

Colwell, R. K. 1986. Population structure and sexual selection for host fidelity in the speciation of hummingbird flower mites. Pp. 475-495 *in* Karlin, S. and E. Nevo (eds.). Evolutionary Processes and Theory. Academic Press, Orlando, FL.

POPULATION STRUCTURE AND SEXUAL SELECTION FOR HOST FIDELITY IN THE SPECIATION OF HUMMINGBIRD FLOWER MITES

R. K. Colwell

Department of Zoology
University of California, Berkeley
Berkeley, California 94720

ABSTRACT

The rigid patterns of affiliation of hummingbird flower mites (Acaridae: *Proctolaelaps* and *Rhinoseius*) with their host plant species may be more a result of selection for mate-finding than for food-finding. A simple model shows that, at low densities, a significant fitness advantage due to differential mating success is enjoyed by individuals that preferentially seek out the host species favored by prospective mates. Selection for host fidelity by this frequency-dependent mechanism can be viewed as a form of sexual selection. The effects of predispersal mating, relative density, and sex ratio alter the quantitative outcome, but not the qualitative effect. Selection for host fidelity (obligate or learned) very likely plays an important role in the extinction and speciation of hummingbird flower mites. Taking into account population structure, conditions appear favorable for local speciation.

I. INTRODUCTION

When resources do not limit population density, mate-finding may be a more important focus of selection than food-finding, particularly among mobile species with highly subdivided and ephemeral populations. In such

species, differential mating success--the basis of sexual selection--can sharply focus host or habitat affiliation.

The effect of this phenomenon on community structure is the principal subject of a previous paper (Colwell, 1985b), where I discussed the history of ideas about selection for mate-finding in relation to habitat and host fidelity. Here, I present a model that attempts to capture the essence and explore a few of the ramifications of the "host fidelity hypothesis," especially its implications for processes of extinction and speciation.

The inspiration for this work came from my efforts to understand the distribution and patterns of host affiliation among hummingbird flower mites (Colwell, 1973, 1979, 1985a, 1985b). The flowers of many species of hummingbird-pollinated plants are inhabited by mites of the genera *Rhinoseius* and *Proctolaelaps* (Ascidae). On their host plants, these mites feed on nectar and on pollen substances, mate, and oviposit. From all indications, females must mate more than once to realize their maximum fecundity. Males clearly mate numerous times--especially in species with highly female-biased sex ratios (Wilson and Colwell, 1981; Colwell, 1981, 1982).

The mites live in small breeding groups, each group virtually confined to a single inflorescence, which may produce flowers over a period of days, weeks, or months. However, when the inflorescence finishes flowering, all inhabitants must disperse or die, and the group is no more. Meanwhile, other inflorescences, coming newly into flower, represent large potential fitness gains to successful colonists. The mites move between inflorescences in the nostrils of hummingbirds. It appears that considerable emigration occurs during the "life" of the inflorescence, followed by a mass local exodus as flowering nears an end on each inflorescence.

In tropical lowland forest, typically 10-20 species of hummingbird flower mites coexist, each affiliated with different species of host plants. Most of the mite species are monophagous--affiliated with only a single host species. Moreover, as a rule, each host plant species supports only one mite species ("host monopoly"), but in several cases two mite species are regularly affiliated with the same host, in sympatry; in these cases of "host-sharing" the two mite species are invariably of different genera (one *Rhinoseius* and one *Proctolaelaps* [Colwell, 1985b]).

The high incidence of monophagy and host monopoly in these mites cannot be fully accounted for by differential adaptation of morphological, behavioral, or physiological features, nor by interspecific competition (Colwell, 1985b). Densities often remain quite low (Colwell, 1973; Wilson and Colwell, 1981), rarely approaching carrying capacity. The restriction of "host-sharing" exclusively to non-congeners might seem to suggest within-host resource partitioning in these pairs of species, yet we can find no evidence for partitioning, and considerable evidence against it (Colwell, 1985b).

I suggest that sexual selection (differential mating success) may be largely responsible for the evolution of host plant fidelity and monophagy among hummingbird flower mites: individual mites that disembark from birds at the "correct" host plant find more mates. Thus affiliation with a particular host plant species becomes focused by frequency dependent selection--a special case of Fisher's "runaway process" of sexual selection (Fisher, 1958; Lande, 1980; Kirkpatrick, 1982; Arnold, 1983). The affiliation of non-congeners with the same host may be permitted by differences in courtship or morphology sufficient to avoid mistaken courtship or mating, while the two species of the pair exploit the same host plant as a mate-finding cue (Colwell, 1985b).

Host fidelity, however it originates, perpetuates genetic isolation of populations associated with different host species. If host fidelity is indeed an adaptation that promotes mating success *per se*, then selection for host-fidelity becomes self-reinforcing, and may be expected to lead to rapid genetic isolation of errant lineages, under appropriate circumstances. What those circumstance might be, for hummingbird flower mites, and the role that sexual selection for host fidelity may play in the speciation of these mites will be discussed in the final section. First, I will show by means of a simple model that the key principle is valid.

II. A MODEL FOR THE EVOLUTION OF HOST FIDELITY THROUGH DIFFERENTIAL MATING SUCCESS

Envision a habitat with two or more potential host plant species, all equally suitable for habitation by hummingbird flower mites, and all equally visited by hummingbirds. Into this habitat the model sends a population of dispersing adults of a single species of hummingbird flower mite. Let the density of mites in the *i*th host plant species after dispersal be n_i mites per inflorescence. If there is no host preference (no host fidelity), then n_i will be the same for all host plant species.

If one of the host species is preferred, however, mite density will be greater in inflorescences of the preferred species, and less in other species. The goal of the model is to estimate the component of mite fitness due to mating success among mites, as a function of mite density.

Now suppose that, among dispersers, proportion m are males, and proportion $(1-m)$ are females. Then the mean density of males per inflorescence, for host species *i* is

$$\bar{y}_i = mn_i \quad (1)$$

and the mean density of females on host species *i* is

$$\bar{x}_i = (1-m)n_i . \quad (2)$$

Given these means, the model assumes that the number of male or female mites per inflorescence in each of the host species is a Poisson variate, with the sexes independently distributed as a function of their mean densities \bar{y}_i and \bar{x}_i . The proportion of inflorescences that have y male mites or x female mites in host species i is therefore

$$P_z(z) = \frac{e^{-\bar{z}} \bar{z}^z}{z!}, \quad (3)$$

where $\bar{z} = \bar{x}_i$ or \bar{y}_i , and $z = x$ or y .

To keep things simple, an index of fitness is computed separately for each sex-- V for females and W for males. The present model makes no attempt to combine fitness between sexes or to incorporate genetics.

In the female submodel, each female disperser is assumed to have a maximum potential fitness of V^* , which she will realize if there is at least one male in the inflorescence where she disembarks, regardless of how many other females are present. Of course, there is actually some maximum number of females that a single male mite can fully inseminate (perhaps 10 to 15, allowing for several repeat matings per female). The error introduced by this assumption is negligible, however, because very few inflorescences will have such an extreme sex ratio.

If there are no males in an inflorescence, the realized fitness of a female who disembarks there may nonetheless take on some "baseline" value V_0 , resulting from predispersal mating events. If females mate before dispersal, but require additional matings to realize their maximum potential fecundity (as we believe to be true for hummingbird flower mites), then V_0 will be greater than zero, but less than V^* . Thus the mean fitness of females in plant species i is a weighted average of the

fitness of females that land in zero-male inflorescences and the fitness of females that land in inflorescences with at least one male:

$$\bar{V}_i = P_0(\bar{y}_i)V_0 + [1 - P_0(\bar{y}_i)]V^* . \quad (4a)$$

$$\bar{V}_i = e^{-\bar{y}_i} V_0 + (1 - e^{-\bar{y}_i})V^* . \quad (4b)$$

The male submodel is more complex. The fitness gained by a male mite after dispersal is a function not just of the local density of females, but of the local density of competing males as well. This local fitness function, which I will call $w(x,y)$, could take many forms. The simplest is just the local number of females per male

$$w(x,y) = x/y, \quad x \geq 0, \quad y \geq 1 . \quad (5)$$

To calculate male fitness in progeny units, this ratio would have to be multiplied by the mean number of progeny produced per mated female after dispersal. Here, however, the simple sex ratio is sufficient because the concern is with relative fitness of males at different mite densities.

Like females, males may arrive at an inflorescence with a baseline fitness-- w_0 -- achieved through predispersal matings. To this baseline, matings in the new inflorescence contribute additional fitness--in principle, up to some lifetime maximum w^* . In fact, as already mentioned for the female submodel, the number of females per male in an inflorescence will so rarely permit w^* to be reached that w^* can safely be ignored in the male submodel.

Thus, mean male fitness on plant species i is a weighted average of local male fitness in inflorescences with each combination of x females ($x \geq 0$) and y males ($y \geq 1$):

$$\bar{W}_i = w_0 + \sum_{x=0}^{\infty} \sum_{y=1}^{\infty} [P_x(\bar{x}_i)P_y(\bar{y}_i)yw(x,y)] / \bar{y}_i . \quad (6)$$

After substitution for the Poisson terms and for $w(x,y)$, male fitness can be written as

$$\bar{w}_i = w_0 + \frac{1}{\bar{y}_i} \left[\sum_{x=0}^{\infty} \frac{e^{-\bar{x}_i}}{x!} \frac{x}{\bar{x}_i} \times \sum_{y=1}^{\infty} \frac{e^{-\bar{y}_i}}{y!} \frac{y}{\bar{y}_i} \right] \quad (7)$$

The first summation is just \bar{x}_i , by definition; the second summation equals $[1 - P_0(\bar{y}_i)]$, so that \bar{w}_i reduces to

$$\bar{w}_i = w_0 + \frac{\bar{x}_i}{\bar{y}_i} (1 - e^{-\bar{y}_i}). \quad (8)$$

(Alternatively, the sex ratio \bar{x}_i/\bar{y}_i can be expressed as $[1-m]/m$.)

III. RESULTS OF THE MODEL

Consider, first, the female submodel (Eq. 4), and recall that predispersal female fitness v_0 is assumed to be less than the maximum potential fitness v^* --in other words, there is some potential benefit from dispersal. Clearly, female fitness increases monotonically with increasing male density \bar{y}_i , as the proportion of inflorescences with zero males $[P_0(\bar{y}_i)]$ declines. Females do well to disembark at the host species that males prefer.

Likewise, in the male submodel (Eq. 8), for a given sex ratio (which sets \bar{x}_i/\bar{y}_i as a constant), male fitness also increases monotonically with mite density, most simply parameterized by male density \bar{y}_i .

Figure 1 shows female fitness \bar{v}_i and male fitness \bar{w}_i as functions of total local density n_i and proportion males m . First of all, notice that the fitness of both males and females is clearly quite

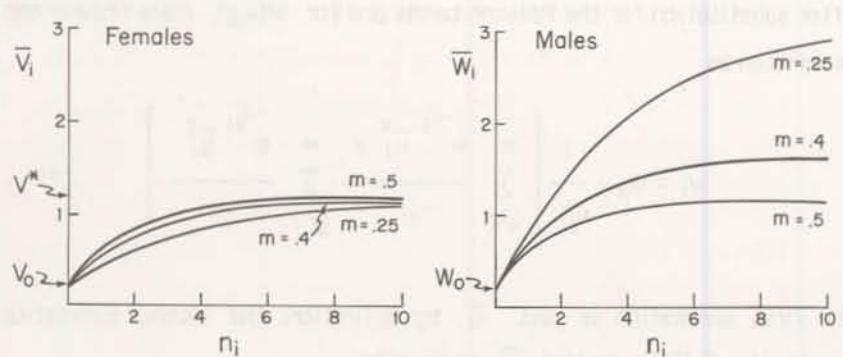


Figure 1. Mean female fitness (\bar{V}) and mean male fitness (\bar{W}) of mites disembarking from hummingbirds, as a function of mite density on host plant species i (n_i) and as a function of mite sex ratio (proportion males m). For each sex, fitness increases with density as a consequence of greater mating success. Fitness differences between mites that disembark on host species with low mite density and those that disembark on host species with high mite density promote self-reinforcing selection for fidelity to the most-favored host. The density n_i is the average number of mites per inflorescence of host species i , disregarding mite gender. V_0 and W_0 are pre-dispersal fitnesses for females and males, respectively, and V^* is maximum female fitness. See the text for discussion of the effects of sex ratio, scaling of the ordinate, and maximum male fitness.

sensitive to the number of mites per inflorescence (n_i) when the density of mites on at least one host species is fairly low.

Population sex ratio also affects the fitness of both sexes, for a given total mite density. Female fitness declines only slightly with decreasing proportion males (m), for a given value of n_i , because zero-male inflorescences become slightly more common. The effect of sex ratio on female fitness diminishes as overall density increases, and all female fitness curves converge on V^* .

The net effect of increasingly female-biased sex ratios (declining m) on male fitness is much more dramatic, and opposite in direction to the

effect on female fitness. For females, only the declining relative density of males affects fitness. For males, on the other hand, both the declining density of competing males and the increasing relative density of females boosts male fitness when the sex ratio is more female-biased, for a given overall density.

In the figure, predispersal fitnesses V_0 and W_0 have both been set arbitrarily to .2, and the maximum fitness for females (V^*) has been set equal to the asymptotic maximum fitness for males ($W_0 + [1-m]/m$) for the case of an unbiased sex ratio ($m = .5$). (Eqs. (4) and (8) are identical for these conditions, and, therefore, so are the curves.)

For both sexes, the figure shows that the curves approach their asymptotes more rapidly for unbiased sex ratios ($m = .5$) than for female-biased sex ratios ($m < .5$)--in other words, density n_i has a significant effect on fitness across a broader range of densities for species with female-biased sex ratios, such as hummingbird flower mites (Wilson and Colwell, 1981), than for species with unbiased sex ratios. Thus female-biased sex ratios amplify selection for host fidelity.

Finally, note that an increased level of predispersal mating would simply raise the intercepts on the fitness axis in Figure 1, without changing the asymptote for either sex, and thereby decrease the effect of postdispersal density on fitness.

IV. DISCUSSION OF THE MODEL

The use of the Poisson distribution in the model carries the assumption that density is low, and that each individual mite disembarks at an inflorescence of its chosen host species completely at random--without regard to the actions of other individuals.

The assumption of randomness is in fact violated in a variety of ways in real populations of hummingbird flower mites. First, hummingbirds do not visit all inflorescences of a given host species with equal frequency (summed over the "flowering life" of the inflorescence), even on the same individual plant (Colwell *et al.*, 1974). Some inflorescences are less accessible than others, some less defensible (for territorial hummingbirds), some too isolated to be energetically worthwhile. Second, female hummingbird flower mites tend to aggregate--at least in laboratory settings, whereas males tend to avoid one another (S. Naeem and R. Colwell, unpublished data). Third, reproduction within inflorescences is rapid, amplifying initial discrepancies among inflorescences set up at the time of colonization (Colwell, 1973).

With the possible exception of mutual avoidance among males, each of these violations of randomness has the effect of producing an aggregated distribution of individual mites among inflorescences. However, distributions more aggregated than random simply magnify the effects demonstrated by the model--for a given overall density of mites, inflorescences with few or no mites, and thus few or no mates, become more frequent.

In fact, statistical analysis of distributions from field data for several species of hummingbird flower mites from Costa Rica (Fig. 4 in Colwell, 1973) and from Trinidad, W. I. (Colwell, unpublished data), consistently show aggregation for both sexes, with zero-male, zero-female, and completely unoccupied inflorescences forming a substantial proportion of the total (10 to 40%). In principle, these aggregated distributions could be wholly the result of differential visitation by hummingbirds, with mites disembarking at random hummingbird foraging visits, but I am quite sure that behavioral aggregation among mites, and certainly, local population growth, are involved as well (Colwell, 1973).

We have so far been unable to demonstrate a role for pheromones that promote aggregation, but they cannot yet be ruled out. Field experiments are underway to yield quantitative estimates of the rates of immigration, emigration, and local population growth for the hummingbird flower mite *Proctolaelaps kirmsei* in its host plant *Hamelia patens* in Costa Rica.

Another assumption of the model is that mites remain where they first disembark. In the real world, fitness losses befalling individuals that land in mateless inflorescences (for both sexes) or mate-poor inflorescences (for males, especially in female-biased mite species), are undoubtedly mitigated to some extent by further episodes of dispersal. On the other hand, mounting a hummingbird, putting one's itinerary completely in the bird's control, and disembarking elsewhere surely is not risk-free, and in any case takes up valuable time. One of the major risks of disembarking in an alien host species, in the real world, is that the inflorescence is very likely to be already occupied by mites of another species of hummingbird flower mite, who may (Colwell, 1985b) or may not (Colwell, 1973) be altogether hospitable, and may further waste one's time with mistaken mating attempts.

The positive fitness effect of host fidelity, through increased mating success, seems certain to be stronger on males than on females in quantitative terms, even though the qualitative effect is quite similar for the two sexes (Fig. 1). In common with classical sexually-selected traits (Fisher, 1958), within-sex variance for mating success due to host fidelity is doubtless greater among males simply as a result of their higher reproductive potential. There are as yet no quantitative data for hummingbird flower mites, but female mites of the allied family Phytoseiidae have a lifetime potential fecundity of 50 to 100 eggs, whereas males may produce ten times as many progeny (Amano and Chant, 1978).

Moreover, the expected difference between the sexes in the variance of mating success is magnified by female-biased sex ratios. The matter is complicated by the fact that primary sex ratio in hummingbird flower mites is not only female-biased, but the degree of bias varies systematically among species, as a function of breeding group size (Wilson and Colwell, 1981). The rate of male dispersal, relative to female dispersal, also varies among species of hummingbird flower mites (Colwell, 1985b and unpublished data). Yet a further complication is the likelihood that hummingbird flower mites are parahaploid (a form of functional haplodiploidy [see Hoy, 1977]). My next modelling objective is to work these complexities into the present model, and to combine male and female submodels by incorporating simple population genetics.

In summary, the host fidelity principle illustrated by the model seems qualitatively valid, in spite of diverse simplifications and violation of the assumptions of randomness. The key condition for its applicability, of course, is that populations be at sufficiently low density that host fidelity significantly increases mating success.

V. IMPLICATIONS FOR EXTINCTION AND SPECIATION

A. Extinction

Extensive study of hummingbird flower mites in lowland wet forest areas of Costa Rica and Trinidad (Colwell, 1985b) strongly suggests that each mite species occupies no more host species than necessary to maintain a year-round floral resource base. Thus, in the relatively aseasonal tropical lowland forest, each host plant species typically has its own species of monophagous mite. This one-on-one matchup has two kinds of exceptions. The first, mentioned in the introduction, is the

phenomenon of "host-sharing": in six known cases, one species of *Proctolaelaps* and one species of *Rhinoseius* occupy the same host species. The second class of exception concerns host species with seasonal flowering patterns. These are inhabited by polyphagous hummingbird flower mites that occupy successively flowering alternate hosts seasonally (sequential specialists) or have a year-round "home base" from which seasonal hosts are colonized annually. A detailed account appears (and names are named) elsewhere (Colwell, 1985b).

Extinction threatens monophagous mite species as well as most sequential specialists; all it takes is a flowering failure of a few weeks' duration over the geographical range of a host plant. (The mites have no resting or "resistant" stages.) Thus monophagous mites affiliated with host plants of limited geographical range are the most vulnerable to extinction, and very likely do go extinct frequently, on a geological time scale. We have actually documented a local "temporary extinction" in Trinidad (Colwell, 1985b); the mite *Rhinoseius bisacculatus* disappeared for a period of four years after a ten day flowering failure in its obligate host plant, *Costus scaber*.

Short-term natural selection is of course blind to the long-term risk of extinction from rare extrinsic events. Meanwhile, sexual selection for host fidelity (or any other trait) potentially acts in every generation, at least in a stabilizing mode. In effect, mites are constantly pushed by the selective force of differential mating success towards monophagy, if the yearly resource base permits it, whether it is "good" for them or not in the long run. Extinction--local or complete--is the check on such extreme phenotypes, just as predation often defines the limits of classical sexually-selected characters, such as the colors of male guppies (Endler, 1983), which are otherwise constantly impelled by the agency of female choice toward ever brighter and more contrasting patterns.

B. Host Shifts

The existence of sequential specialist mites presents a challenge to the theory of host fidelity, as well as an opportunity to test it. At our Volcan Colima study site in Mexico, for example, the mite *Rhinoseius epoecus* shifts from its fall-winter host *Castilleja integrifolia* to its local spring-summer host *Lobelia laxiflora* during a one-month period of flowering overlap, and back to *Castilleja* again each fall. In Trinidad, *Proctolaelaps kirmsei* occupies the host plant *Hamelia patens* in the wet season and shifts to *Palicourea crocea* in the dry season; the two plants overlap in flowering period for a few weeks during the two annual transition periods. How do these shifts in host affiliation occur? The host fidelity model predicts that the mites would remain loyal to the current host, whichever it is, even when flowers of the current host are waning in abundance while the alternate host is coming into full flower.

We have carried out many "T-chamber" experiments to investigate preference for various host and non-host nectars and control substances for several species of hummingbird flower mites, among them these two sequential specialists (Colwell 1985b; Heyneman, 1985). In general, mites prefer the nectar of their current host plant to matched sugar solutions, to nectar of the host plants of other sympatric species of mites, and to the nectar of non-host plants pollinated by hummingbirds--presumably, these preferences permit the mites to identify, by olfactory means, flowers appropriate for occupation and mate-finding.

The Mexican sequential specialist mite *Rhinoseius epoecus* was tested during December, when both of its host plant species are in flower, and are occupied by mites of this species. Mites from both host species significantly preferred nectar from the host species from which they were taken for the test (Heyneman, 1985). This result begs the question of how

the shift is initiated, but fulfills the expectation that host fidelity may shift rapidly among sequential specialists.

In Trinidad, *P. kirmsei* was tested for its host preference during the dry-season-to-wet-season transition period; although larger sample sizes would be desirable, it appears that *P. kirmsei* prefers its wet-season host *Hamelia*, just coming into flower during this transition; indeed, mites are sparse in the dry season host *Palicourea* during transition, and relatively more common in the first flowers of *Hamelia* (Heyneman, 1985). The shift from *Hamelia* back to *Palicourea* has not yet been explored, but it is possible that mites on *Hamelia* when it nears the end of its flowering season may become dense enough to starve, which may relax host fidelity (Hoffman and Turelli, in press), and facilitate the shift to *Palicourea*. It may well be significant that *Hamelia* is the sole host plant of *P. kirmsei* elsewhere in the range of this widespread plant, in areas where it flowers all year (e.g., the Atlantic lowlands of Costa Rica).

Although there may be seasonal genetic shifts in sequential specialists associated with these cyclic host shifts (generation time is about a week), associative learning very likely plays a role--and could in principle be sufficient. We have carried out several very-short-term "transplant" experiments in the field, forcing mites to live in (unoccupied) inflorescences of sympatric host plants normally occupied by other mite species (Colwell, 1985b, and in preparation). We carried out identical preference tests before and after the experiments. *P. kirmsei* was among the species capable of significantly shifting preference to a novel host plant (*Centropogon cornutus* [= *C. surinamensis*]).

Mites at higher latitudes and elevations (such as *Rhinoseius epoecus*) are virtually all sequential specialists--by necessity. A single mite species may occupy four or five seasonal hosts, but have no overlap

with other mites in the same habitat, each of which has its own set of hosts spanning several plant families and orders (Colwell, 1985b). It seems more likely to me that host fidelity in such species is based on learning than on genetic "hard-wiring," whereas monophagous species whose host has a wide geographic range (making complete extinction of the mite highly unlikely) are good candidates for "hard-wired" host fidelity.

The literature on adult conditioning among plant-associated arthropods is growing (Jaenike, 1982, 1983; Prokopy *et al.* 1982; Prokopy and Roitberg, 1984; Rauscher, 1983; but see Hoffman and Turelli, in press). Where densities are low, this phenomenon (where genuine) may be primarily an adaptation for mate-finding, rather than food-finding.

C. Speciation

The annual host shifts in *P. kirmseii* and other sequential specialists may well represent, in many respects, models for incipient speciation in hummingbird flower mites. If host fidelity does indeed shift seasonally through associative learning, gene frequency changes, or a combination of the two, the process of speciation might very well begin in the same way. How much isolation is required, and how does it occur?

At this time in evolutionary history, the most likely stimulus for a speciation event is probably the extinction of an existing species of hummingbird flower mite, although it is possible that "doubling up" of non-congeners on the same host species may be an ongoing process. Only about one in every two hundred mites is normally found in the "wrong" host species in the field, based on some 12,000 specimens of two dozen species (Colwell, 1985b). Although these errant individuals, had they not been collected, might well have eventually found their way back to their usual host species, these mites probably would not have been among the most successful individuals of their species. On the other hand, the

ancestors of any living species that originated by colonization of an "empty" host species were surely "mistake-makers." Heyneman (1985) has shown that hummingbird flower mites tend to accept unfamiliar novel hosts (those not in the foraging repertoire of their usual hummingbird carriers) more readily than "familiar" novel hosts.

When *Rhinoseius bisacculatus* disappeared from our field site in Trinidad after a brief flowering failure in its host plant *Costus scaber* (see above), within weeks the sympatric mite *Proctolaelaps certator*, a "home base" polyphagous species, appeared in numbers in the newly opened flowers of *C. scaber*. Unfortunately the interlopers were not common enough to risk jeopardizing this unusual natural experiment by taking individuals for preference tests. However, the return of the "extinct" mite *R. bisacculatus* four years later did not signal a return to the previous pattern: at last check, in 1981, both species (non-congeners) maintained a strong presence in the host.

I have treated the issue of genetic isolation of colonists on novel host plants in detail elsewhere (Colwell, 1985b). Factors that promote initial isolation from the ancestral population, and that in combination may initiate local speciation include: (1) the frequency of hummingbird "traffic" between the old and the new host plant species, relative to traffic between individuals of the new host plant (Colwell, 1973, Fig. 5); (2) the effectiveness of rapid associative learning of the nectar chemistry of the novel host; (3) founder effects on morphological and behavioral isolating mechanisms (Kaneshiro, 1980; Templeton, 1980, this volume; Lande 1981; Thornhill and Alcock, 1983; Carson, 1978, this volume); (4) founder effects on genetically-specified host preference (if such a preference exists) (Parsons and Hoffman, this volume); and (5) the rate of local population growth relative to immigration.

If these factors together produce a level of genetic isolation sufficient to permit genetic divergence of mites on the novel host plant, then in the longer term, speciation may be consolidated by selection for host fidelity through differential mating success, as well as by classical sexual selection for male morphology or courtship behavior and the correlated preference among females (Templeton, 1980; Lande, 1981; Colwell, 1985; Carson, 1978, this volume). Adaptation to special local conditions (Futuyma and Petersen, 1985; Colwell, 1985b; Parsons and Hoffman, this volume) may then proceed, unhindered by gene flow from the ancestral population. The existence of local sets of extremely similar sibling species, each affiliated with its own host plant (Colwell, 1985b), testifies to the possibility of local speciation, although more biogeographic data are needed for any firm inference.

The effect of host fidelity on fitness in low-density populations plays a two-fold role in this speciation scenario. In ancestral populations, especially of polyphagous hummingbird flower mites, selection for associative learning of host cues may predispose errant individuals and their offspring on novel hosts to disembark from hummingbirds at inflorescences of the new host species, rather than the ancestral one. Meanwhile, rigid host fidelity in the ancestral population prevents swamping of the incipient species by further immigration, which is surely very much smaller than local population growth on the new host.

I have supported these ideas about speciation with a very general model for a mechanism promoting genetic isolation, which in principle could apply to many different kinds of habitat fidelity or host fidelity. My own familiarity with the natural history of hummingbird flower mites has prompted me to use them as a case history in support of these ideas, but of course I hope others will examine carefully the possibility that sexual

selection for host or habitat fidelity may play a role in community organization and speciation in other groups of organisms.

As I have discussed elsewhere in some detail (Colwell, 1985), certain groups of flies appear to present many parallels with hummingbird flower mites, and seem good candidates for the study of the evolution of host fidelity through selection for mate-finding, and its possible role in speciation. These groups include certain lineages of Tephritidae (the true fruit flies) and of Drosophilidae. Certain monophagous *Drosophila* in the Neotropics, in fact, very likely share some host plant species with hummingbird flower mites (Pipkin *et al.*, 1966). A vast radiation of flower-breeding *Drosophila* awaits investigation in New Guinea (see Okada and Carson, 1982, and references therein).

ACKNOWLEDGMENTS

I am grateful to Carlo Matessi for his critical review of the manuscript and for his useful suggestions about the model, many of which found their way into the final version. I thank Ron Prokopy, two anonymous reviewers, and the participants in the Conference for their comments and encouragement, especially Guy Bush, Hampton Carson, Peter Parsons, Alan Templeton, and Michael Turelli. Students and faculty at Kellogg Biological Station provided spirited criticism at a critical stage. I thank Robin Chazdon for helping when it counted most, and Sam Karlin for his infinite patience.

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