NATURAL HISTORY

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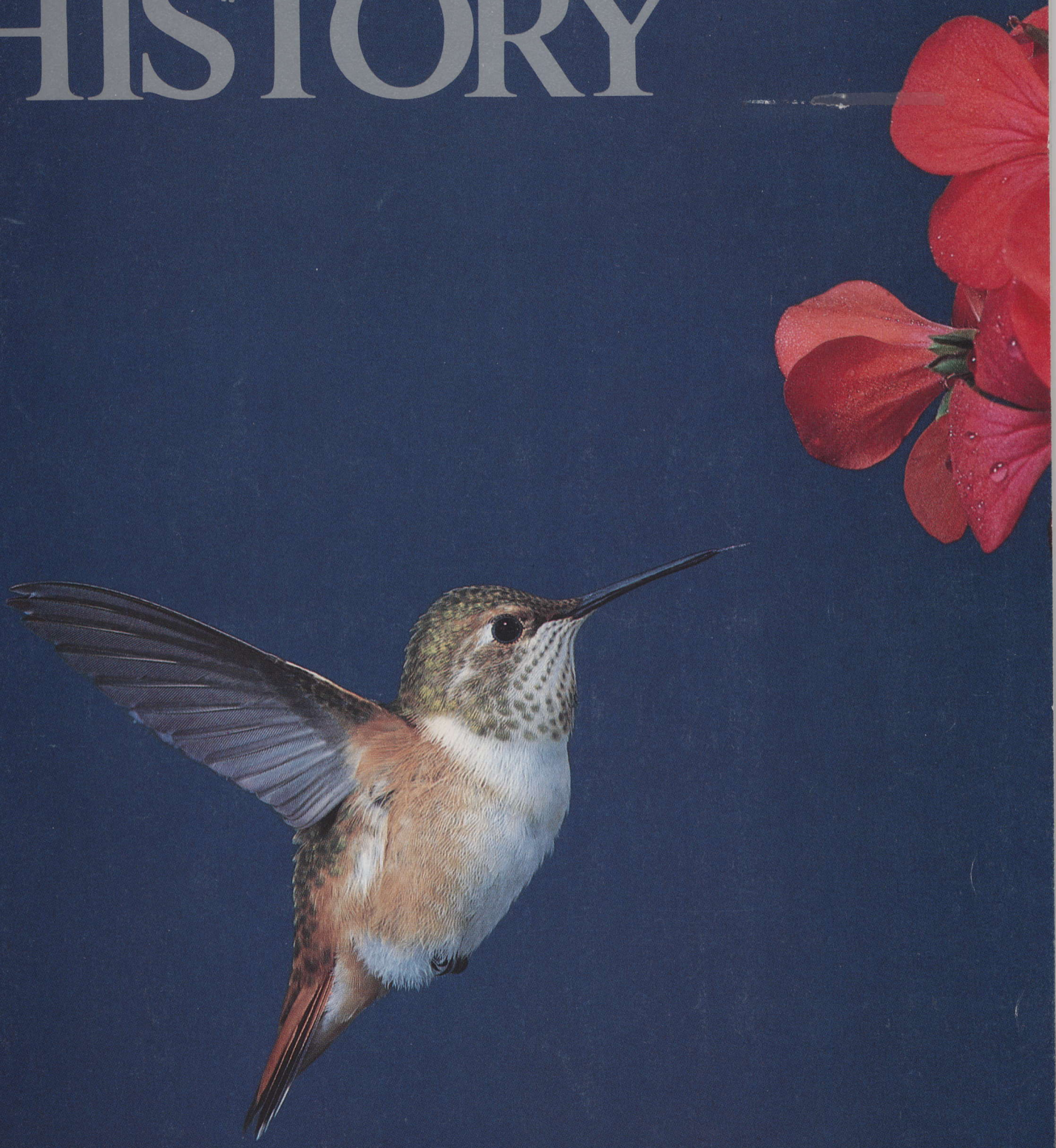

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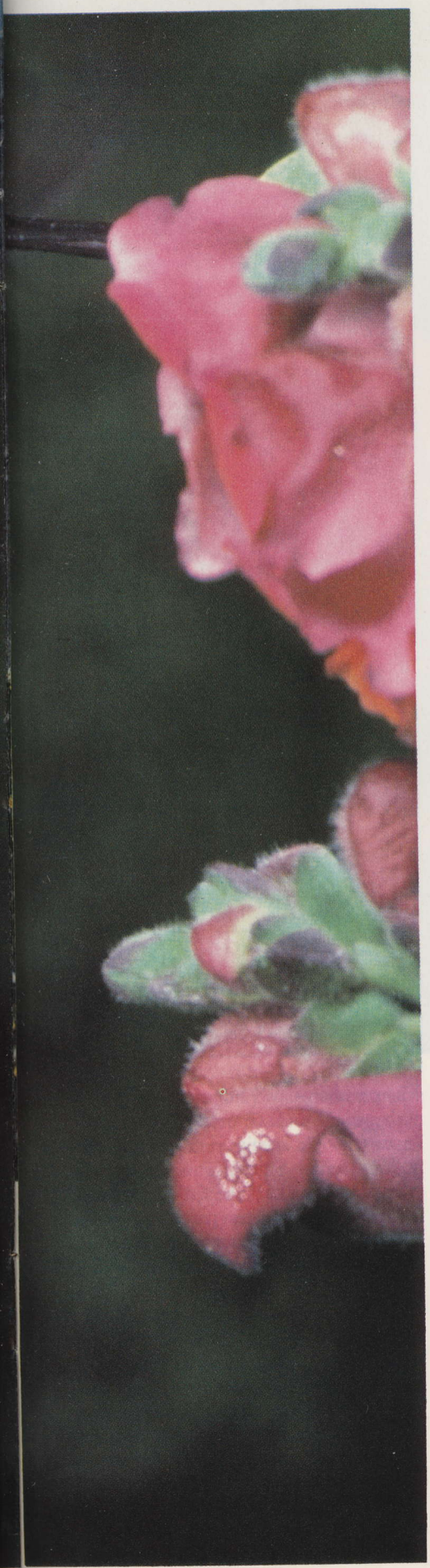


A male Rivoli's hummingbird
Bob and Clara Calhoun; Bruce Coleman, Inc.

Stowaways on the Hummingbird Express

Nectar-sipping mites that hitch rides on hummingbirds are very choosy about where to get off

by Robert K. Colwell

To our eyes, the red and orange flowers of hummingbird-pollinated plants stand out in the deep shade of the rain forest like rubies on green velvet. To hummingbirds—whose range of color vision is even greater than ours—the contrast must be just as striking. But the rich world of odors is closed to hummingbirds, and our own poor olfactory equipment is little better.

The perennial human daydream to fly like a bird surely has its roots, in part, in the similarity of our sensory worlds. Who would not welcome the chance to be a tropical hummingbird for a day, given proper training? The exhilaration of fast and agile flight, the high-calorie diet, the beauty of the forest—all this we can envy and imagine.

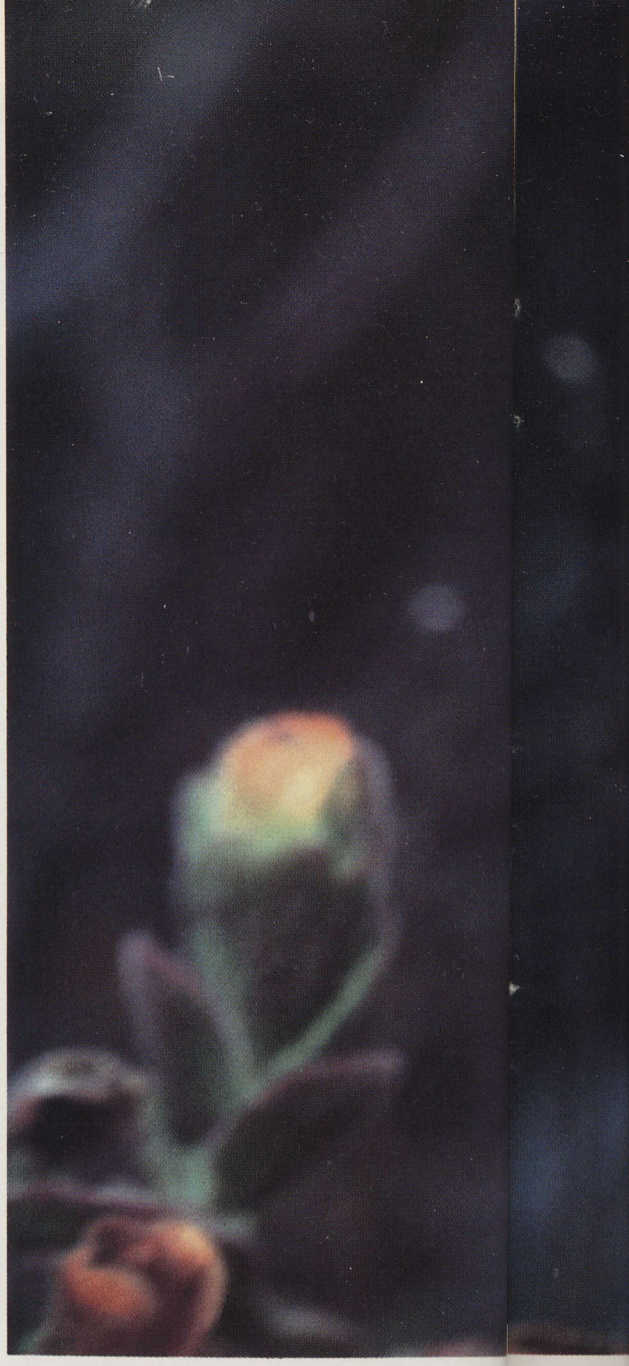
But now enter the same world on a different scale. Imagine yourself a mite just twice the size of the period at the end of this sentence. You are having a breakfast of nectar and pollen with your family and neighbors inside the orange-red, inch-long flower of a *Hamelia* plant at the edge of a rain forest clearing. You have no eyes and need none, because your four pairs of legs and your body are equipped with precisely arranged, minute hairs, called setae, that provide exact information about your special world. When you meet another mite in your flower, a quick touch with your foreleg tells you its sex and age, and the rate of encounter tells you how many other mites share your flower. You can even "smell" with some very special setae on the tips of your forelegs. Although neither hummingbirds nor humans can smell your flower, it has a distinct and very important fragrance for you. It smells like home, and home means safety, your own kind, mates, and food.

Suddenly you sense the vibrant approach of a hummingbird outside the flower. A half second later a bill sixty times the length of your body is thrust deep into your home and you must dodge the rapidly licking tongue that is draining your larder. In the one to five seconds before the hummingbird leaves for the next flower, you must make a decision that will affect the rest of your life. What are the future prospects for food, mates, and the welfare of your offspring on this branch of this *Hamelia* plant, compared with the chance that a risky journey will turn up better prospects elsewhere?

If you decide to leave, you dash up the bill of the visiting hummingbird and run into its nostril, and the odyssey begins. On board, inside the bird's nasal cavity, the accommodations are primitive. There is nothing to eat or drink. The place is crawling not only with your own kind but also with aliens of other species of hummingbird flower mites, hitching rides to their own promised land. You will know them by their smell, perhaps, and by the strange arrangement of their setae—long where yours are short, straight where yours are so beautifully curved.

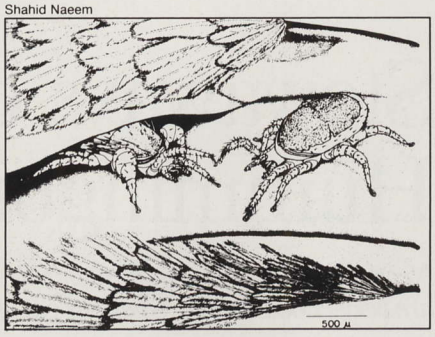
But the ventilation on this feathered freighter is absolutely first-class. A hundred times every minute or so, a hurricane of fresh air rushes in. More than just a source of oxygen, the hummingbird's respiration acts as an odor pump, constantly updating information on the outside world. What you await is that familiar smell—the odor of your own host plant,

David S. Dobkin



Mites that live only in hummingbird-pollinated flowers travel to distant blossoms by climbing on a bird's bill and taking shelter in its nostrils. Below: A Rhinoseius colwelli *mite crouches within a bird's nostril while another stands by. Right: This California species of Indian paintbrush supports a contingent of* R. epoecus *mites, a species discovered recently.*

Shahid Naeem



Hamelia. The hummingbird may visit the flowers of half a dozen other plant species, and the aliens on board may come and go, but you wait until the scent of *Hamelia* tells you the bird has its bill in the flower. You have one to five seconds to disembark. With luck, if you are a male, you will find females in need of a mate in your new home; if you are a mated female, you will find that a nearly empty flower, with a male or two present to replenish your supply of sperm, would be an ideal place to start your own dynasty.

A primary research journal would probably scorn the shamelessly dramatic account you have just read. Yet every good naturalist learns to "see into the life of things," as Darwin put it, in part by identifying with the organisms studied. Even botanists do it. The danger, of course (and the reason for the taboo on exposing such musings in scientific print), is that we may unwittingly and inappropriately impose human capabilities, limitations, or even values on nonhuman organisms. For example, a mite certainly makes a "decision" in a very different sense than we do.

Fortunately, our understanding of the biology of hummingbird flower mites rests on more than daydreams. I first stumbled on the existence of these mites and guessed their relationship with flowers and hummingbirds in 1969 in the Costa Rican highlands. In succeeding years, the project that began at that time broadened geographically and scientifically as my colleagues and I developed new techniques of study and a deeper understanding of the daily lives of hummingbird flower mites. Peter Feinsinger, of the University of Florida, an authority on tropical hummingbirds, has collaborated generously, and my doctoral students, David Dobkin, Amy Heyneman, and Shahid Naeem, have poked their own noses into the flowers of *Hamelia* and other hummingbird plants in intensive field research in California, Mexico, Costa Rica, and Trinidad. Barry OConnor, of the University of Michigan, has scientifically described and named many of the new mite species we have found.

Hummingbird flower mites are freeloaders. As far as we can tell, they do nothing of note for their host plants or for hummingbirds. Yet their survival depends on the interdependence of birds and flowers, which are mutually linked by the exchange of nectar for pollination service. A closer look at hummingbirds and plants reveals the way this network operates.

Within the limits of a very consistent body plan and behavioral repertoire, the more than three hundred species of hummingbirds present an astonishing diversity of body size, coloration, plumage, and bill shape and length. They are strictly a New World group, with outlying species found, at least during the breeding season, from Alaska to Tierra del Fuego. A few acres of tropical forest can contain a dozen or more abundant hummingbird species. The plant species that hummingbirds pollinate number in the thousands and represent dozens of plant families.

Hummingbird flower mites are found nearly everywhere there are hummingbirds. So far, we have recorded the mites from more than one hundred host plant species and from more than sixty hummingbird species, and these records represent only very spotty coverage of the range of hummingbirds. But even where the mites have been studied, not every species of hummingbird-visited plant supports them. Hummingbird-pollinated species in some plant families never have these mites (for example, the mallow, mint, and fuchsia families), and some nearly always do (tropical species in the lobelia, blueberry, and many other families).

Hummingbird flower mites belong to two closely related groups, the genus *Rhinoseius* and a large lineage within the genus *Proctolaelaps*. The dozens of species we have studied so far are nearly all new to science; one or two hundred species are perhaps still undiscovered. As far as we know, only one species resides seasonally in the United States. This *Rhinoseius* mite summers along the California coast in the flowers of Indian paintbrush (*Castilleja*). It spends the winter in the mountains of west-central Mexico with California migrant hummingbirds and in recent times, in the flowers of African aloes in central California gardens. Shahid Naeem and I have named the species *epoecus*, from the Greek meaning "a sojourner from a foreign land." The greatest diversity of hummingbird flower mites is in lowland tropical forests, where a dozen or more species often share an acre.

Hummingbird flower mites are very discriminating in regard to their host plants. In the lowland tropics, each species

typically occupies only a single host plant species, which blooms all year. By contrast, mite species at high elevations and high latitudes, where flowering is more seasonal and less reliable, usually have a choice of two or more host species that they often use sequentially. In most cases there is only one species of hummingbird flower mite per plant species, but in a few cases there are two—always a *Rhinoseius* species and a *Proctolaelaps* species, never two species of the same mite genus.

Host plant species differ strikingly in seasonal flowering pattern, the size and arrangement of flowers, the amount of nectar each flower produces, and the longevity of each flower (half a day to more than a week). These differences in host plant biology profoundly affect the mites.

Life begins for a hummingbird flower mite as an egg nearly one-fourth the volume of its mother's body. (Nonetheless, she can produce half a dozen eggs in a few hours.) Some species whose host plants have long-lived flowers lay their eggs right in the nectary of the flower, where they are bathed in nectar for a few days until they hatch. Mites that live on plants whose flowers open in the morning and drop later the same day lay their eggs among bracts or beneath leaves near the flowers. The eggs hatch into active six-legged larvae; this stage is quickly followed by two active eight-legged nymphal stages that precede adulthood. The mite goes from egg to breeding adult in about a week.

While it is easy to find mites by cutting open their host flowers, it is hard to watch them within the bloom unobtrusively. Fortunately, as long as they have their flowers, even on a cut branch in a vase of water, they seem not to notice being moved into the field laboratory for scrutiny. With a fiber-optic light, which produces intense light but very little heat, we can illuminate their miniature world for study with a dissecting microscope, apparently without disrupting them. Most of the behavior we observe in this way is repeated in glass capillary tubes with nectar.

The inside of a tubular flower is a fairly complicated place. Adult mites tend to congregate near the nectaries, in the base of the flower in most species, while the nymphs and larvae spend more time on the stamens and style. During all these stages the mites drink nectar, which contains proteins, fats, and amino acids, as well as sugars.

Proctolaelaps kirmsei adults avidly

Although imperceptible to humans and hummingbirds, the scent of a host plant, such as Hamelia patens, *below, prompts mites on a bird's bill to disembark. In field and laboratory, mites consistently recognize the odor of the host plant and prefer its nectar to equally nourishing substitutes.* Centropogon cornutus *produces exceptionally long-lived flowers, right. While other mites must lay their eggs on the leaves or bracts of their host plants, those that live on* Centropogon *lay eggs in the nectar, and the young hatch and mature within the blossom itself in a week's time.*

Robert K. Colwell

"process" pollen grains for a short period after entering a new flower of their host plant, *Hamelia patens*. The flowers of this plant open shortly after midnight (at least in Costa Rica), long before its pollinators become active at dawn. The mites rush in as soon as the flower opens. They immediately begin a frenzied attack on the pollen packed in the anther sacs, using a pair of short appendages to move one grain at a time over their mouthparts. We suspect that the mites are removing nutritious substances that coat the pollen grains. In terms of relative size, it would be as if you had before you a large bin of basketballs covered with peanut butter and honey, which you picked up one by one to lick.

When an individual flower has fully bloomed, the mites are able to leave it on foot to lurk about the same flower cluster until the next flower opens. Passage between clusters, however, seems usually to require the unwitting assistance of a hummingbird. In field experiments, uninhabited flower heads closed to mite foot traffic but exposed to hummingbirds are quickly populated by mites.

Hitching a ride on a hummingbird requires timing and agility. Taking the length of the mite as two-hundredths of an inch (some species are smaller), the bill length of the bird as about one and a quarter inches (some are longer), and allowing a generous five-second feeding visit by the bird, the mite must run as fast as a cheetah, for its size, to make it into the nostril before the bird moves on. (In other words, both hummingbird flower mites and cheetahs can run about twelve body lengths per second. We have actually clocked the mites at this speed in wind sprints around the lip of a test tube.)

"Deplaning" presents new difficulties. Before racing down the bill into a flower, the mites must first determine whether or not the flower is of their own host species. Our records for many thousands of mites show that no more than one in two hundred has disembarked in the wrong flower. Yet many hummingbirds visit several species of plants in an hour's time, and often each plant has its own species of hummingbird flower mite. How do they know when to get off?

By far the most likely source of information is odor. With the bird's bill in a flower, mites in the bird's nostrils could quickly determine the species of the flower and act accordingly, based on odors provided by the bird's rapid respiration.

Robert K. Colwell

Our evidence is indirect but convincing.

Given a choice of nectars in a T chamber, hummingbird flower mites choose nectar from their own host plant species. In Trinidad, for example, we offered the mite *Proctolaelaps kirmsii,* which lives in the flowers of *Hamelia patens,* a choice between nectar from uninhabited flowers of *Hamelia* and equally "virgin" nectar from flowers of *Centropogon cornutus,* the home of another mite. We put a drop of *Hamelia* nectar in the tip of a tiny glass capillary tube and a drop of *Centropogon* nectar in another. The open ends of the two tubes lead into an enclosed three-way "intersection" in a small block of acrylic. The third entrance to the intersection (the leg of the T) is another capillary tube with a mite from *Hamelta* in it. Twenty identical chambers were simultaneously set up. We kept track of the location of each mite in its chamber over a period of hours.

The mites in this experiment strongly preferred the nectar of their natural host plant—nearly all of them ended up in the tubes with *Hamelia* nectar, rather than in the tubes with "alien" *Centropogon* nectar. But when we put mites from *Centropogon* (another species, *Proctolaelaps glaucis*) in the same setup, they preferred *Centropogon* to *Hamelia* nectar. The mites are even more consistent in nature, where they are presented with one host plant odor at a time in a moving stream of air rather than two odors in still air.

Many species of hummingbird flower mites from Trinidad, Mexico, Costa Rica, and California have participated in our T-chamber experiments. A consistent pattern emerges. Each species prefers its own host nectar to the nectar of other species of mite plants. The mites also choose their own host nectar over sugar water of the same concentration and over nectar from miteless plants, that is, hummingbird-visited species that never support hummingbird flower mites. Amy Heyneman, who has analyzed dozens of nectars from both kinds of plants, has found biochemical differences between the two groups of nectars. Our field experiments, however, show that, within broad limits, the host nectar of one mite species is nutritionally acceptable to other mite species in the same habitat. We forced mites to live in newly opened, unoccupied host flowers of a plant normally inhabited by another mite species. A nylon mesh bag excluded hummingbirds and thereby prevented escape of the mites, many of which survived to reproduce successfully.

Why, then, are the mites so particular about the host plants they actually use? If every flower were densely populated with mites, competition among mite species for nectar might explain the adherence of each mite species to certain host plant species. However, the density of mites is quite low, relative to the nectar available, so competition between mite species is not a likely explanation for the very rigid plant–mite affiliation. Another possible explanation is that each mite species aggressively excludes "aliens" from its host plant. But most pairs of mite species get along quite amicably in laboratory tests. Moreover, certain pairs of species share the same host plant on a regular basis.

The explanation I favor for host allegiance is that hummingbird flower mites use host plants as a way of finding mates. Once a particular host plant species becomes the most popular jumping-off place for a given mite species, the mating success of mites that get off elsewhere will suffer, on average. Because in these species both males and females must mate many times to achieve their maximum reproductive potential, mites of either sex that disembark at the correct host plant will leave more descendants.

If I am right in thinking that plant affiliation evolved among hummingbird flower mites in large part through differences in

mating success, then host affiliation can be viewed as the product of sexual selection. Darwin first drew the important distinction between evolutionary changes based on inherited differences in survival rate and in the potential for reproduction, the process he called natural selection, and evolutionary changes based on differences in mating success in itself, a phenomenon he termed sexual selection.

Darwin believed that natural selection and sexual selection could, at times, conflict. Some physical and behavioral traits of animals are thought to have evolved largely through their role in courtship and mating, perhaps even at the cost of decreased survival. Well-known examples include the beautiful but cumbersome peacock's tail, the elaborate and seemingly arbitrary bowers constructed by male bowerbirds, and the magnificent songs of thrushes, which can attract predators as well as mates.

Just as more elaborate peacock tails presumably increased their owners' success in attracting peahens, strong allegiance to a particular host plant species boosted the mating success of hummingbird flower mites. Like other sexually selected characters, host affiliation involves a degree of arbitrariness and probably carries an element of risk as well. For a mite that has specialized on a single host species, even a brief flowering failure in the plant could mean the mite's extinction.

My co-workers and I suspect such extinctions must be rather common, on the scale of mere thousands of years. However, unless the flowering of all host species were to fail simultaneously from California to Chile and throughout the New World tropics—a most unlikely event—the future of hummingbird flower mites as a group seems assured. Their dynamic evolution all but guarantees that newly evolved species will eventually replace extinct ones, even in the same host plants. Some species even thrive harmlessly on the nectar of garden plants (including African aloes in California) along with the hummingbird visitors that delight the gardener. Despite the risks that they face daily, stowaway mites are well suited to life on the run. □

A long-tailed hermit hummingbird, bearing mites on its bill, samples the nectar of a scarlet passionflower. The mites will remain on the bird until it arrives at the "right" flower. By sharing an affinity for particular host plants, mites of the same species may expedite mate finding and improve their reproductive success.

Michael Fogden