Extreme environmental conditions lead to a collapsed avian soundscapes; an agent-based model

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Climate change is increasing aridity in grassland and desert habitats across the southwestern United States, reducing available resources and drastically changing the breeding habitat of many bird species. Increases in aridity reduce sound propagation distances, potentially impacting habitat soundscapes, and could lead to a breakdown of the avian soundscapes in the form of loss of vocal culture, reduced mating opportunities, and local population extinctions. We developed an agent-based model to examine how changes in aridity will affect both sound propagation and the ability of territorial birds to audibly contact their neighbors. We simulated vocal signal attenuation under a variety of environmental scenarios for the south central semi-arid prairies of the United States, ranging from contemporary weather conditions to predicted droughts under climate change. We also simulated how changes in physiological conditions, mainly evaporative water loss (EWL), would affect singing behavior. Under contemporary and climate change induced drought conditions, we found significantly fewer individuals successfully contacted all adjacent neighbors than did individuals in either the contemporary or predicted climate change conditions. We also found that at higher sound frequencies and higher EWL, fewer individuals were able to successfully contact all their neighbors, particularly in the drought and climate change drought conditions. These results indicate that climate change-mediated aridification may disrupt the avian soundscape, such that vocal communication no longer effectively functions for mate attraction or territorial defense. As climate change progresses increased aridity in current grasslands may favor shifts toward low frequency songs, colonial resource use, and altered songbird community compositions.

Keywords: Climate change, aridity, agent-based model, vocal communication, evaporative water loss, house finch

Introduction

      Semi-arid ecosystems are especially sensitive to climate change due to their relatively high temperatures, low precipitation, infertile soil, sparse vegetation cover, and low abundance of resources such as food and freshwater (Reynolds *et al.*, 2007; Huang and Ullrich, 2017; Wei *et al.*, 2019). As global warming intensifies, desertification and land degradation in dryland habitats is also predicted to increase (Goudie 2019). In the Mojave Desert, increases in temperature and aridity coupled with a decrease in water resources have led to the collapse of desert avian communities (Iknayan & Beissinger 2018). While increases in temperature can lead to adaptations in heat dissipation (Song and Beissinger, 2019), with increasing aridity birds will also suffer from increased evaporative water loss. Understanding how increased desertification affects avian behavior may provide insight into community collapse and resiliency under new environmental conditions (Buchholz *et al.*, 2019). In response to warmer temperatures, some birds advanced the onset of reproductive and singing behaviors to earlier dates in the breeding season (Dunn, Winkler and Møller, 2010; Rubolini, Saino and Møller, 2010; Dunn and Møller, 2014). Predicting how aridity changes birds' energy and water demand and how these changes may affect their communication behavior will be useful for understanding how other factors, such as reproduction, physiology, and even population recruitment, will be impacted by future weather conditions (du Plessis *et al.*, 2012; Van de Ven *et al.*, 2016; Sharpe, Cale and Gardner, 2019).

      Acoustic signals are used for intra- and interspecific communication among multiple animal species. Rapid changes in these signals can indicate that a population is adapting to environmental change associated with climate or other factors (Sueur and Farina, 2015). Since dry air is a poor sound conductor relative to moist air, we can expect increased aridity to degrade sound transmission fidelity (Henwood and Fabrick, 1979). This effect is most pronounced for high-frequency sounds, such as the songs of North American wood warblers, for

which high frequency songs experienced high atmospheric attenuation (Snell-Rood, 2012). For many bird species, the dawn chorus is a period of high singing activity during the breeding season (Catchpole and Slater, 2008; Gil and Llusia, 2020; Staicer, Spector and Horn, 2020). This period is usually characterized by low temperatures and moderate to high humidity, which generally corresponds to most optimal conditions for sound transmission (Henwood and Fabrick, 1979). Therefore, the dawn chorus may represent a behavioral adaptation that exploits the optimal sound transmission properties of early morning. Yet, climate models predict disproportionate nighttime temperature increases, suggesting that early-morning conditions may become less optimal for vocal communication, potentially reducing the efficacy of the dawn chorus for adjacent neighbors to communicate (Mutiibwa *et al.*, 2015).

Increasing aridity will lead to reduced resources such as food and water (Reynolds *et al.*, 2007, 2011), hence changing territory quality. To maintain suitable body condition for survival and reproduction, individuals need to expand territory sizes to access enough resources (Khoury and Boulad, 2010). For example, in the Central Monte Desert in Argentina, rufous-collared sparrows (*Zonotrichia capensis*) maintain larger breeding territories compared to their temperate or tropical counterparts during the breeding season due to the lower habitat quality of this arid region (Cecilia Sagario and Cueto, 2014).

Birds singing under increasingly arid conditions will not only simultaneously face poorer song transmission and territorial resource qualities, but the cost of singing itself will also increase, as the individual must shift allocations of time and energy resources away from singing (Reid, 1987; Zollinger and Brumm, 2015) and toward thermoregulatory and foraging behavior (Gil and Gahr, 2002; du Plessis *et al.*, 2012; Funghi *et al.*, 2019). Furthermore, aridity likely increases the water costs for singing birds due to accelerated evaporative water loss; singing exposes the high moisture gradient between the bird's respiratory tract and surrounding dry air, causing water loss to the environment (Ward, Speakman and Slater, 2003; Ward and

Slater, 2005; O'Connor *et al.*, 2018). To avoid dehydration, birds will need to exhibit behavioral flexibility to sing at low dehydration conditions (Ducatez *et al.*, 2020) or increase their rate of drinking (Czenze *et al.*, 2020).

Agent-based models (ABMs) are a powerful tool to analyze individual behaviors and their population-level effects (Axelrod, 1997). ABMs are built around a set number of agents, defined behaviors, and rules; each agent's behavior is dependent on external stimuli fed into the model and the agent displays a behavior based on these stimuli and pre-defined rules (Reynolds, 1987; Marceau, 2008). These models are useful in providing information on how behaviors can respond to future scenarios, such as increased temperature and aridity due to climate change, and on how the simulated system dynamics are affected. Studies used ABMs to predict migration start dates and routes for Painted Buntings (*Passerina ciris*) (Bridge *et al.*, 2015) and stopover duration and movement distances in North American dabbling ducks under changing weather conditions (Beatty *et al.*, 2017). ABMs are a valuable tool in predicting how climate change will affect the behavior of individuals, and how those altered behaviors can affect the population (Patt and Siebenhüner, 2005). To our knowledge, ABMs have yet to map out how climate change will affect avian singing and territorial movement, and how these changes will affect the avian soundscape.

We examined how aridity would lead to a disrupted soundscape, and how this disrupted soundscape would affect avian singing, movement, and resting behavior. We developed two hypotheses to test how avian singing behavior changes under a disrupted soundscape: the facultative activity budget (FAB1) hypothesis, which states that singing activity is mainly dependent on individual condition, and the fixed activity budget (FAB2) hypothesis which states that singing activity is fixed regardless of environmental conditions. To evaluate these two hypotheses, we used an agent-based model to simulate a population of individuals each with their own territories and their singing, movement, and resting behavior across contemporary and

climate change induced weather conditions. We varied territory size and mean song frequency to determine which bird species would be most at-risk to increased aridification (Figure 1).

We chose to simulate these disruptions under breeding conditions, both because alterations to breeding behavior would be more noticeable in an applied scenario, and because the consequences of disruptions to breeding behavior have tangible consequences for recruitment and persistence. We predicted that individual contact rate would decrease with increasing frequency and territory size, and that a population of singing individuals would not be able to maintain vocal contact with their immediate neighbors due to sound attenuation and reduced singing activity due to physiological constraints. We tested this hypothesis by using an ABM to model individual territorial vocalizations, within-territory movement, and resting behavior across current and predicted climate conditions.

Methods

Model design. We created an ABM in the program R v4.0.4 (R Core Team 2008) that simulated the singing and movement behavior of individual "virtual birds" (from now on referred to as birds) within their respective territories. The model advanced at 1 min time steps, and at each time step every bird could perform one of three behaviors: sing, move within the territory, and rest. Decisions regarding which action was performed were determined by probabilities assigned to each action. At the first time-step, the probability of each behavior was the same (0.33). When a singing behavior was initiated, a song radius was calculated based on the expected attenuation of the song. We set the threshold between audible and inaudible songs at 30 Db as the minimum amplitude that can be detected by the birds. If a bird's song radius overlapped with the position of any of its neighbors, then a successful instance of communication was recorded for all individuals involved and the neighbors within the song radius were induced to sing during that time step. If a bird's song radius did not overlap with its

neighbor, the focal bird would either move or rest in the following time-step. If a movement behavior was initiated the bird would relocate to a random position within its territory, and if a rest behavior was initiated, the bird would take no action during the time step.

Experimental Design. We ran the model using weather data from an Oklahoma Mesonet station in western Oklahoma (ERIC). For the months of May and June (a period that roughly corresponds to peak singing activity). Each modeled day used weather data from sunrise until 6 hours after sunrise which corresponded to peak singing activity. We averaged corresponding values from measurements at five-minute intervals for air temperature (TAIR), relative humidity (RELH), and air pressure (PRES) from 2011 to 2019. These variables were used to calculate acoustic atmospheric attenuation (Rossing, 2007).

$$\alpha = f^2 \left[\left(\frac{1.84 \times 10^{-11}}{\left(\frac{T_0}{T}\right)^{\frac{1}{2}} \times \frac{p_s}{p_0}} \right) + \left(\frac{T_0}{T}\right)^{2.5} \times \left(\frac{0.10680 e^{-3352/T} \times f_{r,N}}{f^2 + f_{r,N}^2} + \frac{0.01278 e^{\frac{-2239.1}{T}} \times f_{r,O}}{f^2 + f_{r,O}^2} \right) \times \frac{Np}{m \times atm} \right] \quad (1)$$

With α as the attenuation coefficient, *f* is the sound frequency, *T* is the absolute temperature of the atmosphere in degrees Kelvin, *T0* is 293.15K or 20C, *ps* is the local atmospheric pressure and *p0* is the reference atmospheric pressure (1 atm = 1.01325 x 10^5 Pa); $f_{r,N}$ is the nitrogen relaxation frequency, $f_{r,O}$ is the oxygen relaxation frequency and are calculated by the equations below:

$$f_{r,N} = \frac{p_s}{p_{s0}} \left(\frac{T_0}{T}\right)^{\frac{1}{2}} \times \left(9 + 280 He^{-4.17\left[\left(\frac{T_0}{T}\right)^{\frac{1}{3}} - 1\right]} \right) \quad (2)$$

$$f_{r,O} = \frac{p_s}{p_{s0}} \left(24.0 + 4.04 \times 10^4 H \frac{0.02 + H}{0.391 + H} \right) \quad (3)$$

H being the percentage molar concentration of water vapor in the atmosphere or absolute humidity, and is calculated by:

$$H = \frac{\rho_{sat} r_h p_0}{p_s} \quad (4)$$

With $\rho_{sat} = 10^{C_{sat}}$ and $C_{sat} = -6.8346 \left(\frac{T_0}{T}\right)^{1.261} + 4.6151$.

To simulate contemporary drought conditions, we used a subset of the baseline weather data from the year 2011, when there was a severe drought that affected most of Oklahoma and many neighboring states (Tadesse *et al.*, 2015; Khand *et al.*, 2017). To simulate the predicted climate change conditions in 2070, we took the mean weather condition values (TAIR, RELH, and PRES) from 2010-2019 ERIC Mesonet station and added 7.5°C to the TAIR and subtracted 6% from the RELH of the mean values. We chose the ERIC Mesonet station because it has recorded some of the driest temperatures within the state of Oklahoma. These values are based on the predicted climate trends in the North American Southwest for the year 2070 (Huang and Ullrich, 2017). To simulate drought conditions in 2070, we added 7.5°C to the TAIR and subtracted 6% from the RELH from the 2011 ERIC Mesonet weather data. The list of tested conditions can be found in Table 1.

Individual contact rates. We first ran a simplified version of the model with two individuals and their respective territories to test the effects of multiple song frequencies across multiple territory sizes. We tested 12 frequencies (1-12 kHz) and 60 territory size radii (25-1500m by 25m increments) to demonstrate how the different climate conditions listed above would affect the contact rate between two individuals with adjacent territories. We ran this model on the 06/01 date for the contemporary, extreme, climate change, and extreme climate change weather data because it was one of the hottest and driest days (based on 2011 TAIR and RELH, respectively) in our weather dataset. To determine which frequency and territory radii would be affected by extreme weather, we subtracted the extreme and extreme climate change results from the contemporary and projected climate change results, respectively.

Population contact rates. This version of the model contained an array of 110 contiguous territories, represented as a hexagonal grid, such that 72 birds (those not on an edge of the

array) had six neighbors (Figure 2). We increased the number of birds and territories in a population to determine if the changes in individual contact rates would influence the population-level communication system. Once a bird contacted all six of its neighbors it would stop singing because it has met the intrasexual condition of defending its territory against its adjacent neighbors. We also tested three different mean song frequencies, which represented individual bird species: 4, 8, and 12 kHz to determine if contact rates varied as a function of frequency because these frequencies cover the majority of the avian song frequency bandwidth and 8 kHz is the expected hearing range of most birds (Dooling, 2004). We also ran the model with and without the evaporative water loss (EWL) equation included to determine if water budgets, our measure of individual condition, affected contact rates. In the first time-step, the probability of a bird singing, moving, or resting was equal (i.e. 0.33). However, to test if individual condition affected the probability of these behaviors, these probabilities were subject to change as the model progressed based on how much water had been lost due to thermoregulation. To account for this physiological change, we derived EWL equation from (Albright *et al.*, 2017) for the House Finch (*Haemorhous mexicanus*), our model system for singing parameters. Once any bird lost 15% of its body mass due to total EWL (TEWL), it would no longer sing or move and would only rest until the next day. At the beginning of the next day, the TEWL resets back to zero under the assumption that the birds would recover their water reserves.

Each model run consisted of 61 virtual days each of which contained 6 virtual hours or 360 time steps. The six-hour period represented the dawn chorus and morning singing period, and we disregarded the rest of the day because the morning singing period is usually the highest singing period of the day (Gasc *et al.*, 2017). We evaluated the effectiveness of vocal communication based on the percentage of birds that had successfully contacted all six neighbors at the end of each day. We then averaged these values across all days to generate an overall contact rate for each of the 360 time steps (i.e. the completion rate). Birds/territories

that were on the edge of the hexagon array were not used to calculate contact rates as they had fewer than six neighbors. Hence, completion rates were calculated based on the 72 inner territories (Video 1).

Statistical Analysis. To analyze how different environmental conditions, frequencies, and territory sizes would affect individual contact rates, we developed generalized linear models using the lme4 package in R (Kuznetsova, Brockhoff and Christensen, 2014). We also conducted the generalized linear mixed models on the population-level, completion contact rate. These models included weather conditions, frequency, and the inclusion or absence of the EWL equation on bird contact rate. All statistical analyses were done in R v4.0.4 (R Core Team 2008).

Results

Individual effects. Compared to the mean contemporary conditions, contact rates significantly decreased in the mean contemporary drought conditions ($B = -0.160 \pm 0.051$ s.e., t = -3.158, p = 0.002) and the mean climate change drought conditions ($B = -0.184 \pm 0.051$ s.e., t = -3.642, p < 0.001). No significant differences in contact rate were found in the mean climate change conditions ($B = -0.008 \pm 0.051$ s.e., t = -0.157, p = 0.875). When frequency was included in the model, contact rate significantly increased as frequency increased in mean climate change conditions ($B = 1.457e\text{-}05 \pm 6.878e\text{-}06$ s.e., t = 2.119, p = 0.034). Contact rates increased significantly as territory size and frequency increased in the contemporary drought conditions ($B = 4.049e\text{-}08 \pm 7.844e\text{-}09$ s.e., t = 5.161, p < 0.001) and in the climate change drought conditions ($B = 3.916e\text{-}08 \pm 7.844e\text{-}09$ s.e., t = 4.992, p < 0.001). When comparing contact rates between the mean climate change and extreme climate change conditions, contact rates increased in the extreme climate change conditions ($B = 5.110\text{-}08 \pm 7.844e\text{-}09$ s.e., t = 6.514, p < 0.001). To determine which frequencies would be affected by the extreme

arid conditions, we subtracted the results of the simple model under the mean contemporary conditions from the drought conditions results (Figure 3A) and the mean climate change conditions from the climate change drought conditions results (Figure 3B) to demonstrate how extreme conditions affect mean song frequencies under different territory sizes. Smaller territory sizes with higher frequencies had higher contact rates compared to larger territories with lower frequencies. High frequencies in large territory sizes had significantly lower contact rates in the contemporary drought conditions compared to mean contemporary conditions (B = -4.049e-08 $\pm$ 4.892e-09 s.e., t = -8.276, p < 0.001). This significant trend was also seen in the climate change drought conditions (B = -5.242e-08 $\pm$ 5.423e-09 s.e., t = -9.667, p < 0.001).

Population effects - Weather conditions. Compared to the mean contemporary conditions (Figure 4A), completion rates were lower for 4 kHz and 8 kHz in the contemporary drought conditions (Figure 4B, 4kHz: B = -0.072 $\pm$ 0.005 s.e., z = -14.584, p = <0.001; 8Khz: B = -0.164 $\pm$ 0.005, z = -33.253 s.e., p <0.001), and climate change drought conditions (Figure 4D, 4kHz: B = -0.034 $\pm$ 0.005 s.e., z = -6.924, p <0.001; 8kHz: B = -0.041 $\pm$ 0.005 s.e., z = -8.28, p <0.001). The completion rates for the mean climate change conditions were higher than the mean contemporary conditions for all frequencies (Figure 4C, 4kHz: B = 0.031 $\pm$ 0.005 s.e., z = 6.252, p <0.001; 8kHz: B = 0.264 $\pm$ 0.005 s.e., z = 53.327, p <0.001; 12kHz: B = 0.035 $\pm$ 0.005 s.e., z = 6.970, p<0.001). Completion rates for 12kHz were also significantly lower between the climate change drought and mean climate change conditions (12kHz: B = -0.020 $\pm$ 0.005 s.e., z = -3.942, p <0.017).

Population effects - Frequency. Completion rates decreased with increasing frequency for mean contemporary (8kHz: B = -0.600 $\pm$ 0.005 s.e., z = -121.178, p <0.001; 12kHz*: B* = -0.950 $\pm$ 0.005 s.e., z = -192.209, p <0.001), drought (8kHz: B = -0.691 $\pm$ 0.005 s.e., z = -139.846, p <0.001; 12kHz: B = -0.869 $\pm$ 0.005 s.e., z = -175.886, p <0.001), mean climate

change (8kHz: *B* = -0.366 $\pm$ 0.005 s.e., z = –74.103, p <0.001; 12kHz: *B* = -0.580 $\pm$ 0.005 s.e., z = -117.388, p <0.001), and climate change drought conditions (8kHz: *B* = -0.606 $\pm$ 0.005 s.e., z = –122.534, p <0.001; 12kHz: *B* = -0.901 $\pm$ 0.005 s.e., z = -182.256, p <0.001).

Population effects - Evaporative Water Loss. When we included the EWL equation in the model, EWL significantly reduced completion rates at 8kHz for contemporary conditions (8kHz: *B* = -0.283 $\pm$ 0.005 s.e., z = –5.724, p <0.001), the contemporary drought conditions (8kHz: *B* = -0.296 $\pm$ 0.005 s.e., z = –5.987, p <0.001), mean climate change conditions (8kHz: *B* = -0.514 $\pm$ 0.005 s.e., z = –10.395, p <0.001), and climate change drought conditions (8kHz: *B* = -0.097 $\pm$ 0.005 s.e., z = –19.689, p <0.001). EWL also significantly reduced contact rates for 12kHz for the mean climate change conditions (12kHz: *B* = -0.030 $\pm$ 0.005 s.e., z = –6.007, p <0.001).

Population Effects - Territory Size. Since the 8 kHz frequency demonstrated the most significant effects, we tested this frequency at various territory size diameters (1.0, 1.5, 3.0 km) under the climate change drought (Figure 5). Completion rate decreased significantly as territory size increased from 1.0 km to 1.5 km (*B* = -0.213 $\pm$ 0.003 s.e., z = –75.311, p <0.001), increased from 1.0 to 3.0 km (*B* = -0.309 $\pm$ 0.003 s.e., z = –109.266, p <0.001), and increased from 1.5 to 3.0km (*B* = -0.096 $\pm$ 0.003 s.e., z = –33.955, p <0.001). When EWL was included, completion rate decreased significantly as territory size increased from 1.0 km to 1.5 km (*B* = -0.176 $\pm$ 0.003 s.e., z = –62.174, p <0.001), increased from 1.0 to 3.0 km (*B* = -0.220 $\pm$ 0.003 s.e., z = –77.519, p <0.001), and increased from 1.5 to 3.0km (*B* = -0.043 $\pm$ 0.003 s.e., z = –15.345 p <0.001).

Discussion

Based on the ABM results, we concluded extreme arid conditions would lead to reduced contact rates and a degraded avian soundscape for birds with mid to high mean song

frequencies. While we found support for the FAB1 hypothesis, wherein reduced physiological condition (i.e. TEWL) led to lower the completion rates for the 8 kHz mean song frequency under extreme and extreme climate change conditions, the majority of our results supported the FAB2 hypothesis, indicating that species' specific soundscapes are dependent on fixed, species' specific traits (i.e. mean song frequency and territory size). This trait-dependence means that with increasing aridity, certain species will be excluded due to reduced efficacy of the vocal communication system. This species loss will change the community composition of singing songbirds, which can be an indicator of community health. Our model demonstrates that under high aridity levels, the soundscape is no longer functional for certain species. Therefore, the population cannot maintain acoustic contact with each other, which could lead to the breakdown of territorial boundaries and potential mating opportunities. These individual consequences could lead to population level effects such as a decline in population size, which could alter the community soundscape. Alternatively, species that can adjust their singing behavior to accommodate for these extreme conditions by producing signals with optimal transmission distance or by having a more gregarious social system, however not all species would be able to display behavioral flexibility or developmental plasticity accordingly.

Species whose singing and movement behaviors are fixed are more vulnerable to soundscape degradation associated with increased aridity. As song transmission distance decreases, maintaining contact rates will require some combination of lowering mean song frequency, increasing song volume, and altering the timing and intensity of singing to correspond with favorable conditions. For species that are flexible in their singing behavior, they will need to create new song types to sing in an arid environment (which supports the acoustic adaptation hypothesis), or change their peak singing time to periods of low aridity (which supports the acoustic niche hypothesis) (Morton, 1975; Krause and Others, 1993). Selection for more transmissible songs in degraded environments has been noted in multiple species. North

American warblers (Parulidae) decrease their signal frequency bandwidth (max frequency span within a note) and increase the signal length under high atmospheric attenuation (Snell-Rood, 2012). Southern House Wrens (*Troglodytes musculus*) had lower song amplitude at high atmospheric attenuation conditions (Sementili-Cardoso and Donatelli, 2021). In many bat species, which vocalize in ultrasonic frequencies, warmer climates have led to higher frequency calls that attenuate due to high temperatures and low humidity (Luo *et al.*, 2014), which could lead to selection of lower frequency vocalizations and longer vocalizations to transmit information to the intended receivers. This selection for certain song syllables and song types could lead to the selection of low frequency, long songs, which would lead to the decrease of song type diversity in the avian soundscape. Species with higher frequency songs may relocate to habitats that have more favorable acoustic properties or reduce singing under hotter periods of the day (McGrann and Furnas, 2016; Diepstraten and Willie, 2021). Alternatively, selection can favor increased behavioral plasticity for birds to continue to sing in arid environments. Species that are not able to adjust their singing behavior can no longer maintain a vocal communication system in arid environments and will need to move to more suitable habitat.

While our model did not account for behavioral plasticity or intraspecific variation for individual species, this exclusion does not necessarily negate support for the FAB2 hypothesis. Completion rates did shift under the different climate scenarios, but frequency was the deciding factor in difference in completion rates (Figure 4). While plastic behavior is shown in many species, plasticity itself can be fixed, unless selection acts on it to increase (Crispo, 2007). It has been documented that certain species' singing behavior is flexible in disturbed habitats, particularly in habitats with high anthropogenic noise. Many urban birds such as Oregon Juncos (*Junco hyemalis oreganus*; Reichard *et al.*, 2019), Great Tits (*Parus major*; Slabbekoorn and den Boer-Visser, 2006), and White-crowned Sparrows (*Zonotrichia leucophrys*; Derryberry, Danner and Danner, 2016) shifted their minimum song frequency to transmit signals above the

low-frequency anthropogenic noise. Other species, like the Vermillion Flycatcher (*Pyrocephalus obscurus*) sing longer songs during noisy habitats (Ríos-Chelén *et al.*, 2013) and Serins (*Serinus serinus*) increase vocal activity during noisy periods (Díaz, Parra and Gallardo, 2011). Birds in arid environments may also adjust singing behavior by singing during the morning periods when sound transmission is the highest. Altitudinal migrants and resident bird species reduced singing activity when temperatures were high, but Neotropical migrants retained their singing activity even though the risk of heat-stress was high (McGrann and Furnas, 2016). With behavioral plasticity included, the FAB2 still retains support because the limits of plasticity can be limited by species-specific interactions.

If territorial songs are unable to propagate and reach their intended receivers, then the efficiency of the song decreases and the cost of singing increases (Wiley, 1998). This reduced efficacy could result in individuals not able to find mates due to incomplete information reaching the receiver, or potential mates preferring non-degraded songs. In many songbird species, females prefer certain song types over others. In habitats with high levels of anthropogenic noise, an example of a disturbed soundscape, Ovenbirds (*Seiurus aurocapilla*) suffered lower rates of pairing than quieter habitats (Habib, Bayne and Boutin, 2006). Wild male Zebra Finches (*Taeniopygia castanotis*) that sing longer, higher pitched songs predicted hatching success and the number of genetic offspring surviving (Woodgate *et al.*, 2012). Preference can also play a factor in reduced population recruitment; female Lincoln's Sparrows (*Melospiza lincolnii*) have a higher preference for male songs sung in colder temperatures vs. warmer temperatures (Beaulieu and Sockman, 2012). On the opposite spectrum, male Pied Flycatchers (*Ficedula hypoleuca*) singing in cold temperatures are preferred less by female pied flycatchers than males singing in warmer temperatures (Slagsvold and Dale, 1994). Warmer temperatures could also lead to potential mates preferring conspecific songs over heterospecific songs (Coomes,

Danner and Derryberry, 2019), which could lead to missed mating opportunities and ultimately reduced population recruitment.

In addition to reduced preference for certain song types, as aridity increases, resources like food and water will decrease in abundance, and birds will need to expand their territories to have the necessary resources to survive and reproduce (Dean, Barnard and Anderson, 2009; Khoury and Boulad, 2010). This increase in territory size will lead to increased energetic demand for patrolling territories, especially if the vocal signals used to maintain territory boundaries no longer reach their intended receivers. If vocal activity decreases, then individuals will need to increase territorial movement behavior to actively defend their territories from intruders. Increasing resource needs when resources are already low would push individuals past their breaking point (McKechnie, Hockey, and Wolf 2012), and while behavioral flexibility (short-term behavioral plasticity) would provide quick relief, the increased allostatic load would be too much for some species to adapt and develop non-reversible plasticity (i.e. developmental plasticity) to deal with increasingly extreme conditions (Wingfield et al. 2017). Outside of mating and reproduction, for social species the reduced soundscape under arid conditions could lead to reduced flock foraging behavior (Safriel, 1990) as calls may not reach conspecifics. The reduced transmission of predator alarm class could have community level effects, such as elevated depredation events, due to multiple species listening to heterospecific alarm calls (Grade and Sieving, 2016). Pair-bonded individuals will not be able to coordinate parental provisioning or produce effective alarm calls to warn of predators (Rose *et al.*, 2020) if the vocal signals are degraded. Territorial behaviors may decrease if degraded signals reach neighbors because birds rely on ranging or auditory cues to evaluate the distance of a conspecific. If a trespassing neighbor's song is degraded by high atmospheric attenuation, then the focal individual may not respond aggressively enough to the trespassing neighbor because the focal individual thinks the trespasser is farther away than it really is (Fotheringham, Martin and

Ratcliffe, 1997; Farina, 2014). Alternatively, aggressive territorial behaviors may increase due to competition over decreasing resources (Samplonius and Both, 2019). Many avian species use vocalizations to defend territories against rival mates and prevent extra-pair paternity (Mace, 1987). Males that move more could suffer from extra-pair fertilizations occurring on their territory. If the male is unable to defend the territory, territoriality behavior could become ineffective. Alternatively, individuals that are unable to defend a territory or no longer have access to a territory could become helpers on an existing territory of a more dominant/successful individual. With the degraded soundscape leading to fewer mating opportunities and increasing aridity leading to limited resources unable to support multiple breeding individuals, cooperative helpers may assist with dominant individuals to patrol territories and help with nestling provisioning (Koenig and Dickinson, 2004). A direct effect of reduced resources leading to larger territories is smaller population densities, which coupled with attenuated song types/syllables could lead to the loss of vocal culture or reduced vocal repertoires. A decrease in population size and density resulted in a decrease in vocal culture in Regent Honeyeaters (*Anthochaera phrygia*). Male Regent Honeyeater songs in 2011 were shorter and contained fewer syllables than songs in 1968 due to habitat fragmentation (Valderrama, Molles and Waas, 2013). This decrease in vocal culture led to reduced female pairing (Crates *et al.*, 2021). Song type diversity may also decrease due to cultural selection in tandem with natural selection if certain signals are not learned by the next generation (Searcy and Nowicki, 2005). Oscines or birds that learn song types from a tutor would only be exposed to low frequency, long syllable song types in an arid, degraded soundscape and once they mature their offspring will learn those song types as well. One study demonstrated that young Carolina Wrens (*Thryothorus ludovicianus*) prefer to learn undegraded songs than degraded songs (Morton, Gish and Van Der Voort, 1986), and under the predicted extreme aridity conditions, there may be fewer degraded song types to choose from. To reduce degradation, birds may position themselves higher in tree canopies (Mathevon, Dabelsteen and Blumenrath,

2005), which may expose birds to new ecological niches. Our results demonstrated that higher mean song frequencies would be less likely to transmit to adjacent neighbors, indicating that high frequency signals could be lost in arid songbird communities because they will not be heard by young birds. Alternatively, singing activity could potentially increase due to geophonies (i.e. sounds from the natural environment) decreasing due to dry riverbeds (Krause and Farina, 2016). Regardless, species living in variable conditions and unpredictable environments will need to learn and invent new syllables and song types in order to communicate to their intended receivers (Laiolo and Tella, 2006; Laiolo, 2008; Botero *et al.*, 2009), which could lead to an increase in syllable and song type diversity.

Changing song characteristics and song diversity would be an example of adaptation or a plastic response. Increasing phenotypic plasticity can help species continue to function in extreme environments, and these extreme environments can therefore select more plastic traits that reduce trait costs (Chevin and Lande 2010; Hoffmann and Parsons 1993). If the extreme environments continue to persist, organisms may develop non-reversible plasticity, which could lead to trait adaptation (Wingfield et al. 2017). While selection may favor plastic traits, plasticity is dependent on other traits (e.g. behavioral syndromes) that may limit behavioral expression, which could prevent species from expressing the optimal trait in a given context (Lande 2009). Plastic responses can be adaptive if those plastic responses in mild conditions are genetically correlated with responses in the extreme conditions (Chevin and Hoffmann 2017). Species with these correlated, plastic responses may have built-in climate resilience, which would lead to better chances of survival under increasingly extreme environments (Chevin, Lande, and Mace 2010).

Increasing aridity may completely alter soundscapes which can have individual, population, and community level impacts. The acoustic niche hypothesis states that species will occupy individual niches to avoid frequency or temporal overlap (Krause and Others, 1993).

With increased aridity changing the optimal times to sing, increased temporal overlap may occur between species that before did not compete for the same frequency range (Krause, 2012). Highest acoustic activity occurs during the dawn choruses, and while multiple factors like physiology (Thomas and Cuthill, 2002; Thomas *et al.*, 2002), light intensity (Berg, Brumfield and Apanius, 2006), and social factors (Kacelnik and Krebs, 1983) affect the dawn chorus activity, if aridity negatively impacts the sound propagation characteristics during the day, then multiple species will compete for the same temporal space during the dawn chorus (Krause, 1987). With selection favoring lower frequency songs and with a smaller optimal window to produce high frequency songs in arid environments, species that are unable to shift their song frequencies or cannot produce new songs will need to relocate to more suitable habitats. This relocation could lead to interspecific conflict between native species and the relocating species that use the same acoustic niche (Farina, Pieretti and Morganti, 2013), and potentially divergence of species as the colonizing species begins to adapt to the new acoustic environment (Cardoso and Price, 2010). This change in community composition could lead to an avian soundscape dominated by functional diversity (i.e. low frequency songs in large territories or medium frequency songs in small territories) rather than phylogenetic diversity (Gasc *et al.*, 2013).

Soundscapes can represent the health of an environment if acoustical niches correlate with ecological niches of vocal animals (Farina *et al.*, 2011; Kasten *et al.*, 2012; Gage and Axel, 2014; Fuller *et al.*, 2015). Soundscapes can be used to detect early signs of bird stress related to changes in habitat or climate (Sueur and Farina, 2015). Since the 1990s, the avian community soundscape has become more homogeneous, acoustic diversity has decreased, and soundscape intensity has declined in northern and eastern North America (Morrison *et al.*, 2021). Degrading soundscapes could lead to reduced perceived ecosystem value for many habitats (Ferraro *et al.*, 2020). Humans have increased perceived ecosystem value if a habitat sounds more "natural" (Francis *et al.,* 2017). Ecosystem services can be enhanced by making a

habitat sound more natural, which in turn could lead to an increase in conservation support

(Levenhagen *et al.*, 2021). Protecting a soundscape is vital for adding ecosystem value to a

habitat so we can advocate for ecosystems for the public's benefit.

Our model demonstrated how changes in individual singing and movement behaviors

due to extreme aridity can lead to a disrupted or even a collapsed avian soundscape. This lack

of communication could lead to an altered avian community soundscape, with certain species

being able to adapt and continue to sing during these increasingly arid conditions. Identifying

which species would suffer from this communication system collapse can potentially be helpful

in creating mitigation strategies such as adding supplemental water resources or creating

artificial shade refugia, to help reduce the impact of increasing aridity on avian populations.

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Tables

Table 1. Model Testing Parameters

Figures

Figure 1. Pictogram of questions, hypotheses, and predictions for the ABM. The questions, variables, and values outlined in the orange box represent the FAB1 hypothesis, while the blue box represents the FAB2 hypothesis.

Figure 2. Virtual environment for a population of virtual birds. Each hexagon represents a bird's territory in which the bird moves around. Each bird has 6 adjacent neighbors, except for the hexagons on the grid edge, which were not included in the final calculations since they could not contact all six neighbors. An bird will either sing, move, or rest until all neighbors were contacted. Birds that have contacted all six neighbors will turn gray and that bird will stop exhibiting behavior for the rest of the day.

Figure 3. Heatmaps of frequencies affected by extreme temperatures across different territory sizes. We applied the ABM to multiple territory sizes ranging from 25m radius territories to 1500m radius territories across the audible bird song frequencies for the differences in drought vs. contemporary weather data (a) and the differences in climate change drought vs. climate change weather data (b). Cooler colors represent frequencies and territory sizes that would lead to fewer birds successfully contacting all neighbors under extreme conditions in both the extreme and climate change drought data, suggesting that selection may drive bird populations towards smaller territory sizes and higher frequency songs.

Figure 4. Population contact rates across four different environment conditions: a) Mean contemporary, an average of TAIR, RELH, and PRES from the ERIC Mesonet station from 2010-2019. b) Contemporary Drought, the weather data from 2011 drought from the ERIC Mesonet station. c) Mean Climate Change, 7.5C TAIR increase and 6% RELH decrease to the

Mean Contemporary data. d) Climate Change Drought 7.5C TAIR increase and 6% RELH decrease to the Mean Climate Change data. Three frequencies that span the songbird frequency bandwidth were tested (4kHz: orange, 8kHz: blue, 12kHz: gray). Models without (solid) and with (dotted) the EWL equation are included.

Figure 5. Total contacts decrease as territory size increases under extreme climate change conditions for 8 kHz. Total number of contacts is represented on the y-axis and time (min) is represented on the x-axis. EWL equation was included in all of the models run.

Table 1. Model Testing Parameters

Weather Conditions	Territory Size Radius (km)	Song Frequencies (kHz)
Contemporary	1	4, 8, 12
Contemporary Drought	1	4, 8, 12
Climate Change	1	4, 8, 12
Climate Change Drought	1	4, 8, 12
Medium (Climate Change Drought)	1	8
Bad (Climate Change Drought)	1.5	8
Worst (Climate Change Drought)	3	8