

AGGRESSIVE AND COURTSHIP DISPLAYS OF THE MALE ANNA'S HUMMINGBIRD

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ABSTRACT.—The aggressive and courtship displays and vocalizations of the male Anna's Hummingbird (*Calypte anna*) are described in detail, and various types of evidence and observations are used to reconstruct the typical courtship sequence. Initial contact is made by the female flying to the male's territory and attempting to feed; she may have previously visited several other territories in order to evaluate territory quality. The well-known dive display is an aggressive maneuver by the male, although it may play a role very early in the courtship sequence. Following a lengthy chase towards the female's nesting area, she alights low in dense vegetation. The male then gives the displays most critical for courtship: a back-and-forth "shuttle" display and high-intensity song. These hitherto undescribed displays occur immediately preceding copulation, and are probably the most important isolating mechanisms for the species. Many of the elements of courtship in *C. anna* are widespread in hummingbirds. Practice and probably learning play a major role in the maturation of song and dive displays in the individual. The courtship sequence in this hummingbird probably represents the resultant of various selective pressures, some acting mainly on males and others on females.

Hummingbirds are becoming among the best-studied of North American birds, particularly with respect to energetic aspects of nesting (Horvath 1967, Calder 1971, 1974, Calder and Booser 1973, Smith et al. 1974), territoriality and foraging (Stiles 1971a, Ewald and Carpenter 1978, Kodric-Brown and Brown 1979, Pyke 1978, Gass 1979), and relationships with the flowers they visit and pollinate (Stiles 1973, Carpenter 1978, Waser 1978, Kodric-Brown and Brown 1979, Price and Waser 1979). Recent field studies in California have disclosed a striking amount of hybridization among several (newly?) sympatric species (Lynch and Ames 1970, Wells et al. 1978, Wells and Baptista 1979). Study of hybrids and parental types in nature offers a unique opportunity to document the ecological and behavioral effects of such hybridization. Analyses of these phenomena, however, have been hindered by the lack of reliable descriptions of courtship and aggressive displays of the species concerned. The conspicuous dive displays have been described with varying degrees of completeness and accuracy by Bent (1940), Banks and Johnson (1961), Wells et al. (1978), and Wells and Baptista (1979), among others, but except for the perceptive discussions of Pitelka (1942, 1951a, b) their role in courtship has been misunderstood. Moreover, a whole family of close-range displays in these hummingbirds, far more crucial in courtship *per se*, has been overlooked. Finally, I know of no good descriptions of display sequences nor, indeed, of copulation itself in these birds. Be-

havioral isolating mechanisms in North American hummingbirds cannot be properly appraised without a clear understanding of what actually constitutes their courtship.

Through several years of close study of the ecology and behavior of the Anna's Hummingbird (*Calypte anna*) and other California species (Stiles 1973), I was able to observe courtship and aggressive displays of these birds in detail. My purpose here is to describe and interpret the vocalizations and displays of the Anna's Hummingbird, to serve as a basis for comparisons with other species.

METHODS

Most of the field observations reported here were made in the Santa Monica Mountains, Los Angeles County, California, between 1966 and 1970, with supplementary observations made intermittently through 1974. The main study areas and their hummingbirds have been described elsewhere (Stiles 1973). Many of the displays described here were observed either during all-day watches at the territories of male Anna's Hummingbirds (cf. Stiles 1971a) that became habituated to my presence; or on regular censuses in my study areas. I specifically tried to determine the objects of chases and displays given by male hummingbirds on breeding territories. To further clarify the forms and functions of these displays in *C. anna*, I experimented with mounted dummies in March and April of 1969 and 1970. Three dummies were used: a stuffed male *C. anna* in singing position, a female *C. anna* in cop-

ulatory position, and a female Rufous Hummingbird (*Selasphorus rufus*), in erect perched position. In each experiment, I presented a dummy to a territorial male *C. anna* by placing it on a prominent perch in or near the core area of his breeding territory (see below), and observed his reactions to it for 10 min. Males rapidly became habituated to the dummies; hence I made only a single presentation to any given male. The three dummies were used 10, 10, and 9 times, respectively, thus involving a total of 29 territorial males.

Whenever possible, I recorded display sounds using a Uher 4000 Report-L tape recorder and a Griffith fiberglass parabolic reflector. On several occasions I used dummies to elicit displays in order to record the latter. Such presentations were made to males that had already experienced dummies, and these results are not included in the analyses of the dummy experiments.

My overall approach in this paper is first to describe each display of male Anna's Hummingbirds in as much detail as possible. I then present several representative sequences of displays as observed in the field, to show how the different components are integrated. The responses of the birds receiving the displays are also noted, as well as the stimuli that evidently evoked the display. These data, together with the results of the dummy experiments, provide the basis for an interpretation of the information content and functional significance of the displays. For reasons explained below, I have never witnessed a complete courtship sequence, from initial contact to copulation. However, I have observed enough fragments of enough sequences to be able to reconstruct what I feel is the "typical" courtship behavior of the Anna's Hummingbird.

BREEDING AND TERRITORIALITY IN ANNA'S HUMMINGBIRD

In order to place the displays in their proper ecological context, I discuss here the major features of territorial behavior and the annual cycle of Anna's Hummingbirds in the Santa Monica Mountains. The breeding season extends from about November or December to April or early May, during which time males occupy breeding territories in chaparral habitats. These territories are most often located on north- and east-facing slopes where *Ribes malvaceum* and *R. speciosum*, the most important food flowers, grow. A breeding territory consists of a core area of ca. 0.1 ha of relatively low, uniform vegetation containing the male's most frequently-used territorial perches and, often, his major food plants. Surrounding this is a 2–4-ha "buffer zone" much

more variable in vegetation height and presence of flowers, that is used relatively infrequently and irregularly by the male. Most territories are loosely clustered on favorable slopes. Females prefer oak woodlands and gardens for nesting, and tend to occupy canyon bottoms, sometimes far from male territories. During the nonbreeding season, males often occupy feeding territories at rich clumps of flowers, especially the introduced *Nicotiana glauca*. Feeding territories consist essentially of the flowers themselves; often they are only a few square meters in area, and many such territories may exist within a large clump of flowers. Where a feeding territory contains two or more discrete clumps of flowers, the area between them is usually inconsistently defended. Territorial behavior in these hummingbirds has been described further by Pitelka (1951a), Williamson (1956), and Stiles (1971a, 1973).

VOCALIZATIONS

The vocalizations described are given in interactions involving adult male Anna's Hummingbirds, though they are not always given by the males themselves. My account is not a complete catalogue of the vocal repertoire of the species, as I did not study in detail the sounds made by nesting females, nestlings, or fledglings. In general, I use the terminology of Heckenlively (1970) to describe vocalizations.

CHIP NOTE

This is a short, sharp, dry "tzip" given in a wide variety of low-intensity interactions by all members of the species. The note appears to be produced by a very rapid vibration of a single element covering a wide frequency range, from about 10 kHz down to about 3–4 kHz (Fig. 1a). It is the most frequently heard vocalization of Anna's Hummingbirds and is given in various contexts, which probably determine the exact meaning of the chip (cf. Smith 1977). It is probably best regarded as a general contact and spacing note, like corresponding vocalizations in other species of North American hummingbirds (cf. Stiles 1971b). In more intense interactions (e.g., males feeding when a potential intruder is near the territory, or nesting females when another bird is near the nest), many chip-notes may be strung together in an excited-sounding twitter. For my present purposes chip-notes are of interest because they, or elaborations of them, may enter into more complex vocalizations.

CHATTER

The chatter (Fig. 1b) is a rapid series of harsh, buzzy or grating notes given in high-intensity

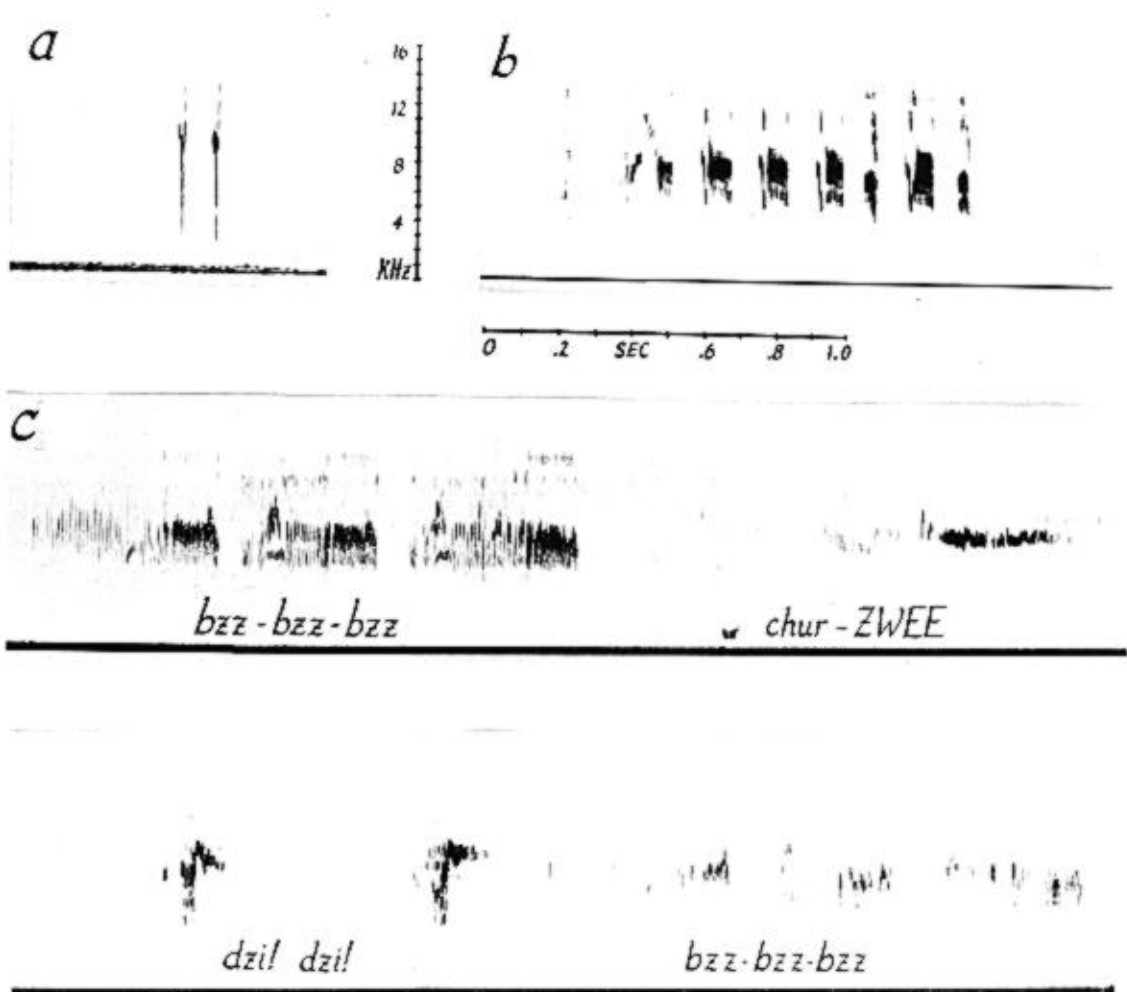


FIGURE 1. Vocalizations of *Calypte anna*: a. chip; b. chatter; c. song (one 'song unit').

aggressive interactions. It consists of an essentially undifferentiated series of buzzy notes given at a rate of ca. 10 per second. Each buzz is composed of ca. 8–18 syllables similar in structure and frequency range to chip-notes, save that the lower frequencies are truncated at ca. 4–5 kHz. A single buzz lasts 0.02–0.05 s, depending mainly upon the number of syllables it contains; syllables are repeated at a rate of ca. 300/s. The chatter appears to consist of a series of bursts of very fast, run-together chip-notes. It is given by both sexes and at least well-grown juveniles, and is directed towards other *C. anna* or other hummingbirds (very rarely towards non-hummingbirds). An Anna's Hummingbird chatters either as it attacks or chases another hummingbird, or as a warning that the vocalizer is about to leave its perch and attack. Chatters are given in the latter context either by females on or near their nests, or by territorial males, as another hummingbird approaches the nest or territory. A

perched male may combine the chatter with the sway display (see below).

SONG

Complex and highly structured, song (Fig. 1c) is the main advertising vocalization of males on breeding territories, although it sometimes occurs in other contexts as well (see below). Previous descriptions of the song (Mirsky 1976, Baptista and Matsui 1979) have not fully described the extent to which the song is structured. "Full" song consists of three different phrase-groups, each of which contains two to four like or unlike phrases. To my ear, the typical song sounds like: "bzz-bzz-bzz chur-ZWEE dzi! dzi! bzz-bzz-bzz." The "bzz" phrases almost always occur in groups of three or (less often, and mostly at the beginning of the song) four. The "chur-ZWEE" note-complex is invariably given as a unit, and is virtually always followed by two "dzi!" phrases. Typically, one or several groups of "bzz"

phrases occur at the start and end of the song, and one group of three "bzz" phrases separates successive "chur-ZWEE dzi! dzi!" phrase groups. The "bzz" phrases may also occur alone, without the other elements, particularly when the bird is singing in flight (see below).

The "bzz" phrases average about 0.4–0.5 s in duration, and are separated by brief pauses of ca. 0.1 s or less. Each "bzz" comprises two components: one containing distinct syllables given at a rate of 100–115/s; and another that appears to be essentially a continuous buzz with no apparent syllable structure. The frequency range of the first component varies cyclically from 6–8 to 5–9 kHz with a period of about six syllables, evidently the result of amplitude modulations. The frequency range of the second component is similar, 6.5 or 7–9 kHz; there is also some suggestion of modulations. The distinction between the components is not clear-cut, and the proportion of the phrase each occupies varies somewhat from one phrase to the next. Usually, the first component occupies the initial half or so of the "bzz," then, after a variable transition, the second comprises the last third or so of the phrase. The general similarity in frequency range and overall structure of both components to the chatter and chip-note suggests that the same vocal elements are involved: the "bzz" is essentially another elaboration of the chip-note.

The "chur" is a clear low-pitched note at about 1.5–2 kHz, lasting about 0.05 s. The "ZWEE" phrase is complex, apparently involving the vibration of two independent elements. The first produces a sustained tone over a narrow frequency range, ca. 7–8 kHz for the most part. This element is evidently vibrating very faintly from the moment the "chur" is produced, but the principal part of the "ZWEE" starts with a burst about 0.4–0.5 s later, and lasts 0.4–0.5 s. Simultaneously with the last two-thirds of the loud part of the "ZWEE" is uttered a series of short syllables with a dominant frequency of 4.5 kHz and a strong harmonic at 9 kHz. These syllables are given at a rate of ca. 35/s over a period of ca. 0.5 s, sounding like a warble or trill to the human ear. The similarity of the dominant frequency of the first component of the "ZWEE" note to those of the preceding vocalizations suggests that it, too, is structurally a derivative of the chip-note, whereas the "chur" and the second component of the "ZWEE" are wholly different.

The "dzi!" phrase is also complex, consisting of faint vibrations without distinct syllable structure at 4.5 and 9 (approximately) kHz, probably made by the same element that pro-

duced the second half of the "ZWEE" at these same frequencies. This faint buzz lasts ca. 0.2–0.3 s and is immediately followed, sometimes overlapped, by several short bursts at 7–8 kHz, the third or fourth of which is especially loud. Then, ca. 0.05 s after this syllable, comes a broad-frequency (4.5–10.5) burst not unlike the individual phrases of the chatter but shorter than most; the lower frequencies of this oscillation are abruptly damped producing a short, narrow-frequency sound that slurs downward from a mean frequency of ca. 9 kHz to about 8 kHz. A faint "echo" of this latter component may follow, suggesting that the frequency change in the last part of this phrase reflects another cyclic modulation. The overall similarity of the different components of the main part of the "dzi!" to those of other vocalizations, particularly the chatter and part of the "ZWEE," implies that here is still another elaboration of the chip-note, produced by yet another sort of damping and modulation.

The total phrase-group "bzz bzz bzz chur-ZWEE dzi! dzi!" may be considered to comprise one "song unit." In normal advertising song, a series of 1–3 such units, followed and often preceded by one or more groups of 3–4 "bzz" phrases, constitutes a bout of singing. However, when a male is perched close to, and singing at, another hummingbird, the song is given more rapidly, and many song units follow one another without a break, often for minutes on end. I term this "high-intensity song"; the posture of the male while giving it also differs from that of normal song (see below).

The chip, chatter, and song represent the three major vocalizations of male Anna's Hummingbirds. Three other vocalizations occur occasionally in particular situations involving adult males, and so will be described briefly here:

FIGHT NOTE

This is a short, sharp "brrrt!," low-pitched and with a rolling or gurgling quality, heard in intense aggressive or courtship interactions (as will be seen, the difference between them is not great) when bodily contact is made. It is generally impossible to tell which of the birds in the interaction is giving these notes; perhaps both do. However, in some dummy experiments (see below) the male gave "brrrt" notes upon attacking the dummy.

"SEET" NOTE

The "seet" note is a high, thin, short whistle given by begging juveniles towards their mother as she approaches; also given by the

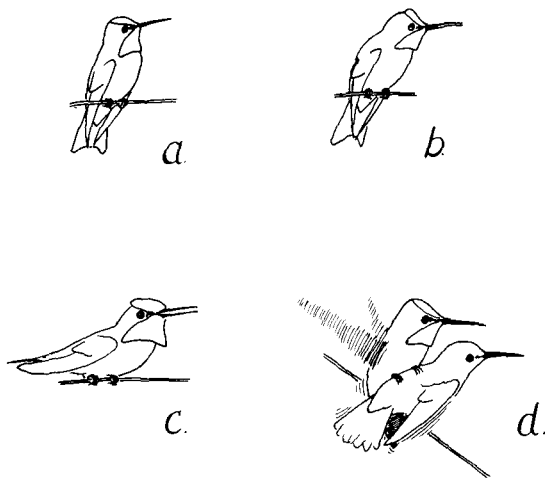


FIGURE 2. Postures and static displays of *Calypte anna*: a. normal perching posture of male; b. singing posture; c. high-intensity song; d. copulation posture.

subordinate bird when hard-pressed in an aggressive interaction. I also heard it once in a courtship interaction, presumably given by the female as the male approached to settle on her back.

KEENING NOTE

A high, thin, long-drawn-out, down-slurred whistle, this is evidently an intense distress note. It is given by a bird being handled as it emerges from torpor or upon being extracted from a mist net; I once heard it given by a young bird that was being attacked by an adult male into whose territory it had wandered; soon thereafter the male ceased its attack.

POSTURES, STATIC DISPLAYS, AND COPULATION

A male Anna's Hummingbird that is neither singing nor displaying normally perches with the body held erectly (60–75° from the horizontal), the bill more or less horizontal, the crown and gorget feathers more or less sleeked (Fig. 2a). The typical song posture, assumed when the bird is singing but not close to another hummingbird, is with the body tilted to ca. 30–45° from the horizontal, the crown and gorget feathers ruffled, often presenting a shaggy appearance, the neck extended (Fig. 2b). In high-intensity song, given when a male is close to another hummingbird (whether in aggressive or courtship situations), this trend is continued: the body is held almost horizontally, the crown and gorget feathers fully erected to present practically a red disk or shield to the other bird (Fig. 2c).

CHATTER-SWAY

This display is given by a male on his perch, apparently to intimidate and repel a potential

trespasser—usually one that has not yet actually entered his territory. In this display a male sits very erectly, his tail held at an angle to the body and at least partly spread, the bill horizontal or slightly raised. He faces the intruder and turns rapidly from side to side while buzzing his wings and chattering loudly. If the intruder does not retreat, he quickly chases it. The chatter-sway appears to be a high-intensity aggressive display, announcing a male's readiness to chase the intruder. It is probably a ritualized flight-intention movement, typically given when the intruder is far enough away that the male's threshold of overt attack has not been reached. The chatter-sway is seen most frequently in two contexts: when a male on feeding territory perceives an intruder approaching but not yet in his territory; and when a male on a breeding territory sees another hummingbird pass by just outside the territory. When males are just setting up breeding territories in late fall, they may perch on common borders; whenever one flies within his own territory, the other may give a chatter-sway. Occasionally this display is directed by a breeding male toward another bird (non-hummingbird) that has just passed close by his song perch. In any case, this display, although occurring in various aggressive contexts, has little if anything to do with courtship.

Also perhaps best considered here are the postures assumed by a female in courtship interactions, and by both sexes during copulation. When close to (but not in contact with) a displaying or singing male, a female holds her body fairly erectly, partly spreads her tail, and points her bill directly at the male. Should he fly back and forth above her (the shuttle display, described below), she "tracks" him with her bill, in effect keeping him "at sword point" until the actual copulation attempt (Fig. 2d). This might be considered a female's defensive display, which effectively keeps the male at a distance until he is ready to attempt copulation. As will be described below, I believe that the male's motivation changes from primarily aggressive to sexual as such a display sequence develops, the longer the female refuses to fly.

During copulation, the female perches on a horizontal twig, her body leaning forward to form only a slight angle to the horizontal; her head is held low, the bill usually pointed slightly upwards (Fig. 2d). Her tail is partly spread and twisted downward and to one side; her partly-open wings flutter against the perch, perhaps for balance. The male perches on her back, his wings buzzing (again probably for balance). His body is erect as he lowers and twists his abdomen and tail down the female's

side to achieve cloacal apposition. Both birds vibrate their rumps and tails during cloacal apposition, which lasts no more than 3–5 s in my experience. The male may or may not grasp the female's crown or nape feathers in his bill tip as he lands on her back to attempt copulation. Allowing for the short legs and long bills of hummingbirds, these positions resemble those that nearly all birds assume during copulation. I regard reports of aerial copulation in hummingbirds as pure fancy, perhaps inspired by such copulations that occur in the swifts. There may be contact between the two birds involved in a chase; occasionally one may grasp the other with bill or feet such that both tumble toward the ground, but in my experience such events have nothing to do with copulation.

DYNAMIC DISPLAYS

Under this heading I include those displays performed while a bird is in motion (which, for a hummingbird, generally means in flight). Male Anna's Hummingbirds have two such displays: the dive and the shuttle. Dives are the most conspicuous and best-known displays of male North American hummingbirds. Shuttle displays, although probably much more important in courtship per se, have not been described previously although they occur in all species of the genera *Calypte*, *Archilochus*, *Selasphorus*, and *Stellula* (Stiles, unpubl. data; Ortiz-Crespo, unpubl.).

Male *C. anna* perform perhaps the most elaborate and spectacular dive displays of any North American hummingbird. I divide this display (Fig. 3) into four phases: hover-sing, climb, dive, and return. In the hover-sing phase, a male hovers 2–4 m above the object of the display and sings one or two sets of three (rarely 2 or 4) "bzz" notes. Next comes a wavering, near-vertical climb to a height of 20–40 m; this is occasionally interrupted by a brief bout of hovering and singing partway up (Baptista and Matsui 1979), though in my experience this is exceptional. Immediately there follows a near-vertical dive that terminates with an explosive squeak just above the display object (usually within 0.5–1 m of it). Then, without pausing, the male returns along a circular arc to a point 2–4 m above the display object, where he may again hover and sing or repeat the entire performance. Sometimes as many as 5 to 10 dive displays are given in rapid sequence.

I have been able to time the components of numerous dive displays. The hover-sing phase lasts from 1 to 2 s (mean 1.65, range 1.0–2.4, $n = 11$), the climbing phase from ca. 7 to 8 s (mean 7.47, range 6.8–8.2, $n = 10$); the dive

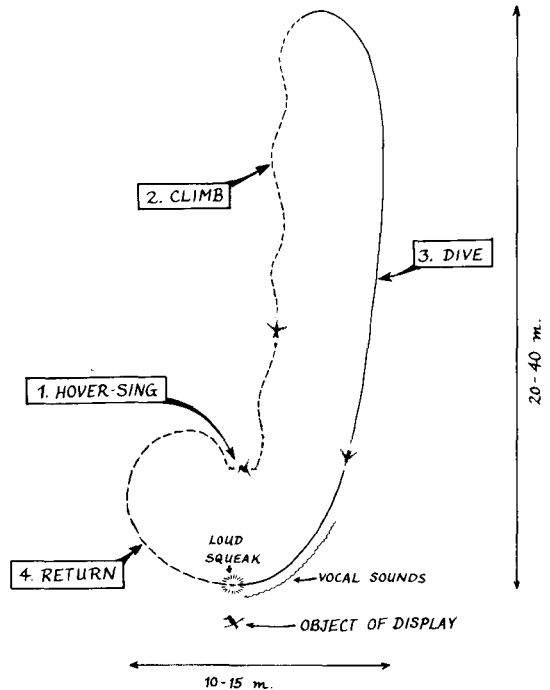


FIGURE 3. Phases of the dive display of *Calypte anna*.

requires just over 2 s (mean 2.32, range 2.0–2.8, $n = 15$) and the return less than 0.5 s (mean 0.34, range 0.2–0.5, $n = 7$). The entire dive display requires about 12 s (mean 12.04, range 10.5–13.3, $n = 10$). The variation in length of time required for a complete display depends mainly upon whether one or two bursts of "bzz" phrases are given in the hover-sing phase, and the height to which the male climbs before diving. For one set of dives at a dummy I determined this height by triangulation to be ca. 32 m; the corresponding dive took 2.2 s. I estimated the male's total flight path during the dive to be about 37 m, giving an average speed of just under 17 m/s. The highest speed attained during the dive was probably at least 20 m/s. By contrast, the normal speed of a male flying around his territory was observed to be ca. 13 m/s (depending upon wind speed, inclination of flight, etc.), and the speed attained during the vertical climb phase of the dive display is only around 4–5 m/s. Hamilton (1965) reported that the dive display of Anna's Hummingbird was oriented towards the sun, probably to enhance the reflectance from the crown and gorget, especially near the bottom of the dive. My data strongly support Hamilton's finding: of 41 dives that I observed closely on sunny days, at least 35 were sun-oriented. On several occasions when a male performed the dive display at me, I could clearly see the brilliant rose-red flash of crown and gorget as he passed close over my head.

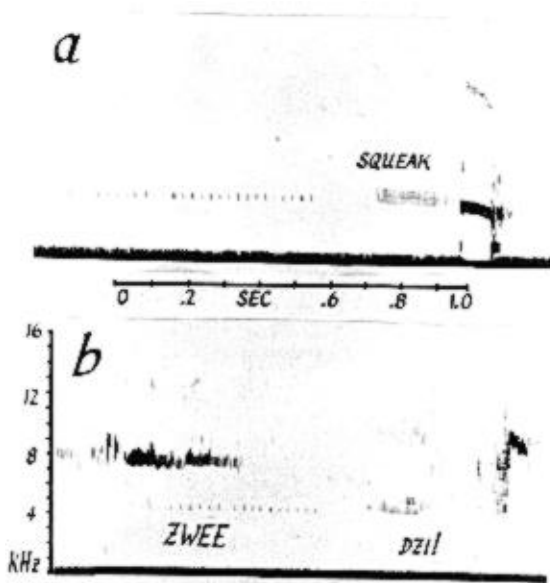


FIGURE 4. Sounds associated with the dive display of *Calypte anna*.

Aside from the “bzz” phrases of the hovering phase, three distinct sounds are associated with the dive display, specifically with the dive itself (Fig. 4). The most noticeable is the startlingly loud squeak at the very bottom of the dive, as the bird passes closest to the display object. This squeak is audible for several hundred meters; it has a frequency of 4.5 kHz at the start, dropping to ca. 4 kHz, and it ends abruptly with a low-pitched snap or click that covers a wide frequency range but with a dominant frequency of 1.5–2 kHz. The squeak has a duration of ca. 0.05 s.

Two different sounds precede the loud squeak: a series of short notes with frequency of about 4.5 kHz, identical to the trill of the “ZWEE” note of the song but lacking the harmonic; and a short buzz at a frequency of ca. 5 kHz, lasting for ca. 0.15 s, that precedes and may even overlap the squeak. This buzz may actually be composed of two separate notes, one at ca. 4.5 kHz, the other at ca. 5.5 kHz, which overlap in the sonogram due to the use of the wide-band filter. An identical soft buzz, in which the two components are sometimes merged and sometimes clearly separated, occurs at the start of the “dzi!” phrase of the song (cf. Fig. 2c); moreover, the latter follows the trill of the “ZWEE” at exactly the same interval as the buzz in the dive display follows the trill (ca. 0.15 s). Both of these sounds seem to me to be vocal in origin, as concluded by Baptista and Matsui (1979). However, I do not

agree with these authors that the squeak is a vocal sound as well, even though its frequency range is similar (albeit not identical) to that of several of the notes mentioned above. First, the note seems too loud in relation to the size of the syrinx and airsac system of a hummingbird. To project a squeak with such penetration the sound would probably have to be delivered with the beak open—and it is inconceivable that this would not drastically offset the flight pattern of such a small bird traveling at upwards of 20 m/s. Finally, I have never heard a definitely vocal sound from an Anna’s or any other hummingbird that approaches the squeak in explosive loudness. Both circumstantial and experimental evidence show that the squeak is produced by air passing suddenly through the specially modified rectrices. The experiment was performed by Rodgers (1940), who mounted *C. anna* rectrices on a whip in such a way that when he “cracked the whip,” the squeak was produced. Moreover, adult males that dive during the period when they are molting the rectrices make only a muted “whiff” at the bottom; the squeak is not produced again until the new rectrices are grown (F. A. Pitelka, pers. comm.). Similarly, young males often dive prior to the postjuvinal molt, but do not make the squeak until they have grown adult-type rectrices.

SHUTTLE DISPLAY

In this display (Fig. 5), a male flies rapidly back and forth in tight arcs 15–25 cm in length above another hummingbird (usually a female *C. anna*) that is perched ca. 20–30 cm below him. The male holds his body fairly horizontal, his head and bill pointed downward toward the object of the display; at the end of each arc, he reverses direction with a rapid flick of the spread tail (though in this case I have not heard any sound). During the shuttle display the male sings, but as in the “hover-sing” phase of the dive display, the song consists entirely of “bzz” notes, usually in groups of three. However, preceding or following the shuttle display, a male may perch near the other hummingbird and indulge in a bout of high-intensity song.

DISPLAY SEQUENCES

In this section I present several representative observations of courtship and aggressive display sequences, as abstracted from my field notes. These should help to illustrate how the displays and vocalizations are integrated in nature, as well as possible sources of variability between sequences and problems of observa-

OBSERVATIONS

1. *Copulation sequence, Stone Canyon, Santa Monica Mts., 21 February 1969, ca. 14:00.* For the preceding two hours I had been watching a female building a nest in an oak grove at the end of a garden in the canyon bottom. At 13:58 she flew off over a hill to the east, where ca. 200 m away were the breeding territories of three males on a chaparral-covered hillside. About one minute later I heard three dive displays from the vicinity of this hillside. Shortly thereafter (ca. 14:00), the female flew in from the east hotly pursued by a singing male. The chase zigzagged down through the nest tree into a thick clump of herbage. The female evidently perched on or near the ground, and there followed some violent-sounding bodily contact (although within 2 m, I could not see the birds at this time), accompanied by "brtt" notes. After ca. 15 s of this, the male flew up just above the foliage (ca. 40–50 cm) and gave a rapid series of shuttle flights for ca. 20 s; the female, now perched on a horizontal twig ca. 15 cm above ground, tracked him with her bill. The male then dropped down to a twig ca. 10 cm from and slightly above the female and gave high-intensity song at her for at least 30 s. The female vibrated her wings, and the male flew directly to her, alighted on her back, and copulation followed; cloacal apposition evidently lasted ca. 5 s. The male, without further displays, then flew directly off to the east. About 10 s later the female flew to her regular perch and preened vigorously for several minutes, especially about the rump and vent. She then flew off to the west, returning 2.5 min later with nesting material.

2. *Copulation sequence, Franklin Canyon, Santa Monica Mts., 22 April 1969, ca. 10:00.* During hummingbird censuses along a chaparral-covered ridge, I repeatedly noted a female *C. anna* in a grove of walnut trees ca. 100 m south of a male's breeding territory. After passing by the territory I heard three or four dive displays therein, then ca. 3 min later a singing male *anna* chased a female along the ridgetop towards me from the territory, now ca. 150 m away (I did not see the chase begin). The chase came to earth in a dense *Encelia* patch 2 m from me. The male perched ca. 20 cm from the ground and gave high-intensity song for 20–30 s, his bill indicating the location of the female, who was perched low and out of sight. She then flew up onto a dead twig ca. 25 cm from the ground; the male followed her closely, and as she perched he lit directly on her back and attempted copulation, grasping her crown feathers in his bill tip. The copulation lasted 3–5 s, then one bird gave a "brtt" note,

the female broke free and flew back toward the walnut trees, pursued by the male. Six days later I found an Anna's Hummingbird nest with two fresh eggs in a walnut tree.

3. *Attempted copulation, Pine Cove, San Jacinto Mts., 13 May 1969, ca. 11:30.* At this highland (elevation ca. 1,700 m) site a large aggregation of presumably postbreeding *C. anna* was present at a group of feeders. A male chased a female from the feeders into a young cedar tree ca. 20 m away. She perched ca. 1 m from the ground, and the male alighted 15 cm away and gave high-intensity song at her for nearly 1 min. When she flew, he dashed out, struck her in mid-air, and to the accompaniment of "brtt" notes forced her to the ground ca. 3 m away, in a patch of bare ground about 5 m from me. He immediately performed shuttle displays over her at a height of ca. 20 cm for about 15 s, as she tracked him with her bill. He then landed on the ground facing her and ca. 8 cm from her and sang intensely for perhaps 20 s. She twice attempted to fly and was forced to the ground, one or the other bird giving "brtt" notes. Then, still singing, he flew to her back and attempted copulation. Again she tried to fly but was forced to earth by the still-singing male, who continued to try to copulate; this time the birds appeared to be in the normal copulatory position, but I am not sure cloacal apposition actually occurred. The female broke free after 1–2 s and escaped into the nearby evergreen. The male then returned to the feeders; the female chattered, then perched and preened her rump and vent. This incident was unusual in being outside the normal breeding season of *C. anna* in southern California (cf. Stiles 1973), and in involving a male that almost certainly was not holding a breeding territory.

4. *Aggressive interaction and (?) attempted copulation with young male, Franklin Canyon, Santa Monica Mts., 23 April 1968, ca. 09:30.* As I walked the ridgetop trail mentioned in the second incident, a male *C. anna* chased a second bird from his territory ca. 50 m away, up towards the ridgetop. The latter bird flew into a thick, low clump of *Salvia* bushes, and the territorial male was apparently unable to get to it. The male perched ca. 0.5 m away and sang at high intensity for ca. 15 s, then flew to a perch ca. 1.5 m away on the other side of the *Salvia* and sang again for 25–30 s; then he flew to still a third perch and again gave high-intensity song. This entire performance was repeated several times, the territorial male effectively making four circuits of the second bird's refuge, giving high-intensity song nearly continuously except for brief flights between perches. Finally, the second

bird attempted to flee but was knocked down by the male after less than 1 m, and flew into a more open low shrub (at which point I was able to identify it as a young male *anna*, with scattered red feathers in crown and throat). The adult male gave a brief shuttle display, then dropped down and perched ca. 15 cm from the young bird and sang intensely at it for ca. 10 s. He next flew to the young male and attempted to land on its back, presumably to attempt copulation; simultaneously the latter attempted to fly again. Both birds tumbled out of sight into the vegetation, whence I heard violent-sounding body contact and "brrt" notes for several seconds. The young bird then escaped, streaking off under several shrubs, then up and out of sight over the ridgetop. A moment later the adult male hovered up, singing and evidently looking all about. Failing to spot the young bird, he flew directly to a song perch of his territory and sang for ca. 15 s, afterward dropping to feed at a *Ribes* bush.

ANALYSIS

These four display sequences appear to represent a gradient from what I consider to be a fairly typical copulation sequence in the breeding season, through two copulations with increasing proportions of aggression present, to an essentially aggressive interaction in which elements of sexual behavior were present. In fact, the male in sequence 4 probably did attempt to copulate with the young bird, but its response was to attempt to escape or fight rather than submit (as finally did the almost equally reluctant female in sequence 3; this female was probably postbreeding and therefore sexually unreceptive, but apparently finally submitted to copulation in order to escape the male). These sequences, especially the latter two, suggest that adult males may remain sexually active longer than females, and that sexually active males may attempt to copulate with any other hummingbird that they can force to remain perched at close quarters.

I have observed two other copulations in Anna's Hummingbirds in circumstances similar to sequence 1 above, and four other incidents that I thought were copulations but was able to watch less adequately owing to the dense vegetation where they occurred. Assuming that these all represented copulations, several points stand out: all occurred well away from the territories of breeding males and were preceded by lengthy chases (leaving aside the evidently atypical sequence 3 above). In four of the eight cases, copulation occurred within 30 m, and twice within 10 m, of the nest site of the female. The two most prominent displays given were shuttle displays (six of eight

cases) and high-intensity song (all eight cases). In only two instances were dive displays given near the site of copulation, and in each case they were followed by shuttle displays and/or high-intensity song, prior to the copulations themselves. I never observed the initial contact of the male and the female, but in at least four cases circumstances indicated that it occurred on the male's breeding territory (cf. sequence 1). Conversely, in over 80 h of intensive timed observations on male territories, I never saw shuttle displays or anything resembling copulation on the territories (although I heard several examples of high-intensity song similar to the incident reported in sequence 4 above). Moreover, dive displays, so infrequently seen prior to copulation, were observed frequently in and near the core areas of the breeding territories. I turn now to events in the males' territories to clarify the functions of the dive display and to attempt to determine how courtship sequences typically start.

THE DIVE DISPLAY: CONTEXT AND FUNCTION

In 56 h of timed observations of a single marked Anna's Hummingbird on breeding territory, I was able to observe closely 64 bouts of dive displays, comprising 142 dives. In most cases I could determine the circumstances leading up to the dive display, the object of the display, the number of dives given, and the subsequent behavior of the male and the display object (Tables 1 and 2).

In general, dive displays are given mostly in the core area of the territory, less often in the buffer zone, and rather seldom beyond it. I may have underestimated the number of dives given outside the territory, however, either due to confusion with other males or because the distances involved were too great to permit detection of the squeak. Certainly a few copulation sequences involved dives, usually at sites closer to the female's nesting area than to the male's territory (see above). Dive displays were directed more often toward *C. anna* than to any other hummingbird, although this may reflect merely the fact that for most of its breeding season, this was the only hummingbird species in the chaparral (Stiles 1973). The number of dives per display bout averaged highest in the core area, declining with distance away from it (Tables 1, 2).

Male Anna's Hummingbirds gave the dive display most frequently at other hummingbirds that were perched or hovering inside the bushes of *Ribes speciosum*, their main food flower during the breeding season (Stiles 1973). Except for birds feeding low in *Ribes* bushes virtually all dive displays in the core area of

TABLE 1. Locations and objects of 64 bouts of dive displays by a marked male Anna's Hummingbird in 56 h of timed observations during February–May 1969, Franklin Canyon, Santa Monica Mountains.

	No. bouts	No. dives	Dives/Bout
A. Location of dive displays			
Core area of territory	45	118	2.62
Buffer zone of territory	16	21	1.41
Outside territory	3	3	1.00
B. Objects of dive displays			
<i>Calypte anna</i> : adult ♂	8	18	2.25
adult ♀	8	21	2.63
juvenile	3	9	3.00
not determined	7	22	3.14
Total <i>C. anna</i>	26	70	2.69
Other hummingbird species	10	25	2.50
Other birds (nine spp.) ^a	20	35	1.75
Humans	4	7	1.75
No discernible object	4	6	1.50

^a *Aphelocoma coerulescens*: 6 bouts, 13 dives; *Carpodacus mexicanus* and Rufous-sided Towhee (*Pipilo erythrophthalmus*), 3-5; Hooded Oriole (*Icterus cucullatus*), 2-3; Bewick's Wren (*Thryomanes bewickii*), Brown Towhee (*Pipilo fuscus*), Mockingbird (*Mimus polyglottos*), White-crowned Sparrow (*Zonotrichia leucophrys*), each 1-2; Audubon's Warbler (*Dendroica coronata auduboni*), 1-1.

the territory were given toward perched birds. Moreover, dive displays were directed toward adult males and juveniles, as well as females, to all appearances indiscriminately. The sight of another hummingbird perched in or near his territory may be the stimulus that releases the dive display in breeding *C. anna* males. The most frequent reaction of the recipient hummingbird was to flee the territory, almost always hotly pursued by the displayer; the former usually attempted to flee while the latter was in the hover-sing or climb phases of the dive display and so gains ground—but very few hummingbirds escaped unchased.

TABLE 2. Activities of object of display immediately prior to and following receiving dive displays by a marked male Anna's Hummingbird, spring 1969.

	Recipient of display				Σ	
	<i>C. anna</i>	Other hummingbird	Other birds	Humans		
Activities before receiving displays						
Feeding at <i>Ribes</i>	2	2	2	0	6	
Perched in <i>Ribes</i> (usually following feeding)	8	4	4	0	16	
Perching or standing conspicuously in core area	4	1	5	4	14	
Perching low in core area	4	2	2	0	8	
Perching in buffer zone	5	1	1	0	7	
Perching outside territory	3	0	0	0	3	
Activities after receiving displays						
Ignore	} male usually returns to perch	0	1	6	2	9
Hide in vegetation		5	3	8	0	16
Flee; chased by male	20	6	2	0	28	
Flee; not chased	1	0	4	0	5	
Write notes	0	0	0	3	3	
Totals	26	10	20	5		

The fact that a male Anna's Hummingbird will give the display towards other birds perched conspicuously in his territory emphasizes the aggressive and rather indiscriminate nature of this display. Various birds that were displayed at, especially Scrub Jays (*Aphelocoma coerulescens*), which are relatively large and which perched conspicuously atop tall shrubs. Usually, the dive-bombed bird would seek cover, but if it ignored the displays (as did most House Finches, *Carpodacus mexicanus*, when they were feeding on *Ribes* flowers), the male hummingbird would soon desist. He occasionally displayed at me when I stood conspicuously on the skyline in his core area—allowing me an excellent opportunity to perceive the visual and auditory effects of the display!

These observations prompt me to interpret the dive as basically an aggressive display, intended to intimidate a perched bird (normally a hummingbird) in the male's territory, generally forcing it to flee. Although male Anna's Hummingbirds displayed relatively and absolutely more often to hummingbirds than to other birds, I saw little indication that they displayed selectively to females of their species. Therefore, although the display may play some role early in a courtship interaction (see below), I believe that it is not a courtship display as such.

The other reaction of a male *anna* to a hummingbird that invaded his breeding territory was to chase it without further ado; indeed, chases were the most frequent means of territorial defense (Table 3). Chases were directed most often at other male *anna*, but this prob-

TABLE 3. Locations and activities of all birds chased by a marked male Anna's Hummingbird on breeding territory during 56 h of timed observations, spring 1969.

Location where chase originated: Activity of bird subsequently chased	Identity of bird chased						Other hummingbird species	Other bird species
	<i>C. anna</i>				Total			
	Ad. ♂	Ad. ♀	Juv.	Indet.				
1. Core area of territory								
<i>Ribes</i> spp.: Feeding	11	9	10	4	34	11	2	
<i>Ribes</i> spp.: Perching	7	4	5	3	19	4	2	
Conspicuous perch: Perching	9	1	4	1	15	2	7	
Low perch: Perching	3	2	5	2	12	2	0	
Indeterminate: Flying	7	7	6	6	26	8	4	
Total—Core area	37	23	30	16	106	27	15	
2. Buffer zone of territory								
<i>Ribes</i> : Feeding or perching	2	1	3	1	7	2	0	
Conspicuous perch: Perching	6	2	1	5	14	1	0	
Indeterminate: Flying or perching	5	4	5	16	30	1	1	
Total—Buffer zone	13	7	9	22	51	4	1	
3. Outside territory: Flying or perching								
4. <i>High over territory</i> : Flying	0	0	0	33	33	7	0	
5. <i>Undetermined</i> : Flying or perching	9	4	4	23	40	5	0	
Total chases	306	63	35	44	104	246	44	16
Total display flights (bouts)	56	8	8	3	7	26	10	20

ably reflected frequency of invasion rather than any selectivity of response. Flying hummingbirds in the territory were invariably chased, and perched hummingbirds were chased at least as often as they were displayed at. I believe that whether a male will chase or display at a trespassing hummingbird depends upon whether it perches or flees at his approach. When a male detects a trespasser he is usually on a song perch; he then flies directly at the other bird, singing or chattering. The subsequent course of the interaction is determined by the trespasser's behavior.

Flying non-hummingbirds in the territory were generally ignored. However, one male repeatedly chased two Scrub Jays that flew regularly along the hillside between a fruiting olive tree and their nest in a large bush just beyond his territory. This species frequently preyed upon hummingbird nests, and was regularly mobbed by female *anna*; male *anna*, which took no interest in nesting, seemed to respond more strongly to these jays as well. The male also twice chased Red-tailed Hawks (*Buteo jamaicensis*) and once an American Kestrel (*Falco sparverius*) flying low over his territory.

Male *anna* ignored non-hummingbirds outside their territories, but sometimes chased or displayed at other hummingbirds. Similarly, the only birds chased when they were flying high over the territory were other hummingbirds. When a male took off after a chase in progress passing above, he almost invariably seemed to choose to pursue the bird being

chased rather than the chaser. This occasionally resulted in the male's "taking over" the chasing of a female, perhaps resulting in copulation.

DUMMY EXPERIMENTS

The purpose of these experiments was to determine whether male Anna's Hummingbirds gave certain displays selectively to other hummingbirds depending on species or sex. The results (Table 4) strongly suggest that they do not: all displays were given with similar frequencies to all three dummies. Somewhat surprisingly, the dive display was given only slightly more often than was the shuttle display, and in about the same frequencies as were high-intensity singing and copulation attempts. Moreover, the males attacked the dummies physically at least as often as they attempted copulation; indeed, the Rufous Hummingbird dummy was severely mauled by one male when I was slow to rescue it. Usually one or more dive displays were given first, followed by high-intensity singing and/or shuttle displays, or directly by an attack on the dummy. Often a copulation attempt followed, and the male usually ended by attacking the dummy. In four cases the male attacked the dummy immediately (twice with dummy 1, once each with 2 and 3; one male attempted copulation with dummy 3 with no preliminaries). Usually after interacting vigorously for 2 to 5 minutes with the dummy, a male would return to his song perch and ignore it thereafter, even if I moved the dummy to another

part of the territory. Presentations of the dummy two to five days later normally elicited much weaker responses. Some males never responded to the dummies at all; probably some movements on the dummy's part would have been required to elicit a response.

COURTSHIP IN THE ANNA'S HUMMINGBIRD

I will now try to reconstruct how courtship probably functions in the Anna's Hummingbird. I say "probably" because I have never witnessed a complete courtship from start to finish. I believe that this was simply because courtships are initiated on the territory of the adult male, but are completed only after a long chase, during which it is impossible to follow such tiny, swift-flying birds. Moreover, I hypothesize that such a chase may be essential for a successful courtship.

Courtship sequences are probably started by a female's flying to a male's territory and attempting to feed there. Evidence for this is circumstantial but strong (see above); certainly feeding is the most frequent activity on males' territories, and most chases of, or displays at, females follow such attempts (Tables 1, 2, 3). This makes it likely that females use the richness of a male's *Ribes* supply as a cue to his proficiency in territorial defense. Males with *Ribes*-rich territories spend more time in territory defense and are more rapidly replaced should they disappear, than males on poorer territories (Stiles 1973). In any case, I know of no evidence that males leave their territories to seek out females. In many hours of watching in female nesting areas, I rarely saw males—and when I did they were either visiting flowers, or arrived already in pursuit of a female, coming from the vicinity of their breeding territories (as in sequence 1 above).

Arriving on a male's territory, a female probably attracts his attention as she feeds from his flowers. At his approach she may either perch, thereby eliciting dive displays, or flee, thereby causing an immediate chase. Except when she escapes by disappearing low into dense shrubbery, a female will normally be chased as she leaves the territory. My data indicate that trespassing females are slightly more likely than adult males to perch and draw dive displays than to flee immediately (cf. Tables 1, 3).

The length of the resulting chase is variable, but I suspect that whenever possible the female tries to prolong it and lead the male towards her nesting area (where she will have already started her nest). It is probably advantageous for her to do this, and not only because only a vigorous, strongly motivated male might be

TABLE 4. Responses of *C. anna* males to mounted dummies (1 = male *C. anna* in singing position; 2 = female *C. anna* in copulatory position; 3 = female *S. rufus* in erect perched position) presented to them on their breeding territories, March–April 1969.

Dummy #	Number of presentations in which given response was observed						Total number of presentations of dummy	
	Ignore	Ap-proach	Dive display	Hi-int. song	Shuttle display	At-tempt copulation		Attack
1	2	8	6	6	3	5	7	10
2	3	7	5	5	3	5	5	10
3	2	7	5	4	4	4	6	9

likely to pursue her for several hundred meters. It may also represent a means of manipulating the degree of aggressive vs. sexual motivation of the male himself. It is highly probable that the male's aggressiveness is highest when he is on territory, and declines with distance therefrom; such situations occur in many other animals (e.g., Brown 1963, Willis 1967). The dummy experiments suggest that aggression may override sexual motivation in the male on territory; by submitting to copulation there the female is probably as likely to be attacked as approached sexually. Indeed, the copulation of sequence 2 above, which occurred after only a short chase and only ca. 150 m from the male's territory, involved a much stronger aggressive component than did sequence 1, which in my experience was more typical, and involved a much longer chase. By leading the male to her own "home ground," the female may increase her chances of getting into a copulation rather than a fight—or of defending herself successfully or rejecting the male should she so decide.

The male, on the other hand, might best try to make the chase as short as possible, both to minimize his own expenditures of time and energy and to reduce the female's chances of rejecting him. When the chase ends with the female perched low in vegetation, the male should try to keep her from flying again. This may best be accomplished by such close-range displays as the shuttle, or high-intensity singing from a nearby perch. A dive display at this point would increase the distance between the two birds and facilitate the female's escape; perhaps this is why I so seldom saw dive displays immediately preceding copulation. Whether the male elects to use the shuttle display or perch and sing after forcing the female down, may depend upon his assessment of her readiness to fly again. The shuttle display, by occupying much of the airspace above the female, may be a more effective inhibitor of further flight. If the female seems willing to remain perched, high-intensity song may be

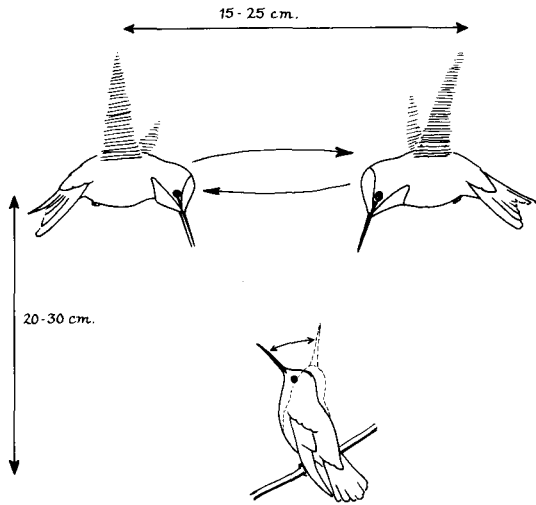


FIGURE 5. The shuttle display of *Calypte anna*.

most effective in inducing her to remain while he attempts copulation. In nearly all copulation sequences I have witnessed, high-intensity song by the male immediately preceded copulation.

Even when the copulation takes place well away from the male's territory, there is evidently a strong aggressive component to his behavior. It may be significant in this regard that the female always keeps her bill pointed right at the male during the close-range displays. This "sword point" posturing may serve to keep the male at his distance through a period of intense displaying, perhaps giving the female a last chance to reject or escape him. It may also serve to tip the male's motivation more from the aggressive toward the sexual.

The arguments presented here regarding display sequences are summarized in Figure 6. Although this scenario is largely hypothetical, it seems the only one able to fit all the facts available to me. Several points should be emphasized, the first being the similarity between aggressive and sexual behavior in male *C. anna*. It is difficult to call any of the displays mentioned here unequivocally aggressive or sexual, although the dive display seems more aggressive in motivation than the shuttle or high-intensity song, which appear to have a stronger sexual component. The dive display may nevertheless function early in courtship, allowing a female to decide whether to permit a male to chase her or to try to elude him in the vegetation. Despite their aggressive component, the displays most crucial in courtship as such are the shuttle and the high-intensity song. They are given close to the female immediately preceding copulation, and in effect represent the final criteria upon which her

choice must be based. The fact that the female always seems to land in dense vegetation probably has more to do with enabling her to reject the male at the last moment by escaping into it, than with simply avoiding interference or predation. Should she be forced down in the open, she may be unable to avoid copulation (e.g., sequence 3 above). Finally, the female's role in determining the course of the interaction is extremely important. She largely determines where the copulation will take place; her behavior can elicit certain displays from the male, and there are several points at which she can, under most circumstances, break off the interaction and reject his advances.

ONTOGENY OF DISPLAYS

Some information on the ontogeny of displays in Anna's Hummingbirds is of interest because of the part played by learning and practice. From a very early age (as little as a few days out of the nest, with bills not yet full-grown), young males begin to spend a great deal of time singing. Their song at first is an unstructured gurgling, often continued for minutes at a time and usually delivered from a low, inconspicuous perch. Over weeks or months, the song gradually becomes more structured. I have not been able to trace fully the crystallization of the song because most juveniles desert the chaparral in late spring, when temperatures rise and flowers become scarcer (cf. Stiles 1973). At this time their songs are still largely unstructured, and they sing only occasionally over the summer. By the next fall as the breeding season approaches, young males have mostly completed the postjuvinal (first pre-basic) molt except for the crown and gorget, and are singing fairly mature-sounding songs. However, some first-year males, doubtless the products of very late nestings, are recognizable as such by both plumage and song well into the breeding season. Such birds may not acquire the full red gorget and crown, or fully adult song, until January or February; this may make it difficult or impossible to obtain a breeding territory during their first year (Stiles 1973).

As with song, the dive display appears early in the post-fledging period of young males, often while they are still associating with their nestmate in the first week or two out of the nest (cf. Ortiz-Crespo 1967, Stiles 1973). The earliest dives are unstructured and variable, the young male simply rising a few meters and making a shallow dive at the other bird. There are no distinct dive phases, no squeak at the bottom, and no suggestion of sun-orientation. Over the succeeding weeks the dive gradually becomes higher, a distinct hover-sing phase

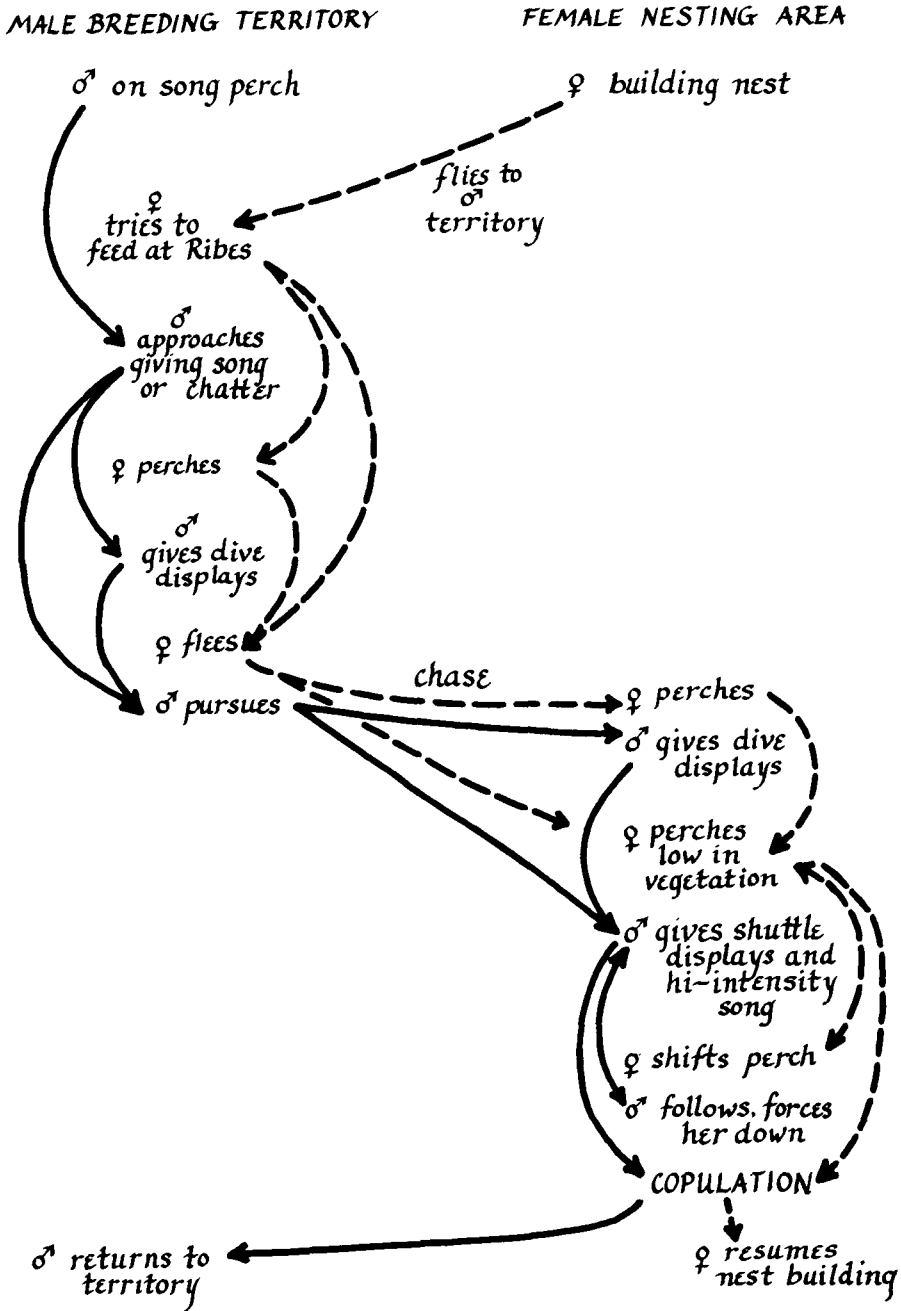


FIGURE 6. Hypothesized courtship sequence of the Anna's Hummingbird.

appears (though the song given is still of the gurgly type), and vocal sounds may be given during the dive. However, the sound at the bottom of the dive is only a muted "whiff"; this does not change until the young bird acquires adult rectrices during its first molt. I have never seen a recognizable shuttle display in very young male *C. anna*. Aggressive displays may appear or mature earlier than those used in courtship, because young males will have to defend territory well before they are likely to engage in courtship (Stiles 1973).

DISCUSSION

SELECTIVE PRESSURES ON ANNA'S HUMMINGBIRD COURTSHIP BEHAVIOR

The courtship system of this species is evidently the result of various selective pressures, some acting mainly on males, others on females. The considerable degree of spatial segregation of the sexes during breeding is probably mutually advantageous in reducing competition for nectar. During the peak of the winter breeding season, only *Ribes speciosum*

flowers are available in natural habitats. Spatial segregation doubtless benefits females in reducing potential interference from males in nesting attempts. During nearly all of the breeding season, *C. anna* is the only resident hummingbird in chaparral (although *C. costae* may be invading in recent years; Wells and Baptista 1979).

Despite this spatial segregation, female Anna's Hummingbirds frequently trespass on male breeding territories (cf. Tables 1-3). They are nearly always seen trying to feed at a male's *Ribes* supply, and males with more *Ribes* seem to attract more female poachers (see above and Stiles 1973). The females are usually chased and displayed at firsthand, and usually do not succeed in obtaining much nectar; I doubt that these visits are crucial to the females' energy budgets. Moreover, *Ribes* is often as common in oak woodlands as in hillside chaparral. It is furthermore unlikely that these females are trying to solicit courtship directly: most of the chases following such invasions are too short (as judged by the duration of the males' absences from their territories) to permit a complete courtship sequence as described above. I suspect that many such visits are to assess the quality of the male's *Ribes* supply, and the vigor of his defense of it. These might influence a female's choice of a male with whom to mate when she is ready. One would therefore expect a female to visit various male territories at this stage. As I did not mark females, I have little direct evidence that this happens; however, one female whom I could recognize was seen on three or four different territories between 18 and 23 March 1968.

If the flowers on a male's territory are a factor in mate choice by females, then males should compete most strongly for flower-rich territories, and the "best" males (in terms of proficiency in territorial defense) should finally control these territories. Although circumstantial, the available data for Anna's Hummingbird are consistent with this hypothesis (Stiles 1973). A considerably better-documented case of female choice based upon the number of flowers in the males' territories is that of the Fiery-throated Hummingbird (*Panterpe insignis*; Wolf and Stiles 1970). These males form longer-lasting associations with females (which greatly facilitates analysis); the male with the most flowers associates with more females, whose eggs he probably fertilizes. In *C. anna* and *Panterpe*, females may choose to mate with any male on a superior territory. In effect, they will select the end product of competition among males. This phenomenon may be widespread in species with promiscuous mating systems (including leks) where contact be-

tween the sexes is fleeting and territory quality may be more easily assessed than any subtle quality of the male himself (cf. Hogan-Warburg 1966, Kruijt and Hogan 1967, Stiles and Wolf 1979).

The resultant strong selection for vigorous territorial defense by males probably makes it advantageous for a male to attack any trespassing hummingbird; this in turn may favor any tendency for a female to lead a male away from his territory for copulation (see above). Conversely, it is probably advantageous for a male to attempt copulation with any hummingbird he can chase to earth; the added expense in time and energy of a copulation attempt, following a lengthy chase, is probably less than the potential benefits of paternity. A female, with her much higher parental investment, is under much stronger pressure to choose correctly. It is probably to her advantage to prolong or complicate the courtship sequence in order to allow maximum opportunity for accepting or rejecting the male. This is probably the principal selective value of such behaviors as leading the male on a long chase, perching low in dense vegetation, and "tracking" the displaying male with her bill.

For males, the ideal courtship sequence would probably be brief and energetically economical, and any behavior tending to shorten the sequence might be selected for. The shuttle display might be an example, as it appears to inhibit further flight by the female.

Another important component of female choice is the avoidance of mating with males of other hummingbird species. For this reason, those male behaviors most effective in inhibiting female flight should also be those that emphasize species-specific, as well as (or even more than) individualistic characters. Thus, high-intensity song and a shuttle display involving song, as well as the associated postures that show the red crown and gorget to maximum effect (Fig. 2c) are probably the most important such displays in Anna's Hummingbird. They are probably also the most critical displays as isolating mechanisms, occurring as they do at close quarters immediately before copulation. However, at an earlier stage the dive display could also function as an isolating mechanism, even though from a male's point of view its function is almost wholly aggressive. The species-specific form and sounds of the dive display therefore might have resulted from selection by females, who might reject males with inappropriate dive displays before the courtship sequence "proper."

The similarity between aggressive and courtship displays of male *C. anna* may also be a widespread phenomenon in humming-

birds. The only other species to receive detailed study in this regard are two members of the genus *Phaethornis*, members of a different subfamily and with lek social systems (Snow 1974, Stiles and Wolf 1979). In these species no appreciable differences exist between male-male and male-female encounters except that females may not give certain displays (or give them less frequently), and females evidently signal their sex by staying perched and allowing males to mount, whereas a male will leave the perch.

OCCURRENCE AND EVOLUTION OF DIVE AND COURTSHIP DISPLAYS IN HUMMINGBIRDS

An early analysis of hummingbird displays was put forth by Wagner (1954). A more objective and detailed scheme is that of Ruschi, who has published an extensive body of comparative information on hummingbird displays, including a general summary of his observations. Ruschi (1962) recognized five phases of courtship in hummingbirds: approach, pursuit, presentation, exhibition, and copulation. According to Ruschi, the *approach phase* involves the male's approaching and "installing himself" in the female's nesting area, giving song and flight displays, sometimes over a period of weeks; the first male into the area chases out others. In the *pursuit phase* the male aggressively attacks and chases the female, who flees. The *presentation phase* involves flight displays, often dives or pendulum flights (*vôo de libração*). In the *exhibition phase* the male makes short and rapid oscillations in flight before or around the female, exhibiting some brightly colored part of the plumage in a highly species-specific manner. Dull-colored species in particular may give distinctive vocal or nonvocal sounds at this point as well. *Copulation* occurs with the female perched, the male hovering over and descending onto her back where he clings, half perched and half hovering; cloacal contact lasts ca. 2 s.

Much of Ruschi's scheme seems applicable to the courtship of Anna's Hummingbird; other parts do not, but the difference may be one of interpretation rather than substance. This applies especially to the approach phase, in which the general behavior of males as described sounds very like that of *C. anna* males establishing breeding territories. On the other hand, I have seen no sign in *C. anna* (or in any other hummingbird species I have studied) that the male approaches the female—the reverse is invariably the case. Theoretical considerations also indicate that it should be the males who establish mating stations and are approached by females: in a promiscuous mat-

ing system there is no advantage for a male to so confine his attention to a single female (cf. Orians 1969). The potential interference of a male in the nesting attempt would seem to make such a course disadvantageous to a female as well. One possible reason for the discrepancy is that Ruschi evidently made many of his observations under aviary conditions, where, among many hummingbirds present, there were only one or two pairs of each species. Moreover, he noted that in nature this "frequenting of the nesting area" may actually bring the male only to within 100 m of the nest site (e.g., in *Calliphlox*). This degree of separation may easily occur in *C. anna*, although usually the distances are greater. Another difference involves the placement of the dive display, which Ruschi (1962) considered part of the presentation phase. In *C. anna* (and in North American hummingbirds in general) the dive usually precedes, rather than follows, the chase.

Aside from these differences in order and interpretation, Ruschi's scheme applies quite well to the courtship of Anna's Hummingbird. The shuttle display and high-intensity song correspond exactly with the exhibition phase, and Ruschi's description of copulation is supported by my own observations. This indicates that the major elements of courtship in *C. anna*, including the chase of a female by a male, also occur in many other hummingbird species, at least in the subfamily Trochilinae. In the Phaethorninae (the hermits) there appears to be no regular pursuit phase, and there is no clear distinction between presentation and exhibition. This doubtless reflects the lek social systems of most hermits and the density of lek vegetation, such that displays and copulations are focused around the males' song perches (cf. Skutch 1951, 1964; Snow 1973, 1974; Stiles and Wolf 1979).

In other North American hummingbirds (i.e., those occurring well north of Mexico, in the genera *Archilochus*, *Calypte*, *Selasphorus*, and *Stellula*), dive and shuttle displays corresponding to those of *C. anna* also occur (Stiles, unpubl.; Ortiz-Crespo, unpubl.). The displays of few Central American species have been described, but dive displays seem to be infrequent, having been noted only in species of *Selasphorus* (Wolf 1976), *Philodice* (Feinsinger 1977), *Florisuga* and *Popelairia* (pers. observ.); they may also occur in *Lophornis* (cf. Ruschi 1962). The highland Green Violetear (*Colibri thalassinus*) also has a rudimentary dive display (pers. observ.). All of these species generally occupy open habitats: the outside of forest canopy, clearings and meadows, forest edge. Tropical species of dense vegetation,

either forest interior or second growth, are more likely to give "static" displays, including song, from a perch (Skutch 1931). Even in those North American species found in woodland habitats, male breeding territories are at clearings and edges (Saunders 1936, Bent 1940, Pitelka 1951a, b; Legg and Pitelka 1956, Stiles 1973).

The extent to which dive displays enter into courtship may differ among species, but I suspect that the primary motivation of the displaying male is aggressive, rather than sexual, in most cases (cf. Pitelka 1942). Ritualized dive displays may have evolved from aggressive behavior, and their sexual significance, if any may have been acquired secondarily. In several hummingbird species not known to have ritualized dive displays (e.g., the Fork-tailed Woodnymph, *Thalurania furcata*; Rufous-tailed Hummingbird, *Amazilia tzacatl*; *Panterpe insignis*) I have seen males attempting to expel persistent intruders (often large, dominant hummingbirds) from their territories, resort to diving at the latter. Such dives are typically short and shallow, variable in height, angle, and direction. Often when passing close by the other, the diving bird will vocalize aggressively. Such "aggressive dive-bombing" sometimes occurs in a still more rudimentary form in female hummingbirds as they mob a potential avian predator or another hummingbird near their nests. From such "intimidatory" measures have doubtless evolved the elaborate dive displays of many species.

This hypothetical evolutionary scenario is paralleled by the development of dive displays in the individual. The early dives of young Anna's Hummingbirds resemble the variable, rudimentary dives of, say, woodnymphs; with time and practice the young bird's dives come to resemble those of the adult. The importance of practice in the ontogeny of the dive display, as well as of song, suggests that learning is involved. This raises the possibility that local "dive dialects" as well as song dialects might develop; an analogous example involving a flight display occurs in a lark (Payne 1973). Such a process could explain some of the differences between my description of the dive and that of Wells et al. (1978), as well as some of the variation in sonograms presented by Wells et al. (1978), Mirsky (1976) and me. Of particular interest is the aberrant song which is characteristic of an isolated population of Anna's Hummingbird on Isla Guadalupe, Mexico (Mirsky 1976). This rambling and unstructured song bears a striking resemblance to the gurgling song of very young males. This suggests that young males must hear adult

males at some stage in order to "crystallize" their song. However the Isla Guadalupe population was founded, these hummingbirds do not now have access to normal adult male songs, and the males continue to sing a juvenile-type song throughout life.

In conclusion, I emphasize that the study of hummingbird courtship is still in its infancy. We are still far from being able to make reliable generalizations about the evolution of display types and courtship sequences, because many key displays have either gone unobserved (or unappreciated), or have been seen only in captive birds, where their form may be aberrant and their true significance unclear. Since aggressive behavior and chases are likely to figure in the courtship of most or all hummingbird species, and many displays typically occur in dense vegetation, determining just how the courtship sequence actually functions may all too often be a procedure involving the fitting together of fragmentary observations. Gathering enough fragments often requires long acquaintance with the bird in the field!

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LITERATURE CITED

- BANKS, R. C., AND N. K. JOHNSON. 1961. A review of North American hybrid hummingbirds. *Condor* 63:3-28.
- BAPTISTA, L. F., AND M. MATSUI. 1979. The source of the dive-noise of the Anna Hummingbird. *Condor* 81:87-89.
- BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U. S. Natl. Mus. Bull. 176.
- BROWN, J. L. 1963. Aggressiveness, dominance, and social organization in the Steller's Jay *Cyanocitta stelleri*. *Condor* 65:460-484.
- CALDER, W. A. 1971. Temperature relationships and the nesting of the Calliope Hummingbird. *Condor* 73:314-321.
- CALDER, W. A. 1974. The thermal and radiant environment of a winter hummingbird nest. *Condor* 76:268-273.
- CALDER, W. A., AND J. BOOSER. 1973. Hypothermia of Broad-tailed Hummingbirds during incubation in nature with ecological consequences. *Science* 180:751-753.
- CARPENTER, F. L. 1978. A spectrum of nectar-eater communities. *Am. Zool.* 18:809-819.
- EWALD, P., AND F. L. CARPENTER. 1978. Territorial responses to energy manipulation in the Anna Hummingbird. *Oecologia* 31:277-292.
- FEINSINGER, P. 1977. Notes on the hummingbirds of

- Monteverde, Cordillera Tilaran, Costa Rica. *Wilson Bull.* 89:159-164.
- GASS, C. L. 1979. Territory regulation, tenure, and migration in Rufous Hummingbirds. *Can. J. Zool.* 57:914-923.
- HAMILTON, W. J. III. 1965. Sun-oriented display of the Anna Hummingbird. *Wilson Bull.* 77:38-44.
- HECKENLIVELY, D. B. 1970. Song in a population of Black-throated Sparrows. *Condor* 72:24-36.
- HOGAN-WARBURG, A. J. 1966. Social behavior of the Ruff, *Philomachus pugnax* (L.). *Ardea* 54:109-229.
- HORVATH, O. 1967. Seasonal differences in Rufous Hummingbird nest heights and their relation to nest climate. *Ecology* 45:235-241.
- KODRIC-BROWN, A., AND J. H. BROWN. 1979. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* 59:285-296.
- KRUIJT, J. B., AND J. A. HOGAN. 1967. Social behavior on the lek in the Black Grouse, *Lyrurus t. tetricus*. *Ardea* 55:203-240.
- LEGG, L., AND F. A. PITELKA. 1956. Ecological overlap of Anna and Allen hummingbirds nesting at Santa Cruz, California. *Condor* 58:393-405.
- LYNCH, J. F., AND P. L. AMES. 1970. A new hybrid hummingbird, *Archilochus alexandri* × *Selasphorus sasin*. *Condor* 72:209-212.
- MIRSKY, E. N. 1976. Song divergence in hummingbird and junco populations on Guadalupe Island. *Condor* 78:230-235.
- ORIAN, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103:589-603.
- ORTIZ-CRESPO, F. I. 1967. Interactions in three sympatric species of California hummingbirds in a planted area containing melliferous flowering vegetation. M.A. thesis, Univ. of California, Berkeley.
- PAYNE, R. B. 1973. Wingflap dialects in the Flappet Lark. *Ibis* 115:270-274.
- PITELKA, F. A. 1942. Territoriality and related problems in North American hummingbirds. *Condor* 44:189-204.
- PITELKA, F. A. 1951a. Ecologic overlap and interspecific strife in Anna and Allen hummingbirds. *Ecology* 32:641-661.
- PITELKA, F. A. 1951b. Breeding seasons of hummingbirds near Santa Barbara, California. *Condor* 53:198-201.
- PRICE, M. V., AND N. M. WASER. 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *Nature* (Lond.) 277:294-296.
- PYKE, G. H. 1978. Optimal foraging in hummingbirds: testing the marginal value theorem. *Am. Zool.* 18:739-752.
- RODGERS, T. L. 1940. The dive note of the Anna Hummingbird. *Condor* 42:86.
- RUSCHI, A. 1962. As diferentes fases na parada nupcial dos trochilídeos. *Bol. Mus. Biol. Prof. Mello-Leitao* 33:1-4.
- SAUNDERS, A. A. 1936. Ecology of the birds of Quaker Run Valley, Allegany State Park, N.Y. N.Y. State Mus. Hbk. 16:1-174.
- SKUTCH, A. F. 1931. Life history of Reiffer's Hummingbird (*Amazilia tzacatl*) in Panama and Honduras. *Auk* 48:481-500.
- SKUTCH, A. F. 1951. Life history of Longuemare's hermit hummingbird. *Ibis* 93:180-195.
- SKUTCH, A. F. 1964. Life histories of hermit hummingbirds. *Auk* 81:5-25.
- SMITH, W. J. 1977. The behavior of communicating. Harvard Univ. Press, Cambridge, MA.
- SMITH, W. K., S. W. ROBERTS, AND P. C. MILLER. 1974. Calculating the nocturnal energy expenditure of an incubating Anna's Hummingbird. *Condor* 76:176-183.
- SNOW, B. K. 1973. The behavior and ecology of hermit hummingbirds in the Kanaku Mts., Guayana. *Wilson Bull.* 85:163-177.
- SNOW, B. K. 1974. Lek behavior and breeding of Guy's Hermit hummingbird *Phaethornis guy*. *Ibis* 116:278-297.
- STILES, F. G. 1971a. Time, energy and territoriality of the Anna Hummingbird (*Calypte anna*). *Science* 171:818-821.
- STILES, F. G. 1971b. On the field identification of California hummingbirds. *Calif. Birds* 2:41-54.
- STILES, F. G. 1973. Food supply and the annual cycle of the Anna Hummingbird. *Univ. Calif. Publ. Zool.* 97:1-109.
- STILES, F. G., AND L. L. WOLF. 1979. The ecology and evolution of lek mating behavior in the Long-tailed Hermit hummingbird. *Ornithol. Monogr.* 27:1-78.
- WAGNER, H. O. 1954. Versuch einer Analyse der Kolibrizal. *Z. Tierpsychol.* 11:182-212.
- WASER, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59:934-944.
- WELLS, S., R. A. BRADLEY, AND L. F. BAPTISTA. 1978. Hybridization in *Calypte* hummingbirds. *Auk* 95:537-549.
- WELLS, S., AND L. F. BAPTISTA. 1979. Displays and morphology of an Anna × Allen hummingbird hybrid. *Wilson Bull.* 91:524-532.
- WILLIAMSON, F. S. L. 1956. The molt and testis cycles of the Anna Hummingbird. *Condor* 58:342-366.
- WILLIS, E. O. 1967. The behavior of Bicolored Antbirds. *Univ. Calif. Publ. Zool.* 79:1-127.
- WOLF, L. L. 1976. Avifauna of the Cerro de la Muerte region, Costa Rica. *Am. Mus. Nat. Hist. Novit.* 2606.
- WOLF, L. L., AND F. G. STILES. 1970. Evolution of pair cooperation in a tropical hummingbird. *Evolution* 26:736-750.

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RECENT PUBLICATION

Suggested Practices for Raptor Protection on Power Lines/The State of the Art in 1981.—Richard R. Olen-dorff, A. Dean Miller, and Robert N. Lehman. 1981. Raptor Research Report No. 4, Raptor Research Foundation, Inc. 111 p. Paper cover. Source: Raptor Research Found., Dept. of Veterinary Biology, University of Minnesota, St. Paul, MN 55101. Hundreds of eagles and lesser numbers of other raptors have been electrocuted as a result of perching on power lines, mostly in the western U.S. During the past decade, concern over this situation has engendered research on the biological and the engineering aspects of

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