine replicates per treatment. The point in the upper right was shifted slightly to prevent error bar overlap.

Proctolaelaps kirmsei is a hummingbird flower mite that is monophagous on *H. patens* in the region (Colwell 1986b). At La Selva, *P. kirmsei* enters *H. patens* flowers when the flowers open between 0000 and 0200 hr. Hummingbirds begin visiting *H. patens* at dawn, approximately 0530 hr, and visitation decreases significantly by 1400 hr.

We observed *P. kirmsei* mites consuming the pollen of *H. patens* under a dissecting microscope. To estimate the quantity of pollen these mites can consume, we placed a recently dehisced. *H. patens* anther with three population densities of *P. kirmsei* in plastic footed dishes normally used for tissue culture (Gelman Sciences, 45 mm diam, with absorbent paper insert). Nine replicates were studied over the course of three nights at each of three mite population densities: 25, 60, and 100 mites per dish. Dehisced anthers were used after determining that *P. kirmsei* mites were unable to consume pollen from undehisced anthers. Footed dishes were prepared the day before the experiment by moistening the footed dish paper insert with water and adding the *P. kirmsei* mites. These mites were collected from *H. patens* individuals growing on the station grounds at La Selva. All the mites for one dish were generally taken from one or two flowers to maintain natural sex and age ratios, although we could not be certain that relative proportions of adult females, adult males, nymphs, and larvae were constant across treatments. At approximately 0100 hr on the morning of the experiment, we collected *H. patens* flowers when they were slightly open and their anthers were partially dehisced. At 0130 hr we placed one anther cut from a newly-opened flower into each prepared, footed dish. Anther selection did not take into consideration anther weight or pollen load. The dishes were then kept under natural light and temperature conditions for the first 4 hours and in an air conditioned laboratory subsequently. At 0530 hr, and every 2 hours thereafter until 1130 hr, we estimated by observation the amount of pollen eaten from each anther to the nearest 5 percent.

Pollen consumption as a function of the number of mites and the time elapsed is given in Figure 1. A significant difference among the three treatments at 0530 hr was found (Kruskal-Wallis, df 2, $P <$ 0.001; data after 0530 hr was not statistically analyzed because the data points were not independent). The only significant pairwise comparison was that between the 100 and 25 mite treatment at 0530 hr (Nonparametric Multiple Comparisons by *STP*, $P <$ 0.05, Sokal & Rohlf 1981). No other comparisons differed significantly because estimated data points resulted in large variances.

We calculated that one mite consumes, on average, 1.42×10^{-3} anther's pollen load/hr; due to a lack of information on an anther's pollen load, we did not determine pollen grain consumption/hr. To estimate this consumption rate, each time period of each replicate was used as an independent measure of pollen consumption. Time periods in which consumption had already reached 80 percent of the anther's

TABLE 1.   *Estimation of pollen consumption per flower (proportion of pollen consumed per flower) by natural populations of mites.*

Factor	Lower	Mean	Upper
A. Mites per flower[a]	22	47	72
B. Pollen consumption/mite/flower/hr[b]	0.00020	0.00028	0.00037
C. Pollen consumption/flower/hr			
Minimum interval[c]	0.00818	0.01335	0.01411
Maximum interval[d]	0.00431	0.01335	0.02678
D. Pollen consumption/4 hr[e]			
Minimum interval	0.03274	0.05339	0.05645
Maximum interval	0.01725	0.05339	0.10714
E. Pollen consumption/12 hr[e]			
Minimum interval	0.09821	0.16018	0.16934
Maximum interval	0.05174	0.16018	0.32141

[a] Lower and upper bounds for mites/flower (Colwell, pers. comm.) and pollen consumption/mite/flower/hr using consumption data for one anther's pollen (from the experiments reported here) give the 95% confidence interval for these values from experimental data.
[b] Pollen consumption/mite/flower/hr was calculated as follows: proportion of one anther's pollen eaten/(experimental population of mites × hours elapsed × number of anthers in one flower).
[c] The minimum interval for pollen consumption/flower/hr was estimated by computing the products Line A(Lower) × Line B(Upper) and A(Upper) × B(Lower).
[d] The maximum interval was computed as A(Lower) × B(Lower) and A(Upper) × B(Upper).
[e] Pollen consumption over time was estimated by multiplying the values in Lines C by the appropriate time period.

pollen load at the start of the time period were not used because in such cases pollen scarcity may have affected consumption rate. Applying this estimate of pollen consumption to population data collected by Colwell (1995), and considering that each flower has five anthers, we estimated that the mean *P. kirmsei* population of an *H. patens* flower (47 mites) would consume 5.3 percent of the pollen in a flower (ranging from 1.7–10.7%) between 0130 and 0530 hr, when hummingbirds begin to visit flowers (Table 1, Line D, maximum range). In the 12 hr between first mite entry and the approximate time of cessation of hummingbird visits, an average *P. kirmsei* population could thus consume an average of 16 percent of the pollen in a flower (ranging from 5.2–32.1%, Table 1, Line E, maximum range).

These estimates of pollen consumption may be inflated for several reasons. First, the experimental design did not allow *P. kirmsei* mites access to nectar. This could have increased observed rates of pollen consumption because the mites had no alternative food source. We also did not control for mite demographic ratios in this experiment. Since mites of different ages or sexes may vary in their energetic requirements, this could have affected pollen consumption. In addition, our experiment was a closed system, with no removal of pollen by hummingbirds or immigration/emigration of mites throughout the 12 hr period of each treatment, although hummingbirds would not naturally be a factor until after 0530 hr.

Nevertheless, our estimates of pollen consumption rate by *P. kirmsei* suggest that these mites may decrease the male fitness of *H. patens* by reducing pollen available for dispersal. This is especially important since *H. patens* at La Selva is self-incompatible (Bawa & Beach 1983) and, therefore, mites cannot assist in self-pollination. A possible role for *P. kirmsei* mites in assisting in cross pollination by transporting pollen between *H. patens* individuals requires further study. *Proctolaelaps kirmsei* also consumes large amounts of *H. patens* nectar (Colwell 1995), which could reduce hummingbird visitation rate and, therefore, pollen dispersal rate (Zimmerman 1988). This evidence of pollen and nectar consumption taken together suggests that the mite-host plant interaction of *P. kirmsei* and *H. patens* is not strictly commensal, as previously suggested (Colwell 1985); the mites may actually have a parasitic relationship with their host plant. However, further research may show a more mutualistic interaction if nectar or pollen consumption by *P. kirmsei* mites is found to actually increase rates of outcrossing.

Pollen consumption has been reported previously for mites (Rasmy & Elbanhawy 1975; Dobkin 1984, 1990; Osakabe *et al.* 1986), as well as in numerous insects, such as bees, butterflies, beetles, and,

thrips (Kirk 1985, 1987; Borror *et al.* 1989). Pollen provides higher quantities of nutrients such as amino acids than nectar (Stanley & Linskens 1974). Pollen consumption may be particularly important for female mites (Royce & Krantz 1989), which need protein for egg laying (Gilbert 1972).

Since pollen appears to be an important part of the diet of *P. kirmsei* mites, pollen consumption may play a role in the specialization of hummingbird flower mites on their host plant. Choice experiments examining nectar specificity have shown that hummingbird flower mites prefer nectar from their host plants (Heyneman *et al.* 1991). Evidence for host plant pollen specialization has been found for thrips (Annadurai & Noble Morrison 1987, Kirk 1985), while species of *Heliconius* butterflies differentially exploit pollen of varying sizes (Boggs *et al.* 1981). Future work could determine if pollen specialization by mites influences mite-host specificity.

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Christopher J. Paciorek,[2] Brett R. Moyer,[3] Rachel A. Levin,[4] and Stacey L. Halpern[5]

Carleton College
Northfield, Minnesota 55057, U.S.A.

The Function of Near Neighbors in Decreasing Call Latency Period by the Túngara Frog, *Physalaemus pustulosus*[1]

MEMBERS OF THE NEOTROPICAL FROG, *Physalaemus pustulosus,* aggregate in shallow pools, marshes, and roadside ditches to breed. While there, males produce an advertisement call which functions to space males (Ryan 1983a, b) and attract females (Ryan 1980). However, calls also serve as an acoustic cue to predators (Ryan *et al.* 1981a, b, 1982; Tuttle & Ryan 1981; Tuttle *et al.* 1982). Although chorusing exposes males to greater vulnerability from acoustically-orienting predators (Tuttle *et al.* 1982, Ryan 1985), it also enhances their chance of reproductive success (Rand & Ryan 1981, Ryan 1985). As with other studies (Greer & Wells 1980, Kluge 1981, Woodward 1982, Godwin & Roble 1983), Ryan (1983b) found that the best predictor of reproductive success for túngara frogs was the number of nights a male spent calling. Thus, to cease calling seriously jeopardizes a male's chance of mating and therefore, his fitness.

Predation is believed to represent the strongest selective force opposing chorus-mediated sexual selection by *P. pustulosus* (Ryan *et al.* 1981b, Bucher *et al.* 1982). The presence of predators is detected visually and causes *P. pustulosus* to cease calling, but frogs generally remain in their calling position (Tuttle &