THE RUBY-THROAT AS MIMIC MODEL AND CROSS-POLLINATOR

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I. The Ruby-throat as a Mimic Model

The similarity of form between the hawk moths and the humming birds is noted by even casual observers, but is apparently taken for mere coincidental resemblance rather than for real mimicry. In most cases such explanation suffices, but one of the insects, the Clear-wing Thysbe,(Haemorrhagia thysbe), has elaborated and improved this coincidental resemblance to a remarkable degree.

Quite all the members of the hawk moth family resemble the humming birds in the possession of scimitar-like wings, heavy tapering bodies, and bright bird-like eyes. But to these the Thysbe adds a number of important features. The scales of the body are colored like the feathers of the ruby-throat, and are plume-like in form, giving the thorax and pendulous abdomen much the appearance of the bird's body, for not only do these scales quite cover the insect's body with a feathery sheen, but those at the tip of the abdomen are elongated and spread out fan-wise in a manner that strikingly simulates the tail of a bird. All these likenesses remarkable as they seem might be thwarted by wings opaque as those of most moths, if the transparency, not to say invisibility, of the whirring wings of the feeding ruby-throat is to be simulated. The outline of the humming bird's body when in the act of feeding, presents the appearance of a quite wingless form of green suspended in the air. How shall this feature be simulated? Like other hawk moths the Clear-wing thysbe begins its adult life with the wings opaque; soon, however, the

scales begin to drop from the central portion of each wing; not in a careless, irregular way as if rubbed off on the fingers of a mischievous boy, but in a symmetrical manner in the center of each wing, leaving a narrow margin of scales all about the clear spaces. These wings in motion have much of the invisibility of the whirring pinions of the ruby-throat, and the very movement of the bird is simulated in the way the insect approaches, probes, and backs off from a flower. So striking is the resemblance in fact that the layman's eye is often deceived, and well might a naturalist be struck with the resemblance. The insect seems to make good use of the deception, for while most of its cousins are crepuscular and even nocturnal, it ventures forth boldly to the feeding bowers in broad day thus escaping the nocturnal birds that gorge on the night-flying insects.

Yet another of the Lepidoptera, the long-tailed skipper, (Eudamus proteus), to a keen eye suggests rather than resembles a humming bird as it hovers before a flower. This suggestion comes partly from its hovering flight, partly from the pseudo-transparency of its wings, but largely from the long thick line of green presented by the body and a pair of swallow-tails on the rear portion of the hind wings. Such swallow-tail appendages are usually regarded by naturalists as false antennae, luring lizards and birds to grab at the wrong end of the intended victim thus affording a chance to break away and escape even if the insect does so with the loss of the appendage. However that be, I have noted but one night-flying moth, the Luna, with swallow-tails, and the inference is strong that such fine deceptive points are not noted by nocturnal birds as they are by diurnal relatives.

I believe that the wing-tails of the long-tailed skipper have been evolved under conditions different from those in connection with other such prolongations. Most tail-winged species have the extension on the fifth nerve from the inside of the rear wing as in Grapta, Victoria, Hypanartia, and others.(Fig. I,1). Even the classic examples of swallow-tails, those of the Papilios, get no nearer the inner angle of the wing than the fourth nerve,(Fig.I,2), and the hair-streaks and the tiny blues attach their mere pig-tails to the third nerve form the inside. The long-tailed skipper, however, is unique in prolonging on the second nerve, (Fig.I,3), and at such an angle that the two tails lie almost parallel, even sometimes overlapping, and as Langstaff has pointed out, these extensions, even when the body proper of each wing is held vertical remain at a horizontal angle. Like the abdomen and the inner fold of the rear wing,they are covered with long, soft, plumey scales of a humming bird green. This of course gives an apparently greater length to the insect's body, while the anterior wings are spotted with squarish patches of silver that give an appearance of transparency to the otherwise somber-hued wings when the insect hovers before a flower and vibrates them rapidly. Now birds, according to J.R.Slonaker have a preponderance of color-seeing cones in their eyes while mammals have a preponderance of ray-seeing rods. Acute vision seems to depend on the presence of a fovea in the eye. Man has such:so has the sharp-sighted sparrow-hawk. The dog, uncertain of his own master's identity until tested with his nose has no fovea; the eyes of many birds show the same defect. To such an eye, a slender green body supported by seemingly transparent wings, might easily appear to be a humming bird. Though skippers are scattered thruout the world these long-tailed forms occur only in America the home of the humming birds,and the area where

the long-tailed skippers abound both as species and as individuals corresponds closely to the area where humming birds are most numerous both as to species and as to individuals, for Eudamus proteus has a number of long-tailed relatives. It is the one type that is found in eastern parts of the United States, and strays as far north as New York, protected perhaps by its resemblance to the ruby-throat.

The advantage to be derived from mimicry of the humming bird is obvious. No bird, when we take size in consideration, is more pugnacious than this midget. The martin and the blue-bird hurry to their holes to escape its vicious jabs; the tufted tit attempting resistance from the perch is soon vanquished; the swift finds safety in its rapid wings, and even the bold king-bird is not immune from attack. Some moths mimic wasps and bees and unconsciously threaten their foes with a sting; some butterflies mimic inedible relatives and threaten their devourers with unpleasant tastes. How much more effective the threat that a humming bird's mimic makes! The foe may well desist from attack fearing the onslaught of a rapier beak in a battle that ends only in the aggressor's flight.

Wallace thought a mimic should occur in the same territory with its model, should be more defenceless, less numerous, differ from most of its relatives, and be only externally imitative. With quite all of these rules the Clear-wing Thysbe accords, and so does the long-tailed skipper, with the exception of the doubtful numerical requirement. Such resemblance after all may be mere examples of those remarkable phenomena of nature such as silhouettes a vine and its berries along the midrib of the otherwise plain leaf of the maranta, a tropical plant found in hot-houses, but many details point strongly toward natural selection of more suitable mimics.

II. The Ruby-throat as a Factor in Cross-pollination

Water, wind, insects, and birds have figured in the cross-fertilization of plants as they have risen from the primitive forms, and all these methods are in use today in the cross-pollinization of flowers while the bees and the humming-birds are closely matched in the production of complex and efficient forms.

All humming bird forms of flowers have apparently descended from older insect-pollinated forms, mostly those of bees and moths, though sometimes to be sure a thrip-pollinated flower might be changed by the visits of the bird to such flowers in order to vary its nectar diet with some insect fare, for even the ruby-throat is to a large degree insectivorous, and small spiders and insects constitute much of its food. Most flowers visited by humming birds in the temperate zone are mere compromises. The flame azalea and its relatives are probably pollenized by both moths and humming birds; the fire-pink, or Virginia catch-fly is visited by both butterflies and ruby-throats; dozens of forms divide their time between the bees and the birds. The European columbine is blue that being it seems a favorite color with bees, no humming birds being found in the Old World. The American columbine, on the other hand, is red a favorite color with humming birds. In form the trumpet creeper blossom resembles the Paulownia of the Orient, but the former is arrayed in red, and the stamens have a more definite compact arrangement. Something of the same difference is seen between the honeysuckles of the Old World and those of the New, for these feathered midgets have influenced the form and color of many American flowers which manifest features not seen in similar forms from Europe, where the ancestors of the plant world have been absent from the humming bird influence. This influence appears to produce flowers of red and orange colors, cornucopia and tubular forms of

corollas, and compactly arranged stamens maturing later or earlier than the pistil. Some such forms would probably survive were all the humming birds exterminated, as this arrangement lends itself to pollination by bees, moths and butterflies. Still others have become so specialized that like the jewel weed when introduced into Europe, in the absence of humming birds they can do little more than produce cleistogamous seeds, a dangerous step because in the direction of degeneracy. Let us consider some of the more highly specialized flowers visited by the ruby-throats.

As a first example take the Cardinal flower, (Lobelia cardinalis), and contrast it with another member of the same genus, the Blue Cardinal flower, (Lobelia syphilitica). As might be expected the red caters to the humming bird, the blue to the bees. In the first the anthers are coalesced to form a tube about the pistil, all standing up in stiff military style and making a conspicuous erect column at the back of the flower. The pistil is completely covered at first, but when the bird has visited the blossom, and brushed the pollen from the end of the tube formed by the surrounding anthers we may be sure that the stigma will emerge from the end of this tube enough to receive the pollen from another flower during a later visit. (Fig. II, 1 a and b). This column is found in the bee-visited blue species, but is much more conspicuous in the red form, and one form has evidently been developed from the other, or both evolved from an ancestral form, common to both.

The scarlet salvia, (Salvia splendens), though developed by tropical humming birds is one of the interesting forms introduced into our gardens which show how the cross-fertilizing apparatus developed by bees readily lends itself to the visits of the bird. As it drops downward from the air to probe the flower, it touches first the stigma, which extends farther out from the flower, and is

higher up than the anthers. (Fig. II,2a). It leaves there a touch of pollen from the last flower visited, then dropping even lower, and and probing farther into the flower, touches the anthers and gathers the magic dust for the next, or some later flower. (Fig.II,2b). There are, let us note in passing, but two fertile stamens to the flower out of a probable original four. Glancing inside we see the reason. Two of the four stamens have been developed into elbowed arms that reach out from the walls of the flowers and hold the other two down out of the stigma's way, much in the same manner that a small boy's legs are held down by the arms of an older brother as he is carried in a sitting posture on the latter's shoulders with legs astride the neck.

The wild touch-me-not, or jewel weed, (Impatiens biflora), stores the nectar in a long curved tube to protect it from tongues other than long ones such as the ruby-throat has. In the exact upper middle of the entrance to the flower hangs the pistil, quite covered over by the basket formed by the united stamens and anthers. (Fig II, 3a). Probing for nectar the bird strikes off on its forehead the pollen, bearing it away to another flower. The stamens having served their purpose, dry at the point of attachment, and the entire basket drops from around the hitherto covered pistil, leaving it naked to receive the pollen from a younger flower when next the ruby-throat comes for nectar. Very similar in form is the cross-fertilizing device of the introduced Impatiens sultani of the same genus as the above. It improves its cousin's plan, however, by the use of a triple divergence at the end of the pistil making contact with the pollen-laden forehead trebly assured. Yet another exotic, the nasturtium, originally from Peru, makes use of the long anterior cornucopia to lock away the humming bird's sweets, but cleverly contrives to place its pollenizing stamens and pistil on the lower side of the

flower, so that the feathers of the throat are used in the act of cross-pollination. As most other flowers use the top of the head this is quite a business-like change and enables the flower to use an otherwise quite unexploited field.

More highly specialized flowers with reference to visits of the ruby-throat occur in the genus Macranthera growing along the Gulf Coast from Mississippi to Florida. Here they have so long a season that they can throw the discretion of the northern flowers to the wind, and snubbing the insects woo with a highly specialized ardor the autumnal hordes of ruby-throats fleeing south before the northern winds and collecting along the margin of the mainland. I have had oppurtunity to examine but one species of the genus, Macranthera Lecontei, which may grow as tall as six feet, with the tubular orange flowers standing up like candles in a candelabra, each candle bracket having a certain amount of resilient springiness.Let us consider the part played by the pistil, and that played by the stamens.

Hardly have the mere scallops of the corolla begun to spread apart before the style thrusts itself out and up beyond the flower, the stigma bending outward. (Fig.II,4a). To this golden chalice comes a ruby-throat, its nape hoary with pollen from another flower. To get at the stiffly erect tube it must rise on wing, drop its bill on its breast and thrust it almost vertically downward.(Fig.II,4b). It is an uncomfortable position and the bird resents it and pulls downward on the flower to bring it more nearly into a horizontal position. This act aids in the end to be accomplished, and the flower yields gracefully with its springy curved bracket. As it does so the style with its outward, now downward bending stigma almost with the canniness of intellect, comes down with the flower, and lightly touches the pollen-bearing nape, another spot the other

flowers have neglected, and there receives the magic of cross-fertilizing pollen. As the bird withdraws its beak the flower springs back to its upright position.(Fig.II,4b and a).

Now the stamens come into play. They stand not around nor above the style but back of it like the four fingers of an upheld hand. Every anther is turned outward. One almost feels that military precision is endangering the symmetry of the flower. These anthers green and gummy at the bird's early visit, are hoary now with ripened pollen; then they were much shorter than the pistil, thus keeping out of the way of the magic spot on the ruby-throat's nape. Now they have grown equally as long as the pistil which has dried up and receded as if to get out of the way.(Compare II,4a and c). The scallops of the corolla are blackening with approaching death, and one almost fears the complex machinery is in vain. But there is still honey in the nectary; there is a flash and whirr of wings; the returning ruby-throat thrusts its bill into the vertical flower and again bends it down. The dried style has receded, but the outward, now downward bending stamens come lower, and still lower, then the anthers on the lower side of the very ends of the stamens touch the bird's nape. Like the four fingers of an extended hand of blessing the stamen of the flower rest there a moment, but patriarchal as the act seems there is something of the patriarch Jacob in that touch, which forces the unwitting humming bird to return in transportation service the value of the nectar gleaned. That the arrangement is satisfactory, however, seems well attested by the twittering hordes of ruby-throats found about these flowers, and later in the fall by the thousands of fertile seeds borne in the capsules of the plants.

This flower,like the Salvia appears to have descended from an ~~ancestral bee-form being closely related to the bee-visited members~~s

ancestral bee-form being closely related to the bee-visited members of the Figwort family in which are found such familiar forms as snap-dragons, toadflax, foxglove, and mullen. Highly specialized as it is it is not red, reputed to be the favorite color of the humming bird, but fairly shines in orange, just as the touch-me-not and several other specialized forms do. In fact I believe that observations in the southern states show that the ruby-throat's eye has as much if not more tendency toward orange flowers than toward red ones.

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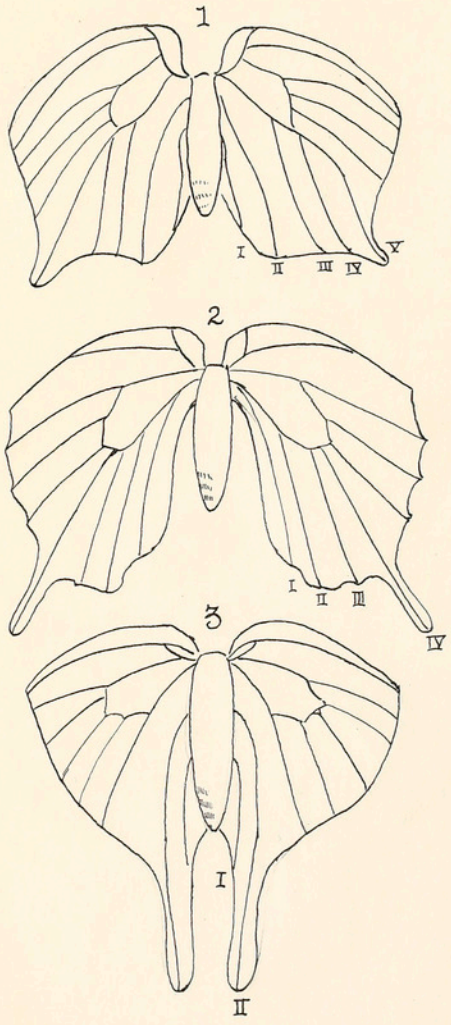

FIG. I.

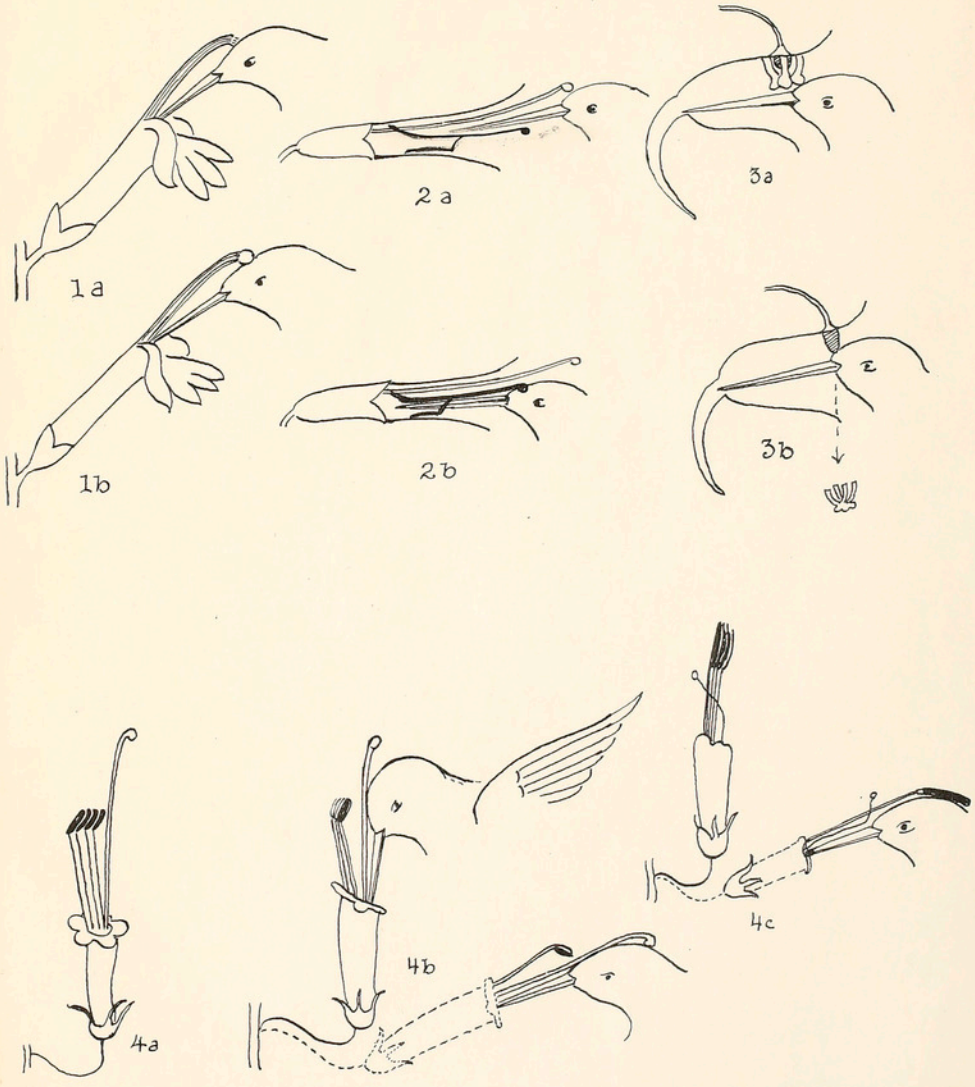

FIG. II.