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The Condor, Vol. 103, No. 3 (Aug., 2001), 647-651.

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- habitat imprinting, and philopatry in a montane, migratory sparrow. *Ornis Scandinavica* 22:98–106.
- OGDEN, L. J. E., AND B. J. M. STUTCHBURY. 1997. Fledgling care and male parental effort in the hooded warbler (*Wilsonia citrina*). *Canadian Journal of Zoology* 75:576–581.
- OLENDORFF, R. R. 1973. The ecology of the nesting birds of prey of northeastern Colorado. Grassland Biome, U.S. International Biological Program, Technical Report No. 211, Fort Collins, CO.
- PERRINS, C. M. 1991. Constraints on the demographic parameters of bird populations, p. 190–206. *In* C. M. Perrins, J. D. Lebreton, and G. J. M. Hiron [EDS.], *Bird population studies: relevance to conservation and management*. Oxford University Press, Oxford, UK.
- PRICE, T. D., AND H. L. GIBBS. 1987. Brood division in Darwin's ground finches. *Animal Behaviour* 35:299–301.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- RAPPOLE, J. H., AND A. R. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- SHANE, T. G. 2000. Lark Bunting (*Calamospiza melanocorys*). *In* A. Poole and F. Gill [EDS.], *The birds of North America*, No. 542. The Birds of North America, Inc., Philadelphia, PA.
- SKAGEN, S. K., T. R. STANLEY, AND M. B. DILLON. 1999. Do mammalian nest predators follow human scent trails in the shortgrass prairie? *Wilson Bulletin* 111:415–420.
- SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *Journal of Animal Ecology* 58:275–286.
- TEMPLE, S. A., AND J. R. CARY. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2:340–347.
- VEGA RIVERA, J. H., C. A. HAAS, J. H. RAPPOLE, AND W. J. MCSHEA. 2000. Parental care of fledgling Wood Thrushes. *Wilson Bulletin* 112:233–237.
- WEATHERHEAD, P. J., AND S. B. MCRAE. 1990. Brood care in American robins: Implications for mixed reproductive strategies by females. *Animal Behaviour* 39:1179–1188.
- WHITE, G. C., AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, New York.

The Condor 103:647–651
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THE FUNCTION OF DISPLAYS OF MALE RUFOUS HUMMINGBIRDS

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Abstract. We observed 26 male Rufous Hummingbirds (*Selasphorus rufus*) on their breeding territories to quantify display behaviors and to interpret their functions. Territory holders responded to intruding conspecific males with aggressive chases until the intruder left the territory. Female intruders received dive displays and shuttle-flights, which we interpret as courtship behavior. Dive displays were J-shaped (concave upward) in both ascent and descent, contrary to other reports of oval-shaped displays. We present a representative sonogram of the sounds produced during these dive displays.

Key words: aggression, behavior, courtship, display, Rufous Hummingbird, *Selasphorus rufus*.

Función de los Despliegues de los *Selasphorus rufus* Machos

Resumen. Observamos 26 *Selasphorus rufus* machos en sus territorios de reproducción para cuantificar sus comportamientos de despliegue e interpretar las funciones de éstos. Los dueños de los territorios respondieron a intrusiones de machos coespecíficos con persecuciones agresivas hasta que los intrusos abandonaron el territorio. Por su parte, las hembras intrusas recibieron despliegues en picada y patrones de vuelo repetidos, los cuales interpretamos como comportamientos de cortejo. Los despliegues en picada tuvieron forma de J (cóncava hacia arriba) tanto en ascenso como en descenso a diferencia de reportes previos sobre despliegues en forma de óvalo. Adicionalmente presentamos un sonograma representativo de los sonidos producidos durante los despliegues en picada.

Manuscript received 2 August 2000; accepted 20 March 2001.

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Male hummingbirds (family Trochilidae) use vocalizations and displays while defending breeding and feeding territories (Kodric-Brown and Brown 1978, Gass 1979, Stiles 1982). Some displays, such as tail-flaring and chasing, are generally interpreted in the context of aggression. Others, such as spectacular U-shaped dive displays (Banks and Johnson 1961, Johnsgard 1997), are more difficult to interpret. It is difficult to precisely describe displays of a tiny bird moving at velocities on the order of 17–20 m sec⁻¹ with acceleration on the order of 70–100 m sec⁻² (Larimer and Dudley 1995). Consequently, most descriptions are qualitative rather than quantitative (e.g., Kobbé 1900, Sprot 1927, Rodgers 1940, Bent 1964, Calder 1993).

Determining the function of hummingbird displays has been hindered by a similar lack of data. Pitelka (1942) dismissed any courtship function of flight displays and concluded that they were used aggressively against conspecifics of both sexes. Some data are provided by Stiles (1982), who counted the number of displays given by male Anna's Hummingbirds (*Calypte anna*) to conspecifics and heterospecifics. He concluded that dive displays were aggressive and indiscriminate, and that chases too were somewhat indiscriminate, with some bias toward adult male conspecifics. Generalizing across hummingbirds, Stiles (1982) speculated that dive displays serve primarily an aggressive, rather than a sexual, function. In contrast, Tamm et al. (1989) demonstrated that male Calliope Hummingbirds (*Stellula callope*) use dive displays primarily for courtship.

Johnsgard (1997) provides the most comprehensive review of the structure and function of hummingbird display dives, but also shows that our knowledge of the subject is deficient. He describes Rufous Hummingbirds (*Selasphorus rufus*) as performing oval-shaped dive displays used primarily in an aggressive context, but does not cite the source of the description. The oval shape is also reported in a field guide (Robbins et al. 1983), but contrasts with inexact descriptions of J-shaped dives in the early literature (Kobbé 1900, Sprot 1927).

Our observations of Rufous Hummingbird behavior conflicted with the descriptions summarized in Johnsgard (1997). Dive displays in our study in southwestern Alberta were not oval in shape and appeared to function in courtship. To document these observations, we describe the displays performed by territorial male Rufous Hummingbirds during the breeding season and quantify the occurrences of these behaviors and the identities of the display recipients.

METHODS

STUDY AREA

We studied hummingbirds in a valley in an eastern range of the Rocky Mountains south of Beaver Mines, Alberta, Canada, (49°29'N, 114°25'W, elevation 1400 m) during June of 1998 and May–June of 1999. In early May, we placed approximately 25 hummingbird feeders containing 14% sucrose solution in various locations along a 15-km stretch of the valley. Feeders were separated by at least 100 m. Within a week most of the feeders were defended, each by a single male Rufous Hummingbird. Territory owners were then marked with a spot of colored ink sprayed on the bird's

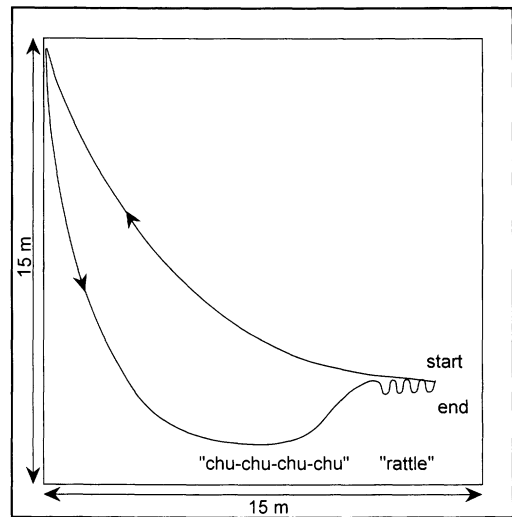


FIGURE 1. Diagram of a display dive of male Rufous Hummingbirds, based upon repeated dives of 4 males.

breast while it was perched at a feeder. Territories were on the order of 1 ha in size.

DATA COLLECTION

We collected data opportunistically within a male's territory during experiments on foraging or memory, recording display rates whenever we noticed them rather than in specific observation periods. Whenever a male engaged in an intraspecific interaction, we recorded the type of interaction (chase, dive display, shuttle-flight, gorget-flash, tail-flare, waggle-flight; descriptions below), and the identity of the individual the male was interacting with. Often the identity of the intruder was unknown. We also counted the number of dives during each encounter and estimated the duration of shuttle-flights. We recorded some dive displays with a Sony condenser microphone and a Sony 35-cm parabola, and made sonograms with Canary 1.2.4 software digitizing at 22 kHz.

DESCRIPTION OF DISPLAYS

Dive display. Males made J-shaped dive displays that were concave upward during both the climb and the dive. We could not record dimensions of these displays with a video camera, so we estimated dimensions of the displays of four subjects using vegetation as landmarks, and measured distances afterward (Fig. 1). Maximum height attained during the climb was noted against nearby trees and then that height was estimated using a 2-m standard.

Males produce a high-pitched whine during dives. Toward the bottom of the arc they produce a distinctive pulsing sound (chu-chu-chu-chu), and then end with a buzzing or "rattle" (Johnsgard 1997) sound during the waggle (Fig. 2).

Waggle-flight. The waggle-flight was sometimes used as a separate display before dives. When this occurred, the waggle at the completion of the dive ap-

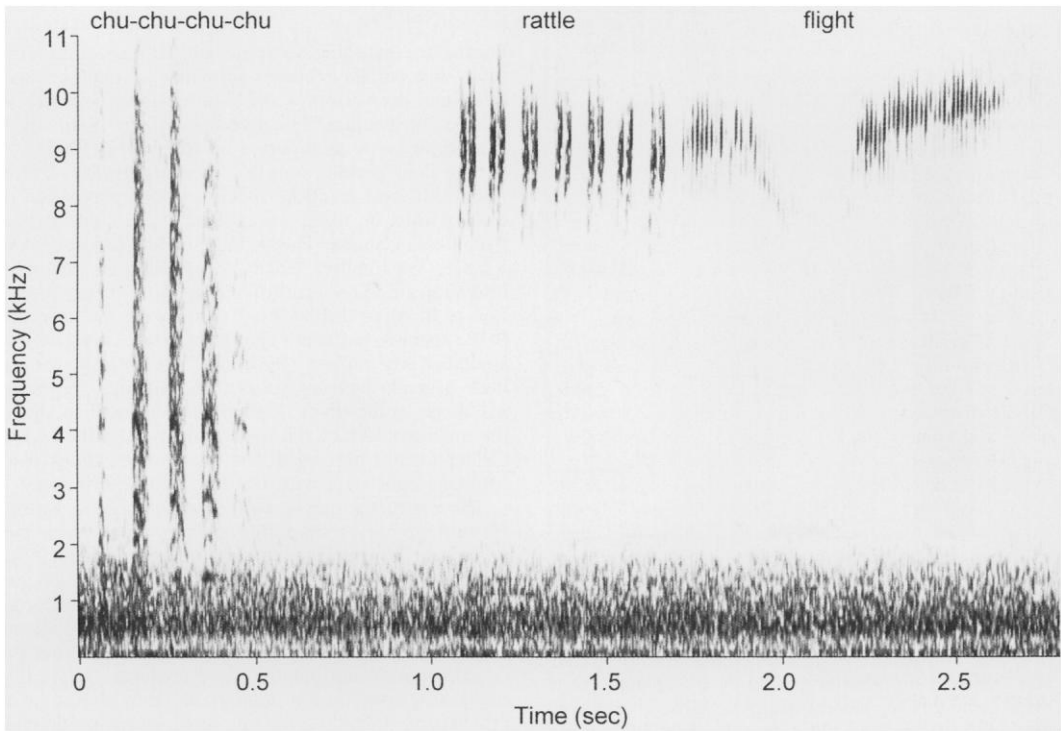


FIGURE 2. Sonogram of sounds produced during the dive-display sequence depicted in Figure 1. The “chu-chu-chu-chu” occurs at the bottom of the dive. The rattle occurs during the waggle-flight. The flight sounds are produced during the ascent to the next dive. Actual timing is preserved in the sonogram, except that the ascent flight is truncated.

peared to follow the same path as the original waggle-flight (Fig. 1).

Shuttle-flight. Shuttle-flight displays were performed a few centimeters above an intruder, usually a female perched in low vegetation. The male hovered in a horizontal orientation and threw himself side to side with his head facing the female and his tail describing an arc on the order of 130° , and approximately 40–50 cm in length, in the horizontal plane. A characteristic throbbing buzz was made as the male moved side to side (see also Bent 1964, Stiles 1982).

Chase. The male approached an intruding bird and pursued it out of the territory. Resident males tended to return quickly following a chase.

Tail-flare. The male flew directly towards an intruding bird, and then hovered approximately 30 cm away in a vertical orientation with the rectrices spread.

Gorget-flash. A perching male faced an intruder and rotated his head. A distinct red flashing of the gorget (i.e., throat) was usually evident to the human observer.

STATISTICAL ANALYSES

Contingency analyses were not appropriate because data points were not independent (multiple behaviors were recorded for each resident). To determine whether resident birds treated male and female intruders differently, we performed repeated-measures ANOVA.

The two within-subject fixed factors were Behavior (chase, dive, shuttle) and Intruder Sex (male, female). Each resident (subject) was regarded as a unit of observation and provided the random variate for analysis. We examined the number of times a resident performed each behavior in the presence of male and female intruders. A behavior \times sex interaction would indicate that the behavior used by the resident depended upon the sex of the intruding bird. The within-subject design controlled for the fact that different subjects received different numbers of intrusions into their territories. The values reported in the Results section are means \pm SE, and the level of statistical significance was set at $P < 0.05$.

RESULTS

We observed 296 chases, dives, and shuttle-flights in 1998, and 923 in 1999. Of these 1219 behaviors, 394 were excluded from analysis because we could not identify the recipient. Statistical analysis revealed a highly significant behavior \times sex interaction ($F_{2, 50} = 39.2$, $P < 0.001$). Most chases (515 of 537) were directed at males and most dive displays (187 of 202) and shuttle-flights (82 of 86) were directed at females (all $F_{1, 25} > 19$, all $P < 0.001$; Fig. 3).

Dives were given 3.2 ± 0.2 times per encounter with females ($n = 182$; range 1–18). Shuttles per-

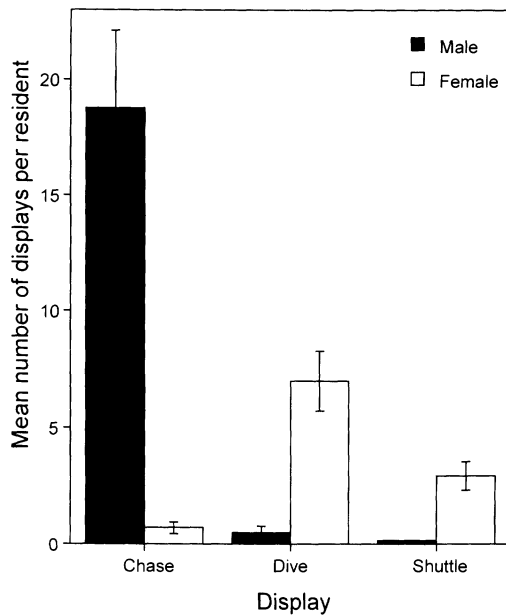


FIGURE 3. Mean (\pm SE) number of chases, dive displays, and shuttle-flights directed at intruding male and female Rufous Hummingbirds by 26 male territorial residents in Alberta, Canada. Most chases were directed at males and most dive-displays and shuttle-flights were directed at females.

formed to females lasted 14.0 ± 1.0 sec ($n = 64$; range 2–46).

None of the 458 dive displays were oval in shape. A dive began with a male ascending in a concave-upward flight to a height of approximately 14.6 ± 0.8 m. The male then dove rapidly in a concave arc, ascended slightly from the lowest point of the dive, and ended the display with a vertically oscillating waggle while moving in a horizontal line. The lowest part of the dive occurred just above (sometimes only a few centimeters) the recipient of the display (Fig. 1). This series of movements brought the male very close to the point in space at which he initiated his ascent. The next display began from this point, with the climb also a concave arc, but always in a path slightly above that of the preceding dive.

Gorget-flashes, tail-flares and waggle-flights were much less frequent than the other behaviors we report here. Analyses are therefore inappropriate, but it appears that gorget-flashes (9 of 9) and tail-flares (15 of 16) were generally directed at males and waggle-flights (4 of 5) were directed at females.

The rattle sound made during the waggle is likely caused by the wings because it is in the same frequency range as for the normal wing noise (Fig. 2). It is more difficult to ascertain the origin of the sound made at the bottom of the dive. The “chu-chu-chu-chu” dive sound has timing similar to that of the rattle, but a much greater frequency range.

DISCUSSION

During the breeding season, male Rufous Hummingbirds directed their chases primarily at male conspecifics and dive displays and shuttle-flights primarily at female conspecifics. The dive display was distinctly J-shaped, not oval as reported by Johnsgard (1997).

Our data pertain only to breeding Rufous Hummingbirds, and could be specific to our population of birds. However, observations from Vancouver, British Columbia, Canada (Hurly and Shields, unpubl.), and Seattle, Washington (John Wingfield, pers. comm.), also indicate a J-shaped dive display. This conformation of the dive display may, or may not, be universal to the species, but at the very least it is relatively widespread. Early reports (Sprot 1927) indicated that the male ascends with his back to the female, suggesting a J-shape to the dive. If the dive were oval in shape, the male would face the female for most of the ascent. Calder (1993) described non-oval-shaped dives from Montana consistent with our J-shaped description.

The courtship function of dive displays in Rufous Hummingbirds is supported by the observation that dives are reported only from breeding populations (Kobbé 1900, Sprot 1927, this study). Detailed descriptions of the defense of feeding territories during migration (Kodric-Brown and Brown 1978) indicate that males employ chases and gorget-flashes, but the descriptions do not mention dive displays. If dive displays were used to intimidate rivals, they should be as effective in defending feeding territories as in defending breeding territories. Since this has not been reported, they may be specific to breeding and courtship.

In the past, much interpretation of the function of hummingbird displays was based upon very few data. For example, although Pitelka (1942) argued that the “frequent claims of amorous intent attached to the display flights of hummingbirds by various observers are largely nonsense,” he presented no data to support this claim. Indeed, such speculative claims have been combined with a few observations and then broadly applied to interpret the evolution and function of the displays of North American hummingbirds (Stiles 1982, Johnsgard 1997). We argue that such generalizations are premature.

Our data do not address directly the function of display flights in other species of hummingbirds. However, our experience suggests that one explanation for confusion about the role of the dive display may be the substantial differences in the detectability of male and female hummingbirds. In Rufous Hummingbirds at least, males intruding into a territory were far more obvious to human observers than were females, both visually and acoustically due to the “wing whistle” of normal flight (Sprot 1927, Miller and Inouye 1983). Females tended to approach feeding areas by flying low and close to the vegetation, and they often moved in short flights, pausing to perch in the vegetation for many seconds. The noise made by their wings was much less than that made by males, but we have not quantified this difference. Often female recipients were identified only after prolonged observation of the vegetation below the dive displays, and were not seen until they flew away, perhaps several minutes after the completion of the dives. Past accounts of dive displays may

have failed to detect some females because the observers were not focused on identifying the recipients of the displays.

We know of only two studies reporting data on dive displays in hummingbirds. Tamm et al. (1989) counted the number of dive displays directed by male Calliope Hummingbirds toward male and female conspecifics and toward heterospecifics. Males directed more chases to male conspecifics and more dive displays to female conspecifics. Tamm et al. (1989) concluded that dive displays played a courtship role in this species.

Stiles (1982) observed that male Anna's Hummingbirds (*Calypte anna*) directed chases more often at conspecific males than conspecific females. Dive displays were directed at 8 males, 8 females, 3 juveniles, and 7 unidentified subjects. Stiles interpreted this apparent indiscriminate use of dives as indicating an aggressive purpose. An alternative explanation is that male Anna's Hummingbirds are indiscriminate in who they court. Indeed, territorial male Anna's Hummingbirds attempted to copulate with a male conspecific dummy as frequently as with a female conspecific dummy (Stiles 1982). Similar indiscriminate behavior was observed in Calliope Hummingbird males attempting to copulate with juvenile conspecifics (Armstrong 1988). Further experimental manipulations may elucidate whether Anna's Hummingbird males use dive displays for aggression or for courtship.

Based on the only quantitative data available (Stiles 1982, this study) it appears that shuttle-flights in Anna's and Rufous Hummingbirds are used primarily for courtship and often precede copulation (Stiles 1982, Hurly, unpubl.). Similar displays are also reported for Calliope Hummingbirds (Tamm et al. 1989). It is interesting that certain display types are used by many species of North American hummingbirds. Variants of the dive display are reported for at least nine species (Banks and Johnson 1961, Johnsgard 1997). We recommend further data collection before interpretation of the structure, function, and evolution of these displays is attempted.

We thank Jay Biernaskie, Lynn Brooks, Richard Ehler, Katheryn Holgate, Julia Lindeman and Beth Shields for assistance with data collection. Ralph Cartar, Lee Gass and one anonymous reviewer provided helpful comments on the manuscript. TAH was supported by the Natural Sciences and Engineering research Council of Canada and SDH and TAH were supported by NATO.

LITERATURE CITED

- ARMSTRONG, D. P. 1988. Persistent attempts by a male Calliope Hummingbird, *Stellula calliope*, to copulate with newly fledged conspecifics. *Canadian Field-Naturalist* 102:259-260.
- BANKS, R. C., AND N. K. JOHNSON. 1961. A review of North American hybrid hummingbirds. *Condor* 63:2-28.
- BENT, A. C. 1964. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. Dover Publications, New York.
- CALDER, W. A. 1993. Rufous Hummingbird (*Selasphorus rufus*), p. 1-20. In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 53. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.
- GASS, C. L. 1979. Territory regulation, tenure, and migration in rufous hummingbirds. *Canadian Journal of Zoology* 57:914-923.
- JOHNSGARD, P. A. 1997. *The hummingbirds of North America*. 2nd ed. Smithsonian Institution Press, Washington, DC.
- KOBBÉ, W. H. 1900. The Rufous Hummingbirds of Cape Disappointment. *Auk* 17:8-15.
- KODRIC-BROWN, A., AND J. H. BROWN. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* 59:285-296.
- LARIMER, J. L., AND R. DUDLEY. 1995. Accelerational implications of hummingbird display dives. *Auk* 112:1064-1066.
- MILLER, S. J., AND D. W. INOUE. 1983. Roles of the wing whistle in the territorial behaviour of male broad-tailed hummingbirds (*Selasphorus platycercus*). *Animal Behaviour* 31:689-700.
- PITELKA, F. A. 1942. Territoriality and related problems in North American hummingbirds. *Condor* 44:189-204.
- ROBBINS, C. S., B. BRUUN, AND H. S. ZIM. 1983. *Birds of North America*. Golden Press, New York.
- RODGERS, T. L. 1940. The dive note of the Anna Hummingbird. *Condor* 42:86.
- SPROT, G. D. 1927. Notes on the courtship of the Rufous Hummingbird. *Condor* 29:71-72.
- STILES, G. F. 1982. Aggressive and courtship displays of the male Anna's Hummingbird. *Condor* 84:208-225.
- TAMM, S., D. P. ARMSTRONG, AND Z. J. TOOZE. 1989. Display behavior of male Calliope Hummingbirds during the breeding season. *Condor* 91:272-279.