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Source: *The American Naturalist*, Vol. 107, No. 958 (Nov. - Dec., 1973), pp. 737-760
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: https://www.jstor.org/stable/2459708
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THE
AMERICAN NATURALIST

Vol. 107, No. 958 The American Naturalist November–December 1973

COMPETITION AND COEXISTENCE IN A SIMPLE TROPICAL COMMUNITY

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This is a study of 10 species in a tropical highland community. Through an analysis of their ecological and evolutionary interactions, I have tried to demonstrate some general properties of competition and coexistence in many-species systems, especially with regard to the effects of seasonality and environmental predictability.

Many species of New World plants rely upon hummingbirds for pollination, and hummingbirds, in turn, depend upon the nectar of these plants for food. Even flowers obligately pollinated by hummingbirds, however, support a variety of "illegitimate" (nonpollinating) nectar-eating organisms, including bees, ants, beetles, birds, and quite probably protozoans, yeasts, and bacteria. But in many hummingbird flowers, the commonest nectar thieves are mites of the genus *Rhinoseius* (Mesostigmata: Ascidae). These mites are dependent not only upon the nectar of hummingbird flowers, like other nectar thieves, but also upon the birds themselves: the primary means of dispersal among *Rhinoseius* mites is on the bill (fig. 1) or in the nasal cavity of hummingbirds. The protagonists of this study are two species of *Rhinoseius*, three hummingbird species, a coerebid bird, and four plant species (fig. 2).

THE STUDY AREA

All observations and experiments were carried out within 2 km of Pensión La Georgina, a wayhouse at 3,100 m elevation on the Interamerican Highway (km 88), Province of Cartago, Costa Rica (09°34′N; 83°41′W). The study site lies not far below tree line, in a region once thickly covered by a hardwood forest dominated by native oaks. Since the construction of the Interamerican Highway, the oaks have gradually been felled for lumber and charcoal, so that today many of the more accessible areas are cleared. Although the yearly rainfall averages only about 2,800 mm, the area is bathed almost daily by clouds and mist, even in the season of no rain (December through March), so that the remaining trees are covered with a variety of

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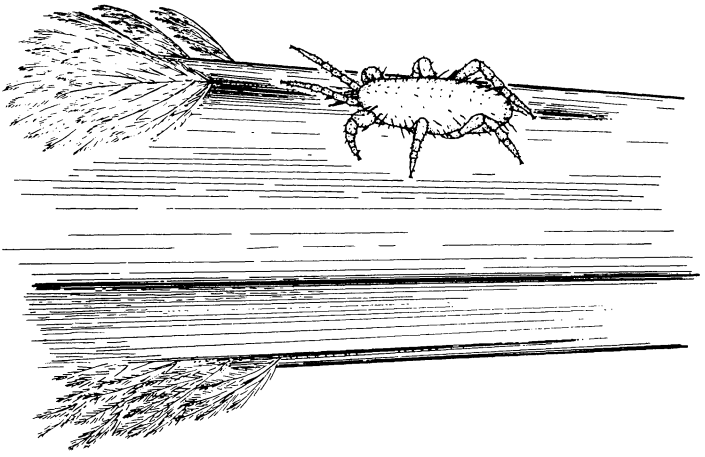

FIG. 1.—*Rhinoseius colwelli* on the bill of the hummingbird *Eugenes fulgens*. The nasal opening of the bird is just out of the drawing to the left. The mite is an adult male (body slightly less than 1 mm in length).

abundant epiphytes, and there is some flowering and fruiting in many plant species all year. The mean annual temperature is 10.8° C, with a difference of only 2.6° C between the lowest (December) and highest (May) monthly means.

THE PLANTS

Of more than 20 species of plants visited by hummingbirds in the study area, only four species commonly support *Rhinoseius* mites. All four of these "mite plants" are endemic to the high mountains of Costa Rica and western Panama. Two of them are in the genus *Centropogon* (Lobeliaceae): *C. valerii* (= *C. grandidentatus* var. *valerii* [Standl.] McVaugh; McVaugh 1943, 1949) and *C. talamancensis* Wilbur (Wilbur 1969; called *C. gutierrezii* in Wolf [1969] and in Wolf and Stiles [1970]). *Centropogon valerii* is a common plant along watercourses and in treefalls in the uncut oak forests of the study area, where it usually forms small patches less than a meter in height. In cleared areas it occurs in clumps up to 2 m high and 5 m in diameter, often with 100 or more flowers per clump during the peak season. *Centropogon talamancensis* appears only rarely in undisturbed forest, as single herbaceous plants in shadier and less open areas than *C. valerii*. In cleared areas *C. talamancensis* forms small patches up to 1 m in height, often in close association with its congener. No consistent difference in habitat between the two species in cleared areas is apparent.

The flowers of the two *Centropogon* species are basically similar in morphology—a long, slender corolla tube with flaring lobes and protruding filament tube (fig. 2). Flowers of *C. valerii* are shorter (corolla tube 25–32 mm long) and orange red in color; flowers of *C. talamancensis* are

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longer (corolla tube 36–43 mm long) and rose lavender in color (see also fig. 1 in Heinrich and Raven 1972).

The two remaining mite plants at the study site are in the family Ericaceae: *Macleania glabra* (Klotzsch) Hoer. and *Cavendishia smithii* Hoer. (Smith 1932). At the study site, *Macleania* is found from deep forest to cleared areas and even on roadbanks. It is characteristically a small epiphytic shrub, and in cleared areas it is usually attached to fallen logs or stumps. *Cavendishia* is a larger shrub (1–5 m high), sometimes epiphytic or scandent, found only in deep forest at the study site.

The flowers of the two ericads are strikingly similar in superficial appearance—deep red corolla tube, cylindrical, about 19 mm long and 5–6 mm in diameter (fig. 2). Since the flowers of other species in the genera *Macleania* and *Cavendishia* in Costa Rica and elsewhere span a wide range in both size and coloration (see Smith 1932), it seems likely that the similarity in the flowers of *M. glabra* and *C. smithii* is the result of convergent evolution under the influence of a shared pollinator, the hummingbird *Panterpe insignis*. *Panterpe* has almost exactly the same geographic range as the two ericad species.

THE BIRDS

Four species of birds commonly forage at the mite plants of the study site (fig. 2)—three hummingbirds and the flower-piercer *Diglossa plumbea* (Coerebidae). Of the hummingbirds, *Panterpe insignis* is the only species commonly resident all year around at the study site. The other hummingbirds, *Colibri thalassinus cabanidis* and *Eugenes fulgens spectabilis,* are both seasonally nomadic, most individuals apparently spending the greater part of the rainy season (about May through November) at lower elevations (Slud 1965; Wolf and Stiles 1970; see also Wagner 1945; Skutch 1967; and Bent 1940). *Diglossa plumbea* is common at the study site all year. All four birds are limited to highland areas from north-central Costa Rica to western Panama (Slud 1964; Vuilleumier 1969).

Competition among Bird Species

During January 1971, a total of some 150 hours was spent studying the foraging activity of birds at mite plants at all times of day. Combining those detailed observations with data from numerous briefer visits in other months of various years, and with the extensive observations of others at the study site (Wolf 1969; Wolf and Stiles 1970; Stiles, personal communication; Slud 1965), allows a fairly accurate description of foraging patterns at the study site.

All four mite plants flower all year around, but the absolute and relative abundance of flowers varies considerably. The peak period for flowering is the season of no rain, from December to March. It is also during this period that *Colibri* and *Eugenes,* both altitudinal migrants, are most abundant

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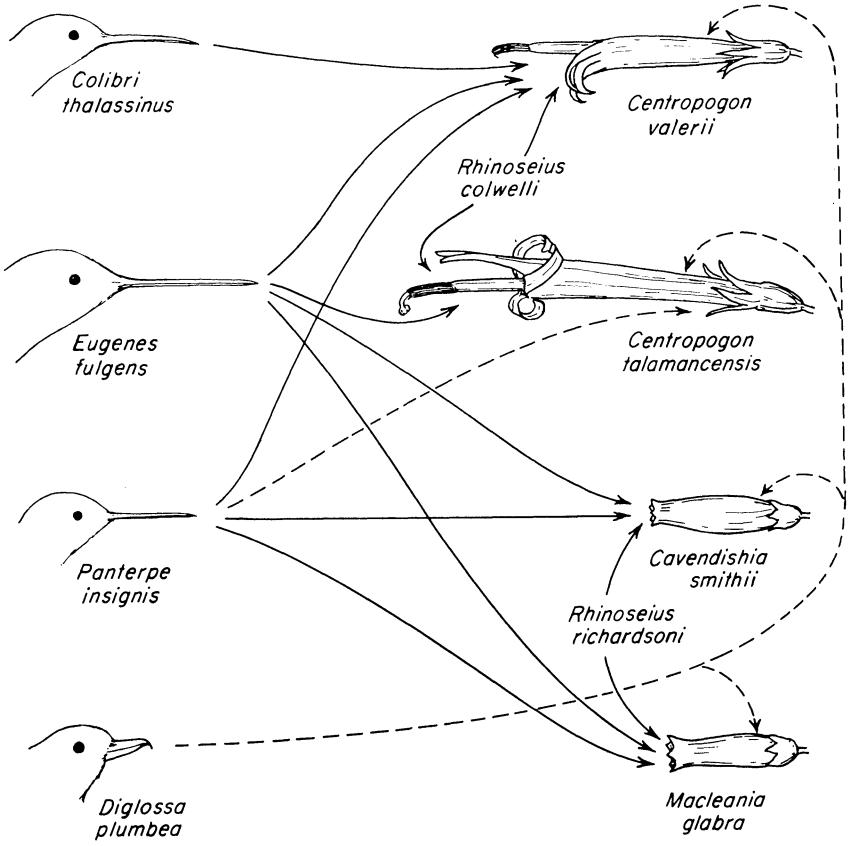

FIG. 2.—Flowers and their visitors. The broken lines indicate illegitimate visits by *Diglossa* and *Panterpe,* which pierce the base of the corolla.

at the site, although a few individuals of these species (particularly *Eugenes*) may remain well into the rainy season.

The relationship between the migrants and the permanent residents, *Panterpe* and *Diglossa,* appears to be quite competitive. Most large patches of *Centropogon valerii* are defended by territorial *Colibri* from December to March, although smaller patches, especially if other desirable plants are nearby, may be defended by territorial *Panterpe* during the same period (see Boucard 1878; Wolf 1969). Aggressive interactions including vocalizations, displays, and chases are frequent among individuals of each species, and between species.

There is a clear correspondence between the departure of most *Colibri* in early March and the takeover of most large patches of *C. valerii* by *Panterpe.* At the same time, alternate sources of food for *Panterpe* are declining in floral productivity, particularly *Macleania* and *Gaiadendron* (Loranthaceae), as also noted by Wolf (1969) and Wolf and Stiles (1970).

During the period when *Eugenes* and *Colibri* are both present at the study

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site, several phenomena suggest strong competition for nectar among the four bird species. *Eugenes* is considerably larger than either *Panterpe* or *Colibri* and has a much longer bill (fig. 2). The long bill allows it to feed on *Centropogon talamancensis,* which is unavailable to *Colibri.* However, when *C. talamancensis* grows near *C. valerii* in an area defended by *Colibri, Eugenes* makes no attempt to visit it during the hours of full daylight, but forages heavily on all the defended plants at dawn and dusk, when *Colibri* is quiescent. By late afternoon many of the flowers of *C. talamancensis* within *Colibri* territories are laden with accumulated nectar, while isolated plants are visited all day long by *Eugenes* and do not accumulate nectar. The same pattern of crepuscular visitation by *Eugenes* occurs with *C. talamancensis* in *Panterpe* territories. There is a marked decline in flower production in *C. talamancensis* at about the same time of year that *Eugenes* begins to depart, and the same pattern occurs with *Cirsium subcoriaceum* (Compositae), another major nectar source for *Eugenes.*

The flower-piercer *Diglossa* (fig. 2) succeeds in foraging within both *Panterpe* and *Colibri* territories. *Diglossa* often escapes aerial attacks by hummingbirds simply by hopping into foliage too dense for the hummingbird to follow. The flower-piercer feeds on a variety of flowers, but nectar of the two *Centropogon* species apparently forms a large proportion of its diet at the study site. *Diglossa* perches near a flower, often on the pedicel itself, and extracts nectar through the base of the corolla by piercing the flower with its lower mandible while holding the flower with its upper mandible (Skutch 1954; Lyon and Chadek 1971).

Even though *Colibri* is unable to take nectar from *C. talamancensis* because of its long corolla (fig. 2), territorial *Colibri* attack and chase any *Diglossa* found feeding on this plant within the territory. This observation was demonstrated statistically by comparing the number of *Diglossa* perforations in *C. talamancensis* flowers from a clump within a *Colibri* territory with the number found in flowers 10 m distant, visited only by *Diglossa* and *Eugenes.* With five perforations per flower possible (between adjacent sepals), 20 flowers protected by *Colibri* had only five perforations (in four flowers), while 20 unprotected flowers had 14 (in nine flowers), a difference significant at $P < .05$ ($2 \times 2\ \chi^2$: 5/100 versus 14/100).

Panterpe is capable of legitimate feeding on *C. valerii,* but (like *Colibri*) cannot feed from the throat of *C. talamancensis* as its bill is much shorter than the corolla tube (fig. 2). Instead, *Panterpe* extracts nectar from the latter plant as *Diglossa* does, through perforations in the base of the corolla, frequently while perching. Many individuals also feed this way on *C. valerii.* No pollination and probably no mite transfer take place, since the mites are apparently unable to pass through the perforation while the bill is inserted. Although *Panterpe* may certainly use perforations made by *Diglossa, C. talamancensis* flowers within *Panterpe* territories (defended against *Diglossa*) have significantly more perforations than undefended flowers, which suggests that *Panterpe* can make its own perforations (19 out of 50 possible perforations, in 10 out of 10 flowers; $P < .001$ by $2 \times 2\ \chi^2$). Be-

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cause of the peculiarity of this method of feeding, and its possible relevance to hummingbird evolution, a more complete behavioral and morphological analysis will appear elsewhere.

Coexistence among Bird Species

At the study site, *Eugenes* coexists with other hummingbirds primarily by "traplining" (sensu Janzen 1971) between and beyond *Colibri* and *Panterpe* feeding territories. A male *Eugenes* may defend certain dense clumps of *Centropogon talamancensis* or *Cirsium* against its own kind, but *Eugenes* territories at the study site tend to be large, loosely held, and rather poorly defined. In encounters with *Colibri* and *Panterpe, Eugenes* is consistently dominated, in spite of its greater size (see Wolf and Stiles 1970, tables 4 and 7). *Eugenes* successfully invades their territories only at dawn and dusk (above). Its greater body volume may allow *Eugenes* to forage more efficiently at lower ambient temperatures than its competitors, and to fly farther for food, as has been shown for large bees (see Heinrich and Raven 1972; Hainsworth and Wolf 1972).

In several ways, then, *Eugenes* is forced by its competitors into the role of an *interstitial species,* feeding in between and beyond their territories and foraging hours, often on plants too widely dispersed to be part of a defensible territory. At least four unrelated species in the local flora, all rare and widely dispersed, exploit the foraging pattern of *Eugenes* for pollination. *Bomarea costaricensis* (Alstroemeriaceae), *Fuchsia splendens* (Onagraceae), *Desfontainea* sp. (Desfontaineaceae), and *Symbolanthus* sp. (Gentianaceae) all have corollas too long to allow feeding by the other hummingbirds. Although body size and bill shape are complicating factors (Hainsworth and Wolf 1972; Snow and Snow 1972), the hummingbird species with the longest bill in any community is likely to be an interstitial species, since its morphology permits nearly exclusive access to flowers with long corolla tubes even without recourse to behavioral defense against other species. Species with shorter bills, on the contrary, must defend their nectar sources behaviorally against the long-billed species. To the degree that this phenomenon occurs, we should find that rare hummingbird-pollinated flowers have longer corollas than common ones.

In organisms for which aggressive interactions are important in interspecific competition, behaviorally subordinate interstitial species are in a precarious position. In a poor year they are likely to suffer the most and may actually be forced out by "diffuse competition" (MacArthur 1972) with several behaviorally dominant species. Thus, although interstitial species probably exist everywhere, the interstitial strategy should account for a higher proportion of the fauna in more predictable environments.

Panterpe is an opportunistic generalist. Resident at the study site all year, both sexes hold feeding territories which shift with the seasonal flowering peaks of *Macleania, Cavendishia,* and several other plant species (Wolf 1969; Wolf and Stiles 1970). Moreover, an individual may feed on

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four or five plant species within its territory in a single foraging excursion, while a nearby individual utilizes a different set of species. *Colibri,* on the other hand, feeds almost exclusively on *Centropogon valerii* at the study site and virtually monopolizes this plant during its dry-season flowering peak. (*Colibri valerii* is an important nectar source for *Panterpe* during the remainder of the year.) *Colibri* very likely specializes narrowly on other species in its wet-season habitats at lower elevations (see Wagner 1945; Skutch 1967).

If the feeding pattern of *Colibri* is indeed as stereotyped during the rest of the year as it is during the annual visit of this species at the study site, then *Colibri* may be called a *sequential specialist.* This strategy depends heavily upon the predictable availability of the particular seasonal resources monopolized by the sequential specialist, as well as the reliable appearance of sufficient alternate resources, to keep its opportunist competitors satiated. In the present case, competition between *Colibri* and *Panterpe* would increase markedly if (1) the flowering peak in *C. valerii* were grossly reduced or delayed, or (2) the aggregate supply of nectar in the other plant species used by *Panterpe* failed to peak as usual during the same period. A certain degree of resource predictability is thus a prerequisite for the coexistence of sequential specialists with their opportunist competitors.

From an evolutionary point of view, the flower-piercer *Diglossa* is entirely dependent on the hummingbird-plant mutualism (see Lyon and Chadek 1971). Ecologically, *Diglossa* is an ectoparasite of the plant and a competitor of the hummingbirds, since it consumes much nectar and accomplishes no pollination whatsoever. Coexistence of *Diglossa* with the hummingbirds is primarily a result of differences in foraging behavior. It has been demonstrated statistically that *Diglossa* tends to forage on different individual flowers than those frequented by *Colibri* in the same *C. grandidentatus* bush (Colwell, in preparation). The perching *Diglossa* feeds on flowers in the interior of the bush which are least accessible (and least defensible) to the airborne *Colibri.*

THE MITES

In 1969, when I began to suspect that the mites common in hummingbird flowers at the study site might also be associated with the birds themselves, J. I. Richardson and I netted several hummingbirds at the site. All of them carried *Rhinoseius.* These mite specimens and others (collected from flowers) were described by Hunter (1972) as two new species of the genus *Rhinoseius* (family Ascidae, Mesostigmata): *R. colwelli* and *R. richardsoni.* Specimens referable to *R. colwelli* have subsequently been taken from *Centropogon* spp. in Oaxaca and near Monteverde, Costa Rica, and from *Bomarea* sp. (Alstroemeriaceae) and *Psychotria* sp. (Rubiaceae) near Monteverde. The distribution of the two mite species among plant and hummingbird species at the study site is discussed in detail below.

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Mite species now included in the genus *Rhinoseius* (Lindquist and Evans 1965) were first reported by Baker and Yunker (1964). They described 11 species on the basis of specimens recovered from the nasal cavities of Panamanian and Colombian hummingbirds, from *Heliconia* sp. in Panama, from *Heliconia* cuttings originating in Venezuela, and from bromeliad cuttings from unknown localities in Mexico. However, only two of Baker and Yunker's species were recovered from both birds and plants and apparently none from birds and plants in the same habitat. An additional species of *Rhinoseius* has been described from a Cuban hummingbird (Dusbábek and Cerny 1970). To date, I have collected *Rhinoseius* mites from a total of 18 additional hummingbird species and 45 additional plant species in various localities in Costa Rica, Ecuador, and Peru; from seven plant species in California; and from four plant species in Chile. These specimens, which include several new species, are presently being determined by P. E. Hunter.

A similar case of phoresy among mites has been found for species in the family Ameroseiidae (Mesostigmata). These mites, which are transported by nectar-eating birds (Honeyeaters and Lories) and by bees, have been reported from Australia, New Zealand, New Guinea, Borneo, and the Philippines (Evans 1963; Gravatt 1969; Allred 1970). They are also found in a variety of flowers, and they may feed on pollen (Lindquist and Evans 1965; Gravatt 1969), but there is apparently no evidence to rule out nectar feeding.

Little is known about the natural history of mites in the suborder Mesostigmata, with the exception of species that are pests of domesticated or laboratory animals. The most relevant studies are probably those of Treat (1957, 1958, 1962, 1969) on the mites associated with noctuid moths, chiefly the moth ear mite *Dicrocheles phalaenodectes* (in the family Laelaptidae, not far taxonomically from the Ascidae). Behaviorally, these mites are in many ways similar to *Rhinoseius,* with the essential difference that they feed on hemolymph and use flowers to get from moth to moth, while *Rhinoseius* feed on nectar and use birds to get from flower to flower.

Hunter's (1972) descriptions of the two *Rhinoseius* species present at the study site allow field identification of living adults by eye, and of mounted larvae, protonymphs, and deutonymphs with the aid of a compound microscope. Living adult males and females are also easily separable by eye for *R. colwelli,* and with a dissecting microscope for *R. richardsoni.*

Mites on Plants

Mites were censused on plants by removing a flower, then quickly slicing it through longitudinally with a razor blade, counting, and noting the position of any mites present. Flowers were also sliced open in situ on the plant to confirm observations of mite position. Once exposed, the mites may easily be picked up unharmed with a fine artist's brush.

More than 800 mites, taken from over 100 flowers of each of the four species of mite plants, were mounted and positively identified to species

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with phase-contrast microscopy. Without exception, all specimens taken from *Centropogon talamancensis* or from *Centropogon valerii* were *Rhinoseius colwelli,* while all specimens from *Macleania* or from *Cavendishia* proved to be *Rhinoseius richardsoni* (figs. 2 and 3). This complete separation of the mite species included flowers of *Macleania* and *Centropogon valerii* less than 15 cm apart and samples taken in 3 different years and in both wet and dry seasons.

A consistent pattern of spatial distribution of life stages emerged from examination of the flowers. Eggs, when present, are invariably found in the nectaries at the base of the corolla tube, often actually immersed in nectar, usually in groups of five to 20. *Rhinoseius colwelli* larvae, when present, aggregate in tight groups in the narrow space between the style and the surrounding filament tube in young *Centropogon* flowers and in the empty anther compartment after the stigma is exserted. In *Macleania* and *Cavendishia,* larvae of *R. richardsoni* are characteristically found on the medial surface of the anthers, which tend to form a sort of loose compartment. In flowers of all four plant species, adults and nymphs are usually found in clusters on the inside surface of the corolla base, just distal to the nectary region.

In small petri dishes or test tubes, mites also behave in a rather stereotyped fashion depending on age and gender. Immature mites and adult females separately form tight aggregations of three to six individuals,

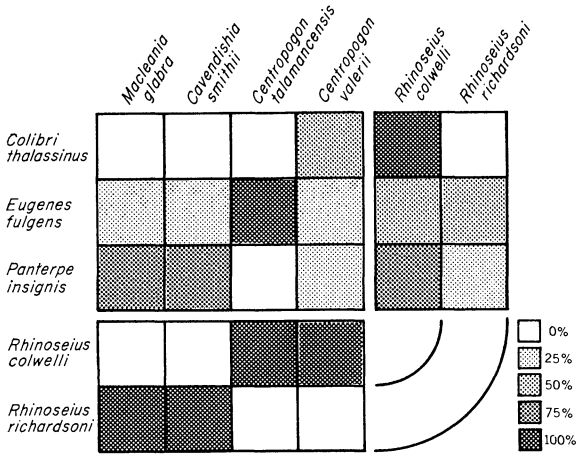

FIG. 3.—Exploitation of the nectar of four species of hummingbird-pollinated plants by three hummingbird species (3 × 4 rectangle) and by two mite species (2 × 4 rectangle), and the transport of the mite species by the birds (3 × 2 rectangle). Intensity of stippling indicates the following: (1) in the 3 × 4 rectangle, percentage of bird visits (by species) for each plant species (each column adds to 100%; rows correspond to vectors **D**, **F**, and **Q** of table 3, part I); (2) in the 2 × 4 rectangle, percentage of mites (by species) found in each plant species (each column adds to 100%); and (3) in the 3 × 2 rectangle, percentage of mite-carrying birds which carry each mite species (each row adds to 100%; data from table 1).

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remaining quiescent for long periods of time except for frequent palpation of one another with the antenna-like forelegs. Meanwhile, adult males move about actively, each male typically centering his activity around a group of females, whom he palpates frequently. (The male : female sex ratio is about 1 : 3.) When two males meet, there is invariably an aggressive interaction, involving lunges and sometimes grappling with the second pair of legs, which are also used for holding the female during copulation.

In petri dishes, the mites showed a 100% preference for sucrose water over plain water, and actually laid eggs in the tiny plastic "nectaries" I provided (caps of Beem electron microscopy imbedding capsules). Ingestion was demonstrated by adding a vital dye to the sucrose water. It is not clear where *Rhinoseius* obtains nitrogen compounds. I could not demonstrate pollen eating, but some pollens are known to release free amino acids or enzymes when mixed with nectar (Gilbert 1972; Mäkinen and Brewbaker 1967), and many nectars themselves contain amino acids (Baker and Baker 1973*a*, 1973*b*). Yeasts or bacteria are another possible source.

The life history of *Rhinoseius* was not followed in its entirety for individual mites. However, by tagging flowers in the field it was possible to know how many days had been available for egg laying and development since each flower opened. By this method I estimate that only 2–3 days are required between oviposition and the subadult stage (deutonymph). Generation time is probably about 5–7 days. (Individual *Centropogon* flowers produce nectar for 7–12 days.) In addition to the fact that all mite life stages are found in flowers, evidence for flowers as the site of mite reproduction comes from data such as those shown in figure 4. None of the frequency distributions in figure 4 for old flowers differs significantly ($P < .05$) from the corresponding distribution for young flowers except for the distributions of juveniles (Kolmogorov-Smirnov two-sample test).

The distribution of mites among flowers of the same plant is strikingly clumped—a few flowers swarm with mites, while most have few or none

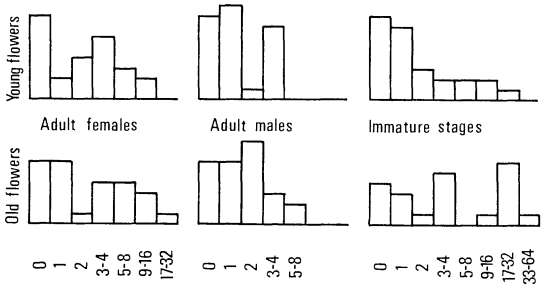

FIG. 4.—Logarithmic frequency distribution of *Rhinoseius colwelli* in 25 "young" (staminate stage) and 25 "old" (pistillate stage) flowers of *Centropogon talamancensis*. The height of each bar represents the number of flowers which held mite populations in the size range indicated on the abscissa. For all mite life stages combined, the distribution would become even more clumped. Frequency distributions of mites in flowers of the other three mite plants show similar clumping.

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(fig. 4). The significance of this pattern is not obvious. The strong tendency to aggregate, combined with subsequent reproduction, would predict a gradual decline in the variance of the number of mites per flower as the mean number per flower approaches the carrying capacity (K) of an average flower—assuming equal access to all flowers. Thus either (1) there is unequal access to the flowers sampled, the more accessible being the more populous; (2) there is a high variance in K, and in fact mean K has already been reached; or (3) something is keeping the mean number of mites per flower below mean K. Although more work is needed, the last alternative appears most likely, since counter to alternative (1), the flowers censused were intentionally chosen for equal accessibility to hummingbirds (and thus to mites), and counter to alternative (2), many uninhabited flowers had more nectar than inhabited ones.

Predation may be one factor limiting the mean number of mites per flower, although other factors are certainly involved. In a flower of *C. valerii,* I recently found a hemipteran (now being determined) which is apparently specialized for feeding on *Rhinoseius.* About 3 mm long, the bug holds a mite down with its forelegs, pierces the dorsum with its beak, and sucks the mite dry, leaving a deflated carcass. The individual I watched killed one mite after another in the flower (which was placed in a petri dish for observation). It died unaccountably after a few hours, but not before consuming some 15 mites. It seems unlikely that hummingbirds themselves consume *Rhinoseius,* as no mites were found in the crops of birds taken as voucher specimens.

Mites on Birds

Mites were normally removed from live birds (caught in mist nets) by aspiration, using a disposable postnatal mucus pump (Bard-Parker Infant Suction Set, no. 3450 with no. 10 French catheter). The tip of the catheter is held firmly against the nostril beneath the operculum, and suction is applied repeatedly to dislodge any mites. Usually, some mites also run out onto the bill as soon as the bird is netted (also noted by Baker and Yunker 1964), so that no attempt was made to collect mites from the two nostrils separately. Any mites found on the bill were also collected. I make no claim to have extracted all mites present in all birds treated in this manner, although the few birds taken for voucher specimens produced no further mites upon dissection immediately after aspiration and subsequent sacrifice. The aspiration method apparently had no ill effect on the birds, since marked individuals were recaptured subsequently in apparent good health.

Twenty-eight individual hummingbirds were netted at food plants and aspirated for mites. A summary of the mite species carried by each hummingbird species appears in table 1. Eleven birds carried no mites. The rest carried from one to 32 mites per bird (median four). Figures 2 and 3 show that the presence or absence of the two mite species on the three hummingbird species is about as expected given the feeding habits of the birds. That

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TABLE 1
SUMMARY OF MITE SPECIES TAKEN FROM NARES OF BIRDS

Carrier	Number of Individual Birds with Mites			
	Rhinoseius colwelli Only	*Rhinoseius richardsoni* Only	Both Mite Species	Neither Mite Species
Colibri ($N = 9$)	4	0	0	5
Eugenes ($N = 9$)	2	2	2	3
Panterpe ($N = 10$)	5	1	1	3

is, only *Rhinoseius colwelli* was taken from *Colibri,* which feeds exclusively on *Centropogon valerii,* inhabited only by *R. colwelli.* On the other hand, both mite species were found on *Eugenes* and *Panterpe,* and both bird species forage on plants inhabited by each of the mite species. Each of the three individual birds which actually carried both mite species was netted near the boundary between mature or cutover forest (where *Rhinoseius richardsoni* lives in *Macleania* and *Cavendishia*) and early second growth (where *R. colwelli* lives in *Centropogon*). The *Panterpe* and *Eugenes* with *R. richardsoni* only were netted in deep forest, and those with *R. colwelli* only were caught in second-growth areas. Two *Panterpe,* netted in second growth, fed on *Centropogon* almost exclusively by perching and piercing, so that it was not surprising to find these birds among those that yielded no mites at all.

Although it was impossible to watch the behavior of mites during hummingbird foraging, their habits when presented with a stuffed "forager" were clear enough. As soon as the bill is inserted into a flower containing mites, several run quickly up the bill (usually the underside) and into the region of the nares. Some mites actually entered the nares of stuffed specimens temporarily, but most wandered rapidly about the area near the nostrils or hid in the frontal feathers. It seems likely that the rapid air flux of a living bird may be an essential guide to the nares for the mites. Mites will board any object even remotely resembling a hummingbird bill, if inserted into a flower (e.g., forceps, twigs, artist's brush). Mites already on a dead hummingbird's bill will frequently disembark when the bill is inserted into a flower. Since I had no method of marking mites or seeing into flowers, I was unable to make detailed observations on individual mites. However, one safe generalization is that mites of older life stages are more likely to be found on birds than are younger mites, compared with the ratio of young and old mites in flowers (2×2 χ^2, $P < .001$ for *R. colwelli,* $P < .005$ for *R. richardsoni*).

Competition between Mite Species

To recapitulate, both species of mites are carried by two of the bird species, and some individual birds even have both species of mites simul-

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taneously. Yet not one of the hundreds of mites taken from flowers and identified to species was found in the presence of its congener. How can this be explained?

A reasonable hypothesis is that the two mite species have nonoverlapping fundamental niches. In other words, each mite species might be simply incapable of feeding and reproducing in the host flowers of the other mite species. If this were true, selection would be strong for some means of avoiding disembarkation from a hummingbird at the "wrong" flower. Some mites are indeed known to have highly specific chemoreceptors (e.g., Camin 1953). The first part of this hypothesis was tested at the study site by introducing mites of each species into uninhabited host flowers of its congener. To accomplish this, I first removed all open flowers (and thus all mites) from a *Macleania* plant and from a *Centropogon gutierrezii* plant and covered each plant with cheesecloth to prevent reintroduction of mites by hummingbirds. After new flowers had opened under the cheesecloth, I gathered about 100 mites of each species from its normal host plant and introduced adults of each species into the uninhabited flowers of its congener's normal host plant. Each separate flower of *Centropogon* and each inflorescence of *Macleania* were then bagged with a piece of mite-proof nylon stocking, and the entire plant again covered with cheesecloth. (The mites left over from each sample of 100 were mounted and identified to verify the purity of the populations used for introductions.) Details of the experimental procedure and results are given in table 2.

These experiments clearly show that each mite species is perfectly capable of reproducing in the host flowers of its congener, which means we must reject the hypothesis of nonoverlapping fundamental niches. Why then are no mixed colonies found in flowers? The answer to this question becomes immediately obvious when mites of both species are placed together in a closed test tube: they kill each other.

The main combatants are adult males, although adult females and younger mites attempt to defend against attack with their legs. In addition, adult male *Rhinoseius richardsoni* are armed with four unusual dorsal spines nearly half as long as the body (Hunter 1972), which are used defensively

TABLE 2

RECIPROCAL INTRODUCTION EXPERIMENTS DEMONSTRATING REPRODUCTION OF EACH MITE SPECIES IN THE HOST PLANT OF ITS COMPETITOR

	Rhinoseius colwelli IN *Macleania glabra**			*Rhinoseius richardsoni* IN *Centropogon talamancensis*†		
BAG	♀♀	♂♂	Imm	♀♀	♂♂	Imm
1	2	1	19	2	0	3
2	2	1	2	3	1	5
3	3	0	5	9	1	7
4	3	0	4	0	0	1

NOTE.—In each experiment, mites were introduced into four virgin flowers, which were then bagged separately. Data in the table were taken after 5 days.

* Two adult males and six adult females introduced into each flower.

† Ten adult mites (not sexed) introduced into each flower.

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with a rapid, upward jabbing motion. Male *Rhinoseius colwelli* use their large second legs, which are armed with opposing sclerotized spines (see fig. 1 and Hunter 1972), as raptorial weapons. In a typical encounter between two males, there is first a momentary touching of forelegs. If the mites are not of the same species, a fight ensues almost immediately, with the *R. colwelli* attempting to get in position for a lateral attack and the *R. richardsoni* attempting to prevent it. If the *R. colwelli* succeeds in grasping its opponent with the second pair of legs, it quickly begins a rapid shaking of the *R. richardsoni*, which is crushed and killed. The entire sequence may take as little as 15 sec. Male *R. colwelli* kill female and young *R. richardsoni* in the same way. Although I was unable to determine the cause of death, many male *R. colwelli* also perish after fighting. Female *R. colwelli* seem relatively immune in equal mixtures of the species. No attempt to set up replicated fights involving different proportions was feasible, due to the relative scarcity of *R. richardsoni*.

Putting together information on the distribution of the two mite species among plant species and bird species, the results of the reciprocal introduction experiments, and observations of behavioral interactions, we clearly have a case of aggressive or "contest" competition (Wilson 1971; MacArthur 1972) for a resource quite usable by either species. The completeness of separation of the two species among host plants strongly suggests some kind of preaggressive avoidance behavior based on plant species recognition (as proposed earlier) in addition to lethal fighting. Although it was possible to introduce mites into either the "right" or the "wrong" flowers with a fine artist's brush for the reciprocal introduction experiments, this was accomplished by wiping them off the bristles onto the interior surface of the corolla with a twirl of the brush—not a very good simulation of live hummingbird foraging. If plant-specific avoidance behavior does not exist, surely some individual mites of both species would have been found on the same plant species in spite of lethal aggression, since many individual flowers have no mites at all and many more lack males (fig. 4).[1]

A new problem now arises: why do the mites avoid particular plant species instead of simply staying out of individual flowers inhabited by the other species? A teleological answer is that they could not coexist indefinitely if there were competition for individual flowers, and an unfalsifiable answer is that flowers are easier to smell than mites. Another answer is given next.

Coexistence between Mite Species

Why are there two mite species and not just one at the study site? To understand the coexistence of *Rhinoseius richardsoni* and *R. colwelli* we

[1] In February 1973, C. H. F. Rowell conducted experiments at the study site which confirm the prediction of behavioral flower selection by the two mite species. Given a choice of two previously unoccupied flowers in opposite corners of a small plastic box, mites placed in the middle of the box (in the absence of congeners) tend to aggregate in their own host flower, avoiding the host flower of the other species.

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must look closely at the structure of their environment. To an individual mite, the world is a series of flowers connected by hummingbirds; the mite is like a perpetual airline passenger required to take all nourishment (and accomplish all reproduction) in airport restaurants. In terms of plant species visited, hummingbirds completely determine the grain structure (Levins 1962, 1968; MacArthur 1968) of the mite's environment.

A perfectly fine-grained mite environment would exist if all the hummingbirds in the study area visited available flowers of the four species of mite plants at random. A perfectly coarse-grained mite environment would exist if every hummingbird visited only one plant species. The real situation is intermediate, but much closer to the coarse-grained than to the fine-grained extreme, as I will now show.

Quantitatively, it is easiest to define and describe the grain structure of the mite's environment in terms of transition probabilities. Assume simply that each mite (*regardless of species*) climbs on the next hummingbird, *of any species,* that visits its present flower, and then gets off at the next flower, *of any species,* that the bird visits. Then what we want is a square matrix (**G**) of the probability g_{ij} that a mite will be taken to a flower of species j, given that the mite was in a flower of species i before the transfer. Vandermeer (1972) introduces the term "grain matrix" for this general method of representing environmental structure and discusses its mathematical properties (see also Pielou 1969, p. 187). The following discussion of the derivation of a grain matrix for mites may be followed more easily by reference to table 3.

The flowers we are concerned with typically occur in single-species patches. Let **N** be a vector of the average number of flowers per patch where n_i is the average for plant species i (table 3, part III). If a hummingbird feeds on each flower in a patch before moving on to the next patch, the probability that the bird will move to a new patch at any one transition is $1/n_i$. Consequently, the probability that the transition will be to another flower in the same patch is $1 - 1/n_i$. For large patches, the effective patch size is actually the average number of flowers visited per foraging bout, if this is less than the true patch size.

To define the grain matrix **G**, we also need to know about the pattern of hummingbird movement between patches. This information can be put in a set of three square matrices of patch-to-patch transition probabilities (**C**, **E**, and **P**)—one for each hummingbird species, since the species differ in flower preferences (table 3, part I). (For example e_{ij} is the probability that a patch transition by *Eugenes* will be from a patch of flowers of plant species i to one of species j.)

We now need the matrix **T** of patch-to-patch transition probabilities for mites. Matrices **C**, **E**, and **P** provide this information, on the condition that we know which species the next bird will be. For plant species i, the probability that the next visiting bird will be a *Colibri* is element d_i of vector **D**. The corresponding "visit probabilities" for *Eugenes* and *Panterpe* appear in vectors **F** and **Q**, respectively (table 3, part I). (Thus $d_i + f_i +$

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TABLE 3
COMPUTATION OF GRAIN MATRIX AND GRAIN COARSENESS INDEX FOR MITES

I. Patch-to-Patch Transition Probabilities (**C**, **E**, **P**) and Visit Probabilities (**D**, **F**, **Q**) for Hummingbirds*

Colibri

$$\mathbf{C} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \qquad \mathbf{D} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ .5 \end{bmatrix}$$

Eugenes

$$\mathbf{E} = \begin{bmatrix} .53 & .27 & .10 & .10 \\ .60 & .30 & .05 & .05 \\ .10 & .05 & .40 & .45 \\ .10 & .05 & .40 & .45 \end{bmatrix} \qquad \mathbf{F} = \begin{bmatrix} .3 \\ .3 \\ 1.0 \\ .3 \end{bmatrix}$$

Panterpe†

$$\mathbf{P} = \begin{bmatrix} .60 & .30 & 0 & .10 \\ .63 & .32 & 0 & .05 \\ 0 & 0 & 0 & 0 \\ .10 & .05 & 0 & .85 \end{bmatrix} \qquad \mathbf{Q} = \begin{bmatrix} .7 \\ .7 \\ 0 \\ .2 \end{bmatrix}$$

II. Combined Patch-to-Patch Transition Probabilities

$$t_{ij} = d_i\, c_{ij} + f_i\, e_{ij} + q_i\, p_{ij}$$

$$\mathbf{T} = \begin{bmatrix} .58 & .29 & .03 & .10 \\ .62 & .31 & .02 & .05 \\ .10 & .05 & .40 & .45 \\ .05 & .02 & .12 & .80 \end{bmatrix}$$

III. Effective Patch Size

$$n_i = \begin{cases} \text{average number of} \\ \text{flowers of species} \\ i \text{ visited sequentially} \end{cases} \qquad \mathbf{N} = \begin{bmatrix} 5 \\ 10 \\ 5 \\ 10 \end{bmatrix}$$

IV. Grain Matrix (Flower-to-Flower Transition Probabilities)

$$g_{ij} = \begin{cases} (1 - 1/n_i) + t_{ij}\,(1/n_i),\ i = j \\ t_{ij}\,(1/n_i),\ i \neq j \end{cases}$$

$$\mathbf{G} = \left[\begin{array}{cc|cc} .916 & .058 & .006 & .020 \\ .062 & .931 & .002 & .005 \\ \hline .020 & .010 & .880 & .090 \\ .005 & .002 & .012 & .980 \end{array}\right]$$

V. Steady-State Vector of Relative Mite Abundance

$$\mathbf{U} = [.16 \quad .13 \quad .07 \quad .63]$$

$$\mathbf{UG} = \mathbf{U}$$

VI. Fine-grained Limit of **G**

$$r_{ij} = r_j = \begin{cases} \text{proportional abundance of flowers of} \\ \text{species } j \text{ at study site} \end{cases}$$

$$\mathbf{R} = \begin{bmatrix} .2 & .1 & .2 & .5 \\ .2 & .1 & .2 & .5 \\ .2 & .1 & .2 & .5 \\ .2 & .1 & .2 & .5 \end{bmatrix}$$

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VII. Index of Grain Coarseness for Mites

$$s = \sum_{i=1}^{m} \sum_{j=1}^{m} |g_{ij} - r_j| = 5.4$$

$$s_{\max} = \sum_{j=1}^{m} [1 - r_j + (m-1)\, r_j] = 2(m-1) = 6,$$

where m = number of columns or rows in **G**

NOTE.—Values in **C**, **D**, **E**, **F**, **P**, **Q**, **N**, and **R** were estimated from netting data, observation at food plants, and flower censuses.

* Order of plant species in the rows and columns of all matrices and vectors is: *Macleania, Cavendishia, Centropogon talamancensis,* and *Centropogon valerii.* Transition probabilities are from the row plant species to the column plant species.

† Although *Panterpe* feeds on *C. talamancensis,* it does so without transferring mites (see text).

$q_i = 1$.) All three vectors were estimated directly from observational data. Each patch-to-patch transition probability for mites (t_{ij}) is a sum of three joint probabilities, as shown in part II of table 3.

The desired flower-to-flower transition matrix **G** (the grain matrix for mites) can now be specified and is computed in part IV of table 3. Diagonal elements represent the probability that a mite will go from one flower to another of the same species, which is the probability of going to another flower in the same patch ($1 - 1/n_i$) plus the probability of a patch-to-patch transition to another patch of the same species [$t_{ij}(1/n_i)$, $i = j$]. Since the elements of **G** represent the transition probabilities of a Markov process, we may compute the proportional abundance of mites in the four plant species (vector **U**) at steady state by solving the equation **UG** = **U** (see Vandermeer 1972). Elements of the vector **U** (table 3, part V) correspond well in rank order with the distribution of mites at the study site.

The degree of departure from a perfectly fine-grained environment, or the "grain coarseness," can be measured by comparing **G** to its fine-grained limit, **R**, in which $r_{ij} = r_j$ is the proportion of all mite flowers at the study site that are of plant species j (see table 3, part VI). Matrix **R** represents the flower-to-flower transition probabilities for mites, given that all birds visit all flowers completely at random. In a perfectly coarse-grained environment, there is no traffic at all between plant species, so the matrix has ones in the principal diagonal and zeros elsewhere (the identity matrix). A simple index of grain coarseness (s) is defined in part VII of table 3 and computed for the mite-grain matrix. MacArthur (1968) gives a normalized index of "departure from fine-grainedness" which is easily modified for application to grain matrices.

The environment, for *Rhinoseius,* is clearly very coarse-grained. The fact that an individual mite may indeed spend its entire life in one grain type makes *Rhinoseius* a classic example of an animal with a coarse-grained environment, by the definition of Levins (1968). Because of the effect of patch size, the diagonal elements of the grain matrix are close to unity. Failure of the assumption that a traveling mite leaves the bird at the next flower simply reduces the effective patch size and corresponding diagonal

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elements, without affecting the relative magnitude of off-diagonal elements in the grain matrix. Failure of the assumption that each mite boards the next hummingbird which visits its current flower has no effect on the grain matrix.

Again, I stress that the grain matrix computed assumes absolutely no flower or bird selection on the basis of species by the mites—although evidence was presented earlier indicating that flower species preferences very likely exist. Even without inclusion of this factor in the model, a close look at the nondiagonal (between-plant-species) transition probabilities in the grain matrix (table 3, part IV) shows that the first two and the last two flower species form two clearly defined habitat units. Mobility between flower species within these units (the four upper left and four lower right values in the grain matrix) is almost uniformly higher than mobility between them (the four upper right and four lower left values). This can be seen also by reference to figure 5*a*. Vandermeer (1972) gives a method of forming "quasi-hierarchical dendrograms" of habitat types from grain matrices by defining (as I have just done in other terms) stochastic submatrices at successively higher transition probabilities. Figure 5*b* gives the dendrogram for the mite-grain matrix.

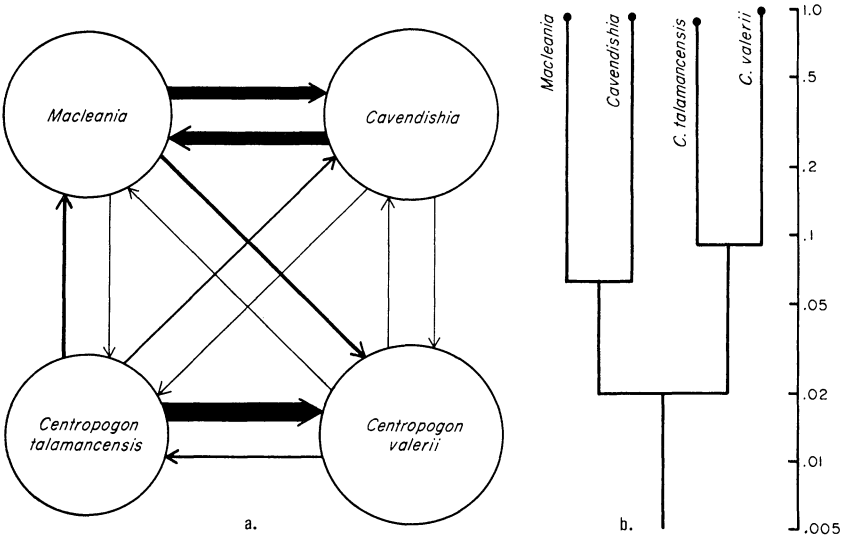

FIG. 5.—Grain structure of the environment for mites. In *a*, the diameter of the circles indicates the probabilities of within-species transitions, and the width of the arrows shows the probabilities (on the same arithmetic scale as the circle diameters) of between-species transitions. The same information is represented in *b*, in terms of the "environmental dendrogram" technique of Vandermeer (1972). It is formed by finding stochastic square submatrices in the grain matrix (table 3, part IV) at progressively higher transition probabilities (the scale on the right margin of the figure).

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The two pairs of plant species defined in figure 5 are the two ericads (*Macleania* and *Cavendishia*) in the first group and the two species of *Centropogon* in the second. *These are precisely the definitive host plants of the two mite species* (figs. 2 and 3), *even though the model yielding the grain matrix assumed that all mites behave alike.* Each pair of plant species forms what MacArthur (1968) has called a "grain type." In general, the existence of two distinct grain types should be sufficient to allow the coexistence of two competing species (MacArthur 1968) with only minimal differential fitness in the grain types. The addition of interspecific aggression (especially if it is lethal) further stabilizes the system by the principle of "aggressive neglect" (Hutchinson and MacArthur 1959). Selection for any behavior which minimizes losses through aggression would clearly be expected to follow the lines of division between grain types and will even further emphasize them.

We now have the answer to the question posed at the end of the previous section. Flower avoidance by mites at the study site is based on flower species rather than on occupancy or nonoccupancy by congeners, since plant species define the limits of the two grain types. Individual mites entering unoccupied (or occupied) flowers within their usual grain type have a higher average fitness than those entering unoccupied flowers of their competitor's grain type. The latter have a negligible chance of getting back or finding a mate and must eventually face hordes of lethal inhabitants. Speculation on the interesting possibility of sympatric speciation must await more complete zoogeographical studies.

The classical competition equations (Gause 1935) predict coexistence on the condition $\alpha < K_1/K_2$, $\beta < K_2/K_1$. Since the mite species kill each other, α and β must each be greater than one, so the condition clearly cannot be met. Very likely, rather, $\alpha > K_1/K_2$ and $\beta > K_2/K_1$. The predicted outcome in this case is no coexistence, with the winner depending on initial concentrations. It is satisfying that this prediction nicely complements the grain analysis of coexistence. Namely, each mite species wins over intruders in its own grain type because its initial concentration is much greater there.

Finally, we must turn to the problem of why there are not *more* than two mite species at the study site. I know of no noncircular method applicable to the present situation which allows quantitative prediction of the upper bound (but see Vandermeer 1970 and Levins 1968). However, the number of species should equal the number of *effective* grain types, which depends upon both the structure of the grain matrix and a threshold probability for transition between possible grain types. This is most easily visualized by reference to the dendrogram in figure 5*b*. The threshold probability for the study site apparently lies somewhere between .020 and .062. Above, I have argued that mobility is too slight between the two grain types defined at that level to allow takeover by one of the mite species, which would occur if the threshold were lower on the dendrogram. If the threshold were moved above .090, we may surmise that four mite species

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could coexist, one on each plant species. At .080, there should be three species of mites.

What factors control the threshold level? Partly the biology of the mites and partly the dynamic characteristics of the grain matrix. For example, the grain matrix computed in table 3 is valid at best only for November to April, and furthermore does not take into account the possibility of unusual climatic fluctuations which could alter radically the structure of the matrix and its dendrogram. In general, the less temporal fluctuation in the grain matrix, the higher the transition probability threshold should be between possible grain types. Even an occasional large increase in mobility between grain types could cause the local extinction of a species. On the other hand, I would predict the possible coexistence of three or four mite species at the study site, were the seasons less distinct and less variable year to year. In general, this means that coexistence of competitors made possible by grain-type separation should be more prevalent in regions of high climatic constancy and predictability. This phenomenon may contribute to high species diversity in the tropics. MacArthur (1968) makes a similar suggestion in terms of the overall grain coarseness of environments.

ADAPTIVE STRATEGIES IN THE TROPICS

The search for general patterns of adaptation in environments with different degrees and kinds of climatic fluctuation has led to rather general agreement, on theoretical grounds, that tropical species should be more specialized ecologically than species at higher latitudes (Levins 1968; MacArthur 1972). I have confirmed this experimentally on a mass basis in a study with arthropods (Colwell 1969, and in preparation). Yet there are many ways to be specialized, and we need a more precise understanding of common adaptive patterns in environments of high climatic predictability and constancy (Colwell, in preparation). The species discussed here demonstrate several adaptive strategies which I suspect contribute significantly to diversity of tropical fauna, although the list below is neither exhaustive nor its items mutually exclusive. Much of my reasoning appears above, so I give only brief definitions below.

Grain specialists, like the two *Rhinoseius* species, depend for their continued coexistence on the maintenance of the grain structure of their environment, which may depend upon a large number of factors. The more dynamically stable the grain matrix, the more grain specialists can coexist, for any particular average values of the matrix elements.

Sequential specialists, like *Colibri,* rely on one or a few resources at any one time, but switch (or migrate) from one to another in a regular way with the seasons (or conceivably night and day). The predictability of timing and quantity of seasonal resources in a complex system affects the possible number of coexistent sequential specialists directly, as well as their relationship with opportunist competitors (above).

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Interstitial species, like *Eugenes* and to some degree *Diglossa* at the study site, depend upon low-density energy sources—that is, either resources which are normally widely dispersed in space or time, or the fringes of high-density resources dominated by other species. There are, of course, interstitial species everywhere, but this strategy should be more common, and more such species may coexist, where the crucial factor of predictability is high for low-density resources, presumed to be the case in the tropics.

Hypercontingent species depend directly for their existence on the relationship between at least two other species. *Rhinoseius* mites, for example, require hummingbirds for transport as well as reliably visited, long-flowering plants with an acceptable floral topology. These mites are dependent not on either the birds or plants, but on the mutualistic interaction between birds and plants. The exploitation of mutualisms (see Janzen 1969 for another case) should be a particularly common hypercontingent strategy, since neither partner in the mutualism can afford to escape exploitation by going it alone. All species, of course, depend ultimately upon many other species. I restrict the meaning of *hypercontingent* to the immediate and direct dependence on the relationship between two or more other species for nutrition, dispersal, reproduction, defense, or support. The number of hypercontingent species should be greater in environments with high constancy and predictability, since their existence is a function of the compound probability of sufficiency in two or more resources. The geographic distribution of the genus *Rhinoseius,* though still poorly known, appears to demonstrate this principle admirably.

SUMMARY

Nectarivorous mites of the genus *Rhinoseius* breed and feed in hummingbird-pollinated flowers and are dispersed in the nasal cavities of hummingbirds. An analysis is presented of the evolutionary and ecological interactions among 10 species in a Costa Rican highland community: two *Rhinoseius* species, three hummingbirds, a coerebid bird, and four hummingbird-pollinated plants. Coexistence of two territorial hummingbirds at the study site is allowed by migration, sequential specialization on seasonal resources, and behavioral interactions. The third hummingbird is an *interstitial* species dependent on a variety of widely dispersed food plants. The coerebid bird, a nectar thief, feeds within hummingbird territories on relatively indefensible flowers. Coexistence of the two mite species, capable of lethal combat, depends upon the grain structure of their environment, which is determined by hummingbird feeding patterns. This is demonstrated by a probabilistic model based on field data.

Tropical environments favor sequential specialists, interstitial species, grain specialists, and *hypercontingent* species. These adaptive strategies probably account in part for high tropical species diversity.

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ACKNOWLEDGMENTS

I thank especially James I. Richardson, without whose help this study would never have begun, and Preston E. Hunter, without whom it could not have continued. I am also grateful to M.-C. King, S. J. Arnold, T. Asami, H. G. Baker, L. Baptista, D. Bradford, L. Carpenter, P. Feinsinger, C. Fitzgerald, D. J. Futuyma, J. H. Hunt, D. H. Janzen, L. Lawlor, M. Mackey, F. Ortiz-Crespo, G. Powell, F. G. Stiles, J. H. Vandermeer, L. L. Wolf, and an anonymous reviewer. William Burger and Robert L. Wilbur kindly identified plant specimens, and Eugene Eisenmann identified bird specimens. Emily Reid drew figures 1 and 2.

This research was supported by an NIH Biomedical Sciences Institutional Grant administered by the University of California and was greatly facilitated by the cooperation of the students, faculty, and staff of the Organization for Tropical Studies.

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