



Differences in daily singing routines reflect male condition along a montane gradient

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Abstract

Vocal communication is used across taxa to convey a range of information. One of the most well-studied vocal behaviors is the song of temperate passerine birds. Among individuals, male song differs across numerous acoustic parameters, many of which are used by females to assess male quality. Males in better condition often produce higher song output and start singing earlier in the day compared to other males. However, the energetic cost of singing varies throughout the day and may be affected by the singer's foraging abilities. Along an elevation gradient, harsher environmental conditions at higher elevations shape foraging abilities in mountain chickadees (*Poecile gambeli*), which are non-migratory food hoarders. High-elevation mountain chickadees exhibit superior spatial cognitive abilities and a higher propensity to cache food, which enables them to forage more efficiently, compared to lower elevation birds. High-elevation males may therefore be able to produce higher song output, especially earlier in the day, than low-elevation males. We compared the daily singing routines of male mountain chickadees inhabiting high and low elevations. We found no difference in total daily song output between elevations; however, high-elevation males sang significantly more than low-elevation males at dawn, when singing is both crucial for reproductive opportunities and most costly due to overnight fasting. Song output at dawn may therefore act as an indicator of condition in male mountain chickadees.

Significance statement

Animals communicate across modalities to exchange information about foraging, predators, and movements. Researchers have studied the vocalizations of songbirds to understand how individual variation affects the behavior of receivers, particularly regarding male song and female mating preferences. The song of many songbirds is learned locally and contains information about the location of origin and respective selective pressures. We tested whether natural access to food via food cache recovery was associated with daily singing routines in food-caching birds. Singing at dawn is thought to be costly as it follows overnight fasting. We found that birds from harsher environments—where selection for enhanced spatial cognitive abilities required for cache retrieval is much stronger—sing more at dawn compared to males from milder environments, where selection on spatial cognition is relaxed. This work shows that environmental selection pressures affect signal production in male songbirds, which may provide information to females during mate choice.

Keywords Song output · Male condition · Food availability · Elevation gradient · Mountain chickadee

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Introduction

Acoustic signals are used across taxa to convey a range of information, including predator presence, foraging locations, movement, and mate condition. Male passerine birds sing to defend their territories and attract mates (Krebs et al. 1978; Searcy 1984; Collins et al. 1994), and females can use the information contained in male song to assess male condition. Passerine females show a preference for males who exhibit larger song repertoires, consistency between songs, higher complexity and performance, and higher total song output (Mountjoy and Lemon 1996; Otter et al. 1997; Drăgănoiu et al. 2002; Ballentine et al. 2004; Byers 2007). For example, higher daily song output has been associated with males who are in better condition and hold higher-quality territories relative to other males (Yasukawa 1981; Hutchinson et al. 1993; Beani and Dessì-Fulgheri 1995). However, daily song output may not always be a reliable indicator of condition because the cost of singing is not consistent throughout the day (Thomas 1999). It is arguably more costly to sing at dawn than at other times because dawn follows the longest period of fasting for birds, who hold relatively limited fat reserves (Bednekoff and Houston 1994; McNamara et al. 1994; Thomas 1999). Previous research indirectly supports this idea, as supplemental feeding increases song output, particularly at dawn (e.g. Reid 1987; Strain and Mumme 1988; Thomas 1999; Berg et al. 2005; Grava et al. 2009), suggesting that food availability is a limiting factor on song output.

While studies have shown the effects of food availability on song output at dawn using supplemental feeding experiments (Strain and Mumme 1988; Berg et al. 2005; Grava et al. 2009), heterogeneous environments provide a natural experiment to test functional hypotheses related to food availability, foraging efficiency, and song output (e.g. Grava et al. 2012). Variation across environments can create differential habitat quality or food availability (Grava et al. 2012), resulting in differential selective pressures (Endler 1986; Kingsolver et al. 2001; Futuyma 2005). For instance, montane ecosystems exhibit predictable decreases in ambient temperature and increases in snow cover as altitude increases, resulting in a stronger selection on ecologically relevant traits at higher elevations compared to lower elevations (Barbour and Minnich 2000; Kozlovsky et al. 2018). One such ecologically relevant trait is food hoarding in non-migratory animals, which has evolved to combat the effects of limited or unpredictable food availability (reviews in Sherry 1989; Vander Wall 1990). Food-caching animals gather and store food when it is abundant (e.g., summer, fall) to be used later when food is scarce (e.g., winter). Harsher environments, such as

higher elevations and latitudes, select for individuals that cache more food and are the most successful at recovering their food stores, providing a buffer against the negative effects of low food availability (Vander Wall 1990; Pravosudov and Roth 2013). In such environments, we would expect individuals that are best able to obtain food via their food stores to be in the best condition, and therefore should exhibit higher song output, particularly at dawn.

Mountain chickadees (*Poecile gambeli*) are non-migratory songbirds inhabiting the montane regions of western North America (McCallum et al. 2020). These birds inhabit a gradient of winter climatic harshness and provide a prime opportunity to investigate the relationship between food availability, selection strength, and male condition via daily singing routines. Mountain chickadees are scatter-hoarding birds that rely on specialized spatial cognitive abilities to recover thousands of individual food stores (Sherry 1989; Pravosudov and Roth 2013). Previous work has shown that mountain chickadees are locally adapted to their respective environments: birds inhabiting harsher, high elevations cache significantly more food items, have better spatial memory abilities to recover their caches, and larger associated brain regions compared to those inhabiting milder, low elevations (Freas et al. 2012; Croston et al. 2016). Furthermore, first-year birds with better spatial cognitive abilities are more likely to survive to the next year than those with inferior spatial cognitive abilities (Sonnenberg et al. 2019). Overall, harsher winter conditions at high elevations result in higher overwinter mortality of juveniles and higher annual survival of adults compared to those at low elevations (Benedict et al. 2020). In other words, only mountain chickadees with enhanced spatial cognitive abilities that are able to recover their food stores will survive the harsh winters at high elevations into the breeding season (Branch et al. 2019a). In contrast, milder conditions at low elevation may allow birds to survive and reproduce even if they have suboptimal spatial cognitive abilities (Branch et al. 2019a; Benedict et al. 2020).

These neural and behavioral differences persist despite a rather short distance between our high- and low-elevation sites (approximately 6 km). Chickadees are highly resident birds, and there is limited movement between elevations. Despite banding 400+ nestlings a year for 7 years, we have never detected a nestling hatched at one elevation breeding at the other. As such, it is unlikely that females at either elevation are making mating decisions among high- and low-elevation males. However, previous work shows that females at high elevations are more discerning and prefer males from their respective elevation, while low-elevation females showed no elevation-related preference (Branch et al. 2015). This work suggests that mating decisions based on male condition have more critical fitness consequences at high elevations due to the harsher environmental conditions.

Indeed, total daily song production may be especially important for females at high elevation, since males in better condition can afford to start singing earlier in the day and should sing more overall (e.g., Thomas 1999).

In this study, we compared daily singing routines between free-living high- and low-elevation male mountain chickadees to test the hypothesis that males in better condition produce more total songs and sing more songs at dawn compared to males in worse condition. Since females generally prefer males that sing more at dawn, and only males in the best condition can forgo foraging to sing at dawn, song output serves as a handicap signal providing information on male condition (e.g., Berg et al. 2005). Among high-elevation mountain chickadees, only males in the best nutritional condition, due to their enhanced spatial learning and memory abilities and high propensity for caching, are expected to survive into the breeding season (Sonnenberg et al. 2019; Benedict et al. 2020); whereas, a greater range of male condition would be expected at low-elevations, as winters are milder and selection on spatial learning and memory abilities is weaker. As such, we predict that high-elevation male mountain chickadees will (1) exhibit higher total daily song output and (2) sing more songs at dawn compared to those at low elevation.

Materials and methods

Study system

Songs were recorded over two breeding seasons (2018 and 2019) from male mountain chickadees inhabiting high (ca. 2400 m) and low (ca. 1900 m) elevations at our long-term field site in northern California, Sagehen Experimental Forest, USA (Sagehen Creek Field Station, University of California Berkeley, approximately 14.5 km north of Truckee, CA). Breeding behavior and male song have been monitored and collected annually from this population since 2013 (Branch and Pravosudov 2015, 2020; Kozlovsky et al. 2018; Branch et al. 2019b). Birds were recorded at their nests from May to July 2018 and 2019 using Swift terrestrial passive acoustic recording units developed by the Cornell Lab of Ornithology's Center for Conservation Bioacoustics. The Swift recording device is a single unit housing the microphone and recorder. Songs were recorded with a sampling rate of 48,000 Hz and a 16-bit resolution. Hourly ambient temperature data were obtained from two snow telemetry (SNOTEL) weather stations, one located at the high-elevation site (SNOTEL 541–Independence Lake) and one at the low-elevation site (SNOTEL 540–Independence Creek) (United States Department of Agriculture, Natural

Resources Conservation Service, <https://www.wcc.nrcs.usda.gov/snow>).

Chickadees are cavity-nesting birds that readily nest in nest boxes. At our field site, there are ~400 nest boxes between high and low elevations, which results in approximately 100 nests per year. Swift recorders were placed ca. 2–5 m from active chickadee nest boxes during the nest-building, egg-laying, and incubation stages of breeding (Table S1). Each male was recorded from 0500 to 2000 h PST for 3 days, for a total of 45 h of recordings per male. Each male was recorded once over the course of 2 years (i.e., no repeats in sampling). Eighteen males were sampled from each elevation for a total of 36 individuals and 1620 h of acoustic recordings. At high elevation, males were an average of 3.18 years old (range: 1–5 years): 16 of the males were > 2 years old, while two were in their first year of breeding. At low elevation, males were an average of 2.39 years old (range: 1–4 years), 15 of the males were > 2 years old, and three were in their first year of breeding. Ages were estimated using multiple plumage characteristics at the time of initial capture (Meigs et al. 1983) and long-term banding records (see ages used for analysis in Table S1).

Acoustic analyses

Song recordings were stored as .wav files on secure digital (SD) cards and uploaded daily for permanent storage. Raven Pro 1.6 was used to visualize and measure all sound recordings. Chickadee song output was assessed using the following presets in Raven Pro 1.6: a Hann spectrogram window with a size of 512 samples, a time resolution of 256 samples, and a frequency resolution of 93.8 Hz. To standardize the selection of a song from a focal male and for it to be included in the analyses, Power Thresholds, which determine the dynamic range of the spectrogram's visual output, were set to 30 dB for the floor and 60 dB for the ceiling. Visual inspection was used to make selections of each song within a recording. Due to logistical constraints, observers were not truly blind to the identity of the sound recordings; however, two observers, DSL and GH, were not privy to the goals of the study. Total daily song output, or the number of songs produced in a day, was calculated for each individual. Songs were then allocated to 1-h bins based on the time of output. Each day of recording was adjusted to begin 30 min before sunrise in Truckee, CA (<https://sunrise-sunset.org/us/truckee-ca/2018/05>). Bins, therefore, represented hours since the start of the dawn but were labeled by an approximate hour of the day (e.g., 0500 h) for ease of reading.

Statistical analyses

The number of songs produced per hour by each individual was averaged over the 3 days of recording to produce one

mean song output value per individual per hour. We first compared the mean total daily song output of each individual by elevation using a two-sample *t*-test, (*t-test()* function) in *R* (R Core Team 2021). Homogeneity of variance was tested using the *LeveneTest()* function in the *car* package in *R* version 4.1.0 (Fox and Weisberg 2019; R Core Team 2021). Mean hourly song output (x) was standardized (z) by the individual bird's mean daily song output (μ) and standard deviation (σ) of each day (e.g. Pitera et al. 2018):

$$z = \frac{x - \mu}{\sigma}$$

The *lm()* function in *R* was used to create a linear model of daily song activity by elevation and time of day (R Core Team 2021). Standardized mean hourly song output was used as the dependent variable, and elevation and timing were used as the independent variables. Year (2018, 2019) and observer (SYH, DSL, and VH) were included in the model along with three additional factors known to influence the timing of song output: mean hourly temperature, male age, and breeding stage, which included five stages of breeding (see Table S1). For example, birds have been shown to sing earlier with warmer temperatures (Hasan and Badri 2016), older birds have been shown to exhibit higher song performance (Ota and Soma 2014), and males have been shown to sing more at dawn during their mates' fertile period (Zhang et al. 2016). Hour-by-elevation interactions were used to assess potential differences in the daily distribution of song output between elevations. Because the dependent variable contained standardized values, significant interactions, which show differences in the distribution of song output between elevations, were the main statistic of interest. Tukey's post hoc comparisons were run to assess hour-by-elevation effects using the *lsmeans()* function in the *lsmeans* package (Lenth 2016; R Core Team 2021). The figure of hourly song output was created using the *ggplot2* package (Wickham 2016; R Core Team 2021), and standardized mean hourly song output was generated with *lsmeans* (Lenth 2016).

Results

There were no significant differences in the total daily song output of individuals at high (mean \pm SD: 433.89 \pm 379.76) and low (594.67 \pm 623.16) elevations ($t = -0.935$, $df = 28.10$, $p = 0.358$, Fig. 1), and variances of high and low song output were homogenous ($F_{1,34} = 1.593$, $p = 0.216$).

When song output was standardized within an individual, there was no significant difference between the total number of songs that chickadees sang in a day at high (mean \pm SD: -0.0003 ± 1.75) versus low (0.0001 ± 1.67) elevations ($F_{1,454} < 0.0001$, $p = 0.997$). However, there was

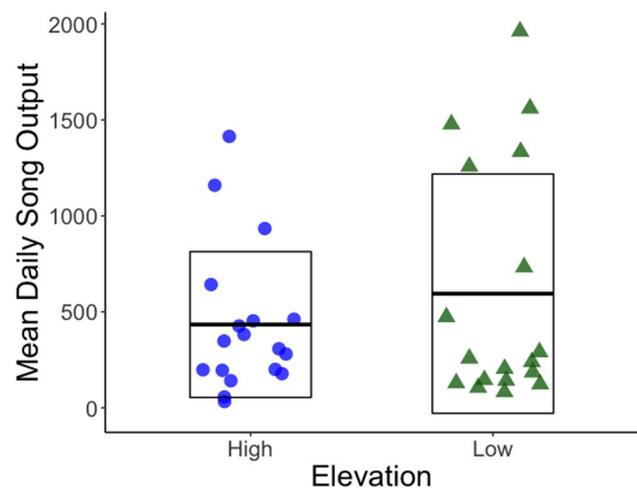


Fig. 1 Mean daily song output of high- ($N=18$, blue circles) and low- ($N=18$, green triangles) elevation males. Each point represents the average number of songs sung by each individual across 3 days of recording. Borders of the boxes represent the mean (bolded middle line) and standard deviation (top and bottom lines). Individual points are adjusted to avoid overlap (*geom_jitter()* function in the *ggplot2* package (R Core Team 2021))

a significant difference in the number of songs sung based on time of day ($F_{13,454} = 33.77$, $p < 0.0001$). Furthermore, there was no effect of year ($F_{1,454} = 0.0328$, $p = 0.567$), observer ($F_{1,454} = 0.0059$, $p = 0.808$), ambient temperature ($F_{1,454} = 0.0993$, $p = 0.320$), male age ($F_{1,454} = 0.014$, $p = 0.906$), or breeding stage ($F_{4,454} = 0.039$, $p = 0.997$) on daily song output.

There was a significant interaction between elevation and time of day ($F_{13,454} = 2.40$, $p = 0.004$, Fig. 2). Across all 14 hourly comparisons, song output at high and low elevations differed at three-time points. High-elevation males sang significantly more songs than low-elevation males in the first hourly bin, including 30 min before and after sunrise (Table 1, Fig. 2). Low-elevation males sang significantly more songs during hourly bin 4, around 800–900 h, and hourly bin 9, around 1300–1400 h, compared to high-elevation males (Fig. 2). All other pairwise comparisons were nonsignificant at $p > 0.05$ (Table 1).

Discussion

After comparing the daily singing routines of high- and low-elevation mountain chickadees, we found support for one of our two predictions. Contrary to our first prediction, male mountain chickadees inhabiting high elevation did not exhibit higher daily song output compared to those at low; however, high-elevation males did sing significantly more at dawn compared to those at low, supporting our second prediction. Although low-elevation males also exhibited a

Fig. 2 Song output of male mountain chickadees (standardized mean and standard error of the mean) at high (blue circles) and low (green triangles) elevations across approximate hourly bins. Asterisks denote significant effects at $p < 0.05$

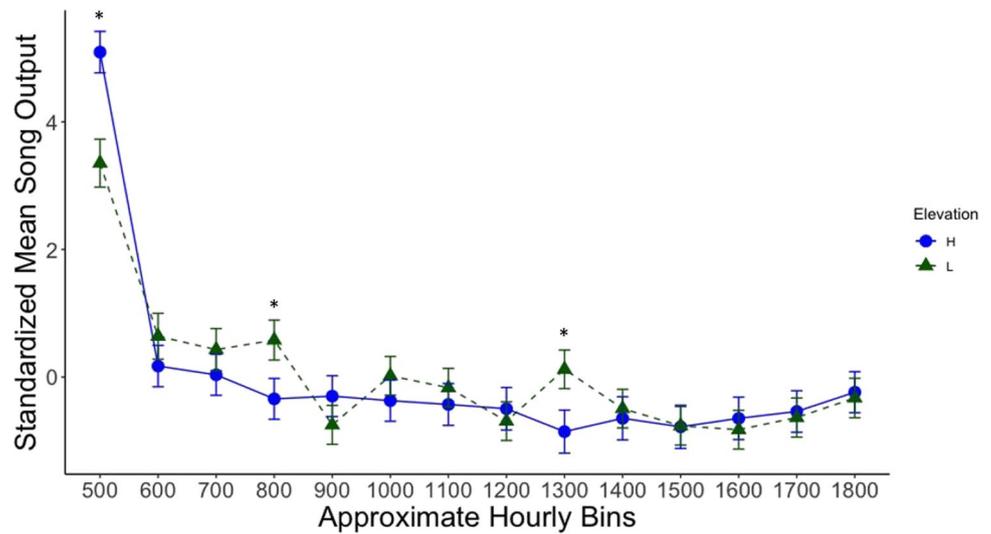


Table 1 Standardized mean and standard error of the mean for every hourly bin at high and low elevations using Tukey’s post hoc pairwise comparisons. Bolded values indicate statistical significance at $p < 0.05$

Hourly bins	High		Low		<i>p</i>
	Mean	SE	Mean	SE	
0500	5.094	0.325	3.354	0.376	0.0002
0600	0.172	0.324	0.640	0.360	0.3011
0700	0.035	0.321	0.430	0.330	0.3704
0800	-0.342	0.320	0.579	0.313	0.0344
0900	-0.300	0.320	-0.750	0.305	0.2979
1000	-0.371	0.322	0.019	0.304	0.3695
1100	-0.430	0.328	-0.168	0.303	0.5483
1200	-0.497	0.333	-0.692	0.303	0.6562
1300	-0.856	0.337	0.121	0.302	0.0270
1400	-0.647	0.339	-0.495	0.303	0.7288
1500	-0.781	0.338	-0.765	0.302	0.9725
1600	-0.648	0.333	-0.825	0.304	0.6903
1700	-0.540	0.325	-0.635	0.306	0.8304
1800	-0.238	0.322	-0.329	0.310	0.8372

peak in singing at dawn, they appeared unable to maintain the high rate of singing, shifting their song output to later times in the day, perhaps once they had an opportunity to forage. Low-elevation males sang significantly more than high-elevation males at 0800 and 1300 h.

Finding that high-elevation males sing more at dawn compared to low-elevation males supports our hypothesis that high-elevation males have more reliable access to food (due to higher propensity to cache and enhanced spatial cognitive abilities to recover food stores) and may be in better condition following overnight fasting. Previous work in chickadees shows that males increase their song

output when provided with supplemental food (e.g. Grava et al. 2009), suggesting that food availability is a limiting resource for song output. In addition, chickadees with larger masses, a proxy for better condition, exhibit higher singing rates at dawn (Lucas et al. 1999). It is advantageous to sing at dawn because it is a critical time for males to settle territory boundaries, advertise themselves, and obtain extra-pair copulations (Gil and Llusia 2020).

Our montane study site sets up a natural experiment to assess the idea that males in good condition can afford to forgo foraging to sing at dawn. Selection pressures are much stronger at high elevations, and only males in the best condition will survive into the breeding season (Branch et al. 2019a). This is likely due to high-elevation birds having superior spatial cognitive abilities to recover their food stores, resulting in lower energetic stress compared to low-elevation males, which have been shown to cache less and have inferior spatial cognitive abilities in this same population (Croston et al. 2016; Tello-Ramos et al. 2018). Although low-elevation males also exhibited a peak in singing at dawn, they appeared unable to maintain that rate of singing and therefore shifted their singing to later times in the day once they had the opportunity to forage. Low-elevation males are likely less efficient foragers due to inferior spatial cognitive abilities and smaller caches and must therefore prioritize early-morning foraging over singing at dawn to prevent starvation (Thomas 1999). Our results suggest that song output at dawn may serve as a handicap signal in mountain chickadees. Individuals must sacrifice vigilance and foraging when singing. Therefore, only males in the best condition are able to forgo foraging at dawn to sing (Møller and de Lope 1994), ensuring song output as a reliable indicator of condition (Zahavi 1975).

The lack of significant differences in total song output between high and low elevations suggests that total daily

song output may not directly reflect the male condition in mountain chickadees. Indeed, male mountain chickadees at high versus low elevation only differ in when they produce their songs, which may suggest the use of different strategies to balance foraging and singing. Harsher conditions at high elevation increase the possibility of an extreme weather event, which can decrease the time available for foraging (Bednekoff and Houston 1994; McNamara et al. 2005). It is possible that males at high elevation may have a smaller or less predictable window for singing compared to males at low elevation. Therefore, they may choose to sing at dawn to avoid foregoing an opportunity later in the day due to weather perturbation. That said, weather perturbations are not restricted to later in the day, and dawn should be an advantageous time to sing for both high- and low-elevation males.

While chickadees at high elevations cache more food and have better spatial cognitive abilities directly involved in cache recovery necessary for survival (Freas et al. 2012; Sonnenberg et al. 2019), they perform worse on a reversal-learning task, suggesting that they may be less cognitively flexible compared to birds at low elevation (Croston et al. 2017; Tello-Ramos et al. 2018). These differences suggest that there may be a trade-off between spatial learning and memory ability and cognitive flexibility (Tello-Ramos et al. 2019). It is possible that female chickadees at low elevation prefer males that are more cognitively flexible, which may be associated with differences in daily singing routines at low compared to high. Perhaps there is geographic variation in female preferences and sexually selected traits, like those documented in the barn swallow species complex (e.g. Møller 1988; Safran and McGraw 2004). Within the mountain chickadee system, it may be that high-elevation females prefer males that sing more at dawn associated with enhanced spatial cognitive abilities, while low-elevation females prefer males that are more cognitively flexible associated with singing throughout the day.

That said, spatial learning and memory are critical for the recovery of food caches, and we have shown that individual variation in spatial cognitive abilities, but not in cognitive flexibility, is associated with differences in survival (Sonnenberg et al. 2019). Furthermore, females from both elevations increased their reproductive investment (laid larger clutches and fledged larger broods) when mated to a male that performed better on our spatial learning and memory task, but not on the reversal task (Branch et al. 2019b). Since cognitive flexibility is not directly associated with cache recovery and survival, it may be less important in harsh winter conditions and less likely to directly affect female preferences and sexually selected traits (e.g. Hill 1994).

Individual variation in birdsong functions across different scales: at the individual level, it advertises male condition, while at the population level, it advertises local

suitability or adaptation (Branch and Pravosudov 2015, 2020). Here, we show that differential strength in selection pressures due to increasing winter climatic harshness can also shape male condition. However, variation in a male song within high and low elevations may be constrained by many additional factors, including social aggression, predation risk, and age (Gil and Gahr 2002). For example, due to the higher overwinter mortality of juveniles at high elevation, there are more adult males that survive into the breeding season compared to those at low elevations (Branch et al. 2019a). Adult males may be more experienced and hence start singing earlier in the day compared to juvenile males, although previous work suggests that age is unlikely to affect the timing of singing (Gil and Gahr 2002), and we did not find evidence of an age effect in our statistical models.

Social dominance rank may also affect daily singing routines, with dominant males singing more at dawn due to their better social and nutritional condition (e.g. Otter et al. 1997). In our system, we do not have data on the social dominance rank of individual males within elevations and their respective song output. However, low-elevation males were socially dominant to high-elevation males in pairwise interactions conducted in the laboratory (Kozlovsky et al. 2014). Unfortunately, this previous finding has little relevance for our comparison here, as males from high and low elevations are unlikely to compete directly. Chickadees are known to be highly sedentary and rarely move across elevations. We have previously suggested that elevation-related differences in social dominance and spatial cognitive abilities restrict movement between elevations; males moving from high to low will likely experience a decrease in fitness due to their subordinate social status (Ratcliffe et al. 2007), and those moving from low to high will likely experience a decrease in fitness due to their inferior spatial cognitive abilities to successfully retrieve their food stores (Kozlovsky et al. 2014).

In addition, population density has been shown to affect the total song output and timing of male song (Stehelin and Ross Lein 2014). Males sing more when the population is denser, likely due to the social influence of hearing others sing and the higher vigilance required for territorial defense. We do not have precise measures of mountain chickadee density at the two locations used in this study; however, both high and low elevations are densely populated with mountain chickadees. At both sites, birds breed in our nest boxes as close as 20 m from one another. Furthermore, the effect we see on song output relates specifically to the timing of singing among hourly bins and not the total number of songs produced or the initiation of the song. Related work in chickadees suggests that males' performance at dawn predicts their competitive ability during midmorning countersinging contests (e.g. Poesel et al. 2004; Mennill and Otter 2007). However, we only

measured natural song output without the influence of playback stimuli, and data on countersinging competitions is outside the scope of our study.

An additional limitation to our study is that the use of autonomous recording units means that we are likely underestimating the total number of songs produced by each male. These units have a limited range of detection, and we chose a rather conservative approach for counting songs from focal males. However, we do not believe that there are elevation-related effects associated with these limitations, specifically at dawn, since males sing by their nest boxes to maximize territorial defense, self-advertisement, and mate guarding (Møller 1991), and the recorders were specifically placed within 5 m of the nest box.

Overall, our study supports the hypothesis that differences in environmental conditions associated with differential selection are associated with variation in daily singing routines but not total song output. The distribution of hourly song production may be more representative of individual condition because it is determined by how efficiently individuals can replenish their energy reserves, while total daily song output can be compensated later in the day, as seen in low-elevation males. Future work aims to investigate individual differences in the timing of song production and variation in male condition both within and between elevations to provide a more refined test of this hypothesis.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-022-03246-x>.

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Author contribution CLB designed the experiment and collected automated song recordings. SYH, DSL, and VH analyzed song data. SYH conducted statistical analyses and wrote the first draft of the manuscript. CLB and VVP advised on statistical analyses and writing of the manuscript.

Data availability Raw data for all analyses is available as supplementary material.

Declarations

Ethics approval To the best of our knowledge, no birds were harmed by the collection of this data. All applicable national and institutional guidelines for the use of animals were followed. All procedures were approved by the UNR IACUC ethics committee in accordance with the UNR IACUC protocol (00046), under California Department of Fish and Wildlife Permit SC-5210 (DocID: D-0019571790-9).

Conflict of interest The authors declare no competing interests.

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