

COURTSHIP AND TERRITORIAL BEHAVIORS OF THREE HUMMINGBIRD SPECIES IN ARIZONA

RICHARD K. SIMPSON, SCHOOL OF LIFE SCIENCES, ARIZONA STATE UNIVERSITY, TEMPE, AZ 85287-4501,
RKSIMPS1@ASU.EDU

ABSTRACT: Many birds exhibit conspicuous courtship and territorial behaviors. These behaviors are often used to secure mates. Courtship territories can function in several ways, including as a defended resource or a lek. Some hummingbird species in Arizona aggressively defend territories during their breeding seasons. I observed hummingbird territories and associated territorial behaviors in three species across the state. In this article, I provide descriptions of hummingbird territories and territorial behaviors and hypothesize about the intended functions of these territories.

Many birds use exaggerated behavioral displays during courtship. Some of the most notable examples include birds of paradise, peacocks, and bowerbirds. These courtship displays are typically used to successfully attract a mate or mates, and most often males are the sex doing the displays (Andersson 1994, Bradbury and Vehrencamp 2011, Ligon 1999). Many species perform their courtship displays on territories they have acquired (e.g. manakins; Endler and Thery 1996, Heindl and Winkler 2003), and males will guard these territories from other males of the same species. Courtship territories can function in several ways: a) males might allow their mate or mates to nest on their territories (e.g. Red-winged Blackbirds, *Agelaius phoeniceus*; Ligon 1999); b) males might provide an alternative resource to females that visit their territory, such as food (e.g. Purple-throated Caribs, *Eulampis jugularis*; Temeles and Kress 2010); or c) male territories might be used only for copulation or breeding, also called a lek (e.g. birds of paradise; Ligon 1999).

In order for males to have successful territories for nesting or resource guarding, males need to locate the desired resources (i.e. nest sites, food, etc.) and set up their territories at or near those resources. However, for lekking species, territory placement can be more complex, such as dependence upon environmental needs for effective communication (e.g. manakins hold leks in sun gaps in the dense tropical rainforests to improve their visibility; Endler and Thery 1996, Heindl and Winkler 2003). Additionally, leks fall upon a continuum from a traditional lek, where males are clustered in the same area (e.g. Sage Grouse, *Centrocercus urophasianus*; Koch et al. 2015), to an exploded lek, where males each have their own breeding territories that are spaced throughout the environment (e.g. Little Bustards, *Tetrax tetrax*; Jiguet and Bretagnolle 2014).

North American hummingbirds are known to have exaggerated courtship behaviors and to vigorously guard breeding territories, especially species from the bee tribe of hummingbirds (McGuire et al. 2014). Species in this hummingbird tribe, such as Costa's Hummingbird (*Calypte costae*), typically have two courtship displays—the dive and shuttle displays (Clark et al. 2012, Clark and Feo 2010, Feo and Clark 2010, Hurly et al. 2001, Tamm et al. 1989). For the dive display, the male flies high into the air and dives down toward the female, whereas for the shuttle display, the male hovers back and forth in front of the female, facing her and extending his colorful throat feathers (i.e. gorget). Male hummingbirds also do not help raise young, and have been suggested to have either lek (traditional and/or exploded) or resource guarding courtship territories. For example, Anna's Hummingbirds (*Calypte anna*) in California have been found to have more exploded lek-based breeding territories during their breeding season, while maintaining resource-based feeding territories outside of their breeding season (Stiles 1982, Powers 1987). There has also been at least one account of a more traditional lek in North American hummingbirds (Broad-tailed Hummingbird; *Selasphorus platycercus*; Barash 1972).

Many observations of hummingbirds occur at feeders, and finding hummingbirds naturally in wild areas can be fairly difficult. However, male bee hummingbirds exhibit conspicuous territorial behaviors. When on a territory, male bee hummingbirds tend to perch in highly visible locations, providing them with a commanding view of the surrounding

area and offering researchers the ability to find them with greater ease. During the breeding seasons of Broad-tailed Hummingbird, Anna's Hummingbird, and Black-chinned Hummingbird (*Archilochus alexandri*), I observed males as they courted females from their territories at various locations across Arizona. In this paper, I will document my observations on where these males have set up their courtship territories and provide anecdotal evidence about the status of these territories (lekking or resource guarding).

OBSERVATIONS OF BROAD-TAILED HUMMINGBIRDS

I found many male Broad-tailed Hummingbirds on courtship territories in the area surrounding Flagstaff (April-July 2014) and on Mount Lemmon near Tucson (June 2015). Near Flagstaff, I found clusters of male territories at the southern base of Elden Mountain near Elden Spring (elev. c. 2100 m), along Forest Road (FR) 128 1.5 km past Marshall Lake (c. 2150 m), and in Walnut Canyon National Monument (c. 2050 m). I found high numbers of territories near Elden Spring and along FR 128, with 10-15 territories detected along a small portion of FR 128 and around 20 territories discovered near Elden Spring, whereas I was able to observe only about five territories in Walnut Canyon National Monument. However, the lack of territories in the national monument is most likely due to the difficulties of exploring the steep ledges there. In both the Elden Spring and FR 128 areas, the males' territories were mostly in the scrubby piñon-juniper forest areas (Figure 1), with males perched on conspicuous branches of the juniper, piñon, or Gambel oak trees (Figure 2). Males rotate between two to five perches in their territories, and it was their use of these perches that allowed me to distinguish different male territories. In both areas, the territories seemed about 100-200 m², though further work would be needed to definitively quantify the territory sizes.

Male Broad-tailed Hummingbirds in these areas seemed to exhibit more exploded lek-based territorial behaviors, as I would rarely find males feeding on their territories. In fact, males typically disappeared from their territories for several minutes to an hour, presumably to feed elsewhere. Because the males near Elden Spring were close to a neighborhood, I often found them leaving their territories and flying directly toward the neighborhood, most likely to feed at hummingbird feeders. If another hummingbird—male or female—ever appeared in a male's territory, he would usually chase it away, and thus these males guarded their territories fervently. However, if the intruder was a female, I would often hear males dive-and-shuttle displaying to them before chasing them off. These observations are similar to those reported elsewhere in



Figure 1. The typical piñon-juniper habitat where I found male Broad-tailed Hummingbird territories near Flagstaff. This photo was taken from Forest Road 128. Photo by Richard K. Simpson



Figure 2. An example of a male Broad-tailed Hummingbird perched on his territory near Flagstaff. Photo by Richard K. Simpson

Arizona and Colorado, though the territory sizes I observed are much smaller (Camfield et al. 2013)—possibly due to higher densities of male territories. Throughout my observations I did not view a traditional lek, as Barash (1971) had in Colorado, and while this does not preclude the possibility that Broad-tailed Hummingbirds exhibit traditional lekking behavior in Arizona, it suggests that this might be a rare behavior.

Interestingly, among the densely packed Broad-tailed Hummingbird territories near Elden Spring, I found one Black-chinned Hummingbird territory and two Anna's Hummingbird territories. Neither of these species is typically found at these high elevations (c. 1800 m), so it would be interesting to understand how successful these individuals were at finding mates.

I had a much harder time defining a given male's territory on Mount Lemmon (c. 2100 m). This was due to the males mostly flying and perching high up in the pine trees, making it difficult to find the males while perched. Although Mount Lemmon was full of male Broad-tailed Hummingbird movement, I was only able to find three to five definite territories. More time and work would be needed to map territories in the dense pine forests of both Flagstaff and Mount Lemmon to see if male territorial behavior varies between these habitats.

OBSERVATIONS OF BLACK-CHINNED HUMMINGBIRDS

I have also observed the courtship territories and behaviors of the Black-chinned Hummingbird. As mentioned previously, I found one male Black-chinned Hummingbird territory near Elden Spring (June-July 2014), and I suspect there are more spread throughout the Flagstaff area. However, Black-chinned Hummingbirds typically do not prefer higher elevations; their territories are most likely not common there. Lower in elevation near Wet Beaver Creek (c. 1200 m; May 2014), I observed a few more male hummingbird territories, but I still did not find them in high numbers.

The situation changed once I started observing Black-chinned Hummingbird territories in southeastern Arizona. I first tried to locate male territories at the Patagonia-Sonoita Creek Preserve (c. 1200 m; May 2014), but despite finding many males at feeders in the area, I could not find male territories. At the Appleton-Whittell Research Ranch (AWRR) of the National Audubon Society near Elgin (c. 4800 m), I found 10-15 male territories that were easily defined (May-June 2015 and 2016)—like the Broad-tailed Hummingbird territories defined above. AWRR is mostly upland grassland, but several ephemeral washes run through the property, and it was along the canyons and ridges of these riparian habitats where I found male territories (Figure 3). Male Black-chinned Hummingbirds also perched in several conspicuous branches of trees, and I tended to find them in oak, mesquite, and juniper trees (Figure 4). The dispersion of male Black-chinned Hummingbird territories was different here than what I



Figure 3. The typical ephemeral riparian habitat where I found male Black-chinned Hummingbird territories in southeastern Arizona. This photo was taken at the Appleton-Whittell Research Ranch. Photo by Richard K. Simpson



Figure 4. An example of a male Black-chinned Hummingbird perched on his territory at the Appleton-Whittell Research Ranch. Photo by Richard K. Simpson

found with the Broad-tailed Hummingbirds. Instead of finding the territories clustered within one large area, I found three to four territories in a given canyon/riparian habitat. The Black-chinned Hummingbird territories seemed similar in size to the Broad-tailed Hummingbird territories, but instead of finding many abutting territories, I would find only a few.

Like the Broad-tailed Hummingbirds of Flagstaff, these Black-chinned Hummingbird males seemed to be exhibiting more of the exploded lek-based behavior, as males would disappear from their territories for long periods of time, presumably to feed. There also seemed to be relatively few flower resources on each male's territory, so I suspect the males in this upland grassland environment had to travel far and wide to find enough flowers on which to feed. Thus, the resource distribution may be driving the territorial behavior of these males. Males would typically chase most other hummingbirds that entered their territories, though not as aggressively as the Broad-tailed Hummingbirds. I also observed some courtship dive-and-shuttle displays, always occurring on the male territories. My observations about males establishing breeding territories partly match other observations in California and Texas, though in both places some resource-guarding was also observed (Baltosser and Russell 2000). Additionally, it seems that the territories of the males I observed were much larger than those reported from California (Baltosser and Russell 2000), which again could be due to resource distribution differences.

OBSERVATIONS OF ANNA'S HUMMINGBIRDS

The third species for which I observed territorial and courtship behaviors in Arizona is the Anna's Hummingbird. Most of my observations of this species occurred in the Phoenix Valley area (c. 400-700 m²), though as mentioned above, I did find two territories near Elden Spring (June-July 2014). Anna's Hummingbirds are interesting because they have actually expanded into the Phoenix area from their original range in California (Zimmerman 1973), and they seem to be mostly reliant on humans for their habitat. I found male Anna's Hummingbird territories at South Mountain Park/Preserve, Cave Creek Regional Park, Lake Pleasant Regional Park, Coon Bluff Campground at the Salt River, and other desert locations surrounding Phoenix (February-April 2015 and 2016), but never too far from urban or suburban areas. Within Phoenix, Anna's Hummingbird territories are very common. On Arizona State University's Tempe campus, I found 10-15 territories (February-April 2016 and February-March 2017; Figure 5), which seemed to be similar in size to the male Broad-tailed Hummingbird and Black-chinned Hummingbird territories. The territory densities are also similar to what I found for the Broad-tailed Hummingbirds near Flagstaff.

Male Anna's Hummingbirds mostly perch on palo verde trees or ocotillos (Figure 6), which is very similar to what I observed with Costa's Hummingbirds in the Mohave deserts of California. Unlike male Broad-tailed or Black-chinned hummingbirds, Anna's Hummingbirds sing while on their territories, which they also use for courtship.



Figure 5. The typical habitat on Arizona State University's Tempe campus where I found male Anna's Hummingbird territories. Photo by Richard K. Simpson

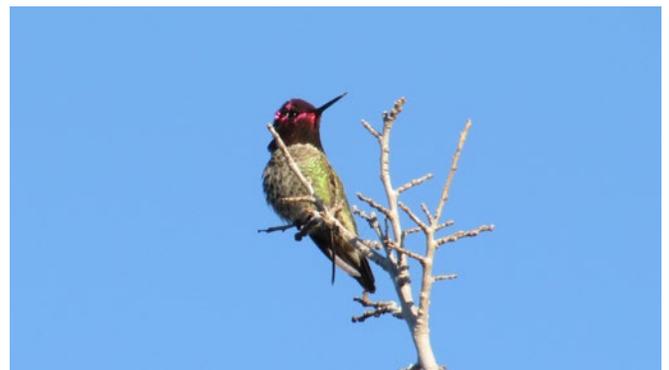


Figure 6. An example of a male Anna's Hummingbird perched on his territory on Arizona State University's Tempe campus. Photo by Richard K. Simpson

Anna's Hummingbirds might also exhibit more of a resource-guarding behavior rather than exploded lekking, as males will often feed on their territories and their territories will be close to several flower patches. However, the distribution of resources on the Tempe campus is much denser than the places where I observed the other two species. Male Anna's Hummingbirds fiercely defend their territories, and I frequently observed males dive displaying and singing to female hummingbirds on their territories. Previous research on Anna's Hummingbirds in California suggests that although males often have food resources on their territories, these male territories are primarily used for breeding (Clark and Russell 2012, Powers 1987, Stiles 1982); this would further support the exploded lek theory.

DISCUSSION

Overall, male territorial behaviors across Black-chinned, Broad-tailed, and Anna's hummingbirds are similar. Males will find conspicuous perches on their territories and guard their territories from other hummingbirds. Males of all species will also perform their courtship displays on their territories when females are present. The distribution of territories varied across the species, with Black-chinned Hummingbirds exhibiting much lower territory densities compared to the other species—though territory size did not seem to vary greatly across species. Based on feeding behaviors, both Broad-tailed and Black-chinned hummingbirds appeared to exhibit exploded lek-based territorial behaviors matching some previous observations (Baltosser and Russell 2000, Barash 1972, Camfield et al. 2013), while Anna's Hummingbirds might exhibit more resource guarding-based territorial behaviors—though as mentioned above, other work has found that male Anna's territories are primarily used for breeding and not feeding (Clark and Russell 2012, Powers 1987, Stiles 1982). More detailed and rigorous quantification of these territorial behaviors and of territory time budgets is necessary to confirm these hypotheses.

While I did generally note the resource distributions at each site, more work could be done to specifically map the flowers or feeders at which these males are feeding and compare their territory ranges to these resources. Finally, in all cases, I did not observe female behaviors outside of their visits to male territories, so further work could be done to match female movements or territorial behaviors relative to male territories to understand how females might be driving male territorial behaviors.

I focused my observations on only three of the bee hummingbird species in Arizona. Costa's and Lucifer hummingbirds (*Calothorax lucifer*) also breed in Arizona, and it would be worthwhile to observe their territorial behaviors on their courtship territories to see if they are similar or different from the species I observed. Additionally, it would be interesting to compare the territorial and courtship behaviors of the bee hummingbirds in Arizona to those of the non-bee hummingbird species, such as the Magnificent (*Eugenes fulgens*), Blue-throated (*Lampornis clemenciae*), and Broad-billed hummingbirds (*Cynathus latirostris*). Other work has found that Blue-throated Hummingbirds exhibit territorial behaviors (Ficken et al. 2002); however, further work is needed to understand whether these territorial behaviors or those of other species represent lekking or resource defense.

Understanding hummingbird territorial behaviors provides useful insight into their breeding biology. The ability for species to have different territorial behaviors suggests that species have adapted to their environments and available resources, which could illustrate how hummingbirds became so diverse across the United States and the Americas. Additionally, knowledge of hummingbird territory systems could help explain the diversity found in hummingbird signals (e.g. coloration, song, displays), as variation in mating systems has often partially explained diversity in animal signals (Dunn et al. 2015). Finally, hummingbirds are highly valued by the public and are unique and entertaining animals to observe, and collecting more information on these birds will continue to demonstrate just how exciting hummingbirds are.

ACKNOWLEDGMENTS

I would like to thank Dr. Kevin McGraw at Arizona State University for providing useful feedback on this project. I would also like to thank Linda Kennedy, Roger Cogan, Suzanne Wilcox, and Toney Leonardini from the Appleton-Whittell Research Ranch, Luke Reese from the Patagonia-Sonoita Creek Preserve, Amy Whipple and Paul Heinrich at Northern Arizona University, Susan and Tom Bean in Flagstaff, and Jessica Givens at Arizona State University's Tempe campus for their help and advice with locating field sites for Broad-tailed, Black-chinned, and Anna's hummingbirds. I would also like to thank Dr. Christopher Clark from the University of California-Riverside for his expertise in locating and studying hummingbird courtship behaviors. Finally, I would like to thank Doug Jenness, Arizona Field Ornithologists, and Sheri Williamson, Southeastern Arizona Bird Observatory, for their insightful and helpful comments on this manuscript. This work was supported by Arizona State University, the Animal Behavior Society Student Research Grant, the Society for Integrative and Comparative Biology Grants-in-Aid of Research, T & E Inc. Grants for Conservation Biology Research, and the Arizona Field Ornithologists Gale Monson Research Grant.

LITERATURE CITED

- Andersson, M. B. 1994. Sexual selection. Princeton University Press, Princeton, NJ.
- Baltosser, W. H., and S. M. Russell. 2000. Black-chinned Hummingbird (*Archilochus alexandri*). The Birds of North America (A. Poole, ed.). Cornell Laboratory of Ornithology, Ithaca, NY.
- Barash, D. P. 1972. Lek behavior in the Broad-tailed Hummingbird. The Wilson Bulletin 84:202–203.
- Bradbury, J. W., and S. L. Vehrencamp. 2011. Principles of animal communication. Sinauer Associates, Inc., Sunderland, MA.
- Camfield, A. F., W. A. Calder, and L. L. Calder. 2013. Broad-tailed Hummingbird (*Selasphorus platycercus*). The Birds of North America (A. Poole, ed.). Cornell Laboratory of Ornithology, Ithaca, NY.
- Clark, C. J., and T. J. Feo. 2010. Why do *Calypte* hummingbirds “sing” with both their tail and their syrinx? An apparent example of sexual sensory bias. The American Naturalist 175:27–37.
- Clark, C. J., T. J. Feo, and K. B. Bryan. 2012. Courtship displays and sonations of a hybrid male Broad-tailed × Black-chinned Hummingbird. The Condor 114:329–340.
- Clark, C. J., and S. M. Russell. 2012. Anna's Hummingbird (*Calypte anna*). The Birds of North America (A. Poole, ed.). Cornell Laboratory of Ornithology, Ithaca, NY.
- Dunn, P. O., J. K. Armenta, and L. A. Whittingham. 2015. Natural and sexual selection act on different axes of variation in avian plumage color. Science Advances 1:1400155.
- Endler, J. A., and M. Thery. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. The American Naturalist 148:421–452.
- Feo, T. J., and C. J. Clark. 2010. The displays and sonations of the Black-chinned Hummingbird (Trochilidae: *Archilochus alexandri*). The Auk 127:787–796.
- Ficken, M. S., K. M. Rusch, S. J. Taylor, and D. R. Powers. 2002. Reproductive behavior and communication in Blue-throated Hummingbirds. The Wilson Bulletin 114:197–209.
- Heindl, M., and H. Winkler. 2003. Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. Biological Journal of the Linnean Society 80:647–658.
- Hurly, T. A., R. D. Scott, and S. D. Healy. 2001. The function of displays of male Rufous Hummingbirds. The Condor 103:647–651.
- Jiguet, F., and V. Bretagnolle. 2014. Sexy males and choosy females on exploded leks: correlates of male attractiveness in the Little Bustard. Behavioural Processes 103:246–55.

- Koch, R. E., A. H. Krakauer, and G. L. Patricelli. 2015. Investigating female mate choice for mechanical sounds in the male Greater Sage-Grouse. *The Auk* 132:349–358.
- Ligon, J. D. 1999. *The evolution of avian breeding systems*. Oxford University Press, Oxford, UK.
- McGuire, J. A., C. C. Witt, J. V. Remsen, A. Corl, D. L. Rabosky, D. L. Altshuler, and R. Dudley. 2014. Molecular phylogenetics and the diversification of hummingbirds. *Current Biology* 24:1–7.
- Powers, D. R. 1987. Effects of variation in food quality on the breeding territoriality of the male Anna's Hummingbird. *The Condor* 89:103–111.
- Stiles, F. G. 1982. Aggressive and courtship displays of the male Anna's Hummingbird. *The Condor* 84:208–225.
- Tamm, S., D. P. Armstrong, and Z. J. Tooze. 1989. Display behavior of male Calliope Hummingbirds during the breeding season. *The Condor* 91:272–279.
- Temeles, E. J., and W. J. Kress. 2010. Mate choice and mate competition by a tropical hummingbird at a floral resource. *Proceedings of the Royal Society B: Biological Sciences* 277:1607–13.
- Zimmerman, D. A. 1973. Range expansion of Anna's Hummingbird. *American Birds* 27:827–835.

 *Accepted April 1, 2017*