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FOOD AND FEEDING HABITS OF MEXICAN HUMMINGBIRDS

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HUMMINGBIRDS have been variously reported to feed on nectar alone, on nectar and insects in varying proportions, or (at least for limited periods) on insects alone. The viewpoint that hummingbirds feed chiefly on nectar, using insects only as occasional supplementary food, has steadily gained ground (Stresemann, 1927–34; W. Moller, 1930; Porsch, 1926–30). But this opinion is apparently based on merely casual observations, while the results of stomach analyses and field records published by a number of authors lead to a different conclusion.* Wetmore's very careful investigations (1916), in particular, deserve attention. He found 100 per cent animal content in 64 stomachs of three species of hummingbirds from Puerto Rico; while in 59 stomachs of two other species, 98.57 per cent of the contents was animal, 1.43 per cent vegetable. My own observations on the food and feeding habits of hummingbirds, as well as on the related activities, drinking, bathing, and cross-pollination of flowers, are given below. They are limited to Mexico and include data on 19 species.†

Variation In Food With Locality and Season

The food of hummingbirds is determined primarily by habitat and season. A given species may feed mainly on nectar or mainly on insects, depending on the time of year. The majority of the hummingbirds found in Mexico are not dependent on flowers, their migrations being determined by food supply in general rather than by the supply of a particular kind of food. When flowers are lacking, or when the food they provide is inadequate, hummingbirds live on insects and other small animal life.

In the high mountains, hummingbirds depend on animal food for the greater part of the year. They do migrate locally, avoiding the extreme temperatures of winter, but it is only during late summer when

* See, for example, Gould (1861) and the authors quoted by Bent (1940:319–472).

† Thanks are due to Dr. F. Miranda of the Biological Institute, University of Mexico, for identifying the plants; to W. J. Gertsch and C. H. Curran, of the American Museum of Natural History, New York, for carrying out the stomach analyses; to Dr. Erwin Stresemann for the encouragement that has led me to devote an increasing amount of my time to the study of this group of birds; and to Dr. Ernst Mayr for his invaluable suggestions and painstaking correction of the translation.

TAWNY FROGMOUTH

Podargus strigoides

Water color from a live specimen captured in early August 1943 in open eucalyptus forest near Wacol, Queensland, Australia.

When captured, the bird emitted loud, rasping wails, then clamped my finger in its bill, nicking the skin with the point of its beak.

The species, which breeds from August to December, is fairly common in Australia and occurs also in Tasmania. Male and female are similar, but some adult females show more reddish in the plumage. It is a nocturnal bird with a silent, owl-like flight. By day it sits upright on a branch in a "dead-stick" attitude, feathers drawn tight, bill pointed in the air, the eyes mere slits. It feeds, usually from a perch, on phasmids and other insects. The call, a repetition of a deep *oom oom*, carries great distances.

The nest of the Tawny Frogmouth is an open platform of loose sticks placed on a horizontal limb, sometimes as high as forty feet from the ground. The eggs are two or three in number, white, and rounded.—Richard P. Grossenheider.

everything is in flower that they consume nectar in any quantity. Similarly, in regions with a pronounced dry season an adequate supply of nectar is available for only a few months of the year, and hummingbirds of such regions live chiefly on insects. These birds are, however—and probably without exception—also forced to make regular local migrations. They are found during the dry season in the gallery forests along the streams intersecting their range, where an abundant insect life ensures them adequate food the year round. Following the first rainfall in summer, when the arid regions and barren mountains are green and in blossom again, the hummingbirds return there, and then supplement their animal food with nectar.

On the other hand, there are some species that feed largely on nectar and are in consequence dependent on blossoming plants. I have found them only in the tropical regions of Mexico. Individuals of such species occur in the more northern regions only as summer residents. They do not occur in the high mountains or in areas with a pronounced dry season, even as visitants. Flowers the year round are for them a vital necessity, and consequently they can live only in regions, such as the tropical forests, where climatic changes are slight. Even here their specialized feeding habits force them to make regular local migrations.

An independent confirmation of the pronounced difference in food habits between tropical and highland hummingbirds is supplied by the following observations: On several occasions I took some 40 or 50 live hummingbirds from Mexico and the West Indies to European zoological gardens. En route they were fed the usual mixture of honey, raw sugar, etc. It was not possible to give them the live insects (*Drosophila* sp.) that they are fed in zoological gardens. In the course of years I found that species from the coast of Veracruz and from Havana fared better in captivity than those from the highlands of Mexico. Since species from the warm tropical coasts feed regularly on nectar, they can live without difficulty on the artificial food mixture, which is very similar to their natural food. The birds from the high mountains, on the other hand, had been feeding at the time of capture (March to April) almost entirely on insects. They readily took the syrup offered to them, but it was not an adequate substitute for the food they had been eating, and they soon died of an intestinal affection.

Data from zoological gardens show that Brazilian hummingbirds endure captivity especially well, surviving as long as two years. Since these birds come from the tropical valley of the Amazon, where they feed mainly on nectar, the artificial food given them in captivity suits their requirements.

Modes of Feeding

Hummingbirds feed while on the wing, whether they are extracting nectar from flowers, gathering insects from the vegetation, or capturing flying insects. Usually hummingbirds while perched will capture an insect only if they chance to see one in their immediate vicinity. I have

seen but one species assume a perch for the purpose of feeding. In April, near Mexico City, I regularly observed Heloise's Hummingbird (*Atthis h. heloisa*) feeding at the blossoms of a large tree (*Erythrina americana*). They sometimes hovered before the blossoms but immediately perched on the stem whenever the position of the flower made this possible (Figure 1). Then they inserted the bill between the long bifurcate petals.

Nectar

On the Pacific coast of Chiapas, I observed two species of hummingbird that were predominantly nectarivorous. Near my camp, an enormous leafless tree was in full bloom. It was filled morning and evening with Cinnamomeous Hummingbirds (*Amazilia r. rutila*) and Prevost's Mangos (*Anthracothorax p. prevostii*). The two species divided the tree between them, the Cinnamomeous Hummingbirds taking complete possession of the lower branches of the tree, the Prevost's Mangos occupying the top. If a bird of either species crossed the invisible boundary line that divided the two parts of the tree, it was immediately driven back to its own territory.

From this tree I collected 2 Prevost's Mangos and 8 Cinnamomeous Hummingbirds; the stomachs and crops of all 10 specimens were filled with nectar, a thick whitish liquid, sweet and palatable. With the

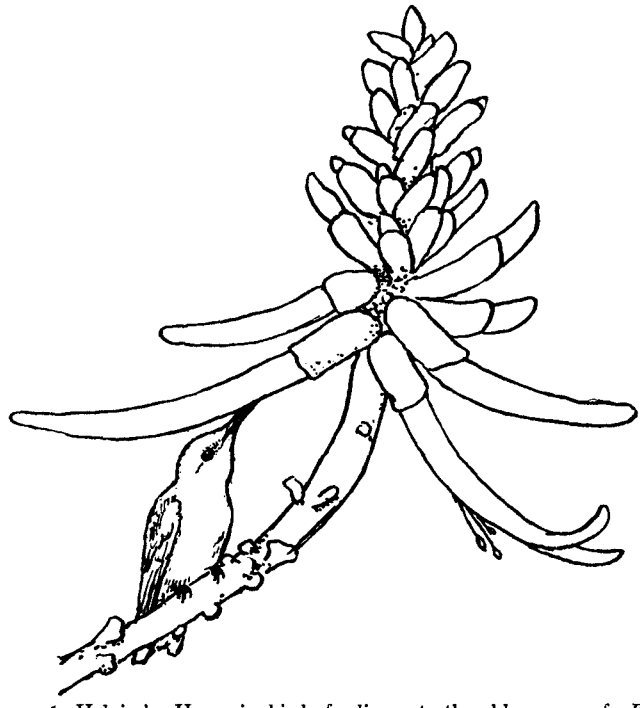

Figure 1. Heloise's Hummingbird feeding at the blossoms of *Erythrina americana*.

nectar a few insects had been taken by one of the Mangos, and two spiders by one of the Cinnamomeous Hummingbirds, but possibly only by accident.

Nectar is so very rapidly used up that large quantities must be stored in the crop for use in periods of inactivity—during the night and during the middle of the day when the temperature of the habitat often reaches 104° F. in the shade. It is known that captive hummingbirds drink daily a quantity of liquid equal to twice their own weight, but this actually tells us very little. In my experience, the amount of liquid consumed by captive birds varies with the sugar content. Since the syrup fed them is more concentrated than the rather watery nectar from flowers, the volume of natural nectar consumed is probably much greater than the amount of syrup determined for captive birds. The fact that carbohydrates are rapidly consumed is probably related to the fact that nectar is the chief food only for birds that live near the equator, where night is never longer than day. Only an insectivorous hummingbird, with crop well filled with insects, can withstand the long winter nights of the temperate zones when the temperature is below freezing. I have observed that captive hummingbirds fed on the honey solution were unable to survive 14 or 15 hours without food.

Insect and Other Animal Food

Most Mexican hummingbirds feed chiefly on insects, spiders, and other small animal life, but there is great variation in their methods of procuring such food. The method is largely determined by environmental conditions, though it also varies in part with the individual species. The prey may be extracted from tubular flowers, picked off from shallow flowers, captured in the air, or taken from crevices in bark, from young shoots, withered leaves, spider webs, fresh fruits that have burst open, and even from the surface of water.

Flowers as a source of food. Whenever possible most species procure their animal food from flowers. When flowers furnish abundant insects, hummingbirds only occasionally hunt them elsewhere.

The exact method of procuring insects from tubular flowers is unknown. Probably the tongue, thrust into the flower, gropes about until an insect adheres to it. The various shapes of tubular flowers are significant in relation to the birds' visits to them. When different types of such flowers bloom simultaneously at the same place, each is usually visited by a different species of hummingbird. In the mountains surrounding the Valle de Mexico, one finds at many spots in August and September the White-eared Hummingbird (*Hylocharis l. leucotis*) at *Salvia mexicana* and *S. polystachya,* the Mexican Violet-ear (*Colibri t. thalassinus*) at *Salvia mexicana* and *S. cardinalis,* while the Blue-throated Hummingbird (*Lampornis clemenciae*) visits only *S. cardinalis.* Convenience is apparently the determining factor. Each species visits the flower from which it can most easily obtain insects or nectar with its peculiar shape of bill. The calyces of *Salvia cardinalis* are too

deep for the White-ear, and those of *S. mexicana* are so small that it is not easy for the large-billed Blue-throated Hummingbird to obtain food from them (although observations have shown that it is possible).

Many species choose shallow flowers when these are available, and the shape of the bill is then not a factor; I have seen species with long straight bills, short and thin bills, and even more or less curved bills, visit the same blossoms.

I have found no evidence for the theory that the long curved bill is a specific adaptation for feeding from certain species of flowers. In fact, not a single species of Mexican hummingbird is adapted to a specific shape of flower. This is not to say that the peculiar bill shapes did not originate as special adaptations during evolutionary development in a different environment. But probably such specialization is not possible in northern latitudes with their extreme climatic changes.

The theory that flowers of a certain color have a particular attraction for hummingbirds has often been discussed. Although the point is not a difficult one to settle by experiment, and observations by Woods (1927:306–307), Sherman (1913), and others seemed to contradict the theory, Bené (1941) was the first to prove conclusively that an innate preference for red does not exist in hummingbirds.

In the summer and fall of 1941, I conducted an investigation similar to Bené's. In a spot frequented by many hummingbirds, I hung several feeding flasks of the usual type covered with paper of different colors. At intervals of 30 minutes to an hour I measured the amount of syrup taken from each flask, in order to determine the comparative frequency of visits to the various colors. I found that the flask most frequently visited was always of the same color as the flower most visited at that particular season. It was purple in July when the purple *Pentstemon campanulata* was in full bloom and was visited by hummingbirds almost to the exclusion of other flowers. In October, when the dark blue *Salvia mexicana* was in bloom, the liquid in the dark blue flask was almost entirely used up, while the purple flasks that had been favored in July were frequently left full and untouched. Further evidence was the observation that, at a given place and time, each species of hummingbird would choose the flask of the color that corresponded with the color of its preferred flower then in bloom. Thus, in season, the Mexican Violet-ear showed a preference for red flasks, in accordance with its preference for the red flowers of *Salvia cardinalis;* while the White-ear, which visited the blue flowers of *S. mexicana* almost exclusively, patronized the blue flasks almost exclusively.

Summarizing his results, Bené says (p. 242): "Color preference may be conditioned by training, as when a hummingbird trained to feed on a colorless syrup remains constant to it, even when the colorless syrup is placed among feeders containing syrup of different colors." It appears that the same conditioning to a given color (varying with the species, the locality, and the season) occurs under natural conditions when a flower of that color provides particularly abundant food.

Hawking insects. The capture of insects by hummingbirds in flight is frequently doubted or else considered an exceptional phenomenon (e.g. Moller, 1930: 677). But I have often observed Mexican hummingbirds capturing insects in the air, and this means of procuring food is essential to some species at certain seasons.

Skill in capturing insects in the air, as well as the method employed, varies from species to species. The technique of capture used by a number of species is described in the following pages and illustrated in Figures 2 to 9. In each drawing, arrows indicate the direction of flight; a dot in the path of flight indicates that the bird hovered at that spot for a certain length of time.

Species that regularly capture insects in the air hover at a given spot and then suddenly dart forward about a meter's distance to seize an insect. Presumably the bird must be at a certain distance from the prey in order to see it and instantly dart upon it with accurate aim. How the bird seizes the insect is difficult to determine since the movement usually takes place too rapidly and at too great a distance from the observer to be accurately followed by the eye. I once observed under favorable conditions, and from quite near by, a Deville's Hummingbird (*Amazilia beryllina devillei*) capturing insects. This hummingbird did not make its capture by using the bill but by darting out the tongue for a fraction of a second so that the insect was caught upon it. Occasionally I saw the bill open to a 15- or 20-degree angle, but this seemed to occur after a successful attack, when the insect adhering to the tongue needed to be moved to the back of the bill.

Deville's Hummingbirds and Pale-crowned Star-throats (*Heliomaster longirostris pallidiceps*) spend the month of April in the gallery forests near Villa Flores in the dry areas of interior Chiapas, where the water level is very low at this season. Innumerable dipterous larvae develop in the many stagnant pools of the drying stream beds, and the insects dance morning and evening in thick swarms.

Deville's Hummingbirds were numerous at these spots and fed chiefly on insects caught in the air though I occasionally saw one hovering at the inconspicuous flowers of a Chalu tree (*Inga* sp.). They would perch on a small twig, some 8 to 15 meters above the ground, at a spot near a dancing swarm of insects, and from there make attacks on the swarm at intervals of three to five minutes (Figure 2). The bird approached the swarm by direct flight, hovered for an instant beneath it, then attacked an insect by darting obliquely upward. Whether the bird captured the prey or the insect escaped could not be determined from a distance, but the bird would hover at the spot for an instant and then attack anew in the same manner. After several flights directed obliquely upward (three to five, depending on the size of the swarm), the bird would reach a point above the insects, hover there for two to four seconds, then return to a point underneath the swarm and again dart upward through it capturing insects. Occasionally I observed two in-

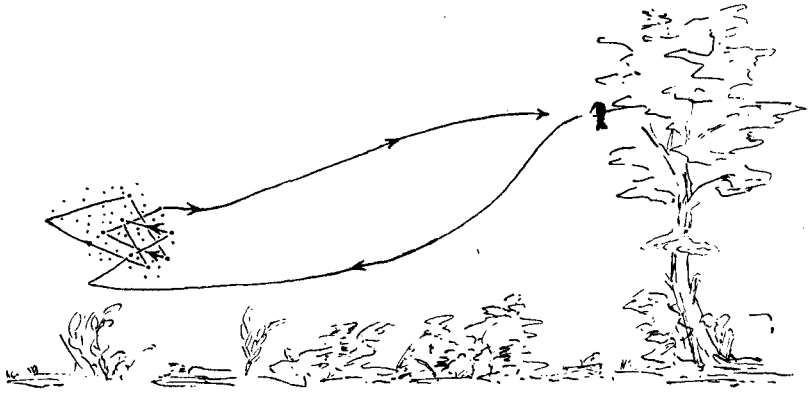

Figure 2. Deville's Hummingbird capturing flying insects.

dividuals of this species hunting alternately through the same swarm.

I have only occasionally observed insect-hawking by Pale-crowned Star-throats, which rarely appeared in my observation area. Like the Deville's Hummingbird, they use a look-out post to which they return after each series of captures. The bird flies out to the swarm of insects and remains for a few seconds beneath it to aim for the first victim (Figure 3). After each attack the bird hovers for an instant to take aim for the next insect. The method of capture is essentially the same as in Deville's Hummingbird, but the individual attacks are less sudden and swift and the line of flight curved. When the bird has reached the highest diptera, it returns in gliding flight to a spot beneath the swarm and again proceeds upward. When it has hunted through the swarm from three to five times, it returns to the look-out post on a

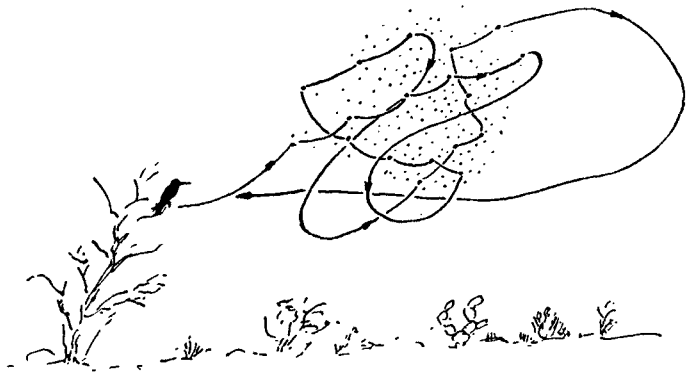

Figure 3. Pale-crowned Star-throat capturing flying insects.

curved line of flight. The length of each period of hunting probably depends on the number of successful attacks. In this species, also, I repeatedly saw the bill opened widely after an attack on an insect; this probably has no connection with the actual capture of the prey.

As a non-migratory forest dweller, De Lattre's Sabre-wing (*Campylopterus h. hemileucurus*) is dependent on locally available food. During the season when a certain ornithophilous flower (*Marcgravia* sp.) produces large quantities of nectar, the Sabre-wing feeds from this, either drinking the nectar or eating the insects caught in it. But during the rest of the year, when flowers are scarce, its chief food is animal, as stomach analyses show. I watched a Sabre-wing capturing gnats from a swarm that danced over a large forest brook (Figure 4). The bird hovered at a distance of 50 to 100 cm. from the swarm

Figure 4. De Lattre's Sabre-wing capturing insects from a swarm over a forest stream.

and then suddenly darted straight forward. It hovered a moment in the midst of the swarm, then flew back to its starting point. After some six or eight such sorties, it disappeared into the neighboring woods. Several times I saw what was probably the same individual capturing insects at the same place.

The Rieffer's Hummingbirds (*Amazilia t. tzacatl*) that occupied the garden of my house in Chiapas used the same method of capture. However, they also hunted assiduously in the blossoming orange trees, whose fragrance attracted countless insects. Blossoming plants were rare at the time of my observation (January and February) outside this small cultivated area, and hence another means of procuring food was necessary. With this species the habit of hawking insects was apparently so firmly fixed that they hawked—at least at this season—even where blossoming plants were plentiful.

In contrast with the species discussed above, there are some that wait on a perch until an insect comes within aiming distance. Heloise's Hummingbird hunts its prey in this fashion, darting out at an insect when it approaches within a meter or a meter and a half. The bird pauses for a fraction of a second at the spot where the insect has been caught. Usually it does not return to the same perch but goes to one near by. In the instance pictured in Figure 5, a female Heloise's Hummingbird perched again and again on the outermost tips of maguey (*Agave*) leaves. At the edge of a field bordered with maguey plants, several hummingbirds were busy capturing insects at the same time, each maintaining its own territory. Feeding conditions were favorable here because the larvae of the insects, a species of minute fly, developed in countless numbers in the damp mouldering stalks of the maguey plants destroyed by the pulque makers.

In the same group were also White-ears, which live in the high mountains of central Mexico and are among the few hummingbirds that remain (at least in part) in the breeding range even during the non-breeding season. To survive the food scarcity of winter (when the temperature is sometimes as low as 15° F.), as well as the hot rainless season from March to May, they must employ every possible method of procuring food. During much of the year, this species "gathers" almost all of its animal food, for the organisms that form its prey are mostly sedentary in cold and inclement weather. But occasionally it

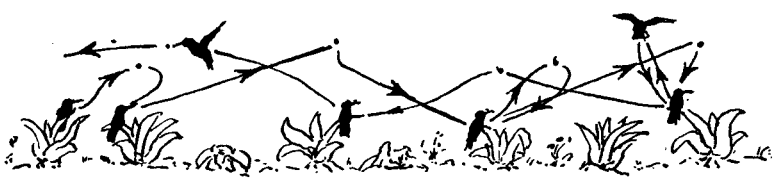

Figure 5. Heloise's Hummingbird capturing single insects along a field border.

catches insects in the air—which it is able to do with great dexterity. It waits on a perch until an insect approaches within 30 or 40 cm., then suddenly pounces upon the prey, hovers for a moment, and returns to the same perch or, exceptionally, to one near by. Very rarely—apparently after missing its prey—it makes a second attack from closer range. The attempts at capture occur at intervals whose length apparently depends on how often an insect comes near the bird. Occasionally they occur in quick succession, as I have observed when a White-ear was perched near a swarm of gnats dancing in the sun. It would remain only two to four seconds on the perch before aiming at new prey.

Besides the habitual insect hawkers noted above, I observed a number of occasional hawkers—so described not only because I rarely observed them hawking, but also because their technique (as shown by the frequency of unsuccessful attempts) was less well developed.

To this group belongs the Mexican Violet-ear, which is very common in late summer in the mountains surrounding the Valle de Mexico. It obtains its food mainly from flowers, and most individuals of the species migrate as soon as flowers in the high mountains begin to diminish in fall. A few males remain for the winter in especially favorable localities (Wagner, 1945:166), but even these feed chiefly in the sparse *Salvia cardinalis, S. elegans,* and *Calamintha macrostema,* which in sheltered places do not freeze. Rarely, however, I have observed a Violet-ear awkwardly catching insects in the air. On one occasion, when the conditions for observation were extremely good, the hunting took place from a perch in an oak sapling. Near the tree danced a small swarm of gnats in which my eye could follow the movements of individuals. Again and again I saw the hummingbird miss a gnat for which it had aimed or a gnat evade capture at the last moment. The Violet-ear perched on the outermost tip of a twig and waited until an insect approached, then took aim and darted forward—usually with negative results. Before returning to its perch, the bird usually made several attempts at capture, hovering momentarily each time to take aim at the nearest insect. Several such sorties are shown in Figure 6.

The Broad-tailed Hummingbird (*Selasphorus p. platycercus*), which is common in the Valle de Mexico, especially in late summer, has still another technique. I have on a number of occasions watched this bird catching insects from a perch on the tip of a corn stalk. Apparently seeing an insect, the Broad-tail would fly to a point some three to five meters away, then turn sharply, and suddenly begin darting back and forth, hovering for an instant before each change of direction (Figure 7). After several such attempts to capture one insect (whether with or without success did not appear), the Broad-tail would suddenly dart after another that came in sight a few meters away. It repeated this a few times before returning to its perch on the corn stalk. This occurred at a season (August and September) when there was no lack of

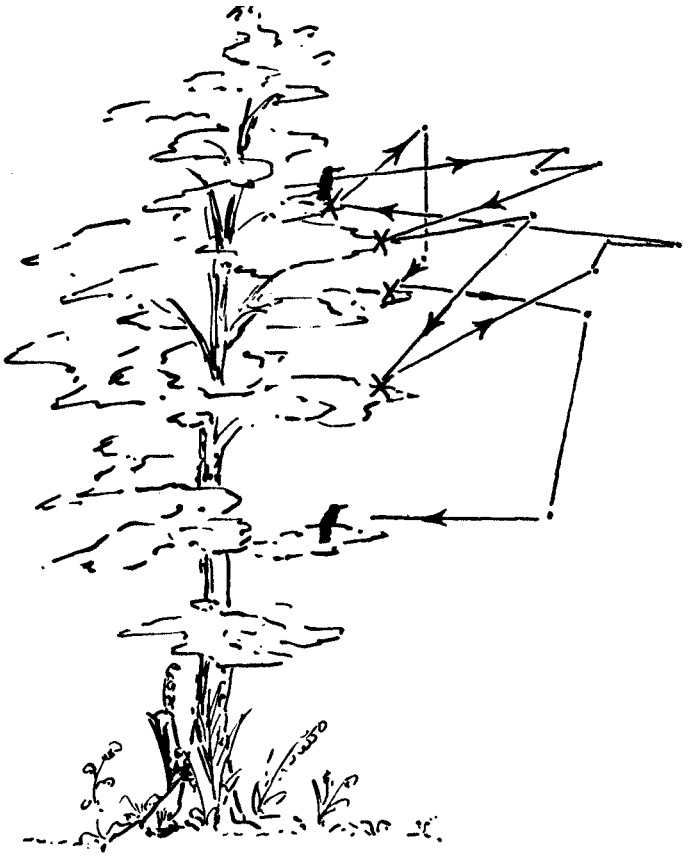

Figure 6. Mexican Violet-ear capturing flying insects that pass its perch.

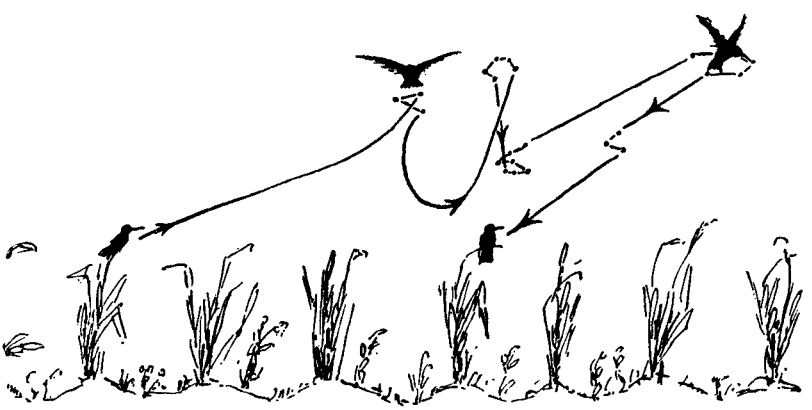

Figure 7. Broad-tailed Hummingbird capturing insects above a cornfield.

flowers holding a rich medley of insects. I never saw Broad-tails capturing insects in the air when feeding conditions were unfavorable; instead they always "gathered" them. And I consider these instances of their hawking merely a form of play.

Rivoli's Hummingbirds occasionally capture insects in the same manner. In contrast to the quick, darting flight of other species, that of Rivoli's Hummingbird is slow, almost deliberate. In the spring, in the Valle de Mexico, I observed Rivoli's Hummingbird attacking the diptera dancing in the sun a few meters from its perch in the top of an oak or pepper tree (Figure 8). After flying out to the insects, the bird moved back and forth in almost horizontal flight, attacking insects at ranges of 20 to 40 cm. It is amazing to see this species turn from one direction to another while hovering at one spot.

The Blue-throated Hummingbird has a different method of capture from those described above. The bird darts here and there to the points where it sees its prey, without hovering even an instant when it changes direction. In the mountains, early one morning in October, I saw a Blue-throat attempting to capture a few flying insects from a perch in the top of a spruce some 20 or 25 meters high (Figure 9). The bird was not a skillful hunter, and it zig-zagged back and forth again and again, apparently in an attempt to capture a single insect. When the weather is inclement and flowers scarce after this hummingbird arrives in the high mountains in spring, it obtains the necessary food by gathering small animal life from bark and vegetation; capture of insects in the air is of minor importance to the species.

Collecting food from bark, vegetation, spider webs, and fruit. When gathering animal food from various surfaces and crevices, a hummingbird first sees the prey, hovers to take aim, then suddenly pounces. The importance of this "gathering" method varies greatly, from species such as Abeillé's Hummingbird (*Abeillia abeillei*), which takes only an occasional insect that it happens to see, to those such as the White-ear, which hunts its food almost entirely in this manner.

The short bill of Abeillé's Hummingbird (measuring between 9 and 11 mm.) is less suited to obtaining food from flowers than that of most other hummingbirds. I have often observed the species in the humid primeval forest of Chiapas; it lives in the half-darkness of the undergrowth beneath the tall thick-crowned forest trees and is very rarely seen more than a few meters above the ground. Only a few and rather inconspicuous flowers grow in this habitat. In May the arum plants (Araceae), with their large, thickly-flowered spadices, are in bloom, and Abeillé's Hummingbird is then seen gathering the insects attracted to these flowers by their fragrance. But they usually hunt their food on leaves and young shoots. I have also seen them moving in their characteristic hovering flight up and down the trunk of a tree, stopping suddenly to pick an insect from a crevice, from moss, or from

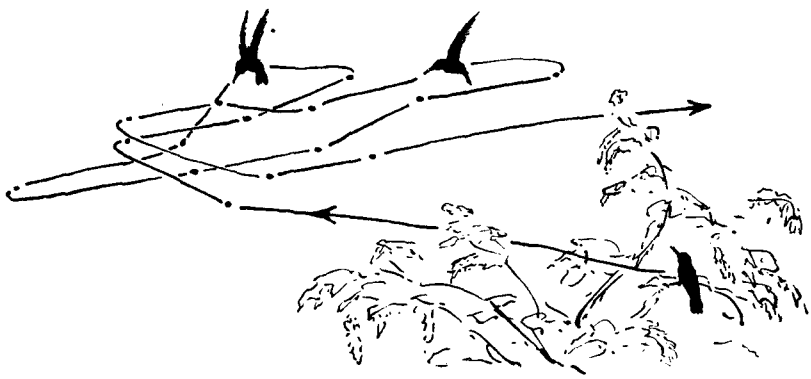

Figure 8. Rivoli's Hummingbird capturing diptera near its look-out in a treetop.

Figure 9. Blue-throated Hummingbird capturing flying insects.

a smooth stem. Microscopic analysis of the stomach contents of two of these birds collected in May showed only fine insect pulp with no admixture whatever of vegetable substance.

Unlike Abeillé's Hummingbird, the White-ear has a bill well adapted to procuring food from flowers, but individuals of the species that do not leave their mountain habitat in fall obtain their food for seven months of the year from crevices in bark, from withered leaves, and similar places. Sleet storms, or heavy snows, which occur occasionally and cover the prey, may have catastrophic results. Only a fraction of the normal White-ear population will be found in such areas in the next breeding season. In mild winters, plants such as *Euphaterium glabratum, Stevia salicifolia,* and *Physalis acuminata* begin to bloom in well-protected spots as early as January, and where these are available, the White-ear obtains the greater part of its insect food from their minute flowers. In spring, the new green spruce shoots are a productive source of food. A small species of aphid (plant louse) is then found in great abundance among the needles and attracts this and other species of hummingbirds. I also once watched a male White-ear picking around in a spider's nest where the young were hibernating. The disturbed young spiders ran in all directions from the nest and were captured one by one.

In May, when the Blue-throated Hummingbird returns to its breeding range in the vicinity of the Capital, no flowers are in bloom, for the rains have not yet begun. The species then resorts to the new green spruce shoots to find its food. In a few places *Salvia elegans* and *Bouvardia ternifolia* grow under the trees, but the hummingbirds do not visit them, apparently because they are a much less productive source of food during the drought than spruce shoots. Examination of 50 blossoms from these plants yielded only three insects, two of them very small.

In the high mountain rain forest of Chiapas, the Guatemalan Cazique (*Lampornis amethystinus salvini*) hovers at thick moss-covered tree trunks looking for small animal prey. For some time it rises and sinks in hovering flight for a distance of about 30 cm. along the trunk, then suddenly stops for an instant and quickly projects its tongue to capture the prey. The next instant the bird is rising and sinking again in steady quiet flight at a place farther along the same trunk. In the spruce woods near the Capital, I observed another race of this species, *Lampornis a. amethystinus*. Usually it fed at flowers, but occasionally I saw it hunting along tree trunks.

During the dry season Rieffer's Hummingbirds occasionally come to the coffee plantations. They hunt over the young coffee shoots for small animal organisms and gather the insects caught in spider webs among the twigs. Near Mexico City I noticed a female Elliot's Hummingbird (*Atthis heloisa ellioti*) in July eagerly hunting food among spruce shoots. Since at this season there was no lack of flowers there, I assumed that the bird was hunting spiders for its young.

Some Broad-tailed Hummingbirds breed in the neighborhood of the Capital from the end of September through November. The breeding territories are frequently in the Petregal lava fields, which have a luxuriant vegetation during the rainy season. At the time of the birds' arrival everything is in full bloom. But in many years the dry season begins so early that when the young are developing and require abundant nourishment, the greater part of the flowers are already withered. At such times I saw the females seeking food among dry shrubs and foliage. The numerous males go elsewhere (exactly where is unknown) as soon as feeding conditions become unfavorable, whereas the females are held to the spot until their young are independent and can leave with them.

On several successive days I observed Prevost's Mangos feeding at the dried out, open fruit husks of a certain tree. They hovered about the bare branches, stopping at the old husks, apparently feeding on various small animal organisms.

Ripe fruit is also occasionally a source of insect food. Thus in May, in Teotitlan, Oaxaca, I regularly observed Dusky Hummingbirds (*Cynanthus sordidus*) at the burst open fruits of the candelabrum cactus (*Cephalocereus*). Stomach analysis proved that the birds consumed only animal food, disregarding the sweet watery pulp of the fruit. I had supposed that this juice was taken like nectar, since the feathers about the base of the bill were sticky with the substance.

In the coffee plantations, open stands of Chalu trees (*Inga* sp.) are cultivated as shade trees, and these are in bloom for a week or two in March. The small pale green flowers are far less conspicuous than pear blossoms but resemble them in structure. With a twig in the hand, one can readily see the great numbers of insects that crawl about the blossoms. When these trees are in bloom, hundreds of hummingbirds visit the coffee plantations, which at other times are visited by only an occasional individual. I have estimated 10 to 15 hummingbirds to a thousand square meters. They stream in from all directions, the radial distance depending on the type of terrain but estimated to extend up to 20 kilometers. They gather during the first week of the blossoming in constantly increasing numbers from the surrounding forest, from the oak-pine forest lower down, and from the savanna, which at this season is quite parched and dry. I have watched the following species collecting insects at these trees: De Lattre's Sabre-wing; White-bellied Emerald (*Amazilia candida*); Deville's Hummingbird—in numbers; Red-billed Azure-crown (*Amazilia c. cyanocephala*)—in great numbers; Pine Star-throat (*Heliomaster constantii leocadiae*); Dupont's Hummingbird (*Tilmatura dupontii*)—in numbers; and Dusky Hummingbird. As soon as the blossoms fall, the birds disappear.

Capturing insects from the surface of water. I have only once observed a hummingbird capturing insects from the surface of water. I was unable to identify the bird positively, but it was probably a Red-

billed Azure-crown, which at that place was very common. (Anyone who has done field work in the Tropics knows how difficult identification is when there is no distinctive peculiarity of pattern or form. The light usually makes color recognition impossible.) The bird appeared suddenly and hovered some 50 cm. above a quiet spot in a mountain stream. At intervals of 5 to 20 seconds, the bird darted upon the small aquatic hemiptera (*Rhagovelia* sp.) moving along the surface of the water. The bird hovered there for a brief instant and rose again. After three to six of these attempts it would disappear for a few minutes in a tangle of vegetation, then return to resume its hunting.

Composition of animal food. The animal food consumed by hummingbirds includes all sorts of small organisms, size, apparently, being the only limitation—bugs, flies, gnats, and plant lice, mosquitoes, leaf hoppers, ants, parasitic wasps, beetles, weevils, spiders, daddy-long-legs, as well as other organisms, have been found in analyses of stomach contents (Wetmore, 1916:70–73; Cottam and Knappen, 1939:160–162; Beal and McAtee, 1922:13–15). I have found that diptera often constitute the major portion of the diet of hummingbirds. This is not necessarily because the hummingbirds have a preference for them; the habits of the diptera may make them easy prey. In some species, as shown by crop analysis, spiders constitute a large proportion of the food given to the young during the first weeks.

It is surprising how large an insect a hummingbird can swallow. Mosquitoes of the genera *Anopheles* and *Culex,* which are quite bulky, were captured in flight and apparently swallowed whole. The largest prey that I have found intact in the crop of a White-eared Hummingbird was a spider of the genus *Neosconella.* The total length was 4.8 mm.; the body diameter, 2.6 mm. In the crop of a Blue-throated Hummingbird, which is larger than the White-ear, I found, in addition to many large diptera, a spider of the genus *Metepeira* 5.4 mm. long.

Formation of pellets. I have twice found pellets (consisting of chitin) in the stomachs of hummingbirds. Fine pieces of chitin are ground by ordinary stomach action and excreted through the intestine, as analysis of feces shows. But pieces of chitin too large and hard for digestion are apparently regurgitated in the form of pellets. I found both pellets in March, when the drought was most severe and the species I encountered were feeding entirely on animal prey. A specimen of the Red-billed Azure-crown had in its stomach a round pellet, 4 mm. in diameter, made up entirely of coarse pieces of chitin pressed tightly together. The other pellet, found in a specimen of the Pine Star-throat, was the same size, but rather more oval in shape. Wetmore (1916:73) says that Green Mangos (*Anthracothorax viridis*) "undoubtedly regurgitate waste matter, in the form of pellets, from which the nutriment has been digested. Several of these, 2 millimeters long by 1 wide, ready to be expelled, were found on opening the stomachs, and in each case consisted of a firmly compressed pellet containing chitinous fragments of insects and spiders."

Drinking and Bathing

Hummingbirds drink and bathe far more often than is generally supposed. When nectar is abundant, they doubtless have little need of water to quench their thirst—which would explain why they are rarely seen drinking except during the dry season, when they are feeding on insects.

In the vicinity of the Capital in winter and spring, I regularly saw White-ears drinking and bathing in a forest stream. At the foot of a small gorge, there was, during the latter half of the rainy season, a waterfall with a drop of some five meters over rocks; this, during the dry season, became a mere trickle of water. The White-ear would hover near the tiny fall and plunge its tongue into the water. After drinking several times in this manner, the bird would disappear unless a bath was to follow. This is the simplest and easiest method of drinking but not always possible, and the White-ear employs others. It will hover close above the surface of a stream, then suddenly plunge downward, rising again immediately. Thus, for an instant, either the bill or the tongue is dipped. The White-ear also drinks when it has settled in shallow water to bathe; then only the tongue is dipped. Elliot's Hummingbird quenched its thirst in a similar way (Figure 10), but it remained hovering close above the water for a longer time and from that position dipped its tongue or bill, causing each time a tiny ring to appear on the water.

When bathing at the waterfall described above, the White-ears would hover beneath a spot where the water fell drop by drop and thus in a minute or two become quite wet. They would then perch on a

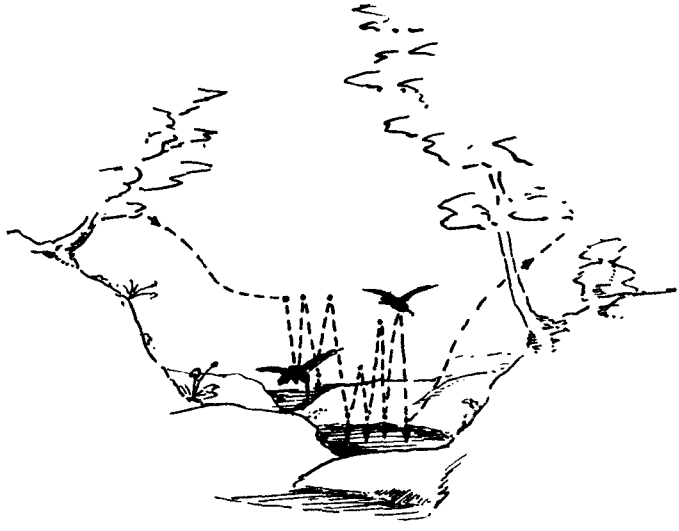

Figure 10. Elliot's Hummingbird drinking.

sunny twig, spread their wings and tail, and preen and arrange their feathers as they dried in the sun. A female Blue-throated Hummingbird that was building a nest in the gorge bathed in the same fashion. Three times in one morning she bathed, preened, and arranged her feathers—apparently because she frequently gathered nest material from steep overhanging slopes and trunks, and her plumage was soiled by the dust and dirt she dislodged.

White-ears also bathe at shallow spots in small streams, alighting in the water and splashing their feathers. Rising from the water again seems to cause them no difficulty. Some mornings after the sun was up I would see two or three hummingbirds bathing and drinking together. C. C. Lamb (1925:90) observed nine Xantus Hummingbirds (*Hylocharis xantusii*) bathing at the same time. They would sit in the water and splash themselves with their wings, then fly into a tiny waterfall near by. I twice surprised several Red-billed Azure-crowns bathing early in the morning at a curve in a small stream where the water was shallow and the shore sandy. They seemed to be familiar with the spot, for they alighted in the flowing water without hesitation.

One of the White-ears that I held captive would bathe at once when in the mornings I put a saucer of water in the cage. Its cage mates (of the same species) paid no attention to the water—perhaps because they were liberally sprinkled with water while the other was bathing. I have never observed hummingbirds drinking dew drops or flying through wet leaves to dampen their feathers (see, for example, Woods, 1927:307; Skutch, 1931:482).

Cross-pollination by Hummingbirds

The importance of hummingbirds to pollination of flowers is far greater in tropical South America than in Mexico. Since hummingbirds probably immigrated to Mexico in relatively recent times, it is understandable that there are very few ornithophilous plants * in Mexico compared with the abundance there of plants primarily adapted to pollination by insects. The ornithophilous plants of Mexico are without exception also immigrants from tropical South America.

The Marcgravia group of ornithophiles has a wide range in the tropical belt of the continent. Southern Mexico is the northernmost limit of their range, and only two species are known from there: *Marcgravia mexicana* and an unnamed species discovered by F. Miranda in northern Oaxaca, shown in Figure 11. The Marcgraviae are epiphytic, a character that limits them to the rain forest where the humidity is high. They thrive on more or less horizontal branches in the crowns of the forest trees. The flower of the Mexican species is a chandelier-like inflorescence with the fertile blossoms—numbering 120 to 150—arranged

* In my opinion, the term 'ornithophilous' is correctly applied only to flowers that are phylogenetically adapted to pollination by hummingbirds, not to those originally adapted to pollination by insects and whose evolutionary development is in no way correlated with birds.

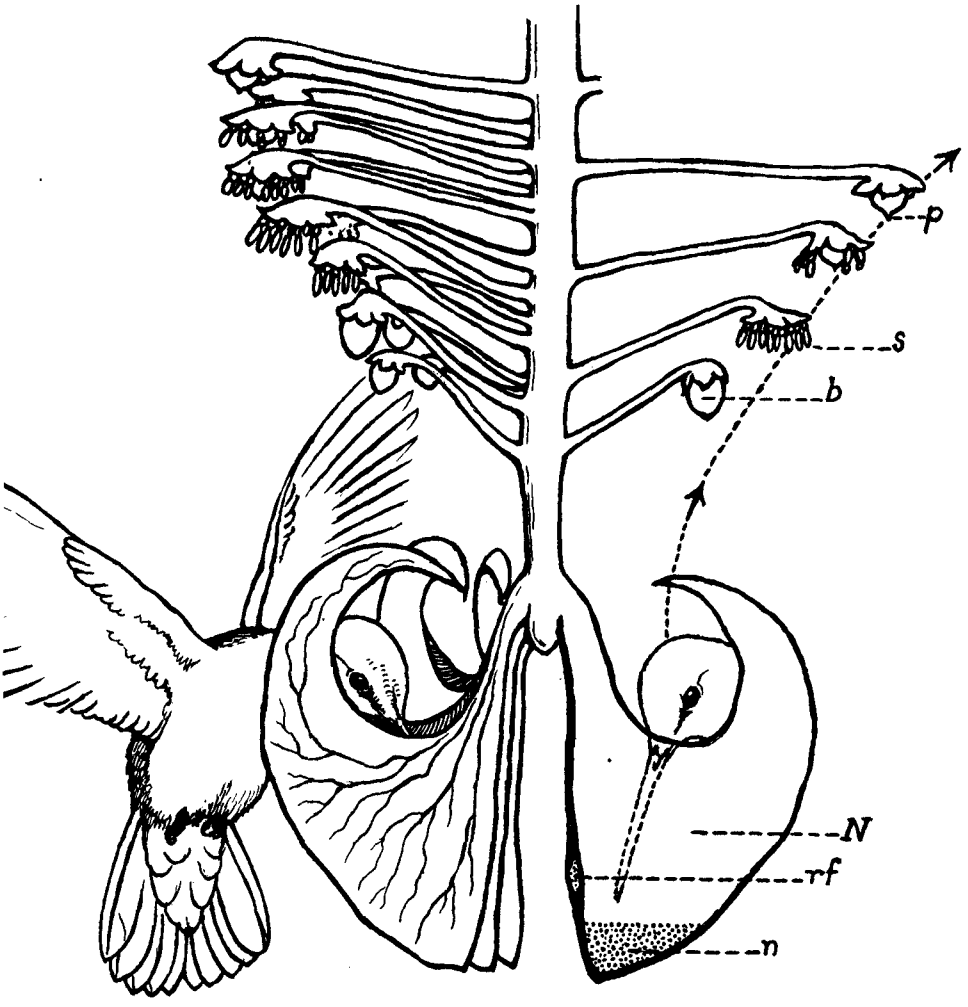

Figure 11. Hummingbird feeding at a flower (*Marcgravia* sp.). *After* F. Miranda. p = pistil; s = stigma; b = bud; N = nectary; rf = rudimentary flower; n = nectar.

on long thick stalks (pedicels) about the upper part of the hanging main axis (rachis). These blossoms face downward at right angles to their pedicels, which, in turn, are arranged at right angles to the rachis. These fertile blossoms are protandrous, that is, in each blossom the pollen-bearing anthers develop first, the stigmas later. The blossoms at the lower tip of the hanging inflorescence (morphologically speaking, the *upper* flowers) are abortive; the pedicel and bract of each are

transformed into a narrow bag-like nectary with a horn-shaped extension above and a pointed lower end where quantities of honey collect.

Because of the upward curving horns of the nectaries, a hummingbird seeking honey is forced to push close to the central axis of the inflorescence between two nectaries. In moving away again, its flight upward and backward brings it in contact with the fertile blossoms above, so that pollen is brushed from the anthers of blossoms in the first stage of development and picked up by the stigmas of blossoms in the second stage. The path followed by the bird's forehead is indicated by dots on the sketch. The shape of the nectary prevents flight directly backward once the bird's bill has been inserted.

Ornithophilous flowers such as *Marcgravia* produce nectar in great quantities, which is the reason that the flower is visited. This is not generally true of flowers originally adapted to pollination by insects. Their small supply of nectar is readily taken by birds, but for the most part it is insects that are attracted to such flowers either by the nectar or by the structure of the flower (as a hiding place and shelter).

In two plants—*Centropogon cordifolius* (Lobeliaceae) and *Lamourouxia exserta* (Scrophulariaceae)—I was able to study both the structure of the blossoms and the manner of their pollination by hummingbirds. (Both plants are also frequently pollinated by large insects, notably bumblebees of the genus *Bombus*.)

In *Centropogon cordifolius* the pistil reaches maturity only after the stamens have withered. When the stamens are mature they droop forward in such fashion that the crown of a hummingbird coming to sink its bill in the flower grazes them in passing and is covered with pollen (Figure 12). Hummingbirds that have hovered at these shrubs wear broad caps of pollen. The stamens wither in a few days and tilt upward, making room for the pistil, which now increases in length and droops forward, the stigmas coming in the way of the crown of a bird feeding at the flower. When a hummingbird comes to a flower in the second stage of development after having visited a flower that is still in the first stage, the stigmas brush pollen from the bird's crown, and thus fertilization is accomplished. Pickens (1927) describes and illustrates the pollination by the Ruby-throated Hummingbird (*Archilochus colubris*) of a flower (*Macranthera LeContei*) that has similar stages of development.

Centropogon cordifolius produces only a small quantity of nectar. Insects and other small animal organisms come to the blossoms less for the nectar than for shelter from inclement weather. Mornings before the sun begins to shine there are four times as many insects and other small organisms in such shrubs than later when it becomes warmer—which explains the large number of birds attracted during the early part of the day.

In the mountains near the Capital, above 3,000 meters, my interest was aroused by several Violet-eared Hummingbirds with crowns yellow

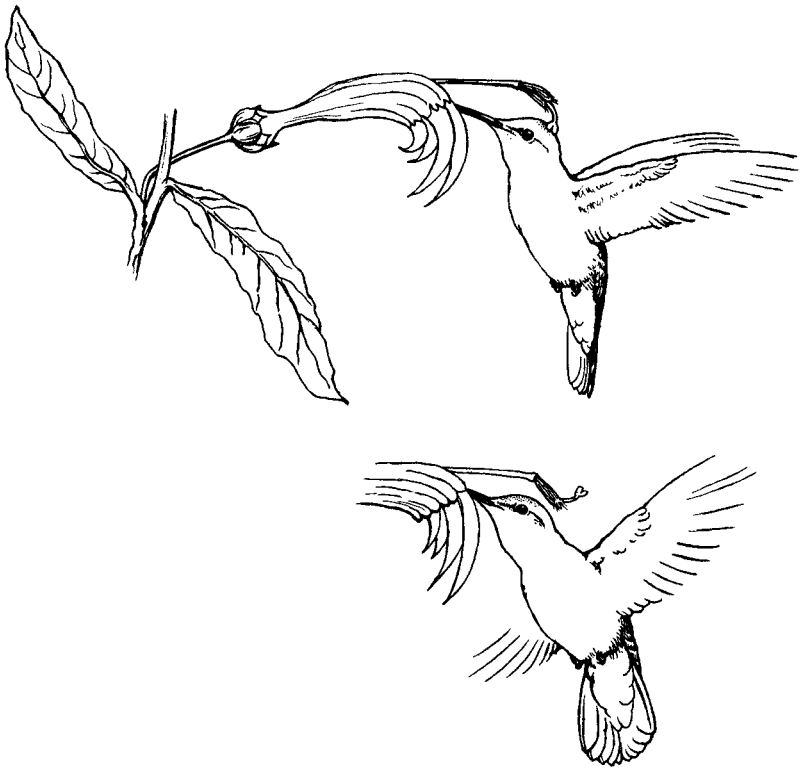

Figure 12. Hummingbird feeding at *Centropogon cordifolius*. *Upper*. During the first stage of the flower's development, when the bird's crown brushes the pollen-bearing anthers. *Lower*. During the second stage of the flower's development, when the stamens have withered and the bird's pollen-covered crown brushes against the stigmas.

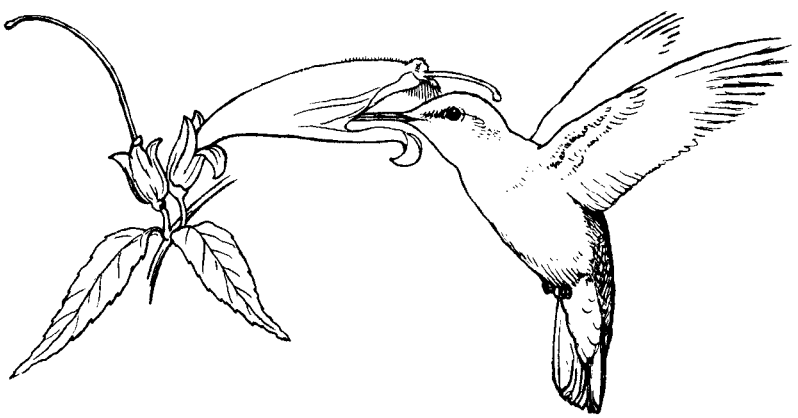

Figure 13. Hummingbird feeding at *Lamourouxia exserta*. The tuft of stigmas brushes the flower's own pollen, or pollen brought from another flower, from the bird's forehead. In the flower shown here, the stamen is not fully developed, and only cross-pollination can occur.

with pollen, and I observed another typical example of pollination by hummingbirds. *Lamourouxia exserta* is a small bush with red and yellow flowers that thrives both in woods and in clearings. It is very resistant to frost and blooms in January and February. The nectaries produce honey only in small amounts and only during the first few days. After that the hummingbirds are attracted by the insects that have sought shelter in the blossoms. The stigmas of each blossom are ready for the pollen before the stamens produce it, although for a short time both parts are mature so that if cross-pollination has not occurred, self-pollination may be possible. When the petals have opened, a small capsule bursts, releasing a brush-like stigma. This tuft brushes the pollen from the forehead of a bird that has visited a flower in a later stage of development as shown in Figure 13. Later, the four stamens mature and droop forward. The stigma then withers, while the stamens remain in the middle of the calyx and continue to cover visiting hummingbirds with pollen. At this time the production of nectar ceases. Neither the flowers of *Centropogon* nor of *Lamourouxia* are strictly ornithophilous, since insects are in both cases the primary agents of pollination.

Conclusions

Many investigators of the bill and anatomy of the tongue of hummingbirds are of the opinion that nectar is the birds' chief food. But, as we have seen, most field observation and stomach analyses do not support this opinion.

Granted that flower visiting, with its associated consumption of nectar and small insects, is the favored mode of feeding, it is not a vital factor for the majority of Mexican species. With them, on the contrary, the vital factors in the struggle for existence are frequently the capture of insects on the wing and the various methods of "gathering" insects.

Phylogenetically the shape of the bill is presumably an adaptation to the extraction of small animal life from tubular flowers. (The ontogeny of the bill, tongue, and stomach anatomy, as well as the food given the young during the first weeks, shows that the original food was animal.) I imagine that the taking of nectar and the correlated transformation of the tongue first began when the form of the bill had become so modified that it easily reached the nectar in the flowers. Then, with the progressive development of the tongue as a pump, nectar became more important as a food. The bird's preference for nectar is not surprising. If a captive bird is given the choice between sweetened water and pure water, it uses the sweetened, and the amount of liquid taken by the bird daily is greatly increased.

In connection with food we can distinguish three stages in hummingbird phylogeny:

1. Insect food as the chief item of diet
   a) Captured in flight with a broader bill—indicated by the

morphology of the young and the hummingbirds' relationship to the swifts.

b) Extracted from flowers with a bill becoming progressively longer as it adapts itself to this mode of feeding.

2. Nectar as the chief item of diet
The tongue develops into a highly specialized pump.

3. Return by a certain number of species to insects as major item of diet

The third stage is contemporary. We are familiar today with all the transitions, from birds that feed chiefly on nectar to birds that feed almost exclusively on insects. There is no evidence so far of any morphological adaptation to the renewed preference for animal food, but this is not surprising, since it is a well-known phenomenon of biology that when an organ has reached a high degree of specialization it seems to have less plasticity for radical transformation.

The fact that hummingbirds hover while procuring their food, even when capturing insects in the air, is also significant. I have never observed them catching insects in the manner of swifts, swallows, or flycatchers. This fundamental difference in method of insect capture indicates that hummingbirds developed their present method after they had in the course of their evolution become adapted to other modes of feeding.

There remains the question of what made the change in feeding habits necessary. The family Trochilidae originated in tropical South America, perhaps late in the Cretaceous or in the early Tertiary—at any rate, at a period of exceptionally stable tropical climate (Mayr, 1946). This permitted an adaptation to a diet consisting largely of nectar, and not subject to shortage caused by the pronounced flowering seasons that characterize all temperate, and even subtropical, regions. The deterioration of the climate in the latter part of the Tertiary, and the development of pronounced seasons nearly everywhere except in a small portion of the tropics, favored a return to a greater utilization of insects. This was particularly true for the species that had colonized subtropical and temperate zones, where nectar food was not available at all seasons. Such species either became migratory or adapted themselves to a seasonal diet of insects.

Summary

Observations were made on 19 species of Mexican hummingbirds to determine the composition of their food, techniques of procuring food, manner of drinking and bathing, and method of pollinating ornithophilous flowers.

The food of hummingbirds is determined by the ecological conditions under which the individual species live. Every degree of dif-

ference occurs between feeding, at least temporarily, exclusively on animal food to feeding temporarily exclusively on nectar.

In areas with pronounced dry seasons, in the high mountains, and in the temperate zones, a medley of small animal organisms constitutes the principal food. In many of these regions the birds migrate at seasons of unfavorable feeding conditions. In tropical habitats, nectar predominates in the food.

Under natural conditions, hummingbirds are conditioned to the color (varying with the species, and with locality and season) that corresponds with the color of the flower that is the most productive source of food.

As long as nectar from flowers is available, it is the preferred food. When the supply of nectar is inadequate, insects are eaten, preferably from flowers, but when these are insufficient, hummingbirds are forced to feed on insects gathered from other vegetation and from crevices, or captured in flight.

Hummingbirds feed while on the wing whether they are extracting nectar or insects from flowers, gathering insects from the vegetation, or capturing flying insects.

The method of capturing insects in flight varies from species to species.

The animal food consumed by hummingbirds includes all sorts of small organisms, size, apparently, being the only limitation.

Pellets are formed of the larger pieces of chitin and regurgitated.

Hummingbirds drink and bathe far more often than is generally supposed.

Two flowers especially adapted to pollination by hummingbirds occur in Mexico (*Marcgravia* sp. and *Marcgravia mexicana*). Both hummingbirds and ornithophilous plants are tropical in origin, having spread in recent times into Mexico from the south. In many cases where pollination by hummingbirds occurs, pollination by insects is also possible.

Hummingbirds were originally insectivorous. At a later stage of development, nectar became their principal food. Paralleling this change, the tongue developed as a suction pump. With the general deterioration of climate in the latter part of the Tertiary and the colonization by hummingbirds of the subtropical and temperate zones, certain species were forced to return to a greater utilization of insects as food.

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