

CORRELATION BETWEEN BOLDNESS AND AGGRESSION OF URBAN AND
RURAL SONG SPARROWS

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ABSTRACT

CORRELATION OF BOLDNESS AND AGGRESSION IN URBAN AND RURAL
SONG SPARROWS

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A behavioral syndrome is the term used to describe suites of correlated behaviors in animals. One behavioral syndrome that has been the focus of many studies is the correlation of aggressive and bold behaviors. Previous studies in song sparrows have found a correlation between territorial aggressiveness and boldness towards humans in rural populations, but not within urban populations. However, boldness was measured as flight initiation distance (FID) in response to humans. Recording flight initiation distance is a common measurement for assessing boldness in birds, but rural birds are not accustomed to humans and so respond to their presence much like they would to a predator. It was hypothesized that song sparrows in urban areas had become habituated to human presence thus a new method to record boldness was required. Playbacks of alarm calls were used to elicit a boldness response. Data were collected from 25 birds from both an urban and a rural site for a total of 50 test subjects. FID trials, Carolina wren alarm call playbacks, and male conspecific song playbacks were conducted on each bird. Results showed that urban birds were bolder in response to alarm call playback as well as human presence. Boldness and aggression were correlated in rural birds with each method of measuring boldness but only in urban birds when using alarm call

playback studies. This suggests that there is a behavioral syndrome between these behaviors but that some flexibility exists in urban birds.

INTRODUCTION

A behavioral syndrome is the term used to describe suites of correlated behaviors in animals (Sih et al. 2004b). Behavioral syndromes can have ecological and evolutionary significance within populations. If the behaviors are tightly linked, then the effects of selection on one behavior can be limited by the correlated effects on the other behavior. This in turn may be detrimental to an organism by leading it to behave in ways that are not conducive to increasing fitness (Pruitt et al. 2008, Pruitt and Riechert 2009). For example, female *Dolomedes* sp. fishing spiders that are aggressive hunters and territory defenders will consequently have access to greater resources and therefore have increased fitness. However, these more aggressive individuals seem to be unable to adjust their level of aggressiveness in different situations and will often eat all potential mates that approach (Arnqvist and Henriksson 1997). One behavioral syndrome that has been the focus of many studies is the correlation of aggressive and bold behaviors (Sih et al. 2004a). Correlations between boldness under predation risk and aggression toward conspecifics have been described in many taxa including: stickleback fish (Bell 2005), great tits (Verbeek et al. 1996), fiddler crabs (Reaney and Backwell 2007), and song sparrows (Evans et al. 2010, Scales et al. 2011). Correlations between boldness under predation risk and aggression also have the potential to lead to suboptimal behavior. Consider an individual that consistently shows higher levels of aggression toward conspecifics. That individual will may gain a better territory, or access to more resources, and thus may have increased fitness. However, if that individual also shows higher levels of boldness in all contexts, it could also have a higher risk of predation. An

optimally flexible individual would be boldest when predators are absent, but less bold when predators are present, thus behaving adaptively in both contexts. Mismatches between optimal behavior and observed behavior might occur most commonly when environments are changing rapidly, such as due to urbanization, or other forms of human induced rapid environmental change (Sih et al. 2011).

Organisms living in an urban habitat often display traits that are atypical of their rural counterparts due to different selection pressures (Evans et al. 2010). The focus of many studies has been to find traits that allow a species to “cope” with urbanization. For example, male white-crowned sparrows (*Zonotrichia leucophrys*) in urban habitats had higher baseline levels of stress indicators such as corticosterone than did rural males (Bonier et al. 2007). Partecke and Gwinner’s (2007) study on captive-raised European blackbirds (*Turdus merula*) found that birds with an urban ancestry were genetically predisposed to migrate less and develop their gonads earlier than those with rural parents. However, it is often unclear if such changes in urban animals represent evolutionary and genetically based adaptations or changes due to learning, habituation, or other forms of physiological acclimation.

Studies of song sparrows have found differences in behavior between urban and rural populations with urban males showing higher levels of aggression and higher levels of boldness than rural males (Evans et al. 2010, Scales et al. 2011). In addition to changes in individual behaviors, the behavioral syndrome appears to differ between urban and rural populations as well. A significant correlation has been found between territorial aggressiveness and boldness towards humans in rural populations of song sparrows. However, a similar significant correlation was not found in urban populations (Evans et

al. 2010, Scales et al. 2011). Population differences in behavioral syndromes have also been described in sticklebacks (*Gasterosteus* sp.) (Bell 2005, Bell & Sih 2007, Dingemanse et al. 2007) where the correlation between boldness and aggression disappears when predators are absent. Sih & Bell (2008) argue that a correlation between aggression and boldness reflects a trade-off between effective resource gathering and costs of predation for aggressive, bold individuals. If predation is low, then all individuals can be flexible and express higher levels of boldness so that the syndrome disappears. This hypothesis may apply to song sparrows if indeed urban birds experience lower predation pressure. However, the apparent lack of a behavioral syndrome in urban birds may also be an artifact of the method used to measure boldness. In studies on song sparrows boldness was measured using flight initiation distance (FID), or the distance to which a human observer can approach a subject before it flies away or takes cover (Evans et al. 2010, Scales et al. 2011). FID has been widely used as a measure of boldness and has been proposed to explain differences in where individuals will settle in relation to human disturbance (Carrete and Tella 2011). FID is also argued to be a trait under selection, explaining why urban animals typically have lower FID scores than rural animals (Moller 2008). However, FID may to some degree represent also habituation to humans, and thus for urban birds exposed to a high amount of human activity humans may not be seen as a potential predator. Rural birds are not accustomed to human interactions and so respond to this method much like they would to an approaching predator.

In this study, playbacks of heterospecific Carolina wren (*Thryothorus ludovicianus*) alarm calls were used as a novel method to test boldness in song sparrows.

Measuring boldness in urban birds by using alarm calls to simulate a predator could lead to a better understanding of the degree to which urban boldness is an inherent trait and the degree to which it is shaped by habituation to humans. Further, we suggest that using heterospecific alarm calls, rather than conspecific alarm calls, simulates the presence of a potential predator without signaling the presence of a conspecific rival to the male birds. Birds that have failed to react strongly to human interaction may be found to have a different boldness score when faced with the simulation of a natural predator. If urban birds appear bolder due as a result only of acclimation to humans, their FID scores will be lower than rural birds, but, the distance that they approach the alarm calls will not differ from the rural birds. However, if urban birds are inherently bolder, their boldness as measured by response to alarm calls should be greater than rural birds. Further, aggression and boldness as measured by response to alarm call playback may be correlated in both populations of song sparrows suggesting that both of these behaviors are linked as part of a behavioral syndrome.

MATERIALS AND METHODS

Data were collected from two distinct populations of song sparrows. One population inhabited an urban site on the campus of Western Carolina University in Cullowhee, North Carolina. This site is well-developed with sparse natural cover and any local birds are subject to nearly constant urban noises and bustle. Many of the territories at this site consisted of little more than a few trees or a hedge in front of a building. The other population of song sparrows was located at Kituwah Mound near Bryson City, North Carolina. This rural site has historical significance to the Cherokee people and so has been somewhat preserved. The song sparrow territories at this site were located on the edge of fields and hedgerows of trees.

Territories of male song sparrows were mapped at both locations during April and May of 2011 by observing singing males and marking where they employed countersinging towards neighbors. Once a breeding season has begun, male song sparrows have been found to almost always defend the same territory (Hughes and Hyman 2011). Therefore, it was not necessary to capture and band each bird for identification purposes, although some birds from each site had already banded during previous experiments. Each male song sparrow was instead given an identifying name based on its territory location. A total of 50 male birds, 25 from each of the two populations, were mapped out and used as experimental subjects.

Three experiments were performed on each of the males at the two sites: flight initiation distance (FID), alarm call playback trials, and song playback trials. Flight initiation distance trials were conducted as a measurement of boldness towards humans.

All FID experiments were initiated 20 to 25 meters away from a singing male to keep the data as consistent as possible. Starting distance was recorded from the bird in question, the distance at which the bird flew away or took cover, and the approximate height of the bird at the start of the experiment. FID scores are equal to the hypotenuse of the triangle formed by the distance from the observer at which the subject took flight and the height of the bird.

Alarm call playback was also used to test for boldness and playback of male conspecific song to determine the level of aggression of the birds. The playback methodology for the alarm call boldness trials and the aggression trials was as follows. Before the trial, a speaker was placed within cover near the center of a territory and the location marked with a flag. To measure the distance that the male displayed to the speaker, other markers were placed at intervals of 2, 4, 8, and 16 meters. Sound playback was then started and the location of the bird in respect to the flags was recorded every 5 seconds. Distance from the speaker was recorded as being either 0-2m, 2-4m, 8-16m, or greater than 16m. The number of songs that the male sang during playback were also recorded and totaled for each set of data. Data were recorded for 6 minutes during the length of the playback during which one song was played every 10 seconds. Data were then recorded for an additional 3 minutes once the playback had stopped for a total of 9 minutes per playback session. All sound files were recorded from birds at a rural site in Pennsylvania. A total of 30 song sparrow songs and 3 Carolina wren alarm calls were used. In order to keep one playback experiment from affecting the results of another, experiments were spread out such that neighboring birds were not subjected to playback

on the same day. All experiments were conducted either between the hours of 6:00AM and 12:00PM or 6:00PM and 7:30PM during May-June 2011.

The average distance to the speaker for the course of each 9 minute playback experiment was calculated and used to give boldness and aggression scores to each male. Pearson's correlation was used to test for significant correlation between the aggression and boldness values. The correlation coefficients were calculated for the relationship between both the FID scores and alarm call boldness scores with the aggression values for each male. Unpaired t-tests were used to compare the FID, alarm call playback, and conspecific song playback scores between the urban and rural sites.

RESULTS

At the rural site a positive correlation was found between conspecific song playback averages and FID scores ($r_p=0.646$, $N=25$, $p<0.001$, Figure 1). There was also a positive correlation detected between the conspecific song playback averages and alarm call average scores ($r_p= 0.524$, $N=25$, $p=0.007$, Figure 2). At the urban site, there was no significant correlation found between the conspecific song playback averages and the FID scores ($r_p = -0.001$, $N=25$, $p=0.997$, Figure 1). However, there was a positive correlation found between the alarm call scores and conspecific song playback averages ($r_p= 0.662$, $N=25$, $p<0.001$, Figure 2).

Conspecific song playback average distances were found to be significantly different between the urban and rural populations of birds ($t = - 6.592$, $df = 48$, $p<0.001$). The mean playback average from the WCU site was 7.56m while the mean value from the Kituwah population was 16.32m. FID scores collected from the urban birds and rural birds varied significantly as well ($t = - 6.859$, $df = 48$, $p<0.001$). Male song sparrows from the urban population allowed for a closer approach by the observer and had an average FID score of 5.52m. The rural birds in comparison had an average FID value of 12.3m. Alarm call boldness scores were also found to vary significantly between the two populations ($t = - 5.948$, $df = 48$, $p<0.0001$). The mean alarm call average value for WCU birds was 6.44m while the average from the Kituwah Mounds population was 14.56m.

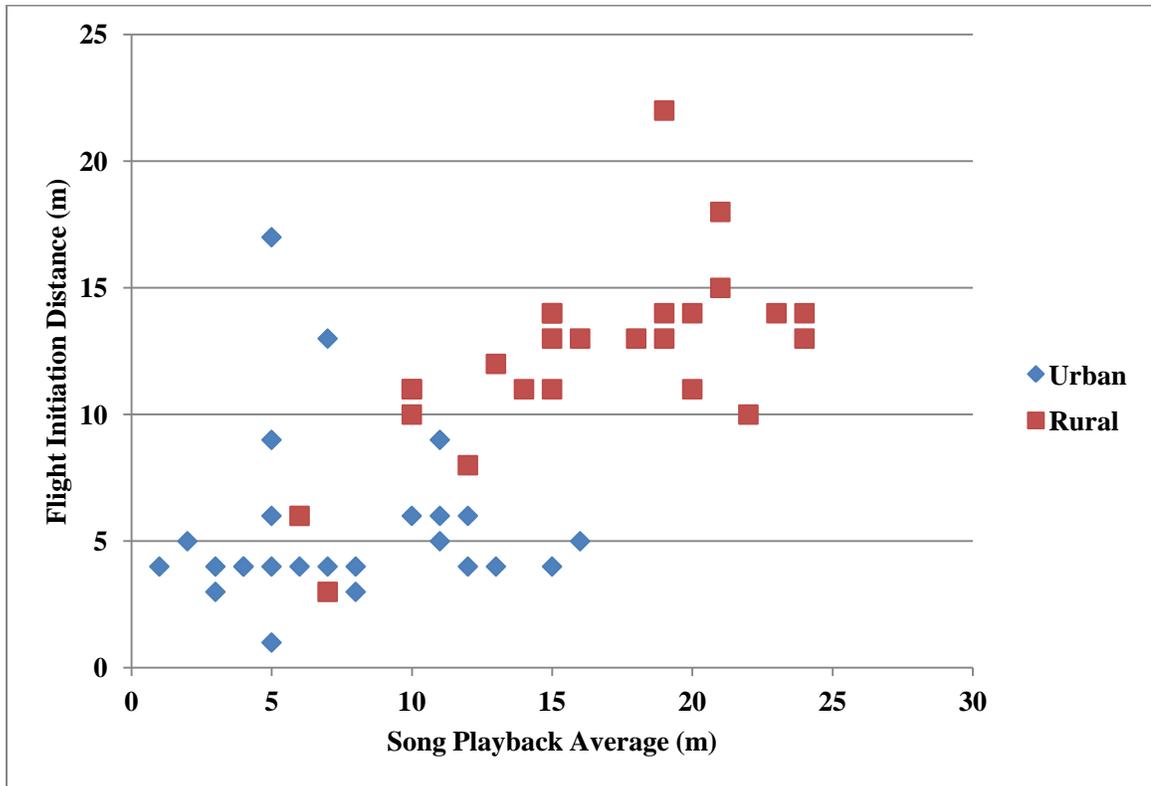


Figure 1: Correlation of song playback averages (aggression) and flight initiation distance scores (boldness) in urban and rural song sparrows.

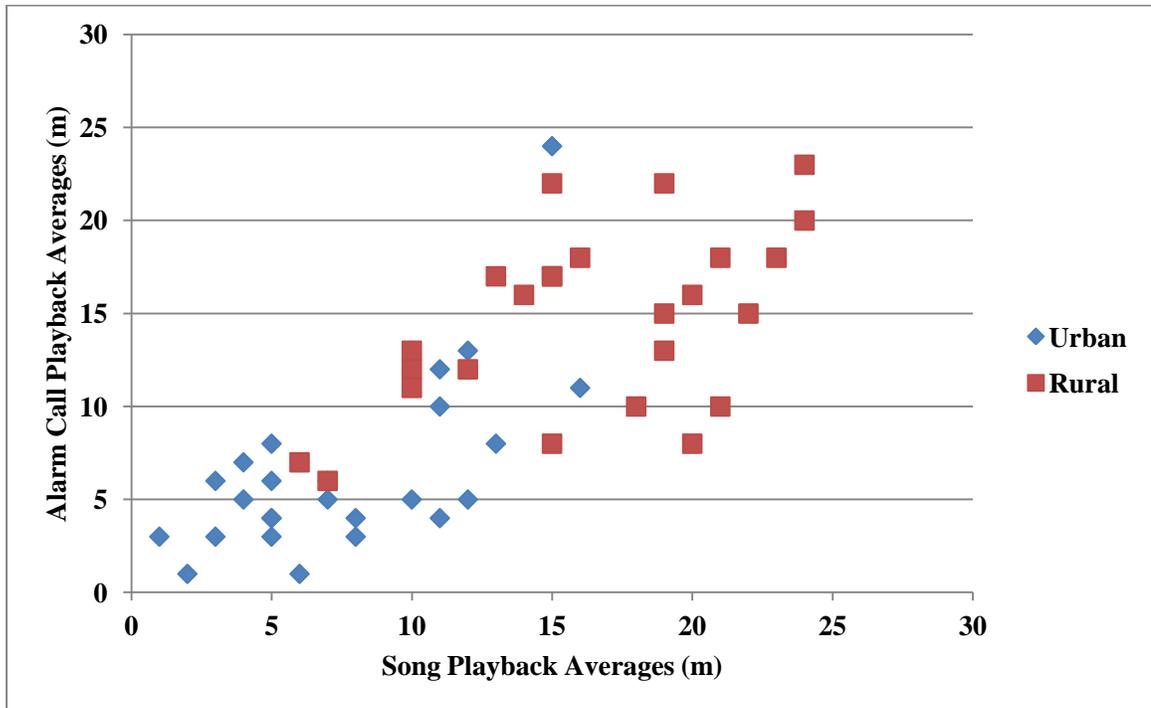


Figure 2: Correlation of song playback averages (aggression) and alarm call playback (boldness) in urban and rural song sparrows.

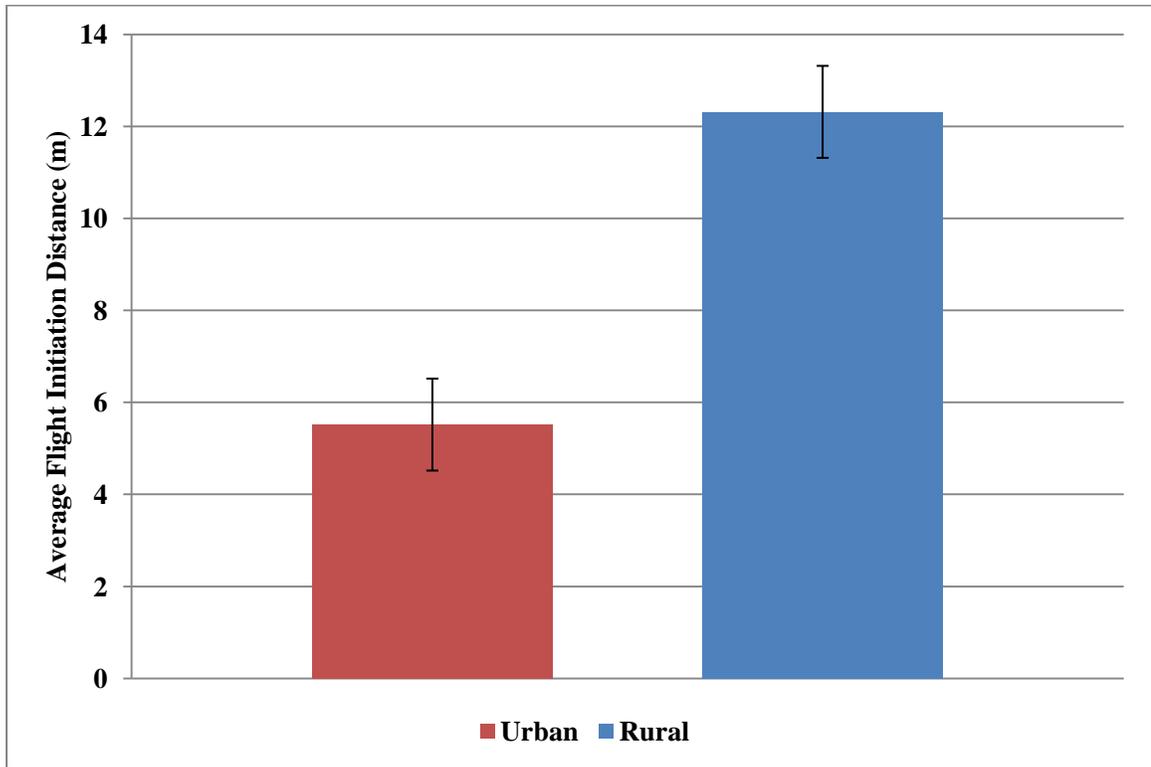


Figure 3: Average flight initiation distance scores (in meters) for birds at the urban and rural sites.

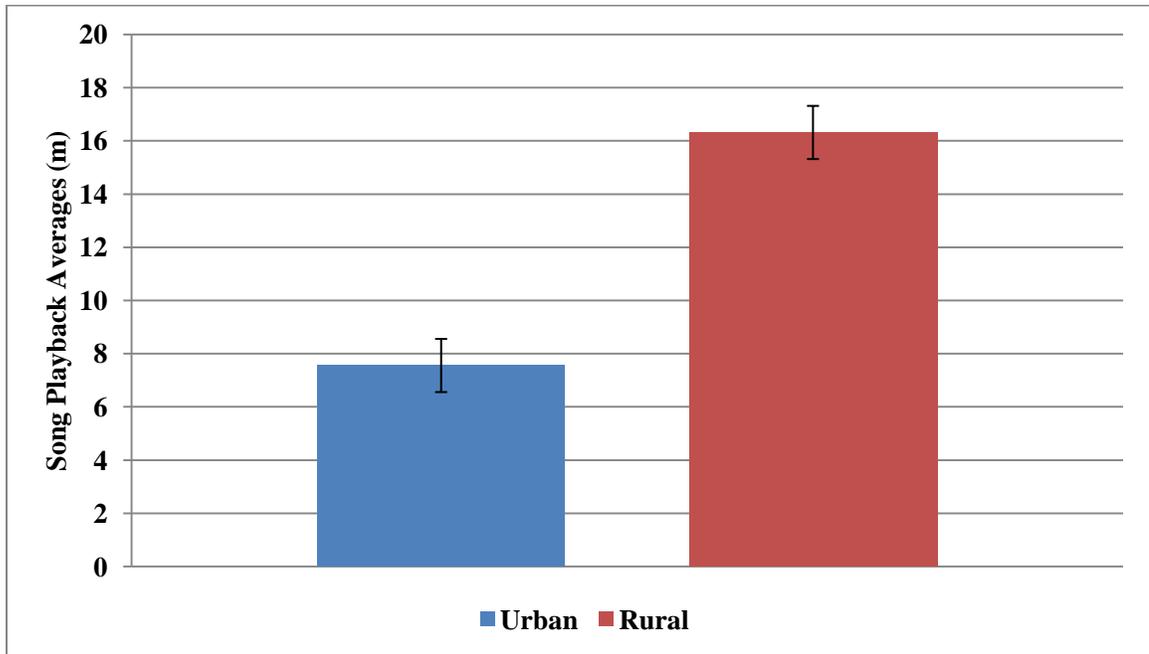


Figure 4: Song playback averages (in meters) for birds at the urban and rural sites.

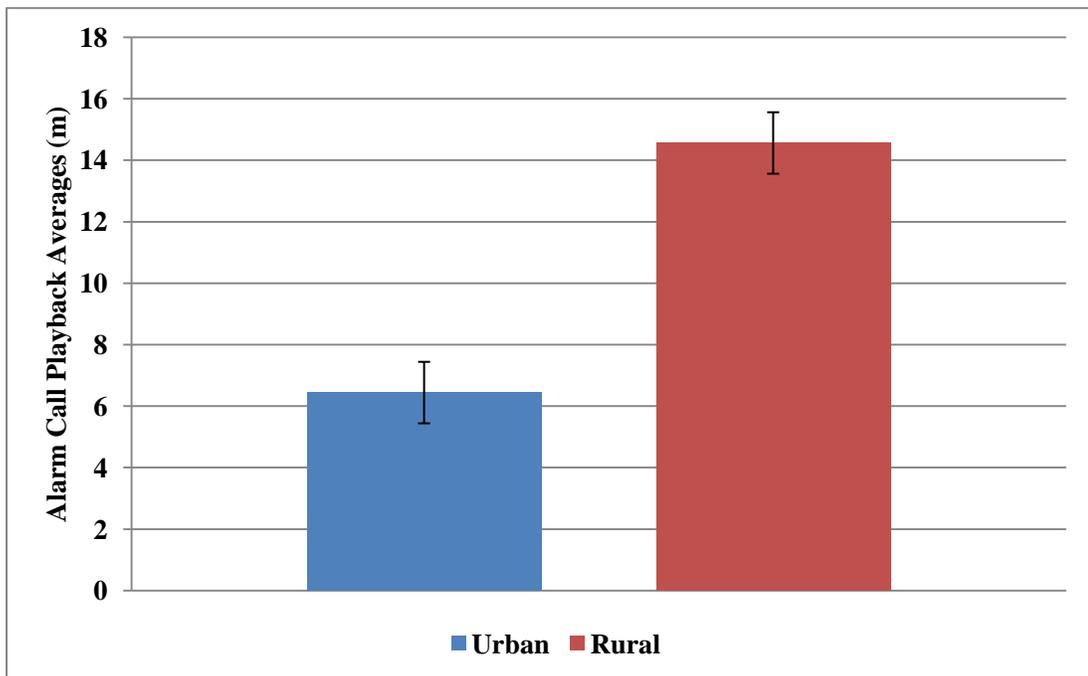


Figure 5: Alarm call playback averages (in meters) for birds at the urban and rural sites.

DISCUSSION

The results of each type of playback experiment varied significantly from population to population. Results were consistent with other studies in that urban birds showed a bolder response during experiments than their rural counterparts (Evans et al. 2010, Scales et al. 2011). Lower scores for boldness trials, indicative of a bolder response from the subject, were expected within the urban population of song sparrows. Boldness towards potential predation within other urban populations of animals has been documented before (Moller 2008, Sih et al. 2011). Although many males did decrease their singing intervals as the observer approached during FID trials, they often did not take flight until we were within a few meters of their perch. On the other hand, the rural birds occasionally flew to cover before the observer could visually locate them.

We expected that the urban birds would be bolder than rural ones using FID trials, but they also showed bolder responses in the alarm call playback experiments. Urban song sparrows are therefore not only bolder towards humans, perhaps due to habituation, but are also bolder towards natural predators. It could be that urban birds have to be bolder in order to survive in habitats with little cover. Rural males have generally larger territories often with dense foliage for cover when threatened. Sometimes the urban birds that were not as bold would have to flee their territories entirely during the experiments as they lacked adequate cover. Since leaving his territory at every sign of danger may eventually end with the loss of those resources to another male, urban birds may need to learn to be bolder towards predators. It could be that urban birds have a constantly higher predation risk as well since they are generally more

exposed in an urban environment than rural birds. Considering all of this, urban birds may become habituated towards natural predators as they do towards humans in urban habitats. It is also possible that defending an urban territory may only be possible for individuals that are inherently bolder.

Urban birds were also found to have significantly more aggressive responses to a conspecific song playback than rural males (Evans et al. 2010, Scales et al. 2011). There are many reasons why this could be. A study of song sparrows in a rural habitat found that aggressive birds appeared able to gain high quality territories (Scales et al. 2013). Male song sparrows may in fact find urban territories preferable to for display to attract females or to defend, so urban territories may be more desirable than rural ones. In this case only the more aggressive males would be capable of defending these prime territories. Alternatively, the higher aggression of urban birds might be linked to their greater boldness. If urban birds must be innately bolder in order to cope with the stressors found in urban habitats and boldness is linked with aggression, then the higher level of aggressiveness could be due to the behavioral syndrome. However, many things remain unknown regarding territory selection in song sparrows.

As expected, results showed a significant correlation between flight initiation distance scores and conspecific song playback experiments at the rural site. The results of the FID experiments at the urban site were not correlated with song playback. Other studies have shown a correlation between boldness and aggression in rural populations of song sparrows using FID trials, while the urban ones were not correlated (Evans et al. 2010, Scales et al. 2011). However, the data collected using the Carolina wren alarm call playback as a measure of boldness were significantly correlated with aggression scores in

both of the populations. This indicates that boldness and aggression in song sparrows are indeed part of a behavioral syndrome when an appropriate measure of boldness is used.

FID trials continue to be an excellent measurement of boldness towards a potential predator in rural populations of birds who do not often come into close proximity with humans. However, using alarm call playback experiments for the urban song sparrows provided a way to more accurately display the threat of a predator to an animal that may have become desensitized to close human interaction. Using this novel method we found the behavioral syndrome between the two behaviors that had been missing in the urban population, leading to a consideration of the implications of this species having the syndrome. Studies have shown that behavioral syndromes can lead to maladaptive behaviors in species, especially within boldness and aggression studies (Pruitt and Riechert 2009, Pruitt et al. 2008). A more aggressive male may have better access to females but may also be too bold towards predators. The ability to change one behavior within the syndrome could therefore be the difference between life and death. It is interesting that the correlation between the behaviors within the urban birds was only seen when using a measurement for boldness that was more indicative of a natural predator. Rural birds treat human presence as they would against the threat of a natural predator. Urban birds have seemingly learned to mostly ignore humans in order to survive. These birds are bolder towards human presence than to warning calls that a predator is nearby. Consequently, the birds seem able to adjust their boldness response even though it is part of a behavioral syndrome. The capacity to change a behavior found in the syndrome could provide a level of adaptability that has been highly selected for.

There have been some studies on behavioral flexibility in individuals showing behavioral syndromes. For example, Bell and Stamps (2004) found that stickleback fish, in which there is a behavioral syndrome between boldness and aggression, did not show the same results for certain behavioral experiments through all of their developmental stages. That is, even though the data consistently indicated a behavioral syndrome existed between the behaviors, individual fish had different strengths of responses to conspecifics and predators over time. A study by Lee and Berejikian (2008) sought to determine whether behavioral syndromes could lead to selection of undesirable traits in hatchery raised fish and found additional evidence that there is some flexibility even between strongly correlated behaviors. Individual fish did not always take the same amount of risk when under the threat of predation but there was always a significant correlation between feeding rates and response to predators (Lee and Berejikian 2008). Behavioral flexibility may also be related to behavioral phenotypes or personality of the individual. Quinn and Cresswell (2005) found that the ability of some birds to adjust their behavior to certain situations can vary with their individual personalities. Chaffinches that exhibited a hyperactive (bolder) response in the face of a predator were less likely to show some flexibility within their behaviors than the hypoactive (less bold) individuals. The differences in personality traits within individuals could be one of the leading factors determining what populations succeed in new habitats.

Future studies testing the capability of rural birds to survive in an urban habitat could help to reveal if these animals can modify their behavior to succeed in locations with less than ideal conditions. Currently we assume that urban birds have certain behavioral or physiological characteristics that allow them to live in the urban

environment but are unsure as to what exactly these attributes might be. It would also be interesting to see if male song sparrows select different environments in which to establish their territories from year to year. That is, would a male that defended an urban territory one year continue to choose an urban habitat in following years? And if so, would that choice be based on the desire to have a territory located within an urban habitat or would it simply be geared towards remaining in the same geographical location? Long-term studies could reveal more about what males choose to select in a territory as well.

One interesting new area of research may help to understand what populations of song sparrows can utilize the urban habitat. The research was based on the idea that certain behavioral traits, boldness in this case, may be linked to how successful a species is in dispersing to new habitats (Rehage and Sih 2004). For a species to invade new habitats it must have the ability to successfully disperse (Ehrlich 1986) but not all individuals in a species have the same dispersal rates (Kot et al. 1996). Rehage and Sih (2004) found that bolder fishes, or those that explored new surroundings at a higher rate than others, were significantly more successful in reaching new habitats. Since boldness has been found to be an important factor for the ability of some species to invade new environments it would make sense that bolder animals would be the first to invade urban habitats. Bolder birds would be the most likely to explore new environments, even those with widespread anthropogenic impacts. As urbanization continues to occur and human populations increase we have to consider how this will affect local species. If only some individuals in each species are capable of living in urban habitats then we could be facing the loss of many populations, even within a species that seems to do well in close

proximity to human influences. Understanding what a species may find useful in an urban environment and what pressures prove to be too much for them is essential to protecting the future of our native wildlife. For song sparrows, having significantly bolder and more aggressive responses along with the likelihood of flexibility within their behaviors may be essential to their success in thriving in an urban habitat.

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