

DISPLAY BEHAVIOR OF MALE CALLIOPE HUMMINGBIRDS DURING THE BREEDING SEASON¹

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Abstract. We studied the breeding behavior of male Calliope Hummingbirds (*Stellula calliope*) in south-central British Columbia where they defended breeding territories from late April through late June each summer. We describe dive displays, hover displays, "buzzing," chasing, and vocalizing, and include a description of a complete mating sequence. Territorial males always performed dive displays in response to intrusions by female conspecifics. In contrast, they usually chased male conspecifics, although chases were occasionally preceded by dive displays. We conclude that dive displays play an important role in the courtship of Calliope Hummingbirds, although this does not preclude a possible role in aggressive interactions. We detected no seasonal trend in overall display activity, but at least in 1 year, more dive displays were given to males than to females early in the breeding season, and the reverse was true later in the season. There was a strong diel pattern in display behavior in that both dive and hover displays decreased gradually over the day. We discuss differences between the courtship behavior of Calliope Hummingbirds and Anna's Hummingbirds (*Calypte anna*).

Key words: Calliope Hummingbird; *Stellula calliope*; courtship; mating; display behavior; diel variation; interspecific differences.

INTRODUCTION

Most evidence suggests that contact between sexes in North American hummingbirds is limited to courtship and copulation (Johnsgard 1983), although male North American hummingbirds have occasionally been reported to feed nestlings or nesting females (Bailey 1927, Welter 1935, Cottam 1941 as cited in Pitelka 1942) or to remain perched near nests (Wheelock 1916 as cited in Moore 1947, Clyde 1972). Except for a few cases of females nesting in males' territories (Stiles 1973), there is a fairly clear habitat separation between sexes during the breeding season; females nest in partially wooded areas and males defend territories in more open areas nearby (Pitelka 1942, 1951; Legg and Pitelka 1956; Williamson 1956; Stiles 1973). On their territories, males exhibit many conspicuous displays and vocalizations which have often been interpreted as courtship behavior. However, without de-

tailed observations of male-female interactions, it is difficult to determine which of these are important in courtship, agonistic interactions, or both.

Conspicuous dive displays have been described for most North American species (Bent 1940, Stiles 1982, Johnsgard 1983), and have traditionally been assumed to be courtship displays (e.g., Grinnell and Storer 1924, Bent 1940 and references therein, Skutch 1977). However, Woods (1927, 1940), Pitelka (1942), and Stiles (1982) noted that male hummingbirds dive display towards both male and female intruders, and suggested that the display is primarily agonistic in nature. Stiles (1973, 1982) also described a number of close-range displays that he interpreted as being more important in courtship. The most extensive and detailed observations are those in Stiles (1973, 1982). More descriptions of the social context of displays are required if we are to determine whether courtship behavior maintains reproductive isolation among North American hummingbirds, and whether display behavior by males is a basis for choice of mates by females.

In this paper we report behavioral observations of Calliope Hummingbirds (*Stellula calliope*) during three breeding seasons. Calliope Hummingbirds breed in the mountains of west-

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ern North America, from northern Mexico to southern Canada (Bent 1940, Johnsgard 1983). Except for general descriptions of their natural history (Bent 1940, Johnsgard 1983), and a few analyses of the energetics of their territoriality (Armstrong 1987) and their nesting (Calder 1971), little is known about their reproductive behavior. We used our data to determine what behaviors males use in interactions with other hummingbirds on their territories, and to suggest some conclusions regarding the "functions" of those behaviors.

STUDY AREA AND METHODS

Our study site is in a narrow valley in the Twin Lakes area of the Ashnola Provincial Forest about 25 km SW of Penticton, British Columbia, Canada (119°47'W, 49°18'N). The elevation of the bottom of the valley is about 800 m. The male Calliope Hummingbirds we studied defended territories in a strip of meadow about 100 m wide on the valley floor (see map in Armstrong 1987). The females we observed nested in Douglas-fir (*Pseudotsuga menziesii*) forest on the north side of this meadow. A few Calliope Hummingbird males held territories in the nesting area, and both Calliope Hummingbird and Rufous Hummingbird (*Selasphorus rufus*) males defended territories 100–200 m above the meadow on the north-facing slope of the valley.

Male Calliope and Rufous hummingbirds arrived and established territories in this area in late April, and stayed until late June or early July. Since females were less conspicuous, it was difficult to determine exactly when they arrived, but our first sightings were in early May each year. On 3 May 1985, we placed feeders where females had fed from feeders of the same type in previous years. No females appeared at these feeders, but several females appeared when we placed feeders at the same locations on 7 May. At least some females stayed well into July. Egg laying occurred from late May through early June 1983 (Tamm 1985). The latest clutch we observed was laid on or about 3 July 1984, but was later abandoned.

We marked birds individually, either by spraying them with thinned enamel paint when they visited feeders or perches (Ewald and Carpenter 1978, Ewald and Rohwer 1980), or by catching them in a feeder-baited trap and applying paint by hand. The latter birds were banded. In 1984, we banded 11 birds (eight males, three females); in 1985, we banded 13 (11 males, two females).

We observed for 67.5 hr on five territories in 1983, 67.5 hr on five territories in 1984, and 88.5 hr on six territories in 1985. On each observation day, one or two of us observed males' behavior during three 30-min sessions starting at 06:30, 11:00, and 15:30. We recorded and timed all behaviors used in interactions with territory intruders. We also recorded and timed apparent displays performed in the absence of obvious intruders. We examined diel and seasonal variation in display data collected by all observers. However, because intruders were often difficult to detect and identify, we compared responses to different types of intruders using only data collected by ST in 1984 and DPA in 1985, when each of us had had a previous year's observational experience.

Each year, there were virtually no flowers containing nectar in the valley or on the slopes when the males arrived. Squaw currant (*Ribes cereum*) bloomed in early May, about the time we saw the first females, and was the main source of nectar during most of May. During this time, males may have obtained much of their nectar from sources on their territories (Armstrong 1987). Although plants of other species bloomed throughout June, far less nectar than the birds required was produced on the territories (Armstrong 1987), and we observed almost no foraging on the territories in June. During this time both males and females visited undefended patches of flowers on the slopes south of and above the meadow and in the woods north of the meadow. In addition, sapsuckers were present and we saw one Calliope Hummingbird female feed at a drilling (see Sutherland et al. 1982, Miller and Nero 1983, Kattan and Murcia 1985), but the drillings we found were not used regularly by hummingbirds.

BEHAVIOR OF TERRITORIAL MALES

Up to 12 males defended territories in the meadow in May, and at least some of the territories were contiguous. However, by June each year, no more than six of the territories remained, and these were all well separated, with on average over 100 m between territory centers. Three of the five banded males that we observed defending territories in 1984 defended the same territories at the beginning of the 1985 season. Territory owners were occasionally challenged by one or more intruding males over a period of several days. In some cases, challengers dive-

displayed to owners. Some individuals that we marked in the meadow in early May were not observed again until they took over one of the territories in late June.

Territory owners were visible 57% of the observation time in 1983, 55% in 1984, and 65% in 1985. An unknown portion of the time out of sight was spent off the territories. At least some of this time was spent feeding on flowers in other areas (Armstrong 1987).

During 10 hr of observation of two incubating females, and over 30 hr of observation of three nests at the nestling stage, we never saw a male approach a nest. We therefore have no evidence that males assisted in the rearing of young.

DESCRIPTION OF INTERACTIVE BEHAVIORS

Dive displays. Males first ascended to 20–30 m, then dived, producing a loud whistle at the bottom of the dive. After a dive they either ascended again until they reached approximately the same altitude and made another dive, or changed direction early in the ascending phase. Most dive displays were directed towards another bird perched on the territory, but displays were occasionally given when we detected no other bird.

Hover displays. Males often started hovering bouts several meters above the ground (sometimes 10 m or more) and slowly descended in discontinuous stages, alternating between sudden vertical drops of a few dm to 0.5 m, and stationary hovering or slow descent. While hovering, males often turned from side to side. Hovering males usually faced the display object (usually a female, see below) but did not necessarily hover directly above it. Similar behavior has been observed in Ruby-throated Hummingbirds, *Archilochus colubris* (Tyler 1940), and Broad-tailed Hummingbirds (*Selasphorus platycercus*) (Bent 1940). Males sometimes hovered after returning from chases. We usually detected no display object in such cases.

Buzzing. When a female perched on a male's territory, the male often hovered in front of and slightly above her, and produced a loud buzz. Sometimes the female left her perch and both birds spun around in circles ("circle dance"), facing each other with the male slightly higher than the female. Wyman (1920) reported a male and a female holding each other's bills during a circle dance. We believe that many of the "mid-air matings" described for several hummingbird species (Bent 1940) were displays similar to the

circle dance of Calliope Hummingbirds. We often saw buzzing bouts that appeared to be directed towards birds of other species, or nonliving objects such as twigs or leaves. In 1984, a male performed a series of dive displays and buzzings to two fledgling conspecifics (Armstrong 1988). Buzzing is similar to the shuttle display of Anna's Hummingbird males (Stiles 1971, 1973, 1982).

Chasing. Males chased conspecifics and Rufous Hummingbirds of both sexes, passerine birds, and less often bumblebees. Sometimes more than two hummingbirds were involved in a chase. Although we have no firm evidence for this, we felt that chases often were less vigorous when the chased bird was a female hummingbird, suggesting that the male was "following" rather than "chasing" her.

Vocalizing. Males typically chattered during chases. They sometimes chattered when perched, often in response to chattering by neighbors. Some males often chattered when leaving their territories. This behavior was similar to the "low intensity threat" described by Stiles (1971, 1973, 1982), Ewald and Carpenter (1978), and Ewald and Orians (1983) in Anna's Hummingbirds.

RESPONSES TO DIFFERENT TYPES OF INTRUDERS

Territory owners usually displayed towards female Calliope Hummingbirds on their territories. In contrast, they almost always chased male intruders (both conspecifics and Rufous Hummingbirds), although dive displays sometimes preceded the chases (Table 1). Males often dived at passerine birds (flycatchers, *Empidonax* spp.; Nashville Warblers, *Vermivora ruficapilla*; and Chipping Sparrows, *Spizella passerina*) that perched conspicuously on their territories (Table 1). Responses to males were significantly different than responses to both females and passerines in 1984 (Chi-square test, $P < 0.001$ for both comparisons), but responses to females were not significantly different than those to passerines ($P > 0.1$). All three comparisons were statistically significant in 1985 ($P < 0.001$).

Dive displays directed towards conspecific females included about three times as many dives per encounter as displays directed towards either unidentified or Rufous Hummingbirds, passerines, or unknown/no objects (Fig. 1). We have insufficient data to estimate mean number of dives in encounters with males in 1984. Hover displays towards females were also of much lon-

TABLE 1. Differences in responses of territorial males to intrusions by male conspecifics, female conspecifics, and passerines in 2 years. Intrusions that evoked no response by territory owners were excluded because we could not be certain that such intruders were detected by the resident. Because many encounters involved more than one type of recorded behavior, the sum of the percentages for the three behaviors exceeds 100% for all display objects.

	Display object	No. of intruders responded to	% responses involving:		
			Dive displays	Hover displays	Chases
1984	Male	54	2	9	98
	Female	15	100	73	13
	Passerine	22	86	27	32
1985	Male	151	9	11	92
	Female	30	100	67	9
	Passerine	65	85	9	15

ger duration than displays towards all other objects (Fig. 2).

MATING SEQUENCE

The following description illustrates use of diving, hovering, and buzzing displays in a complete courtship sequence that culminated in copulation. A marked male encountered an unmarked female near the center of his territory at 16:23 on 3 June 1984. The female moved from perch to perch, all on vegetation near the ground but clearly visible, while the male dive-displayed. The mating took place about 0.5 m above the ground in a bush about 3 m from the perch that had been the male's main perch that day. Mounting occurred 7 min after the female appeared on the territory, and was preceded by a series of 19 dives interspersed with four hover-display bouts (total duration 256 sec), and six buzzing bouts (total duration 51 sec) the longest of which (26 sec) immediately preceded mounting. During this

long buzzing bout, the female perched with her body almost horizontal, and wings partially open. After buzzing in front of her, possibly in direct contact, the male mounted for 2 sec. Immediately after the mating the female flew to another bush. The male made 13 more dives, two hover bouts (27 sec), and one buzzing bout (1 sec) before the female left the territory 3.5 min after the mating. The female chirped ("chip note," Stiles 1971) throughout the interaction.

Earlier the same day, an unmarked female displaced this male from his perch and landed on it herself. We noticed similar behavior by unmarked females on another territory twice the same day. In all three cases the males responded with series of dive displays, and at least one of these interactions involved a circle dance.



FIGURE 1. Mean number of dives per encounter in displays to female conspecifics ("Female"), unidentified or Rufous Hummingbirds ("HB"), passerines ("P"), no or undetected objects ("?"), and male conspecifics ("Male"). 95% confidence intervals are indicated.

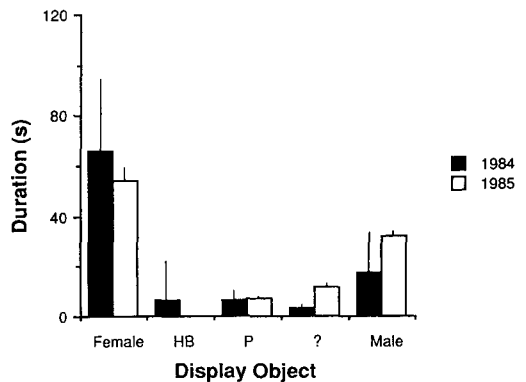


FIGURE 2. Mean duration of hover displays per encounter with female conspecifics ("Female"), unidentified or Rufous Hummingbirds ("HB"), passerines ("P"), no or undetected objects ("?"), and male conspecifics ("Male"). 95% confidence intervals are indicated.

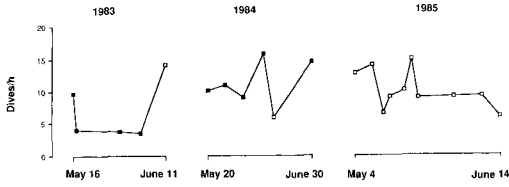


FIGURE 3. Mean frequencies of dive displays between 06:30 and 09:45 by Calliope Hummingbird males during three breeding seasons. The lines connect mean display rates on five territories for 1983 and 1984, and six for 1985. Open squares indicate that each territory was observed for 30 min by one observer, and filled squares indicate that each territory was observed for 30 min by one observer, and then for another 30 min by a different observer. Seasonal and yearly variation is not statistically significant.

SEASONAL AND DIEL PATTERNS OF DISPLAY BEHAVIOR

We detected no difference in number of displays per hour between years (Kruskal-Wallis test, $df = 2$; dive displays: $H = 3.29, P > 0.1$; hover displays: $H = 1.83, P > 0.1$; two-tailed tests here and below), nor did we detect any seasonal trend in overall display activity (Fig. 3; Spearman's rank correlation between number of dive displays per session and date, $r_s = -0.099, df = 60, P > 0.4$; between duration of hover displays and date, $r_s = -0.007, df = 60, P > 0.5$). However, there was a seasonal pattern in 1985 in that more dive displays were directed towards conspecific males than towards conspecific females early in the season, whereas the opposite was true later in the season (Fig. 4). No such trend was apparent

in the other years, presumably because we started observations later in those years (Fig. 3).

Both dive and hover displays decreased markedly during the day. Median number of dives per hour was 9, 4, and 1, for morning, midday, and evening sessions, respectively (Kruskal-Wallis test, $df = 2, H = 22.91, P \ll 0.001$). Median duration of hover displays was 27, 14, and 2 sec, for the three sessions ($H = 14.32, P < 0.001$).

DISCUSSION

The courtship behavior of Calliope Hummingbirds, while similar to that of Anna's Hummingbirds as described by Stiles (1973, 1982), appears to differ in at least two ways. First, copulation in Anna's Hummingbirds is preceded by a chase from the male's territory, usually to the vicinity of the female's nest. In contrast, the Calliope Hummingbird mating we observed took place near the center of a male's territory and was not immediately preceded by a chase, although the male followed the female when she moved from perch to perch (usually by adjusting his position while hovering above her). It should be pointed out that we observed only one mating, and found no nests prior to egg laying, and most of our intensive observation was on territories. Therefore we probably would have missed any matings that took place away from the males' territories.

Second, Stiles mentioned no female initiatives other than visiting males' territories to feed. Stiles used expressions like "the male forces her down" (fig. 6 in Stiles 1982). In contrast, the Calliope

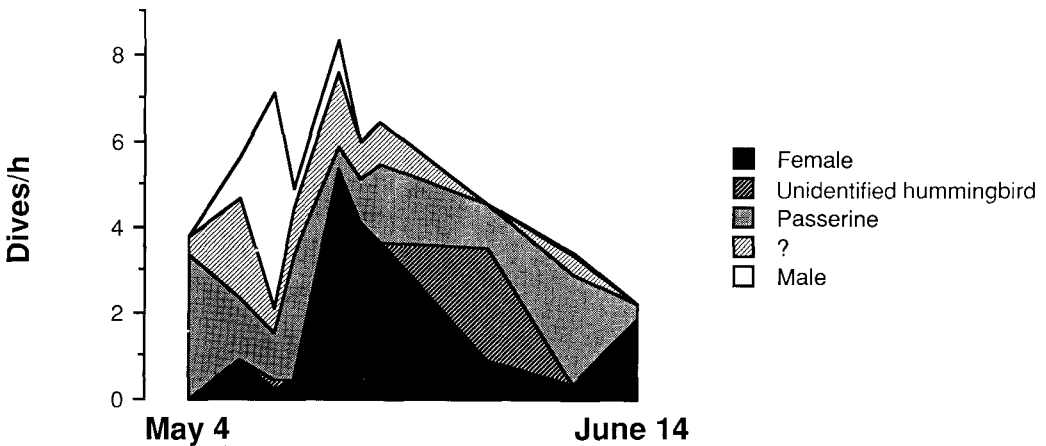


FIGURE 4. Frequencies of dive displays by category of display object in 1985 averaged over all times of day.

Hummingbird female we observed did not appear to be trying to escape the male. She chirped continuously and moved between fairly visible perches in the core area of the male's territory. Furthermore, we saw at least two different females actively approach, and displace perched males on three separate occasions the same day. Also, females often visited territories that contained no profitable flowers (Armstrong 1987).

Pitelka (1942) and Stiles (1973, 1982), suggested that mate selection in Anna's Hummingbirds may be mediated through male territory quality: females visit territories of males primarily to feed, and males who have successfully competed with other males for high quality territories encounter more females than do males on poorer territories. Female choice would act through acceptance or rejection of particular males. In contrast, it is our impression that female Calliope Hummingbirds may visit males for the purpose of mating, as do female hermit hummingbirds (e.g., Snow 1974, Stiles and Wolf 1979). The breeding system of the Calliope Hummingbirds at this site is perhaps best described by the term "exploded lek." Calliope Hummingbird females might still use energetic quality of territories as an index of male quality in other areas, but at our study site there was little nectar available on any territory when matings occurred (Tamm 1985, Armstrong 1987), so under this hypothesis many females would have to choose mates one or more weeks before they laid their eggs.

It is not surprising to find behavioral differences between these two species, given that Calliope Hummingbirds migrate whereas many Anna's Hummingbirds remain in the same general area all year. Furthermore, while Calliope Hummingbird males are smaller than the females, the reverse is true for Anna's Hummingbirds. This suggests that the mating systems are different.

The dives of North American hummingbird males have traditionally been regarded as courtship displays (e.g., Grinnell and Storer 1924, Bent 1940 and references therein, Skutch 1977), but this interpretation has been questioned on the grounds that dives are directed to conspecifics of both sexes, and to members of other hummingbird and nonhummingbird species (Woods 1927, 1940). In contrast, Pitelka (1942) and Stiles (1973, 1982) considered the dives primarily, but not exclusively, aggressively motivated. Female hummingbirds sometimes dive at intruders (Pi-

telka 1942 and references therein; Stiles 1982; ST, pers. observ.), and juvenile Anna's Hummingbird males perform rudimentary dive displays within 2 weeks of fledging (Stiles 1973, 1982). However, only mature males perform dives in the highly ritualized manner characteristic of each North American hummingbird species. Furthermore, although Woods (1940) reported that dive displays by Anna's Hummingbirds occur during "at least the greater part of the year," and Wagner (1954) reported display flights by Black-chinned Hummingbird (*Archilocus alexandri*) males on wintering grounds, Stiles (1973) reported that dive displays were rare or absent outside the breeding season in several species, but became progressively more frequent as the breeding season approached. According to Pitelka (1942), the peak of diving coincides with the peak of gonad development, and may be closely correlated with testosterone levels.

Stiles (1982) recorded almost as many dive displays towards conspecific males (18) as towards females (21) by Anna's Hummingbird males, but more chases of males (63) than of females (35). The Calliope Hummingbird males we studied always dive-displayed towards all females they encountered on their territories, and rarely chased them, but typically chased intruding males, and rarely dived at them (Table 1; Tamm 1985). Furthermore, the only mating we observed was accompanied by the most intense series of displays we recorded (32 dives, six hover displays, and seven buzzing displays in 10.5 min), and displays directed to females usually consisted of more dives than displays to other objects (Fig. 1). We therefore conclude that dive displays play an important role in the courtship of at least this species, although this does not preclude a possible role in aggressive interactions (Tinbergen 1952, Wingfield 1984 and references therein). Alternatively, it is possible that there are two types of dive display that differ in ways too subtle for us to detect.

It is conceivable that females could compare the relative responses of males whose territories they visit, but we have no evidence for any influence of display rates on female choice. However, given the risk of interspecific matings (e.g., Banks and Johnson 1961, Wells et al. 1978, Wells and Baptista 1979), it would be surprising if females did not use the conspicuous and highly species-specific dive displays in addition to other means of identifying conspecific males. In par-

ticular, the sounds produced by displaying males of different species are both loud and easily distinguishable by humans (Bent 1940, Woods 1940).

We do not know why male hummingbirds display to passerines. Stiles (1982) pointed out that male-male and male-female encounters are very similar in many hummingbird species, and suggested that females signal their sex by perching, whereas males leave. Pitelka (1942) and Stiles (1973, 1982) noticed that males were more likely to display towards perching than towards flying intruders. It is therefore possible that passerines often elicit courtship behavior because they perch on males' territories. A Calliope Hummingbird male at our site displayed to and appeared to attempt copulation with juveniles (Armstrong 1988), and similar behavior has been observed in other hummingbird species (Snow 1974, Stiles and Wolf 1979, Stiles 1982). However, when we attracted both male and female intruders to feeders on males' territories, owners dive-displayed to females and chased males although birds of neither sex perched.

There are several possible explanations for the decrease in display activity over the day. We initially hypothesized that this decrease was related to diel variations in nectar availability, because males dramatically increase their display rates when they have access to artificial feeders (Tamm 1985). Such a decrease in nectar availability did occur on 19 and 21 May 1985, when the average afternoon standing crop of *Ribes* flowers on territories dropped to 8% of the early morning level (Armstrong 1987). However, this pattern was not observed in *Ribes* flowers sampled on 10 and 13 May, nor in *Castilleja miniata* flowers sampled off territories in June when that species appeared to be the birds' primary source of nectar (Armstrong 1987). Given that our observations suggest that the diel variation in display activity persists throughout both *Ribes* and *Castilleja*-based phases of the breeding season, we conclude that nectar availability is unlikely to be the primary reason for this variation. Other explanations include the possibilities that there are more or more active competitors in the morning, that it is important for territory owners to establish their presence early in the morning, and that females are more likely to visit or to observe territories in the morning than later in the day. We have no data that would allow us to distinguish between alternative explanations.

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