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TERRITORIALITY AND RELATED PROBLEMS IN NORTH AMERICAN HUMMINGBIRDS

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During late June and July of 1939, a behavior study of the Ruby-throated Hummingbird (*Archilochus colubris*) was made at the Baldwin Bird Research Laboratory at Gates Mills, Ohio. Intensive observations were limited in scope and secondary to the research program of the laboratory; nevertheless, certain informative data about territorial behavior and the relations of the sexes in that species were obtained. Subsequent observations on western species of hummingbirds (especially *Calypte anna, C. costae, Selasphorus alleni,* and *Stellula calliope*) together with a review of literature have enabled me to formulate, at least in tentative form, the main features of territoriality in the North American hummingbirds.

Hudson (1920:3) and Woods (1927:307) have emphasized the uniformity of general life habits among hummingbirds—a uniformity perhaps as extreme as that in any other taxonomic group of similar rank. This fact is conspicuous in the life history monographs of Bendire (1895) and Bent (1940). But observations are interpreted variously and considerable confusion remains as to the significance of certain traits and patterns of hummingbird behavior. Nice's recent review of territory in birds (1941) attests to the need of study of the Trochilidae. Her survey reveals evidence of territoriality in that group, but only a suggestive classification of members of this family was made with respect to types of territory.

In the following pages, the term territory is used in the simplest sense, referring to any defended area (Noble, 1939:267). This definition makes the term available for a more general usage than previously; but at the same time certain precautions may well be emphasized. (1) Among birds, territoriality shows diverse trends and different degrees of development. Attempts to recognize and compare kinds of territories (Nice, 1941) call for many data on the biotic, sociologic, and behavioristic factors which operate to space individuals, pairs, or groups within a habitat. Territories have been classified in terms of the function each appears to perform in the biology of the species—chiefly mating, nesting, feeding or combinations thereof. In the face of this natural trend toward accumulation of particulate data, it is well to remember that to speak of territoriality within a species is to say merely that a member of that species defends an occupied area. (2) Further, in spite of this simplified definition, the term territory generally carries with it certain associations concerning song, display, aggressiveness, and combat. A reciprocal relation of any of these to territoriality is often assumed or implied by particular usage of the term. Yet, one of these traits or patterns of behavior may be well developed without necessarily direct relation to territoriality. Among hummingbirds, for instance, aggressiveness is shown by most individuals and at most times; it may or it may not contribute to the defense of an area. (3) It is difficult to treat territoriality in general terms since the evidence for such behavior is always to be discussed in correlation with differing life requirements

and ecological relations among different groups and species. This indisputable fact is cited by those who question recent attempts to consider territory as a broad, basic problem.

The materials of this paper are presented in two parts: The first deals with details of behavior in the Ruby-throated Hummingbird. The second is a general discussion based on original data and evidence from the literature. This discussion concerns primarily Nearctic species, but certain valuable references on Neotropical species are also included. My own observations on western species were made chiefly in the San Francisco Bay region since 1939 and in Mono and Inyo counties, California, in late May and June of 1942. These observations for the most part only corroborate data already available in the extensive literature and, therefore, are not reported in detail.

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THE RUBY-THROATED HUMMINGBIRD

The present study centers about a single male, his feeding territory, and his relations with other hummingbirds. The intense feeding and territorial activity occurring in mid-summer evenings provided one- to two-hour periods (between 6 and 8 p.m.) of fruitful observation, which was made on ten different evenings between June 21 and July 2. Following the latter date, hummingbird activity subsided and only brief observations were made through July 25. This defines the extent of intensive observations (totalling approximately 25 hours), but repeated visits were made to the study area almost every day in the course of other investigations. Unless otherwise stated, the described behavior occurred during the evenings of the earlier period (through July 2).

The domain.—The feeding territory of the single made Ruby-throat which constistituted the study area covered a semi-formal flower garden approximately one-quarter acre in size (see fig. 66; also Kendeigh, 1941:8-9, and accompanying figures). The garden formed a rectangular, open area bounded by a low wall; an open lawn lay to the south and an orchard to the west, while shrubs and trees bordered the north and east sides. Hummingbirds were attracted here by the tall racemes of larkspur blossoms (*Delphinium*), and the preference shown by several hummers for this species resulted in numerous encounters between each of them and the male who was established here at least from June 21 to July 2. After July 2, defense of the territory subsided when the larkspurs passed their flowering period, and the male was established briefly (at least from July 6 to 9) at a smaller bed of larkspurs that was retarded in blossoming because of shade. (A male, believed to be the one studied, remained about the gardens until July 25.) The latter area was situated along a garden wall some 200 feet to the south of the main territory (see Kendeigh, *loc. cit.*), and during the later days of his occupation of the main territory, the male would absent himself for brief periods that were spent at the fresher larkspurs of the second location. Similar relations of Ruby-throats to food plants are described by Saunders (1936:139). (See also Hudson, 1920:3, on the Argentine Glittering Hummingbird, *Chlorostilbon splendidus;* Grinnell and Storer, 1924:256, on the Calliope Hummingbird, *Stellula calliope;* and Linsdale, 1938:73, on the Broad-tailed Hummingbird, *Selasphorus platycercus.*)

The perches used by the dominant male were tips of four-foot iron rods scattered about the larkspur beds and other higher perches along the margins of the entire feeding area. Each post was occupied for varying periods of several seconds to several minutes between flights and feeding. Changes of post were irregular except for a more frequent

use of the centrally located post A (fig. 66). During the greater part of each day, the male was seen within or in the vicinity of the territory only occasionally.

Attack flights and chases.—The male chased other hummers regardless of sex and often followed an attack flight with a display flight at the site of the outsider's intrusion.

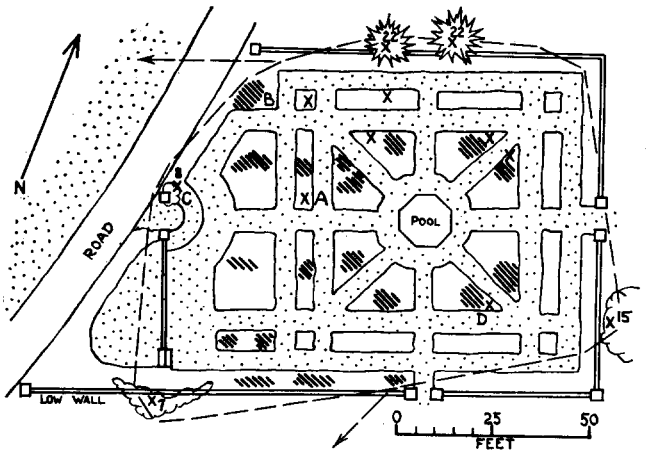

Fig. 66. Map of study area. *Delphinium* beds are shown by heavy diagonal lines. Territorial posts about periphery marked by X's, with figures indicating heights; posts within the garden all four feet high. Dotted areas mark lawn; clear areas within walls, low plants or shrubs. Light broken line circumscribes area of territorial activity.

This latter behavior was shown toward hummers of both sexes. In addition, a sphinx moth and bees were attacked or chased occasionally (see Saunders, 1935:67 and 1936: 152). Fights, that is, actual clashes accompanied by squeaking, occurred between outside hummers about the larkspurs on at least three occasions.

One of the chief stimuli for an attack flight (flight from post to intruder) is the buzzing-humming sound of the wings. Attack flights of 50 to 60 feet were made from posts on which the bird was so perched that it could not see the intruding hummingbird. One exceptional attack flight of about 75 feet was made from perch C to the larkspur beds at D. Feeding was often interrupted and followed abruptly by an attack and chase. On one occasion when a strange hummer passed overhead, the male rose from his feeding, remained poised in the air watching the direction of the passer-by, and then resumed feeding. One 40-foot flight was made toward an intruder that turned out to be a bee. No chase followed, although on another occasion the male hummer actually chased a bee for three feet. At times the bees were fairly abundant and the hummer usually paid no attention to them. Such encounters as occurred followed immediately the return from other encounters with hummers as though the preceding event affected the bird's ability to recognize any differences in the sound of bee flight. Forbush (1927:317) describes a male hummingbird which cleared a feeding area of bees before feeding himself, while Roberts (1936:655) reports clashes of bees and hummingbirds, the bees chasing hummers and the hummers showing great fear of the bees!

Actual attacks were noted only twice: The male was seen to strike a bee and, on another occasion, a female at B, following which he displayed. During the chase of another female, considerable squeaking occurred, and a clash probably took place here,

also. But such contacts occur frequently among hummingbirds when individuals are abundant locally (see Sherman, 1913:154; Bolles, 1894:592; Bowles, 1910:125). Clashes and chases were accompanied by squeaks and high-pitched chatters which were more intense than the occasional chatter given during ordinary flight. The notes of this species correspond in intensity with those of the Allen Hummingbird (*Selasphorus alleni*).

The chases varied in length and usually continued beyond the bounds of the feeding area, although on at least one day (June 24), the male did not fly beyond those bounds. Chases usually were directed toward the open lawn and orchard (area between arrows to the left side of fig. 66). This was due in part to the fact that one persistent female intruder took this as her usual route of escape. The male himself frequented that area outside of the garden and made many of his flights over it in going to the south *Delphinium* patch.

Chases within the feeding area were occasionally interrupted and the male would break off his flight to feed. On one occasion, the male, perched at A, waited 10 seconds while he watched a female moving about larkspur bed B and then made an attack flight and chase. On another occasion he delayed chasing for half a minute. At other times there was another male hummer who fed about the southeast beds; the dominant male failed to detect him and retained his post (A), facing westwardly.

Here it may be repeated that during the day only a weak vigil was maintained. One might more properly say that such clashes as occurred on the feeding area then were merely manifestations of the usual intolerance and belligerence, since clashes and chases were observed about other gardened portions of the estate at various times of the day. But at least during the late afternoon and crepuscular hours (probably also during the morning, although no satisfactory observations were made), a definite surveillance was maintained by the male. This laxity during the day might be explained by the abundance of food in areas in the vicinity of the main territory and by the absence of additional established males. Where food plants are more restricted and where competition is keener, the male may retain his posts continually and observe more definite limits (Saunders, 1936).

Display flights.—Various features of the display or pendulum flights of the Ruby-throated Hummingbird have been described by a number of authors. The dominant male usually performed through 180-degree arcs with amplitudes of 5 to 10 feet. Forbush (1927:318) states that the amplitude may vary from three to forty feet. The plane of the arc was noted to turn as much as 45° about a vertical axis running through the bottom of the arc. Three to six short grating squeaks were given during each swing of a full display flight. At least on one occasion, when an arc of 10-foot amplitude was followed, one complete revolution was made at the end of several swings. Several displays were also performed close to an intruding female within the vegetation so that the back-and-forth flights could be made over a distance of only 10 or 12 inches. Judging from the marked difference in intensity of wing hum in one direction as against the other, it is possible that the male did not turn right-about-face but merely moved forward and then backward. During such performances, the male would rise gradually, the amplitude of the swings would increase as he emerged from the vegetation, and the display would end with arcs of normal distance.

At various times of the day about the garden, display flights were noted, but these were considerably more frequent during the evening hours when vigil was held. On several occasions, two or three performances occurred within one or two minutes. Displays were last seen on July 2. Attack flights were followed by direct chases or by

display flights. The type of behavior at the point of encounter seemed in part, at least, to depend on the response of the intruder. If the latter was reluctant to leave, a display usually followed. If the intruder left during a display, a chase followed (Woods, 1927: 302). Following display flights, the male might (1) fly off wildly up into the air and usually outside of the feeding area to return within the minute to one of the posts, might (2) return directly to a post, leaving the intimidated intruder to make its escape, as in the first case, or might (3) follow a display flight with a chase. On one occasion the male was noted to display before one female and then turn to chase another female intruder (July 2). Displays occurred not only after the attack flights against the individual female, but also at the site of clashes between other hummers within the garden (June 21).

Responses of intruding hummingbirds.—One female frequenting flowers at B repeatedly demonstrated reluctance to leave and came to feed there regularly as well as at other neighboring patches throughout the period of June 21 to July 2. Almost invariably she approached from over the shrubs at the northwest corner. During the earlier evening periods (June 21, 23, etc.), the female usually left promptly after an attack flight and chase by the male. But in the later ones, she exhibited a definite cautiousness in entering the feeding area: her flight was close to the ground; she entered the larkspur beds and then progressed upward onto the larkspur heads to feed; at times she remained poised watching in the direction from which the dominant male usually came. This uneasiness on her part was almost uncanny. She was always alert to the flight-sound of bees and to the rustling noise of wrens near by; on one occasion she even ducked in flight when a bee flew overhead. At such times feeding always was interrupted while she maintained a watch, and indeed her activities within the territory were reduced to short feedings followed by a prompt departure whether or not the male appeared.

When the male approached to chase or display, the female on at least four occasions sought shelter in the lower parts of the vegetation, which prompted the abbreviated display flights already mentioned. In three of these, they left the area in a chase or she left directly after his departure. But during the fourth, while the male swung back and forth through the shortened arc within the vegetation, the female darted at him from beneath three or four times in succession, with her bill poised upward and tail outspread. Following another clash with the dominant male, this female dashed quickly into neighboring conifers; she resumed feeding after this encounter and a minute later the male chased her as she departed of her own volition.

Another male exhibited similar uneasiness in entering the feeding area. On some occasions a chase followed; once he was noted to leave promptly as the dominant male approached.

Territorial function.—The territorial occupancy of the male Ruby-throat was not definite: The male chased intruders over variable distances beyond the limits of the feeding area, often as much as 100 or 150 feet; he did not confine himself to the territory during all routine activity and defended it offensively only during feeding periods. This territorial activity appeared to center about a source of food, although it is probable that mating occurred on the area so that the feeding territory might serve secondarily as a mating station.

There was no nest within the immediate vicinity of any of the feeding areas. One female, which visited the flower heads repeatedly, apparently had a nest in an orchard several hundred feet to the southwest. Saunders (1938:55) observed that the male's territory bore no relation to the female's nest.

Feeding.—The dominant male exhibited a somewhat remarkable efficiency in feeding about the individual patches of larkspur heads, though there was no order in his feeding movements between the various islands. The blossoms of *Delphinium* are arranged in checkerboard fashion about the peduncle. The hummer would progress down usually from the tip, feeding in flowers of two rows and moving left, then right, between alternating blossoms. At the bottom he would turn to either of the adjacent two rows and follow upward in the same fashion, then downward again, so that practically all the blossoms of a single head were visited. There was a 5 to 10 per cent "error" through repetition. At the height of feeding activity and in the absence of interruptions, the male systematically fed thus from one head to another, then moved on to another patch. Flights between patches were always low and usually followed the lawn paths. Both sexes were observed to perch on the flowers to reach inside more effectively.

Insects were picked from the air while the male was perched or while he was flying, the flight being stopped short to seize the prey. Recorded instances of flycatching by hummingbirds are numerous (Mailliard, 1919; Bassett, 1920; and Linsdale, 1938). On several occasions, I have noted the Anna Hummingbird (*Calypte anna*) prey upon swarms of gnats in the manner of a flycatcher.

Summary.—Behavior of the Ruby-throated Hummingbird with particular reference to territoriality and relations of the sexes was studied in northeastern Ohio during late June and July, 1939. Territorial defense by a single male became pronounced during periods of active feeding in the early evening hours. This male maintained an imperfectly defined territory one-quarter acre in size including beds of *Delphinium* which provided food. Territorial activity subsided with the closing of the flowering period of these plants. Prominent posts were maintained by the male during the period of active defense. Other, intruding hummingbirds of both sexes were chased from the area. Display flights of intimidation were performed before intruders who did not leave promptly upon arrival of the established male. Other hummingbirds persisted in entering the territory to feed; their behavior gave evidence of learning, through frequent encounters, of the presence of an established male. A positive reaction of self-protection on the part of an intimidated female is recorded. Several features of feeding behavior are also described.

GENERAL DISCUSSION

General features of behavior.—The general belligerence and intolerance observed in the behavior of the Ruby-throated Hummingbird prevails apparently in all trochilid species on which information is available (Bent, 1940). Fighting occurs not only among the sexes of one species, but as frequently among several species when they occur on a common feeding ground (Henshaw, 1886:76; Ridgway, 1892:278; Moore, 1939*b*:445; for tropical species, see Berlioz, 1932:128 and 1934:420). Numerous attempts have been made to contrast species with respect to these characters of behavior. But my own observations as well as a survey of literature support Wood's statement (1927:304) that a general aggressiveness is characteristic and that there are no constant differences in such traits. Berlioz (1934:420) suggests differences in pugnacity among Brazilian species on which more data are needed.

The independence shown by North American hummers in their activities is so positive that it becomes necessary to doubt any statement suggesting communal or cooperative relationships of any sort except actual mating (Skutch, 1940*a*:33). Stone's comment (1937:648) that "in Hummingbird gatherings, it is always everyone for himself, there is no flocking" is borne out in the literature on practically all species. Dixon

(1912:76) suggests a colonial nesting in the Costa Hummingbird (*Calypte costae*) which is unlikely. Bryant's (1925:100) similar suggestion for the Allen Hummingbird seems unfounded; he found a concentration of nests which, however, may have been accounted for by abundance of suitable habitat for both nesting and feeding. Needless to say, the criteria for colonialism call for more than mere proximity of nests, and the other features of hummingbird behavior do not favor such a thesis. In British Guiana, Nicholson (1931:536) noted that several nests of *Topaza pella* were often close to each other in favorable habitat; but territoriality prevailed.

In no species of hummingbird is the male known to participate normally in nesting activities. This fact has been obscured by observations of members of both sexes on common feeding grounds and of nests close to territorial posts maintained by male hummingbirds. The role of the male as protector to the nest suggested by numerous writers is doubtful. It is astonishing that so recent a work as Todd's (1940:310) states that a "pair (*sic*) of ruby-throated hummingbirds . . . will drive off intruders of their own kind from their chosen domain." All my assembled information agrees with Whittle's statement (1937:172) that, in general, a male's interest in a female one day is not manifested toward the same female the next day. Berlioz (1934:421) has noted the independence of the sexes in certain tropical species, as for example *Thalurania glaucopis*.

Two exceptions to these statements may be cited: Cottam (1941:59) observed a male Calliope Hummingbird feed a female on the nest several times. As regards Neotropical species, Mulsant's statements (1877) that males participate in nest building and incubation may be substantiated in part by future study. In Ecuador, Moore (1939*a*:315) observed male and female of the Violet-ear (*Colibri iolatus*) incubating alternately.

On the basis of this evidence concerning relations of the sexes, one may surmise hummingbirds to be polygamous. This has been suggested by Schlag (1939:17) in the Ruby-throated Hummingbird, Aldrich (1939) in the Allen Hummingbird, and Nicholson (1931*b*:583) in *Topaza pella* of the British Guianan rain forest. Both Schlag and Nicholson observed low ratios of males.

Territoriality.—Evidence of territoriality in hummingbirds appeared as early as 1824, when Bullock described defense of nest surroundings by the Lucifer Hummingbird (*Calothorax lucifer*). In 1877, Henshaw published observations on the defense of the nest and of the male's "vested rights" in the Allen Hummingbird (see also Bendire, 1895:217). In 1892, Anthony noted defense of a feeding area over Agave blossoms by a Rufous Hummingbird (*Selasphorus rufus*) against at least two other species of trochilids.

The first definite and clear statements describing sexual and territorial relations in hummingbirds appear in the studies of Grinnell (1908:73) and Grinnell and Storer (1924:357). In the Calliope Hummingbird, the male does not participate in nesting duties; indeed he is routed from the nest surroundings if he approaches. His location "seems to have no relation to that of a female or an occupied nest." Males maintain feeding territories, but may be seen foraging on "neutral tracts" with other males and females (see also Grinnell, Dixon, and Linsdale, 1930:244).

The male.—All available evidence suggests that territorial behavior of male North American hummingbirds centers around a food supply. This relationship seems most conspicuous in the Ruby-throated Hummingbird, which, while known to feed upon insects, depends extensively upon nectar from flowering plants. In the season and region of breeding, territorial behavior tends to extend over the flowering periods of certain

favored plant species. Such behavior is increasingly positive where individuals are more numerous and competition is keener. Of course the phylogeny of this behavior involves considerably more: (1) Though territoriality might now appear to be concerned with food—a year-around problem, after all—the peak of such activity occurs during the breeding season and its explanation obviously demands more than food considerations. (2) The relation of display flights to territoriality, though direct in its present form, still awaits study with respect to the development of diverse behavioristic traits among the sexes of a species. (3) In all this, more data on reproductive physiology and exact environmental relations are needed before analyses of behavior will begin to take on final form. The fact that maintenance of a territory may coincide with availability of food suggests that whatever the former importance, historically speaking, of courtship and a mating station, these now assume a secondary place. Yet the mating station is the important thing in the survival of the species, and the food and territorial factors may better be said to be conspicuous parts of a complicated mechanism which operates to bring the sexes together.

Aldrich's study (1939) of the Allen Hummingbird led him to recognize two types of territories: (1) a transitory feeding territory of limited extent and time occupancy, as a few square feet of blossoms guarded against neighboring hummers with similar food claims, which may be given up within one or two hours without intrusion or may be taken away by a more aggressive individual; (2) the "semi-definite" territory maintained by resident hummingbirds over suitable feeding areas, which are deserted intermittently, depending apparently on presence of better feeding locations elsewhere, in which case the individual may revert to type one. The territory of the Allen Hummingbird, as in other species of hummingbirds, is set up with no reference to the female, although a nest may be placed within the bounds of the territory.

Territorial limits are not observed as rigidly among hummingbirds as they are in numerous passerine forms. The territory of any male is definable chiefly in terms of the lengths of the attack flights he will undertake to chase an intruder. The chases often extend considerable distances beyond the area which might reasonably be regarded as the territory. But other hummers of both sexes will intrude, especially if the territory includes a good food supply. Males, in absenting themselves from their own territories, may cross territories of other hummers as do females seeking food or nesting material. However, observance of territorial rights has been noted among males in the Central American White-eared Hummingbird, *Hylocharis leucotis* (Skutch, 1940*b*:455).

The above is probably typical of migratory hummingbirds, but in resident forms such as the Anna Hummingbird, posts may be maintained throughout the year, apparently by the same birds (Woods, 1940:383; and the writer's observations). In this as in certain other species, insects are the predominant food (Beal and McAtee, 1922) and there does not seem to be the direct dependency on flowering plants seen in the Ruby-throat and other hummingbirds. The established males appear to hold territorial posts with remarkable permanency; at least certain known posts and territorial sites are occupied practically at all times. Such permanent territories are defended at all times through "song" and chasing; display flights are given almost exclusively during the spring months. But evidence given beyond indicates that migratory species may adopt and defend feeding territories during migration and in regions of winter residence. Even Bullock (1824:264) noted a Jamaican species defending a feeding area in the *non-breeding* season.

Concerning differences between migratory and resident species, data on the non-

migratory, insular form of the Allen Hummingbird (*S. a. sedentarius,* Grinnell, 1929) would be of value. Further studies of such Central American species as the Rieffer Hummingbird (*Amazilia tzacatl*) which nests at all seasons of the year would be informative; Skutch (1940*a*:434) noted, however, that singing of the males of this species subsided in the dry season.

The female.—The female hummingbird performs all nesting duties (Woods, 1924:4; Whittle, 1937:171; Bent, 1940) and maintains a nesting territory. Defense of the nest surroundings by the female against males of the same species has been noted in the Rufous (Finley, 1905:62), Calliope (Grinnell, 1908:74), Anna (Dawson, 1921:940), Black-chinned (*Archilochus alexandri*) (Grinnell and Storer, 1924:353), and Allen (Orr, 1939:17) hummingbirds. Defense, of course, is directed against other birds and animals as well (see Saunders, 1915:113; Chapman, 1928:285; and Schlag, 1930:198).

The female's territory appears limited to the precinct of the nest and from it she makes excursions in search of food. In the Ruby-throat, the female may transgress the male's territory to get food unless food plants are more extensively distributed and are available in the vicinity of the nest; she may then hold a territory of larger extent against neighboring males or females (Saunders, 1936:161). A feeding territory may be maintained by a female with no reference to a nest (Bolles, 1894:591). In *Topaza pella,* Nicholson (1931:536) recognized a territory about the nest, which, however, was not "self-contained" since the female, of necessity, foraged away from this area. In the Black-throated Hummingbird (*Anthracothorax nigricollis*) of Panama, Chapman (1929:133) observed defense of an entire home tree by the female. The females in these various instances display territoriality which approaches that of the males most closely in the case of feeding areas. They exercise belligerence in the vicinity of their nest as well as in occupied feeding areas when other hummers appear. But such territoriality is obviously not as fully developed as that of the male since no posts are maintained and display flights are generally not given.

Further evidences of territoriality (in both or either of the sexes) is available for the following hummingbird species: Costa (Woods, 1924), Rufous (Hammersly, 1928; Aldrich, 1939), Broad-tailed (Woodbury and Sugden, 1938), Heloise, *Atthis heloisa* (Bent, 1940:418), and Guiana King, *Topaza pella* (Nicholson, 1931:538).

Display flights.—The various dives, gyrations, and pendulum flights of hummingbirds are fairly well known. Woods (1927:301) properly questions terming these "nuptial" flights; in *Calypte anna* and *C. costae,* he (1923:198 and 1927:301) observes that the "nuptial" flight is directed toward both sexes of the same species as toward individuals of other hummingbird species. Aldrich (1939) has noted the same in *Selasphorus alleni,* and the reader will recall similar observations already mentioned for *Archilochus colubris.* The territorial significance of display flights seems to lie primarily in their effect as an intimidating device (Dawson, 1929:938). Allen (1934:182) observed that male Ruffed Grouse (*Bonasa umbellus*) display before males as well as females and emphasized the importance of intimidation in such displays. Just as the meaning of song was given a more sound explanation with the development of the concept of territoriality (Nice, 1941:460), so the display flights of male hummers may have meaning in protecting a territory centering about food requirements. Into this territory a female may enter incidentally and through some mode of behavior make known her sexual readiness to the male so that mating ensues. Allen (1934:190) has observed that the occurrence of mating in the Ruffed Grouse is conditioned by the mode of behavior evinced by the intruder upon being intimidated by the characteristic display. The frequent claims of amorous intent attached to the display flights

of hummingbirds by various observers are largely nonsense. Stone's views (1937:648) that aerial flights are of significance only in courtship and that a mid-July performance indicates earlier nesting failure seem to be erroneous.

Woods (1940:372) suggested that the intimidation display of the Anna Hummingbird originated as a "courtship" display. That these displays bear a sexual significance cannot be doubted since the peak of such activity coincides with the peak of gonad development, and display flights may well have had a direct relation to courtship. Among passerines in which nesting duties are shared, the mechanism for bringing the sexes together may operate through courtship and invitation as well as territoriality. But among hummingbirds in which the sexes are independent, the mechanism appears to operate through a territoriality based at least in part on food supply; courtship and invitation are not apparent.

The extension of the territorial interpretation of song to display flights of hummingbirds is supported further by Skutch's interesting differentiation (1940*a*:443) of two "modes of courtship" (or, preferably, territorial defense) among members of that group: the "dynamic" type, exemplified by the Broad-tailed Hummingbird, in which display flights are given; and the "static" type, exemplified by the Rieffer Hummingbird and other Central American species, in which males merely sing or call. Skutch states that so far as he knows, the two types of "courtship" do not occur in the same species. The Anna Hummingbird is a species that practices both types of behavior, the "singing" more frequently than the displaying. The Costa Hummingbird, belonging to the same genus, displays but does not sing. Display as well as calling have been recorded in certain tropical species (Nicholson, 1931*a*; Davis, 1934). The Allen, Calliope, and Ruby-throated hummingbirds do not call or "sing" from their posts. With further study in Mexico and Central America, it may be possible to establish a gradual transition among the numerous species in the proportion of song to display with reference to territorial defense.

Finally, additional support is found in the fact that the displays of the Allen Hummingbird, for instance, are sometimes performed over a territory in the absence of females or other intruders (Aldrich, 1939). The writer has noted this in the Anna Hummingbird, and there are suggestions of the same in the literature on the Ruby-throated Hummingbird, although as regards the last species, the minds of the authors seem so conditioned to the courtship idea that their statements regarding this point are not clear. The various modes of display may, therefore, function in territorial announcement as well as defense. Further, on one occasion, I noted a male Anna Hummingbird "sing" and then display near his post while another male sang some twenty yards away. Thus, territorial competition may stimulate display (Skutch, 1940*b*:455).

In his studies of the White-eared and Heloise hummingbirds, Skutch (1940*b*:453) describes what he terms "singing assemblies." Certain precautions should be heeded in recognizing such assemblies: (1) Concentrations may appear in more favorable habitats. Skutch himself states that in the former species he has never seen more than seven males in a single group, most of the others containing fewer. The individuals within such a group are territorially spaced and scattered lone males also occur. This territoriality seems similar to what Grinnell and Storer (1924:358) describe of normal spacing among male Calliope Hummingbirds. Favorable habitats do not necessarily hold maximum densities of their characteristic birds; and, of course, favorable habitat may be limited locally. (2) Regarding gregariousness, Aldrich (1939) suggests: "Although male Allen Hummingbirds are instinctively solitary because of their belligerency toward other males, their apparent great urge for belligerency in turn makes

them somewhat gregarious. The latter instinct is the stronger, and thus we find males protecting for the sake of combat a small feeding territory in juxtaposition to males with other similar territories." (See also Sherman, 1913:155.)

The foregoing comments, however, merely suggest possible explanations for apparent sociality. That Skutch recognized assemblies of males with probable justification is supported by studies of communal display among the males of tropical hummingbirds. In British Guiana, Nicholson (1931*a*:76) observed groups of up to 20 males of *Phaëthornis superciliosus* all calling more or less continuously and displaying plumage intermittently. Rivalry through more active calling was noted among closely neighboring males. Yet these apparently did not maintain definite posts, as exchanges of perches occurred. At another time, however, a certain territoriality about a perch was observed. Brewster and Chapman (1895:207) observed similar singing assemblies in *Pygmornis longuemareus* and *Phaëthornis guyi* of Trinidad, but in these, the males maintained definite perches to which they returned after encounters with other individuals. It is instructive to note that two instances of solitary display have been recorded in *Phaëthornis superciliosus* (Davis, 1934:733); further, less frequent communal display occurred in a related species, *Pygmornis ruber* (p. 738). No sociality was noted in *Topaza pella* by Nicholson (1931*b*). In most avian species in which communal display occurs, it bears a sexual significance (Winterbottom, 1929); however, there is no evidence for any sexual function in these assemblies of male hummingbirds (Nicholson, 1931*a*:82).

Thus, among the tropical species, certain ones as *Topaza pella* may resemble Nearctic species in territorial relations; but in the latter neither singing assemblies nor plumage display (except gorget and tail expansion) are known. Among the males of the communal species, no suggestion of a feeding territory has yet been made. It is noteworthy that the degree of sociality differs among different species; here is a trend which may be likened to the trend from "singing" to flight display in territorial defense among Central and North American species, as already noted.

In female hummingbirds, display flights have also been observed. According to Bendire (1895:211) and Linsdale (1938:75), the female Broad-tailed Hummingbird may perform the display flight of that species, although the latter author observed these performances to be given only when the male displayed also. Bowles (1910:125) and Poling (1890:403) observed intimidation dives performed by females of the Anna Hummingbird and Rivoli Hummingbird (*Eugenes fulgens*), respectively. Modified, semi-display flights may be given by the female Ruby-throated Hummingbird, also when facing the male (Bent, 1940:336, and Whittle, 1937:171). Such displays appear to be more protective and retaliatory in function than is true in males since, in most instances, females have been noted to behave thus in the presence of enemies or under intimidation by male hummingbirds. In my opinion, displays in which both male and female participate do not mark the height of any courtship but rather the contrary. The female's display may be an effort to resist the male. The female Ruffed Grouse (Allen, 1934:182) is known to display, but here the performance is made to intimidate weaker individuals, regardless of sex.

"Neutral tracts."—At times of subsidence of territorial activity, at least in migratory forms, females may feed freely in the presence of males without a chase or display taking place. Even if a female intrudes in an occupied area, the male may complete a display before a female which then feeds (Grinnell, Dixon, and Linsdale, 1930:244). If the intruder holds his place, no chase occurs (Schlag, 1930:199); if he departs, the display may be interrupted or followed by a chase (Woods, 1927:302; and writer's observations). Furthermore, there may be feeding areas outside those occupied by

males which may be visited by both males and females. Feeding concentrations may occur during migration and before establishment of more definite territories in the spring (Tyler, 1940:334; Aldrich, 1939). Dawson (1923:934) noted a dozen hummers (*Selasphorus rufus*) feeding about a currant bush. Such concentrations occur generally on common feeding grounds in the fall (Grinnell, 1905:384; Taverner and Swales, 1907:137; Woods, 1927:305); however, the individuals of these congregations remain hostile toward each other, and the characteristic belligerence may be manifested to the extent that a sort of vestigial territoriality is seen. An interesting observation was made available to me by Robert W. Storer, who watched eight females and young of Rufous and Broad-tailed hummingbirds about a mass of flowering shrubs on August 17, 1940, in the Medicine Bow Mountains, Wyoming; these birds maintained, at least for brief periods, small areas over the shrubs which they defended against neighbors. Bolles (1894:591) observed two males and one female of the Ruby-throated Hummingbird holding rights over a sap supply resulting from activities of sapsuckers.

Copulation.—The mode of mating has been described variously for hummingbirds, but most of these descriptions, in my opinion, are merely examples of the usual clashes which happen to appear suggestive of actual sexual union (see Ridgway, 1892:279; Knight, 1908:304; Sprot, 1927:71; Arnold, 1930:303; Whittle, 1937:171). It is possible that coition may occur in mid-air (Orr, 1939:19), but there are no sufficiently clear or convincingly complete accounts to confirm this. The most credible description of copulation in hummingbirds is Wyman's (1920:207) of the Calliope Hummingbird. Here, it conforms to the usual avian manner: "A female sat . . . on a horizontal dead weed, when a male shot up the hillside . . . , passed the female, and darted down. . . . As he passed the female, she fluttered and swung head downward on her perch. The male alighted above her, with vibrating wings, and coition took place in this position."

General comments.—At this point, let us review our evidence in terms of the tenets of the theory of territoriality (Nice, 1941:441). Whereas in most passerine species pairs are spaced during the breeding season, in hummingbirds the members of a mated pair are independent. Polygamy probably occurs. The males are generally spaced. The females, likewise spaced, place their nests with no positive relation to male territories and defend at least the nest surroundings. Pugnacity is displayed among all individuals and species of hummingbirds, not just males toward other males of the same species. The displays of the male hummingbird are a warning to other hummingbirds, *whatever the sex*; in the light of our limited evidence, they cannot be regarded as an "invitation to a female." Defense is a paramount feature of territorial occupancy in hummingbirds; announcement and competition through song and display probably occur in at least some species, but more data are needed on these points. Further, hummingbirds do not appear to observe territorial limits as rigidly as do numerous passerine species. A male may defend a certain area; but if so disposed, other hummingbirds of both sexes will enter the territory unhesitatingly unless, as described for the Ruby-throat, there is some learning with reference to the site of an established male through previous encounters with him.

Nice's classification of territories seems to call for an additional category: mating and feeding. This would probably include most male hummingbirds. To be sure, our observations of actual mating in hummers are exceedingly sketchy. But it should be remembered that the conspicuous factor in male territoriality seems to be food supply, not mating as suggested by Nice's mention (1941:462) of "some hummingbirds" under her "type C—mating station only." There can hardly be any doubt that mating occurs

on the feeding territory, since where such behavior has been recorded, it occurred at the site of display flights, the site of territorial defense. The female territory is Nice's "type D—restricted to narrow surroundings of nest," though a reservation should be added regarding possible enlargement, especially to include a feeding area, as mentioned above.

Clearly the aggressiveness of hummingbirds is a general feature of their behavior displayed by most individuals and at most times. Its part in defense of an occupied area seems secondary, since territoriality hinges about attachment and relative confinement to a more or less specific area. Yet, if the trait contributes to defense of an area, it becomes a part of the mechanism functioning to space individuals (Noble, 1939:267).

It is therefore questionable whether hummingbirds may be said to demonstrate a hypertrophy of territorial behavior in terms of the increased pugnacity and positive defense of territory (Nice, 1941:469). The apparent hypertrophy is merely a manifestation of normal aggressiveness. The belligerence of the male is not to be associated with such protective instinct for mate, nest, or young as is displayed by males of many passerine species. If we may evaluate the importance of territories in hummingbirds on the basis of our present knowledge, in males of most species it may be said to be based on a food supply and to serve in the defense of the individual only; in the female, it is based on a protection of nest and young and serves in their defense as well as that of the individual.

Summary.—Belligerence and intolerance characterize the behavior of most trochilid species. In at least North American species, the independence of individuals is conspicuous, and except for mating, the sexes bear no relation to each other. The male hummingbird, who probably is polygamous, maintains a territory centering about a food supply; secondarily the territory may serve as a mating station. Length of occupancy and definiteness of territorial claims depend, among other things, on type of food involved and seasonal status of the species. There is imperfect observance of territorial boundaries. Defense is the chief feature of hummingbird territoriality; announcement and competition through song and display occur less frequently. The female maintains a nesting territory. Both sexes may maintain feeding territories of varying extent and transitory occupancy, probably at all times of the year. The display flights of hummingbirds are essentially an intimidation device. In addition, their function in territoriality may be compared with certain aspects of song in passerine species. The female display is probably a protective device.

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