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# THE GEOGRAPHICAL ECOLOGY OF HUMMINGBIRD FLOWER MITES IN RELATION TO THEIR HOST PLANTS AND CARRIERS

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## INTRODUCTION

Hummingbirds, and the plants they pollinate while visiting for nectar, present a richly textured portrait of mutualistic coevolution. The association is found, at least seasonally, from Alaska to Tierra del Fuego on the American Mainland, throughout the Caribbean, on several continental Pacific islands, and on the oceanic Juan Fernandez archipelago.

Throughout most of this range, mites of the genus *Rhinoseius* and certain species of the genus *Proctolaelaps* (Mesostigmata: Ascidae, Lindquist and Evans, 1965) exploit the relationship between hummingbirds and plants. These "hummingbird flower mites" live inside the corolla, usually tubular in shape, of many kinds of hummingbird pollinated flowers. There, they feed on nectar and probably on pollen exudates, mate, and reproduce. Adults and sometimes deutonymphs then board the bill of a visiting hummingbird, enter the nasal cavity of the bird, and later disembark at another flower. On plant species producing dense inflorescences, mites may also move short distances on foot between flowers of the same inflorescence, but ultimately they must disperse with the aid of a hummingbird. The relationship with the birds is almost certainly purely phoretic—these mites apparently exploit birds only for transportation (Colwell, 1973; Colwell *et al.*, 1974).

## BIOGEOGRAPHY

Since flowers adapted for pollination by hummingbirds are visually advertised, usually with bright red or yellow corolla or bracts, all but the most inaccessible epiphytes may be examined in a few hours' field work at a given locality. Supplemented with collections from the nares of netted hummingbirds

(which may be marked and released since the mites are easily extracted by aspiration), the complete local fauna of these mites is relatively easy to assess. Many of the forms involved await formal description, but it is clear that patterns of species richness in hummingbird flower mites parallel closely those of most other organisms, including their host plants and carriers. The diversity of all elements of the system decreases with elevation, latitude, and isolation.

Based on our work in Trinidad, W.I. (which has essentially a "mainland" biota), lowland tropical wet forest supports about a dozen species of these mites, all of which can be found within a few hectares of mixed secondary and mature forest. They occupy the flowers of some 20 plant species in nearly half as many plant families, including both monocotyledons and dicotyledons, and are regularly transported by 7 to 10 species of resident hummingbirds. At Monteverde, Costa Rica (elevation 1400 m), there are 6 mite species living in the flowers of a dozen plant species, carried regularly by 5-6 species of hummingbirds. At 3000 m in Costa Rica (Villa Mills/Cerro de la Muerte), only two species of *Rhinoseius* are found; they are associated chiefly with 4 species of plants, and are carried by 3 hummingbird species (Colwell, 1973). At 4000 m in Ecuador, there is but one species of *Rhinoseius*, whereas on the Chilean altiplano (5000 m) there are none, although hummingbirds are resident.

The complexity of the system also decreases with latitude. Intensive work in California, has turned up only a single, primarily coastal, species of *Rhinoseius*, found no more poleward than about 100 km N of San Francisco. This species has so far been taken from 5 native plant species, all in the genus *Castilleja* (Scrophulariaceae), and from two species of hummingbirds. Likewise, at similar latitudes in coastal Chile, I found but one species of *Rhinoseius*. In neither hemisphere do the mites reach nearly as high latitudes as hummingbirds, nor have we succeeded in finding them east of California in the USA.

Isolation apparently produces similar patterns. On the island of Martinique, W.I., with only 4 hummingbird species (Lack, 1973), a brief survey produced 2 mite species in 4 plant species. There are no hummingbird flower mites on more isolated San Andres Island in the western Caribbean, nor on Masatierra Island in the Juan Fernandez Archipelago 600 km off Chile, with 1 and 2 hummingbird species respectively.

To date, 29 species of *Rhinoseius* and hummingbird-associated *Proctolaelaps* have been described (Baker and Yunker, 1964; Dusabek and Cerny, 1970; Hunter, 1972; Fain *et al.*, 1978; Hyland, *et al.*, in press), based on material taken from 17 hummingbird species and *ca* 6 plant species. Collections under study in my laboratory represent an additional 32 hummingbird species and nearly a hundred plant species in 17 families. On the basis of our current interpretation of host plant distributions and the well-studied zoogeography of hummingbirds, we surmise that no more than 200 species of hummingbird flower mites exist—less than two-thirds the number of hummingbird species, and a tiny fraction of the number of potential host plant species.

## ASSOCIATION OF MITES WITH PLANTS AND BIRDS

This prediction rests in large part on the patterns of association of these mites with host plants and avian carriers in well-studied communities on a local scale. In every locality for which we have adequate data the same pattern appears: with very rare exceptions, each host plant species supports a single species of mite in its flowers, whereas 2 or more mite species very commonly occur together simultaneously in the nares of the birds. (The record is held by an individual *Glaucis hirsuta* in Trinidad, who carried 18 mites representing 6 species when captured.)

Although each host plant species typically has only one species of hummingbird flower mite, a particular mite species often monopolizes more than one species of host plant within a community. For some mite species, such as an undescribed *Proctolaelaps* in Trinidad, *Rhinoseius richardsoni* Hunter in Costa Rica (Colwell, 1973), or the single California species of *Rhinoseius*, the species making up the host plant repertoire are members of only one plant genus or family (the *Proctolaelaps* sp. on 2 species in the Rubiaceae, *R. richardsoni* on 2 species in the Ericaceae, the California species on 3 *Castilleja* species). But taxonomic congruence of hummingbird flower mites and their host plants is hardly the rule. At Monteverde, for example, *R. colwelli* Hunter occupies 5 host plant species, spanning 2 orders of dicots (*Centropogon* in Campanulales, *Columnea* in Scrophulariales) and 2 orders of monocots (*Bomarea* in Liliales, an undetermined bromelaid in Bromeliales). The California species reproduces successfully in the flowers of introduced African plants of the monocot genera *Knifophia* and *Aloe* (Liliaceae) in urban gardens as well as in native *Castilleja*. The native host plants of the coastal Chilean species include both monocots (*Puya*) and dicots (*Lobelia*).

Likewise, *Proctolaelaps* and *Rhinoseius*, as genera, show little regard for host plant systematics. In Trinidad, a *Proctolaelaps* species and 2 *Rhinoseius* each monopolize a different species of the monocot genus *Heliconia* (Musaceae), while 2 other *Proctolaelaps* species and another *Rhinoseius* species each occupy one or more species in the dicot family Rubiaceae. In Costa Rica, Guatemala, and Mexico, plants of the genus *Centropogon* are occupied by *Rhinoseius* spp., while *Centropogon* in Trinidad and Martinique are inhabited by *Proctolaelaps* spp.

The rule of host plant monopoly by a single mite species has some intriguing exceptions. There is at least one case of geographical replacement over a very short distance. The plant *Cephaelis muscosa* (Rubiaceae) occurs on the north-facing slope of Trinidad's Northern Range, as well as in the Arima Valley on the south-facing slope; two very distinct species of *Rhinoseius* occupy the flowers of this plant on the two sides of the crest. We also have unequivocal evidence of an apparently permanent temporal replacement (to be reported in detail elsewhere): a *Rhinoseius* species (undescribed) was replaced by *Proctolaelaps belemensis* Fain, Hyland, and Aitken in the flowers of the

ginger *Costus spiralis* throughout the Arima Valley in Trinidad, after a very unusual climatic event interrupted the normally continuous flowering of the plant. Opportunity for such replacements is afforded by rare "mistakes" in host plant discrimination by the mites. Locally, about one individual mite in every 60 occurs in a "wrong" host plant, sometimes mixed with the characteristic mites of the host plant, sometimes alone. At Monteverde, Costa Rica, however, we have good evidence of long-term coexistence between *Rhinoseius wetmorei* (Baker and Yunker) and an undescribed species of *Proctolaelaps* in the flowers of a species of *Heliconia*. This case presents an enticing subject for further study.

In every well-investigated locality, there are plant species with ideally ornithophilous flowers (in the sense of Faegri and Van der Pijl, 1966), similar in every obvious respect to typical mite host flowers, which nonetheless never support mites. The lack of mites is clearly not for want of opportunity. To give only one example, the plants *Heliconia wagneriana* and *Pachystachys coccinea* (Acanthaceae) often grow side by side in dense second-growth vegetation in Trinidad, where they are visited sequentially by the hummingbird *Glaucis hirsuta*. The mite whose primary host plant is the *Heliconia* (*Proctolaelaps belemensis*) abounds both in its flowers and in the nasal passages of the bird (where other species of hummingbird flower mites are often found as well)—yet careful dissection and examination of hundreds of *Pachystachys* flowers has never turned up a mite of any species, or any other arthropod. The mites obviously avoid *Pachystachys*.

Miteless hummingbird flowers appear to follow plant taxonomic lines. This suggests that "mitelessness" is based either on chemical or morphological features conserved in certain plant lineages. We are currently approaching the problem by looking for common traits within and among these phyletic lines that could affect their suitability for mites, examining both chemical and biophysical properties of the intrafloral environment. If the nectar of miteless flowers turns out to be noxious or toxic to mites (and to other arthropods, which may be the primary selection pressure), the compounds responsible could be of considerable practical interest, since they would have to be non-toxic to birds, and perhaps to mammals as well.

### HOST PLANT DISCRIMINATION

It is evident from the distribution of sympatric species of hummingbird flower mites on their host plants, "miteless" plants, and carriers that the mites are capable of accurately detecting the proximity of their own host plant from within the nasal cavity of a hummingbird. In the case of flowers with small nectar rewards (e.g. *Castilleja*, *Hamelia*, *Macleania*), this means that mites have 2 or 3 seconds to detect the flower, run down the bird's bill to a point of contact with the flower, and disembark. If we generously assume that the 0.5

mm mite must run only 20 mm (the distance is 40-70 mm for many hummingbird species) in 3 seconds, then it runs about as fast as a cheetah, for its length. Similar arguments apply to the detection of visiting hummingbirds by mites within the flower, although species discrimination is probably not relevant.

Discrimination among flowers by mites in the bill is almost certainly by olfaction, although other cues are available: orientation of the bill during feeding corresponds to the angle of presentation of the flower, which differs among certain plant species, and there may be other more subtle mechanical differences in the bird's behavior at different flowers. Fairly specific olfactory discrimination has been demonstrated experimentally for a number of allied mesostigmatic mites (e.g. Camin, 1953; Farish and Axtell, 1966; Jalil and Rodriguez, 1970), including one case in the genus *Proctolaelaps* itself (Egan *et al.*, 1975; Egan, 1976). Crude choice experiments with two coexisting species of Costa Rican *Rhinoseius* (Colwell, 1973) and with certain Trinidad species show that the mites prefer contact with floral tissue of their own host plant to tissue of other flowers, when left to explore small enclosures containing tissue samples from virgin flowers (i.e. flowers not previously occupied by mites) of both plants. Further experiments are underway to confirm or refute the use of purely olfactory cues, to explore the cues in detail, to test for differential attraction to fresh and already-occupied flowers, to seek ontogenetic and sexual differences among mites in behavioral responses, and to test for conditioning or "induction" of host plant preference (in the sense of Jermy *et al.*, 1968; Huettel and Bush, 1971).

A persuasive logical argument for olfaction is the undeniable fact that a mite inside a bird's nasal passages is continually bathed in a rapidly reciprocating stream of air as the bird respire, which may well act on an extremely effective "odor pump," carrying up-to-the-moment chemical information on the hummingbird's foraging activities. In fact, the occupation of the nasal passages by these mites, instead of the feathers of the head (for example), may have more to do with exploiting the respiratory system as an odor pump than with protection from the elements.

### COMPETITION AND COEXISTENCE

The ecological interactions among different species of hummingbird flower mites in relation to floral resources are quite unlike those of other phytophagous arthropods. In particular, interference competition between species is apparently the dominant organizing force in local assemblages of these mites. There are few documented examples of the importance of behavioral aggression between competing species of phytophagous arthropods (Rathcke, 1976), although I believe the phenomenon may prove to be far more common than we now realize. The closest parallels to the present case of which I am aware involve the "cactiphilic" *Drosophila* studied by Heed and

coworkers (Fellows and Heed, 1972; Heed and Jensen, 1966), and interactions among heliconine butterflies discussed by Gilbert (1977, 1978). The role of interference mechanisms in restricting resource use by close competitors is discussed in formal terms, and the extensive relevant literature is reviewed by Colwell and Fuentes (1975).

The role of interspecific competition and behavioral interference among hummingbird flower mites was first documented for the two *Rhinoseius* species present at Cerro de la Muerte, Costa Rica (Colwell, 1973). Experimental introductions showed that each is manifestly competent to survive and reproduce in flowers of the other's host plant, and has access to them regularly, yet there is no overlap whatsoever in actual utilization of host species. Staged interspecific encounters led to prolonged conflicts, with males of one of the species (*R. colwelli*), attacking and killing females and males of the other (*R. richardsoni*), suffering considerable mortality themselves as a result of defensive maneuvers by their intended victims. Chelicerae and mouthparts play no part in the carnage, and the survivors make no attempt to feed on dead or disabled mites. I concluded (Colwell, 1973) that the rigid fidelity of each species to its own host plants was a consequence of the unfriendly, possibly lethal reception a wayward mite would receive upon entering a flower occupied by another species.

Adult males of most hummingbird flower mites are armed with opposable, raptorial, spine-like setae on legs II (many *Rhinoseius* spp.); with greatly enlarged dorsomedial setae (mites of the *R. richardsoni* group); or with enlarged, highly sclerotized setal "spurs" (used as a fighting cock uses his spurs) on legs IV (all known *Proctolaelaps* species associated with hummingbirds, but none in the rest of the genus). It is not yet clear to what extent these weapons are the result of sexual selection. Based on limited observations interactions between conspecific males of either genus are generally aggressive, but we have observed no damaging encounters. Much more comprehensive experiments and observations are planned to evaluate the role of fighting among conspecific males of varying degrees of genetic relationship (male polymorphism adds further complexity). Other cases of agonistic behavior in mites are recorded by Lee (1969), Potter *et al.*, (1976), and Woodring (1969), while Hamilton (1978) provides a rich source of ideas and parallels in other organisms.

Coexistence of potentially or actually competing species, and the number of such species in a local assemblage are intimately related concerns. In every case we have examined, to date, there are more species of host plants exploited than the number of species of hummingbird flower mites occupying them. Why are there not more species of these mites—say, one for each species of host plant? The systematic relationships among plants comprising the host plant repertoire of the polyphagous species do not offer a convincing explanation, as the phyletic affinities between host plants of different coexisting species of the mites are often closer than relationships among plants *within* repertoires. Why, on the other hand, are there not fewer mite species present in local

assemblages, or even a single, superaggressive species? The actual host repertoire of each species is apparently determined by the interaction of two factors: 1) the structure of the matrix of flower-to-flower transition probabilities between host plant species for potential mite transfers, which is determined by the foraging patterns of the hummingbird species; and 2) the seasonal fluctuations and long-term predictability (Colwell, 1974) in the structure of this matrix, which is determined by the phenology of the host plants and its year-to-year variation.

Simply stated, the principal community "assembly rule" (Diamond, 1975) for these mites is that every *minimum* subset of the available pool of host plant species that would provide a sufficiently reliable resource base potentially supports a mite species. The minimum level of reliability should require that flowers of at least one host species in the subset be available in each part of the year, for at least as many consecutive years as it takes for the immigration or evolution of a distinct mite species associated with that resource subset.

Actual host-plant repertoires range in complexity from a single plant species that flowers all year; to 2 sympatric plant species with overlapping but largely asynchronous flowering periods; to many briefly-flowering, sympatric plant species that together span the annual cycle; to the asynchronous, allopatric sets of plant species exploited by the California *Rhinoseius*, a species associated with latitudinally migrant hummingbird. In short, it appears that biogeographical patterns among hummingbird flower mites are the result of a complex interaction between the temporal patterns of flowering in potential host plants and the spatial patterns of both local and regional movements by their avian carriers.

## SUMMARY

Mites of the genus *Rhinoseius* and certain species of *Proctolaelaps* feed and reproduce in hummingbird pollinated flowers, and are carried between flowers on hummingbirds. The organization and diversity of local species assemblages of these mites is dominated by interspecific competition for phenologically reliable sets of host plant species, each relatively isolated from other such sets by local avian foraging patterns, each monopolized and aggressively defended by a mite species. The number of coexisting species of these mites decreases with latitude, elevation, and isolation. Their phylogeny follows neither plant nor hummingbird lineages.

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## REFERENCES

- Baker, E. W., and Yunker, C. E. (1964). *Ann. Entomol. Soc. Amer.* **57**, 103-126.
- Camin, J. H. (1953). *Chicago Acad. Sci. Spec. Publ. No. 10*. 75 p.
- Colwell, R. K. (1973). *Amer. Natur.* **107**, 737-760.
- Colwell, R. K. (1974). *Ecology* **55**, 1148-1153.
- Colwell, R. K., Betts, B. J., Bunnell, P., Carpenter, F. L., and Feinsinger, P. (1974). *Condor* **76**, 447-452.
- Colwell, R. K., and Fuentes, E. R. (1975). *Ann. Rev. Ecology and Systematics* **6**, 281-310.
- Diamond, J. M. (1975). In "Ecology and Evolution of Communities," (M. L. Cody and J. M. Diamond, eds.) Belknap, Cambridge, Mass.
- Duasbek, F. and Cerny, V. (1970). *Acarologia* **12**, 269-281.
- Egan, M. E. (1976). *J. Comp. Physiol.* **109**, 69-89.
- Egan, M. E., Barth, R. H., and Hanson, F. E. (1975). *Nature* **257**, 788-790.
- Faegri, K., and Pijl, L. Van der (1966). Pergamon Press. Toronto. 248 p.
- Fain, A., Hyland, K. E., and Aitken, T. H. G. (1977). *Acta Zool. et Pathol. Antverpiensis* **69**, 99-164.
- Farish, D. J., and Axtell, R. C. (1966). *Ann. Entomol. Soc. Amer.* **59**, 165-170.
- Fellows, D. P. and Heed, W. B. (1972). *Ecology* **53**, 805-808.
- Gilbert, L. E. (1977). In "Le comportement des insectes et les signaux issus du milieu trophique." (V. Labeyrie, ed.), CNRS, Paris.
- Gilbert, L. E. (1978). In "Analysis of ecological systems." (D. J. Horn, R. D. Mitchell, and G. R. Stairs, eds.) Ohio State Univ. Press.
- Hamilton, W. D. (1978). Univ. of Georgia.
- Heed, W. B., and Jensen, R. W. (1966). *Dros. Inf. Serv.* **43**, 94.
- Huettel, M. D., and Bush, G. L. (1971). *Entomol. Exp. Appl.* **15**, 465-480.
- Hunter, P. E. (1972). *J. Georgia Entomol. Soc.* **7**, 27-36.
- Hyland, K. E., Fain, A., and Moorhouse, A. S. (1978). *J. N. Y. Entomol. Soc.* In press.
- Jalil, M., and Rodriguez, J. G. (1970). *Ann. Entomol. Soc. Am.* **63**, 738-744.
- Jermey, T., Hanson, F. E., and Dethier, V. G. (1968). *Entomol. Exp. Appl.* **11**, 203-211.
- Lack, D. (1973). *Evolution* **27**, 326-337.
- Lee, B. (1969). *J. Aust. Entomol. Soc.* **8**, 210.
- Lindquist, E. E., and Evans, G. O. (1965). *Mem. Entomol. Soc. Can.* **47**, 1-64.
- Potter, D. A., Wrench, D. L., and Johnston, D. E. (1976). *Science* **193**, 160-161.
- Rathcke, B. J. (1976). *Ecology* **57**, 76-78.
- Woodring, J. P. (1967). In *Proceedings, 2nd Intl. Cong. Acarology*, p. 433-440.