

Vocal Dimorphism in Anna's Hummingbirds

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Ethics Statement

Integrity was our priority during data collection, analysis, and interpretation. All authors made intellectual contributions to this paper and reviewed the manuscript.

Data Availability Statement

Our supplementary data is supplied in files attached to this manuscript submission.

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Conflict of Interest

The authors declare no conflicts of interest.

Ethics Approval

Field data collection at the University of California Santa Cruz Arboretum & Botanic Garden and at the University of California Botanical Garden at Berkeley was approved by Dr. Daizaburo Shizuka and Dr. Rauri Bowie, respectively.

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Abstract

Whereas vocal sexual dimorphism is widespread amongst birds, it has been historically overlooked in non-passerines such as hummingbirds. By evaluating correlations among sex, behaviors, and vocalizations, the meaning and utility of intentional sound production may be inferred. Anna's Hummingbirds (*Calypte anna*) exhibit pronounced sexual dimorphism, with males being larger and having more vibrant coloration than females, but vocal dimorphism in the species is unstudied. A common vocalization of Anna's Hummingbirds is the chip note, which is produced by both sexes in a wide array of contexts. Here, we correlated temporal parameters of chip notes with individual sex and behavioral contexts gathered from field observations and audio recordings. The production rate of chip notes differed significantly between male and female hummingbirds but did not vary much with behavioral context. Although Anna's Hummingbirds produce chips across a broad spectrum of behaviors, dimorphic chip production may be important to territorial behavior.

Introduction

Vocal sexual dimorphism characterizes disparate animal taxa, from teleost fish to humans (Brantley et al., 1993; Puts et al., 2006). Extensive research into the mechanisms and function of vocal dimorphism in passerine birds (e.g., Arnold et al., 1986; Nowicki et al., 1998) demonstrates how sexual selection, territorial defense, and other factors can all influence sex-specific sound production. Although there is little literature on vocal dimorphism within the hummingbirds (Apodiformes), the striking morphological dimorphism in Anna's Hummingbirds is well characterized. Males boast an iridescent gorget and crown, whereas females have either reduced patches of iridescence on the throat or no iridescence at all. Males also surpass females by ~12.5% in body mass, with ~15% longer tails (Clark & Russell, 2020). Males differ behaviorally as well, engaging in diving displays during courtship during which they produce a sharp non-vocal squeak with their tail feathers at the lowest point of their dive (Clark & Feo, 2008).

Anna's Hummingbirds have a relatively small repertoire of vocalizations, including the chip note. A chip consists of a single syllable less than 0.1 s in duration covering a broad frequency band (Figure 1); these are often produced in bursts (Clark & Russell, 2020). Thus, measuring the interval between each chip is a simple way to investigate disparity in vocal

behavior between individuals. Chips are known to serve as alarm and contact calls in several passerines (Gill & Bierema, 2013; Piza & Sandoval, 2016), but contextual production of chip notes outside of the passerines is unstudied. There has been speculation that hummingbird chips serve as general contact calls, as well as expressions of excitement and territorial aggression (Stiles, 1971). For example, chip calls in both Rufous Hummingbirds (*Selasphorus rufus*) and Broad-tailed Hummingbirds (*Selasphorus platycercus*) were uttered during a chase (Camfield, 2006). Ewald and Bransfield (1986) found that Anna's Hummingbirds defended their territory from Black-chinned Hummingbirds (*Archilochus alexandri*), a less dominant species, by chipping instead of chasing, which may have conserved energy. Finally, female Anna's Hummingbirds have been observed hovering in front of predators near nest sites while producing a rapid series of chip notes (Stiles, 1973). These observations suggest that chip notes could serve both territorial and repellent functions, but such possibilities have not been systematically assessed.

Anna's Hummingbirds are generally highly territorial. They guard feeding, nesting, and courtship territories, depending on sex and the season (Clark & Russell, 2020). Males (and possibly females) perform ritualistic dives at intruders in their territory. In addition to the chip note, these birds produce both a gurgling song and a rough chatter call that function as territorial announcements. In non-physical territorial confrontations, hummingbirds produce rapid chip notes, chatter calls, and/or songs towards one other (Stiles, 1982; Ewald & Carpenter, 1978). Males also perform a gorget-flashing display to flying and perching rivals that often culminates in a chase and aerial fight. On rare occasions, these fights become deadly as hummingbirds can impale each other with their bills (Evens & Harper, 2020; Clark & Russell, 2020). As most studies on hummingbird territoriality focus only on males (Ewald & Bransfield, 1987; Ewald & Orians 1983; Powers, 1987; Stiles, 1982), there is a lack of information on territorial dimorphism in Anna's Hummingbirds outside of breeding and display contexts.

In this study, we behaviorally contextualized the rate of production of chip notes in Anna's Hummingbirds and recorded the sex of focal individuals to assess potential acoustic dimorphism. We found that, whereas chips did not vary substantially with behavioral context, there was an overall sexually dimorphic effect on chip production rate.

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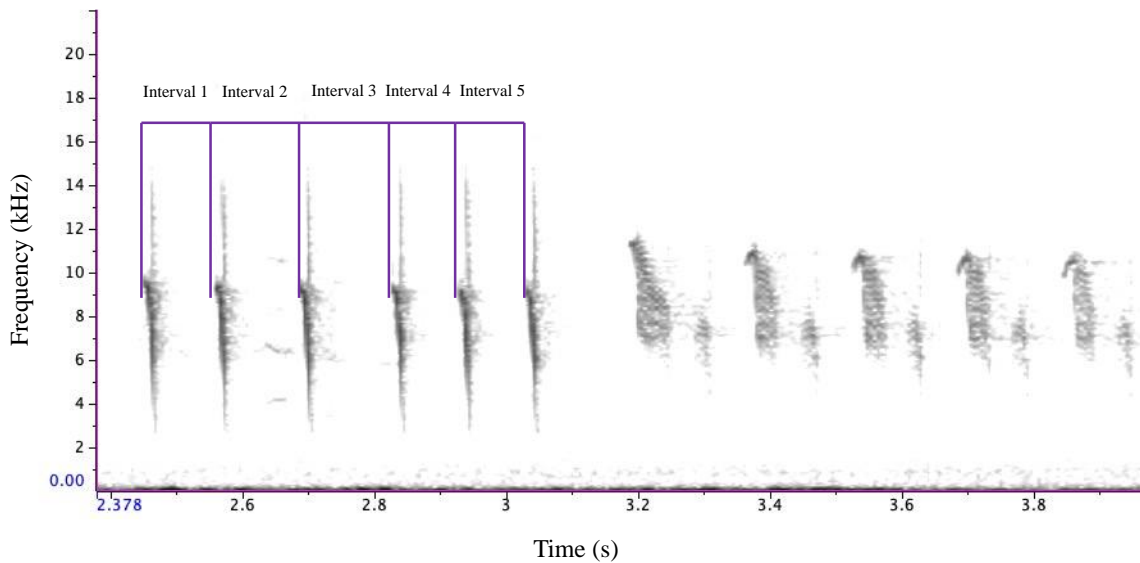


Figure 1: Spectrogram generated in Raven Pro 1.6 of six consecutive chip notes preceding a chatter call made by an Anna’s Hummingbird. Chip Intervals are measured between the beginning of each chip note.

Methods

Field Observations

From November 2022 to March 2023, we conducted twenty rounds of field observations to collect audio recordings (with average duration of 1 hour) between 10:00 and 18:00. We observed hummingbirds at three different locations, all within the boundaries of University of California (UC) grounds: (1) UC Santa Cruz Arboretum & Botanic Garden, (2) UC Berkeley campus, and (3) UC Berkeley Botanical Garden. The UC Santa Cruz Arboretum & Botanic Garden, our main sampling location, is a 135-acre garden primarily featuring plants from Mediterranean climates (Grumbine, 2010). Within the UC Berkeley campus, we most often frequented a stand of eucalyptus trees near the Foothill Dormitory parking lot where many hummingbirds gathered to feed on eucalyptus flowers. The UC Berkeley Botanical Garden covers 30 acres with plants from around the world. All three sites represent either urban or otherwise modified areas where hummingbirds are acclimated to human presence, and these results may thus not apply to wildland hummingbirds (Patankar et al., 2021; Webster & Rutz, 2020).

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Birds were tracked both visually and acoustically at study sites. When possible, we recorded chip vocalizations of focal birds using an Olympus LS-10 recorder. While we collected audio recordings from a focal bird, we also noted behaviors associated with feeding, mobility, and territoriality, as based on an ethogram (Table 1). The initial ethogram used in the field was broader than Table 1, but some behaviors with few representations were either pooled with other behaviors or were removed from the dataset. For example, behaviors such as post-chasing, chasing, and being chased were pooled into an aggregated variable termed Chasing. We also recorded bird sex, classifying birds with substantially iridescent gorgets as male, intermediate to small gorgets as unknown (i.e., subadult male or female), and insubstantial or no gorgets as female (see Clark & Russell, 2020).

Behavioral Category	Behavior	Definition
Feeding	Eating	The hummingbird is stationary at one food source such as a flower, or is moving between food sources in close proximity.
	Not Eating	The hummingbird is not Eating.
Mobility	Perching	The hummingbird is stationary, with one or both feet on a substrate such as a branch.
	Flying	The hummingbird is moving through the air.
	Perching & Flying	The hummingbird displays both Perching and Flying behaviors during the recorded period.
Territoriality	Chasing	The hummingbird is Flying close behind or in front of another hummingbird.
	Confronting	The hummingbird is either facing or glancing frequently at another hummingbird while chipping.
	During or After Territorial	The hummingbird pauses or ends a song and/or chatter call known to

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	Announcement	function in territorial defense (Stiles, 1982; Ewald & Carpenter, 1978)
	None	The hummingbird is not in the vicinity of other hummingbirds, and is not performing any of the aforementioned territorial behaviors.
	Unknown	The hummingbird is in the vicinity of other hummingbirds, but is not engaged in overtly territorial behavior.

Table 1: Ethogram of behaviors occurring concurrently with chips.

Acoustic Analysis

Audio recordings were analyzed in Raven Pro 1.6 to determine intervals between chip notes. Among 198 observations of chipping bouts, we collected 170 recordings. We analyzed 126 out of these recordings, as some were discarded due to low quality. For example, in some recordings, multiple hummingbirds were chipping simultaneously and could not be individually differentiated. These recordings were discarded, many of which represented Confronting behavior.

In Raven Pro 1.6, we used an Interactive Detector to find the start times of each chip note. Typically, we set the detector to make audio selections at a minimum frequency of 8000 Hz, a maximum frequency of 10000 Hz, a minimum duration of 0.01 s, a maximum duration of 0.1 s, and minimum separation of 0.05 s. We also set minimum occupancy to 40%, signal-to-noise-ratio threshold to 11 above, the block size (background noise sample duration) to 2 s, and the hop size (recalculation period of background noise) to 1 s. If the detector was consistently misidentifying chips (e.g., making selections on background noises), the settings were adjusted to yield a more consistent outcome. When necessary, we manually adjusted chip selections.

Data Analysis

To derive rates of chip production, we measured temporal intervals between the start of each chip note using measurements from the Interactive Detector, along with manual selections. Intervals were measured in seconds from the start of one chip call to the start of the next (see

Figure 1). Recordings with fewer than ten chip notes tended to have inconsistent and outlying intervals, and we eliminated these from the dataset, along with recordings with insufficient information as to behavioral context. A total of 106 recordings were thus derived for analysis.

We organized all chip intervals in correspondence to their source recording files. Some recordings also featured long breaks in chipping after a burst (e.g., due to a feeding event). To avoid such long breaks skewing the data, we excluded the highest 5% of all measured intervals from the analysis. Also, to avoid overrepresentation of data within longer recordings, intervals within each recording were averaged.

To correlate chip intervals with sex and behavioral category, we ran a Gamma distributed Generalized Linear Mixed Model (GLMM) using the ‘glmmTMB’ function in the package glmmTMB in R version 4.2.2 (Brooks et al., 2017; R Core Team, 2022). The significance threshold was set to $p = 0.05$. Model fit was assessed with the ‘qqplot’ and ‘qqline’ functions (R Core Team, 2022). The response variable of the GLMM was the chip interval, and the fixed variables included sex, territorial behavior, mobility state, and feeding behavior. Territorial behaviors analyzed included Chasing, Confronting, During or After Territorial Announcement (DAT), None, and Unknown (Table 1). If a confrontation resulted in a chase, it was classified as Chasing. Random factors included the study area (UC Berkeley campus, UC Berkeley Botanical Garden, and the UC Santa Cruz Arboretum & Botanic Garden), along with the species of hummingbird interacting with the focal chipping bird, when present and identified (i.e., either Anna’s Hummingbird or Allen’s Hummingbird; see Table 2). To assess potential differences in territorial behavior between sexes, we ran a Chi-Squared test using the ‘chisq.test’ function in base R (Brooks et al., 2017; R Core Team, 2022) (Table 3). The During or After Territorial Announcement (Table 1) behavior was excluded from this analysis because it was only exhibited by males.

Results

Chip intervals for male and female birds differed significantly ($z = -3.852$, $p < 0.001$) (Table 4), with males chipping on average 1.4 times faster than females (Table 5). Unknown-sex birds had significantly different chip intervals than males ($z = -2.387$, $p = 0.017$), but did not differ significantly from females ($z = 1.586$, $p = 0.113$). When adjusted for multiple hypothesis testing, there was a significant difference ($p = 0.034$) between unknown-sex versus male chip

intervals. Additionally, hummingbirds making chip notes During or After Territorial Announcement (DAT) chipped significantly faster than those chipping during a chase ($z = -2.026$, $p = 0.0428$). No other behaviors exhibited significantly different chip intervals (Table 4). We could not detect significant differences in territorial behavior between the sexes, based on the Chi-Squared test ($6, N = 93$) $X^2 = 10.349$, $p = 0.11$.

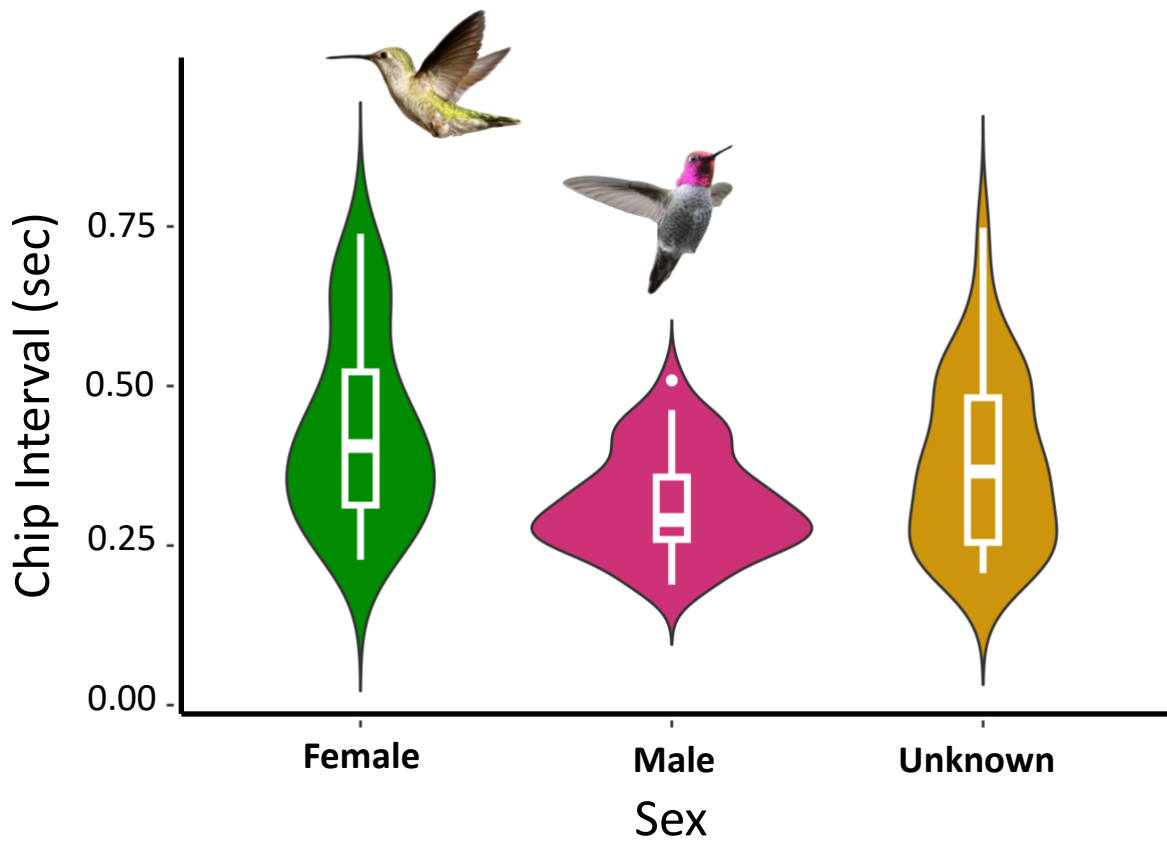


Figure 2: Violin plot displaying variation in chip interval as a function of sex. The colored area displays the data distribution, and box plots indicate the interquartile range and median. Males chipped significantly faster (i.e., had shorter chip intervals) than females.

Groups	Variance	STD Deviation
Location	1.62E-11	4.02E-06
Species	6.45E-12	2.54E-06

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Table 2: Table of GLMM results for the random variables (i.e., conditional effects).

Behavior	Male	Female	Unknown
Chasing	7	3	2
Confronting	6	1	6
None	1	5	2
Unknown	21	17	22

Table 3: Count of territorial variables for each sex classification. The During or After Territorial Announcement was excluded as no females displayed this behavior.

Fixed Effects	Categories	Estimate	SE	Z-score	p
Intercept		0.77	0.11	-7.13	<0.001
Sex	Male (ref. Female)	-0.30	0.08	-3.85	<0.001
	Unknown (ref. Female)	-0.13	0.08	-1.59	0.113
Eating	Not Eating (ref. Eating)	0.19	0.13	1.54	0.125
Territorial	Confronting (ref. Chasing)	-0.04	0.12	-0.31	0.758
	During or After Territorial Announcement (ref. Chasing)	-0.24	0.12	-2.03	0.043
	None (ref. Chasing)	-0.15	0.14	-1.04	0.300
	Unknown (ref. Chasing)	-0.08	0.09	-0.88	0.377
Mobility	Perching (ref. Flying)	-0.14	0.14	-1.02	0.310
	Perching & Flying (ref. Flying)	-0.16	0.11	-1.44	0.150

Table 4: Table of GLMM results for the fixed variables. Significant results are in boldface.

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Categories	N	Mean Chip Interval	Standard Deviation
Male	41	0.32	0.08
Female	26	0.43	0.15
Unknown Sex	39	0.38	0.13
Eating	46	0.35	0.14
Not Eating	60	0.38	0.12
During or After Territorial Announcement	13	0.30	0.09
No Territoriality	8	0.36	0.12
Unknown Territoriality	60	0.37	0.13
Chasing	12	0.40	0.14
Confronting	13	0.38	0.12
Perching	44	0.38	0.12
Perching & Flying	25	0.34	0.11
Flying	37	0.37	0.15

Table 5: Number of measurements, mean chip intervals, and standard deviation of each sex and behavior variable.

Discussion

Male Anna's Hummingbirds produced chip notes around 1.4 times faster than females (Figure 2). Additionally, unknown-sex birds chipped significantly more slowly than males, suggesting that the unknown-sex sample was more heavily weighted towards females.

Hummingbirds chipping DAT tended to chip faster than those displaying the Chasing behavior, possibly because only male hummingbirds chipped DAT. Hummingbirds made chip

vocalizations in all observed behavioral contexts, including perching, flying, feeding, gleaning, DAT, defending territory, chasing, retreating, bathing, preening, mobbing, and when attacking heterospecific hummingbirds. Chip calls of Anna's Hummingbirds are thus more broadly expressed than are chips in other passerines (Gill & Bierema, 2013; Piza & Sandoval, 2016).

In contrast to the finding of sexual dimorphism, there was no significant relationship between territorial behavior and chip rate. Furthermore, we could not detect any difference in territorial behavior between males and females. Nevertheless, we cannot rule out the possibility that vocal behavior is confounded by territorial dimorphism, given our relatively small sample size of territorial hummingbirds. In the Rufous Hummingbird (*Selasphorus rufus*), males must be territorial to gain body mass, whereas non-territorial females gain mass at the same rate as territorial females (Carpenter et al., 1993). Thus, it is crucial for males to hold territory to survive. In Rufous Hummingbirds, males are more dominant than females of comparable ages, possibly for this reason of energy maintenance (Carpenter et al., 1993). If this pattern in territorial dimorphism also occurs in Anna's Hummingbirds, then heightened male territoriality may be manifested via chip production, which can be a low-energy form of territorial defense (Camfield, 2006; Ewald & Bransfield, 1986).

Lethal territoriality has also been reported in Anna's Hummingbird males (Evens and Harper, 2020). Perhaps because physical conflict may result in injury or death, males often rely on chip notes for intimidation (Camfield, 2006; Ewald & Bransfield, 1986). Ewald and Orians (1983) found that immediately after feeding, birds were more likely to chase off intruders using the low-energy gorget-flashing display, rather than engaging in a chase. By contrast, an instance of lethal territoriality between two male Anna's Hummingbirds was observed in near-freezing conditions that presumably limited nectar availability (Evens & Harper, 2020). Our study sites were characterized by abundance of nectar-bearing flowers, and chipping may have been a preferred means of advertisement for territorial and well-fed birds. The higher chip rate of males may thus derive from increased territoriality in comparison to females, along with an abundance of nectar that could de-incentivizes more intense forms of territorial aggression.

Some limitations pertain to the methods used in this study. Our data over-represented feeding behavior given observer bias toward recording at flowers. Additionally, our observations took place in heavily human-modified environments. The urban Berkeley campus is characterized by significant amounts of impervious surface cover, anthropogenic noise, and

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human subsidies (Shultz et al., 2012). The arboreta contain primarily non-native plants, many of which occur on continents where hummingbirds are not present; the UC Santa Cruz Botanic Garden & Arboretum is particularly characterized by a high hummingbird density. Conspecific density, urbanization, and atypical flora are all known to affect bird behavior, including vocalizations (Patankar et al., 2021), so our findings may not apply to hummingbirds in wildland habitat (Webster & Rutz, 2020). Seasonality may have also affected hummingbird behavior, as our study overlapped both the breeding and non-breeding seasons for the study species (Fink et al., 2022; Powers, 1987). Despite these limitations, our study contextualizes Anna's Hummingbirds chip notes, and documents sexual dimorphism in this acoustic trait.

A more targeted study may investigate associations between territorial behaviors and chip production rates, as the broad behavioral sampling used here was not specific to this end. We also averaged chip intervals across each recording, whereas a more detailed temporal analysis of spacing between chips may reveal greater signal structure. Overall, further characterization of chip notes relative to territoriality may reveal additional dimorphic features of acoustic behavior among the highly agonistic hummingbirds.

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