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Acknowledgements

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Evaluating the Effect of Time of Day on Singing Behavior in Anna's Hummingbirds

Adrian D. Macedo^{1*}, Maxine R. Mota²

KEYWORDS—behavior, birds calls, *Calypte anna*, hummingbirds, Pacific Northwest, bird song

INTRODUCTION—Sexual selection has driven the evolution of numerous strategies to attract mates. In songbirds, the most recognized method is the intricate behaviors of song production. However, there are other factors that also influence song behavior in birds. It has long been observed that songbirds put forth the most singing effort during dawn and dusk. Reasons for this temporal pattern in song have raised many hypotheses, such as singing at different times of day may possibly minimize interspecific acoustic interference (Cody and Brown 1969). Alternatively, songs are carried farther and clearer during the dawn and dusk, termed the acoustic transmission hypothesis (Henwood and Fabrick 1979). Empirical support for these hypotheses is equivocal, as they have been supported in some studies but not in others (Keast 1994; Catchpole and Slater 1995; Staicer et al. 1996; Brown and Handford 2002; Dabelsteen and Mathevon 2002).

We wanted to determine if the dawn/dusk pattern is used by non-passerines such as hummingbirds. This temporal pattern in song has been studied in the lekking behavior of white-bellied emeralds (*Amazilia candida*) and Swallow-tailed hummingbirds (*Eupetomena macroura*) (Atwood et al. 1991; Pizo and Silva 2001). Lekking is when the males of one species get together in one area to advertise for mates. Although they do not exhibit lekking, Anna's hummingbirds (*Calypte anna*) employ song, dipping, and shuttle display behaviors in their mating rituals. The effect of time of day on the singing behavior of Anna's hummingbirds has not been described in detail. Perhaps Anna's hummingbirds also sing more frequently at dawn and dusk like the swallow-tailed hummingbirds, white-bellied emeralds, and numerous other birds, or perhaps there is no temporal effect on their singing behavior.

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The Anna's hummingbird is a 3–6 g, medium-sized hummingbird with a straight shortish bill and a broad tail (Russell 1996). When perched, their wingtips meet the tip of their short tails (Russell 1996). Their color pattern is composed mostly of green and gray plumage, without any rufous or orange marks on the body (Russell 1996). Males have iridescent reddish-pink feathers covering their head and throat; this area is referred to as a gorget (Russell 1996).

In the first half of the 20th century, the Anna's hummingbird bred only in northern Baja California and southern California. The planting of exotic flowering trees in gardens and other human-populated areas provided food and nesting resources that have allowed Anna's hummingbirds to expand their range north, as far as British Columbia (Russell 1996). Their primary food source is nectar from flowering plants including currants and gooseberries (*Ribes* spp.), manzanita (*Arctostaphylos* spp.), introduced eucalyptus (*Eucalyptus* spp.), and many others (Russell 1996). They also eat a wide array of smaller insects (Russell 1996).

Behavioral aspects of the male Anna's hummingbird include territoriality, in which resident males will defend a particular area throughout the year (Woods 1940;

Pitelka 1942). They defend this area to protect food and breeding resources (Ewald and Carpenter 1978; Ewald and Bransfield 1987). Behaviors often associated with territorial defense include chasing, display dives, aggressive vocalization, and chatter-sway. The display dive involves a male hummingbird flying upwards of 740 m then diving toward the ground making a sharp chirp sound by pushing wind through its tail feathers (Bent 1940; Banks and Johnson 1961; Clark and Feo 2008). The chatter-sway occurs before chasing an intruder, by vocalizing and swaying back and forth while perched to warn intruders (Stiles 1982).

The behaviors associated with mate attraction include those used in territorial defense (chasing, display dives, and song vocalizations), but shuttle displays are used only in mate attraction. The display dive is generally an aggressive behavior, however is sometimes used to attract a mate (Stiles 1982). Song vocalization to attract mates is distinctly different than aggressive vocalizations (Stiles 1982). Shuttle displays are characterized by the male hovering in front of the female and flying rapidly back and forth in tight arcs while singing (Stiles 1982).

The aim of our study was to test the effect of time of day on the number of songs performed per unit of time (NSPT) in Anna's hummingbirds. We tested the hypothesis that time of day influences the NSPT of Anna's hummingbirds. We predicted that Anna's hummingbirds would follow a pattern of dawn/dusk singing similar to many passerines. If they do follow this pattern, then we would expect to find a higher frequency of song in the morning and evening hours of the day.

METHODS—Study area. We conducted our study on the Humboldt State University (HSU) campus and in the surrounding neighborhoods of Arcata, California, located in the Pacific Northwest region of the USA. Temperatures in Arcata average 7–15 °C over the year with an average rainfall of 101 cm per year. Our study was carried out from March to April, during the middle of the breeding season for the Anna's hummingbird (Woods 1940). The study area is in a semi-urban environment consisting mainly of human infrastructures such as large buildings, roads, and houses. However, there are many pockets of vegetation scattered throughout the area. The types of vegetation within this study area vary greatly as most of the plant communities are the result of intentional planting by humans for ornamental value and food production. Some

of the more common plant families found in the study area include Rosaceae, Ericaceae, Pinaceae, and Liliaceae. Humboldt State functions as a college campus and has a high amount of human activity during the daytime hours when students and other community members make use of the resources available on campus. This also means that there is a great deal of pedestrian and motor traffic throughout the surrounding neighborhoods as people make their way to and from campus. The eastern border of the study area consisted of the Arcata Community Forest (ACF), a mixed-conifer forest dominated by coastal redwood (*Sequoia sempervirens*), and private property, which is of the same forest type as the ACF. We designated the other borders of the study area using K Street/Alliance Avenue as the western border of the study area while the southern border was Samoa Boulevard. The northern border was the Mad River (FIG 1).

Field observation. To gather data on the singing behavior of Anna's hummingbirds, we conducted focal animal observations of male Anna's hummingbirds during different times of the day in order to see if there was a difference in the number of songs performed at different hours. In order to locate male Anna's hummingbirds, we conducted pre-study surveys of the study area looking for males and listening for the distinctive mate attraction

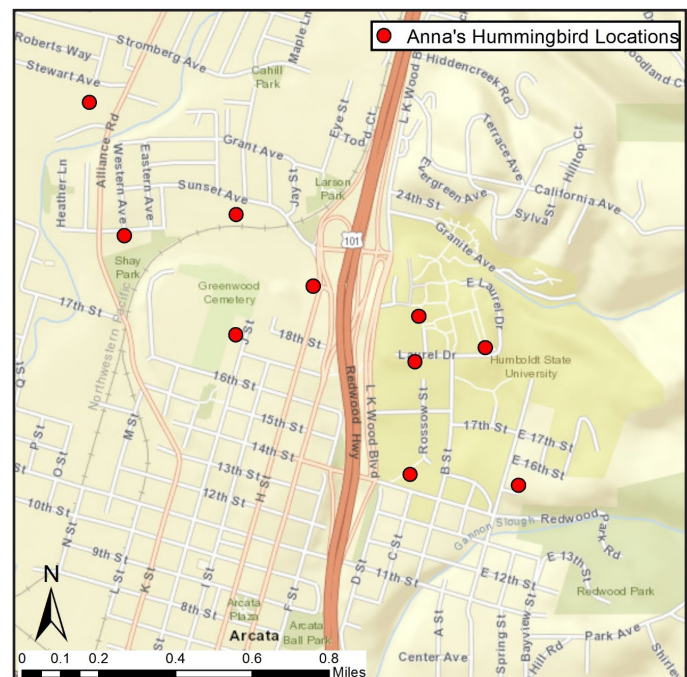


FIGURE 1. Individual male Anna's hummingbird locations in Arcata, northern California, USA.

vocalizations. At each place where a male hummingbird was positively identified, we marked and numbered 10 sites on a map for use during the study. Each site was at least 50 m from other sites, so it could be considered a separate individual male hummingbird as some male hummingbirds can have core territory areas up to 2,023 m² (Pitelka 1951).

When choosing a focal bird to observe for the day, we randomly chose a hummingbird site from among all sites using a random number generator. We then went to the site and attempted to locate the hummingbird within 15 min of arrival. If the bird was not located within 15 min, then we randomly chose another site for observation. If the bird was located within 15 min, we started a stop-watch within 1 min of locating the bird either by sight or sound. We continuously recorded each song vocalization event that happened within a 15-min time frame at the site at three different times throughout the day: morning (7am–9am), midday (12pm–2pm), and evening (5pm–7pm). The song vocalization events that happened during the observation period were then quadrupled to give us an estimate of the number of songs per hour, analogous to NSPT. A new site was randomly chosen each observation day until all hummingbird sites were observed at least once at each of the three chosen times.

We also recorded weather, temperature, time, and date during each observation. Weather was categorized as sunny, partly cloudy, overcast, or light rain. We did not conduct surveys during conditions considered heavy rain due to the lack of visibility. Additionally, we worked under the assumption that most hummingbirds would not be active during heavy rain due to the significant increases in the energy needed for flight during heavy rain (Ortega-Jimenez and Dudley 2012).

We analyzed the data by using time of day as an independent variable and song vocalization frequency as a dependent variable. We completed one survey of each individual at each of the time categories. The NSPT for morning, midday, and evening had a normal distribution and equal variances according to Levene's test and Shapiro-Wilk normality test, therefore an ANOVA test was used.

RESULTS—A total of 10 individual male Anna's hummingbirds were observed in their territories for a total of 150 min for all time groups from 1 Mar 2017 through 5 Apr 2017. Average NSPT was greater in the morning and

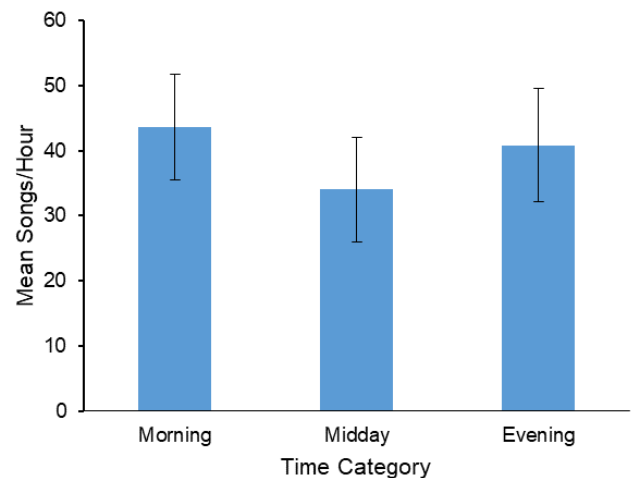


FIGURE 2. Overall mean number of songs per hour (\pm SE) of Anna's hummingbirds ($n = 10$) during different times of day (morning, midday, evening) in Arcata, CA, USA, 19 Apr 2016.

the evening compared to average NSPT at midday, however these differences were not significant (**FIG 2**). Time of day did not have a significant effect on the pattern of NSPT within our sample population ($F = 0.355$, $df = 2$, $P = 0.704$).

DISCUSSION—We surveyed male Anna's hummingbirds throughout a semi-urban area at different times of day to see the effect that time of day had on NSPT. Overall, our results do not support our hypothesis that Anna's hummingbirds will have a significantly greater NSPT during the morning and evening than during midday. Despite observable differences in NSPT between the time categories, the differences were not statistically supported. These results may be due to the sample size, confounding variables, and variation in the breeding behavior among different male hummingbirds. Other possible variables that may have confounded our results was variation in breeding effort over the survey period, weather conditions, and temperature. There was observable variation among individual's NSPT, with some birds singing more than others (**FIG 3**). Some males sang much more frequently; for example, bird 9 had a maximum NSPT of 88 compared to bird 5 who's maximum NSPT was one. This variation in NSPT could be related to a difference in testosterone levels among males, causing some to sing more and others to sing less. This has been experimentally tested in Bengalese Finches. Males of this species who have higher levels of testosterone sang more

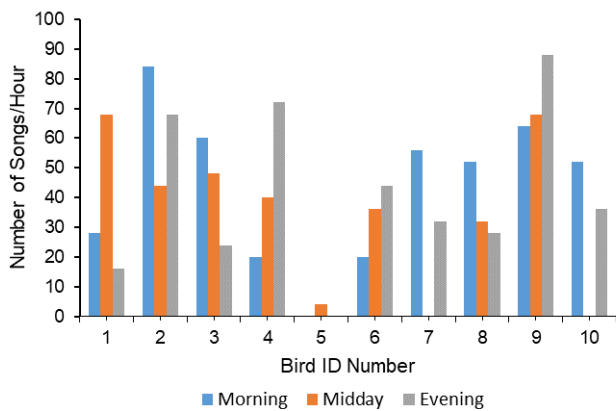


FIGURE 3. Number of songs per hour (\pm SE) of individual male Anna's hummingbirds ($n = 10$) during different times of day (morning, midday, evening) in Arcata, CA, USA, March–April 2016.

than birds with less testosterone (Ritschard et al. 2011). Survey date, specifically when the periods were split between the weeks of 10 Mar 2017 through 19 Mar 2017 and 26 Mar 2017 through 5 Apr 2017, experienced a significant decline in number of songs per hour between the two periods ($t = 2.9738$, $df = 14.606$, $P = 0.009687$) using a Welsh two-sample t-test (FIG 4). Therefore, this significant change in breeding effort is a valuable finding and may explain the minimized response of time of day on NSPT. There were no observable patterns in the NSPT of Anna's hummingbirds in different temperature and weather conditions. This was likely because there were more sampling periods in overcast weather than other conditions, and temperature stayed between 12 °C and 15 °C with less variation. Given a larger data set with more variation and an even distribution of weather observations and temperature, we would have more evidence to identify stronger trends with weather and NSPT (FIG

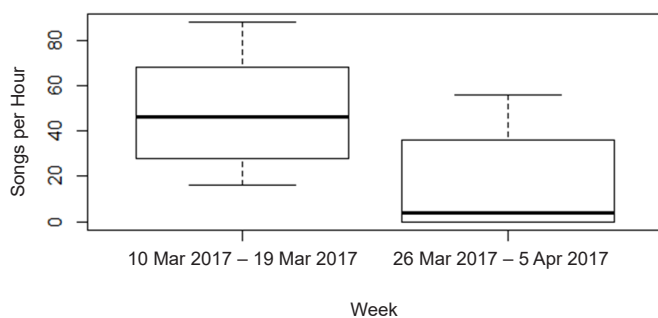


FIGURE 4. The mean number of songs per hour of Anna's hummingbirds ($n = 10$) during the data collection period in Arcata, CA, USA, March–April 2016.

5). Temperature may also have influenced NSPT, but we were unable to analyze this trend as we did not record temperature for all our observations (FIG 6).

These results suggest that males reduced their territorial defense and attempts to attract mates over the course of the breeding season. This has not been studied much in hummingbirds, but our observations suggest that as it gets later in the season, there is a decrease in male song vocalizations and dive displays to attract mates. This has been the case in passerines such as Stonechats (*Saxicola torquata*), which stop singing completely once hatchlings have emerged and females are no longer receptive to breeding (Greig-Smith 1982).

As with all studies, a large sampling size and sample replication are often required to minimize the effects of biases and confounding variables. For greater statistical power we would need to increase our sample size to encompass a larger portion of the male Anna's hummingbirds that live within Arcata as well as a larger sample size of weather types, temperatures, and over a longer course of time.

Although our hypothesis was not significantly supported, there is a trend toward male Anna's hummingbirds having little daily temporal selection pressure—they sing throughout the day with no concentration of song behaviors during a certain period of the day. This could be due to a lack of acoustic interference and miss-transmission at the sites where the hummingbirds were observed. Further research is needed to confirm our results, which could then be used within bird conservation, especially with similar but more cryptic species such as South American hummingbirds.

MANAGEMENT IMPLICATIONS—Knowledge on

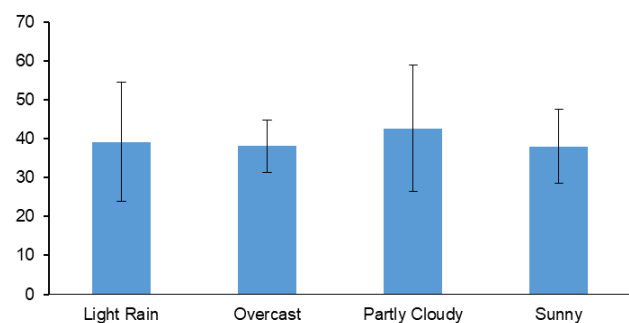


FIGURE 5. The mean number of songs per hour (\pm SE) of Anna's hummingbird ($n = 10$) during different weather conditions in Arcata, CA, USA, March–April 2016.

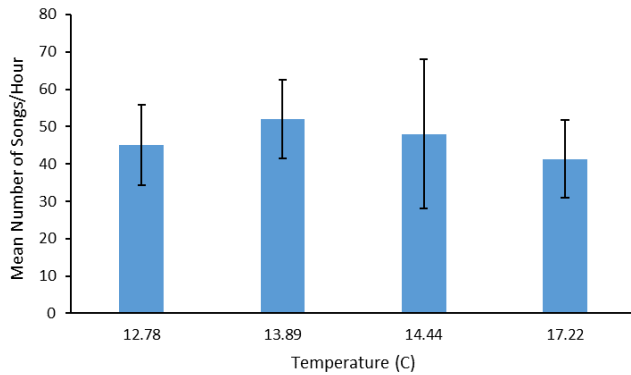


FIGURE 6. The mean number of songs per hour (\pm SE) of Anna's hummingbirds under the effect of varying temperatures in Arcata, CA, USA, March–April 2016.

the mating behaviors of a species is vital to wildlife managers when they are attempting to create appropriate species management plan. This is especially important in areas that have high amounts of human noise, which may disturb the breeding behavior of bird species that rely on acoustic transmission (Patricelli and Bickley 2006). Even though it was not statistically supported, there were differences in the frequency of song of Anna's hummingbirds throughout the day, with more singing during the morning and evening than at midday. Additionally, the frequency of song overall significantly decreased across the survey period indicating that there is more breeding effort during early March compared with later in the season in Arcata, CA. This suggests that certain times of the year and day are used for completing most mating activities. While the Anna's hummingbird is not a threatened species, for a hummingbird species of concern, it may be important to minimize disturbance during peak breeding times to increase the chances of successful breeding. However, further studies must be done to confirm when most breeding activities occur for other hummingbirds as there could be variation within different species that would require different management strategies.

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Responses of *Bouteloua eriopoda* and Soil Stability to Precipitation Extremes in Chihuahuan Desert Grassland

Laura K. Sadorf^{1*}

ABSTRACT—Climate change is expected to increase the frequency and duration of extreme dry and wet years. As water is the most limiting resource in these semi-arid deserts, it is important to understand how semi-arid plants respond to precipitation changes, given that climate change will alter desert ecosystems in the future. To study these responses, I applied an extreme precipitation treatment (10 mm water twice per week) to a *Bouteloua eriopoda*-dominated desert grassland preceding the 2018 monsoon season. I measured soil moisture, soil stability, and vegetative growth of *B. eriopoda* within treatment and control plots, which received no water addition. While two natural rain events increased *B. eriopoda* growth in all plots, growth was significantly increased in response to the extreme precipitation treatment. Yet, control plots responded more quickly to natural rain pulses than continuously watered plots. Soil stability was not correlated with total cover of *B. eriopoda*. Soil stability was also measured at two adjacent long-term precipitation manipulation experiments. In comparison with this experiment, soils were more stable at watered plots in a long-term monsoon rainfall addition experiment and control plots in a long-term drought experiment. These results indicate that extreme precipitation events are beneficial for *B. eriopoda*-dominated grasslands, and *B. eriopoda* is especially responsive to rain pulses between dry periods. Further investigation is needed to determine the interaction between *B. eriopoda* and soil stability, which may provide insight for future success of this dominant desert grass.

KEYWORDS—*black grama*, *Bouteloua eriopoda*, phenology, soil stability, precipitation, semi-arid, pulse-dynamics, productivity

INTRODUCTION—Global climate models predict a more variable climate in the future, including increased frequency of extreme wet and dry years (Knapp et al. 2015). Currently, extreme wet years are rare, and their impacts should be documented through means other than modeling, such as experimental approaches (Knapp et al. 2015; Knapp et al. 2017). Many studies describe sporadic rainfall events via the pulse-dynamics paradigm (Ogle & Reynolds 2004; Reynolds et al. 2004; Thomey et al. 2011; Báez et al. 2013; Collins et al. 2014; Petrie et al. 2014; Thomey et al. 2014). Noy-Meir (1973) first described pulse-dynamics in arid land ecosystems as the biological processes that result after a rainfall event. This refers to sporadic rain events that drive biological responses of plants, such as growth and reproduction (Ogle & Reynolds 2004). More recently, the pulse-reserve paradigm is defined as rain pulses that drive biological activity resulting in a resource reserve, such as biomass or available nutrients (Collins et al. 2014). This reserve is important for driving plant responses well after a rain event (i.e. pulse) has

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occurred (Collins et al. 2014). According to Reynolds et al. (2004), a “pulse” is categorized as a collection of events that are capable of recharging soil water for a significant portion of the season. For example, plant productivity in semi-arid ecosystems responds rapidly to rainfall pulses, and thus is driven by pulse dynamics. Productivity during the growing season is therefore a function of the frequency and intensity of precipitation events (Reynolds et al. 2004; Collins et al. 2014), which are predicted to become more extreme under climate change (Knapp et al. 2015).

Many studies have looked at pulse-reserve dynamics