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Behavioural Syndromes in Urban and Rural Populations of Song Sparrows

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Abstract

Animals in urban habitats are often noticeably bold in the presence of humans. Such boldness may arise due to habituation, as urban animals learn, through repeated exposure, that passing humans do not represent a threat. However, there is growing research suggesting that: (1) inherent traits, as opposed to learned behaviour, influence which species invade urban habitats, and (2) individuals exhibit individual personality traits that limit behavioural flexibility, with the possible result that not all individuals would be able to demonstrate an appropriate level of boldness in urban environments. As a result, perhaps only birds with inherently bold personalities could successfully settle in an area of high human disturbance, and further, we might also expect to see the existence of behavioural syndromes, where boldness is correlated with variation in other behavioural traits such as aggression. In this study, we examined boldness and territorial aggression in urban and rural populations of song sparrows. We found that urban birds were bolder towards humans and that urban birds also showed higher levels of territorial aggression. We also found an overall correlation between boldness and territorial aggression, suggesting that urban boldness may be part of a behavioural syndrome. However, we see no correlation between boldness and aggression in the urban population, and thus, more work is needed to determine the mechanisms accounting for high levels of boldness and aggression urban song sparrows.

Introduction

Animals in urban habitats are often noticeably more bold, or tame in the presence of humans. Such boldness in the presence of humans in urban environments is often considered to arise due to habituation, defined as the gradual decrease in response to repeated stimuli (Anderson et al. 1999; Metcalf et al. 2002). If habituation explains urban boldness, then animals are learning, through repeated exposure, that passing humans do not represent a predator, are unlikely to harm them, and thus the animals eventually come to ignore humans in their habitat. This simple explanation for boldness in urban animals, however, has not been widely tested. In fact, several studies have noted species-specific differences in boldness in response to human observers (Fernández-Juricic et al. 2002; Blumstein 2003; Blumstein 2006; Blumstein et al. 2005; Heil et al. 2007), and it has recently been suggested that short flight initiation distance (FID) for urban birds has evolved as an adaptation to urban environments (Moller 2008). Studies examining bird communities frequently argue that there are inherent species-specific traits that allow some species to successfully invade new habitats when introduced (Sol & Lefebvre 2000; Sol et al. 2002), colonize urban environments (Bonier et al. 2007), or habituate to anthropogenic disturbances (Conomy et al. 1998). It is likely that inherent differences between species in

boldness and ability to colonize urban habitats originated through selection on underlying individual differences within a species, and if this is the case, perhaps inherent traits within a species could determine which individuals successfully colonize urban habitats. In other words, perhaps only animals with inherently bold personalities could successfully settle in an area of high human disturbance and demonstrate an appropriate level of boldness in an urban environment, instead of wasting time and energy hiding from every human that walks past (Diamond 1986; Partecke et al. 2004), while animals unable to cope with disturbance will disperse out of an area, as has been suggested in dolphins (Bejder et al. 2006) and burrowing owls (Carrete & Tella 2009). Few studies have examined if urban and rural animals represent different genetic subsets of a population, though there is evidence from Common blackbirds (*Turdus merula*) that differences between urban and rural populations may partly reflect genetic differences (Partecke et al. 2004; though see Partecke et al. 2006), and studies in dark-eyed juncos (*Junco hyemalis*) and house finches (*Carpodacus mexicanus*) have noted selection can quickly result in phenotypic differences in urban and rural environments (Yeh 2004; Badyaev et al. 2008).

Many recent studies in animal behaviour have focused on the observation that individuals do not seem to be optimally flexible in their behaviour, and that individuals within a population of animals can be defined as being bold or aggressive across a wide range of situations (i.e. territorial, feeding, parental, or antipredator behaviour), while others are non-aggressive or shy. These correlated suites of behaviours are often referred to as 'behavioural syndromes' (Sih et al. 2004). On occasion, the correlation between behaviours may be strong enough to lead individuals to behave inappropriately in a given situation. For example, female fishing spiders (*Dolomedes fimbriatus*) that are highly aggressive in hunting and territory defence also frequently kill and eat every potential mate that approaches (Arnqvist & Henriksson 1997). With respect to predation, it has been noted that aggressive stickleback fish (*Gasterosteus aculeatus*) are also bold in the face of predators (Huntingford 1976), and salamanders (*Ambystoma barbouri*) that are very active in feeding are also overly active in the presence of predators, leading to high mortality (Sih et al. 2003). These examples all highlight the concept that behaviour is not completely flexible, that individuals may have limited behavioural plasticity (Sih et al. 2004), and this could lead to individuals behaving either too bold in the presence of predators or too shy in the absence of a threat. If high urban boldness occurs as part of a behavioural syndrome in which boldness is correlated with aggression, then we might also expect to see high levels of territorial aggression in urban birds.

In this study, we examine the correlation between territorial aggression and boldness in response to humans in the song sparrow (*Melospiza melodia*). We have qualitatively observed that song sparrows in an urban population are extremely bold, showing little alarm in the presence of humans. The questions we examine in this study include: (1) Does aggression or boldness differ in urban vs. rural populations? (2) Does aggression correlate with boldness in a given population? With respect to question 1, we hypothesize that the urban population will be bolder than the rural population, as this was the qualitative observation that led us to propose this study. We have no *a priori* reason to expect the populations to differ in aggression unless boldness and aggression are correlated (question 2). Finally, we examine if the correlation between aggression and boldness varies between populations.

Methods

We conducted the study at three sites: a rural population at the Appalachian Highlands Science Learning Center at Purchase Knob, North Carolina (35°35′N, 83°04′W, elevation 1500 m), an urban population on the campus of Western Carolina University, in Cullowhee, North Carolina (35°18′N, 83°11′W, elevation 640 m), and a rural population studied near Hartstown, Crawford County, Pennsylvania, USA (41°33′N, 80°22′W, elevation 317 m). The two rural populations were found in habitats consisting of open old fields surrounded by hedgerows and forest. The urban habitat was primarily open lawns and parking lots surrounded by ornamental shrubs and hedges alongside university buildings. In the two North Carolina populations, we mapped the territories of approx. 20 male song sparrows without marking individual males. Once the breeding season has begun, males show strong site fidelity to their territories. In a 5-yr study of song sparrows in Pennsylvania, <5% of territorial males switch territories within a season (J. Hyman & M. Hughes, unpubl. data). We can thus assume that males noted singing in a given tree even weeks apart during the breeding season is highly likely to be the same male. If this assumption was ever violated, it merely added noise to our data. The

Pennsylvania rural population has been studied for several years and all males are marked with unique combinations of coloured leg bands for individual identification. We mapped the territories of 24 male song sparrows, and determined territory boundaries through extensive observation of the locations of singing subjects, and by noting the location of countersinging interactions between neighbours. In all populations we performed experiments designed to assay the territorial aggression and the boldness in response to humans of each male. The study sites did not differ noticeably in their population density, nor in their breeding phenology. In all three populations, we performed experiments during the breeding season, from May to Aug. 2007. All observations were performed between 06:00 and 12:00 hours.

We assayed individual males' level of aggression by measuring response to playback of conspecific song (Nowicki et al. 2002; Hyman et al. 2004; Hyman & Hughes 2006). In the playback tests we broadcast 6 min of song sparrow song from near a favoured song perch on the subject's territory, and recorded the response of our subjects during the 6 min of playback, and for an additional 3 min after the playback concluded, for a total of 9 min. Distance to the speaker was recorded every 5 s, and our primary response measure was the average distance between the subject and the speaker over the entire 9 min. A closer average approach to the speaker is assumed to indicate a more aggressive response, as suggested by similar experiments in which close approach to a speaker was a significant predictor of attack (Searcy et al. 2006). Previous studies demonstrate that males show consistent individual differences in their response to playback (Nowicki et al. 2002; Hyman et al. 2004; Hyman & Hughes 2006), and these differences remain consistent across the breeding season, showing only weak seasonal trends (Nowicki et al. 2002). Approach scores tend to deviate from the normal distribution, and thus scores were normalized via a log transformation. We performed playbacks with 17 males at the rural North Carolina site (NC rural), 18 males at the urban North Carolina site (NC urban), and 24 males at the Pennsylvania site (PA rural). The songs used as exemplars all came from a rural population in Pennsylvania. Given that song sparrows are known to respond more strongly to local song (Searcy et al. 1997), using Pennsylvania songs could have biased the study to find stronger responses from birds at the Pennsylvania field site, though this clearly did not happen (see Results).

In order to assay boldness in response to human disturbance, we measured FID, or the distance at which a bird approached by a human takes evasive action by hiding or flying away. This very simple metric has previously been used successfully by researchers examining how bird species differ in their response to human disturbance (Blumstein et al. 2003; Blumstein 2006) including differences between birds in rural and urban environments (Cook 1980). We measured FID by having observers walk quietly towards a male singing on an exposed perch, and recording: (1) the distance at which the observer started, (2) the distance at which the focal bird fled, and (3) the approximate height of the singing perch. FID was then calculated following Blumstein (2006). We made an effort to standardize our starting distance in each trial. Overall, we had no significant correlation between start distance and FID (Pearson Correlation: $r_p = 0.209$, $n = 49$, $p = 0.149$), and thus we were able to simply use FID in our analysis rather than using statistical methods to control for start distance (Blumstein et al. 2003; Blumstein 2006). We performed two FID trials, 2–4 d apart, with some males in the Pennsylvania population in order to determine if males show consistent individual differences in FID. We performed FID trials with 14 males at the rural North Carolina site (NC rural), 14 males at the urban North Carolina site (NC urban), and 21 males at the Pennsylvania site (PA rural).

We compared FID scores of birds in the three populations, using ANOVA, which allowed us to test our qualitative impression of the boldness of urban birds. We compared aggression scores of the populations, using ANOVA, to determine if the populations differed with respect to other behavioural characteristics. We examined the correlation between boldness and aggression in the populations using a Pearson Correlation. This allowed us to determine if these traits tend to vary independently of one another, or if they represented a behavioural syndrome that was common to the two environments. In order to look for differences in the correlations between aggression and boldness in all three populations, we performed *post hoc* comparisons of the correlations each populations. Given that we found a significant correlation between boldness and aggression in the Pennsylvania population but not in the North Carolina populations (see Results below) we calculated the statistical power of our tests in North Carolina populations to find a correlation of the strength seen in the Pennsylvania population. In all statistical tests, p-values were two tailed.

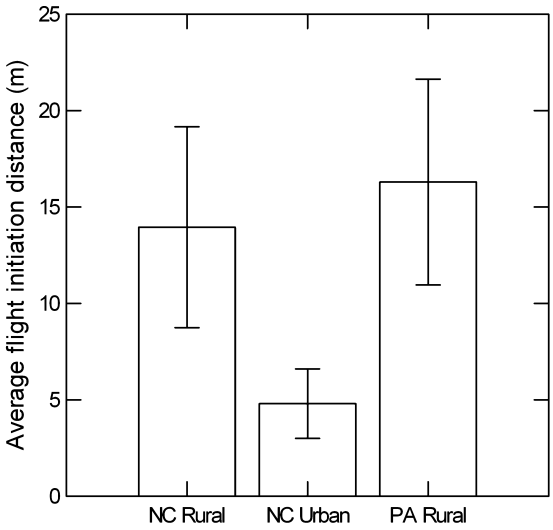

Fig. 1: Average flight initiation distance in response to a human observer ($\bar{x} \pm$ SD) for birds at three study sites: NC urban, an urban site on the campus of Western Carolina University, in Cullowhee, NC, PA rural, a rural site at Hartstown, PA, and NC rural, a rural site at Purchase Knob, NC. Birds in the urban population have significantly smaller FID than birds in either rural population (ANOVA: $F_{2,49} = 25.161$, $p < 0.001$).

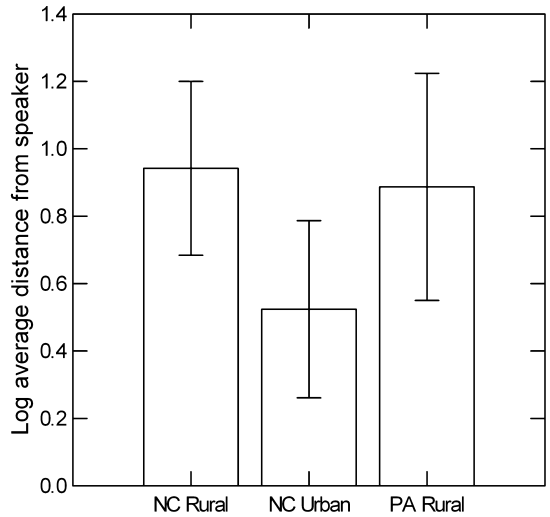

Fig. 2: Average distance to speaker (log transformed, $\bar{x} \pm$ SD) for birds at three study sites. Birds in the urban population show a significantly closer approach to playback than birds in either rural population (ANOVA: $F_{2,59} = 7.352$, $p = 0.001$).

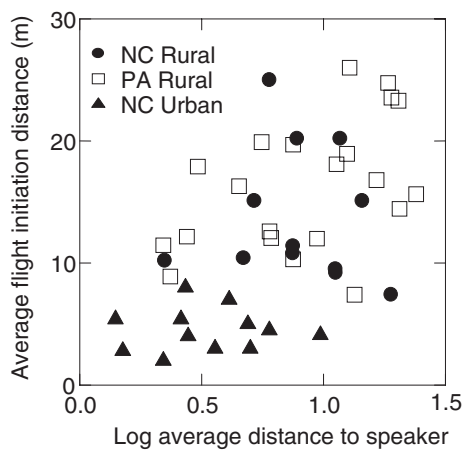

Fig. 3: Correlation between boldness (flight initiation distance) and territorial aggression (log average distance to playback) for birds at three study sites. Overall, there was a significant correlation between aggression and boldness in the three populations (Pearson Correlation: $r_p = 0.539$, $n = 45$, $p < 0.001$). Significant within-population correlation was found only in the Pennsylvania population (Pearson Correlations PA rural: $r_p = 0.470$, $n = 21$, $p < 0.032$, NC urban: $r_p = 0.029$, $n = 12$, $p = 0.929$; NC rural: $r_p = -0.073$, $n = 12$, $p = 0.821$).

Results

The urban and rural populations differed strongly in boldness, as measured by FID (ANOVA: $F_{2,49} = 25.161$, $p < 0.001$; Fig. 1), with the urban birds allowing a significantly closer approach by a human observer. *Post hoc* comparisons show that the Pennsylvania and North Carolina rural populations did not differ in boldness (Tukey test: $p = 0.444$) while both rural populations differ from the urban population (Tukey test: both $p = 0.001$). These observations support our initial qualitative impression of a difference between the populations. We performed two FID trials several days apart with some males in the Pennsylvania population. The correlation in scores from one trial to next demonstrate significant consistency within individuals in FID (Pearson Correlation: $r_p = 0.758$, $n = 17$, $p < 0.001$), and there was no difference in FID from trial 1 to trial 2 (paired *t*-test: $t = -0.023$, $df = 16$, $p = 0.982$).

The urban and rural populations also differed significantly in their response to playback, with the urban birds showing a significantly closer approach to playback than the rural birds (ANOVA: $F_{2,59} = 7.352$, $p = 0.001$; Fig. 2), and again, the two rural populations did not differ (Tukey test: $p = 0.989$), while both rural populations differ from the urban population (Tukey Test: PA vs. NC urban, $p = 0.003$, NC urban vs. NC rural $p = 0.005$).

Overall, there was a significant correlation between aggression and boldness in the three populations (Pearson Correlation: $r_p = 0.539$, $n = 45$, $p < 0.001$; Fig. 3). However, a significant within-population correlations was found only in the Penn-

sylvania population (Pearson Correlation: $r_p = 0.470$, $n = 21$, $p < 0.032$). We could not detect a correlation between aggression and boldness within either population in North Carolina (Pearson Correlation: NC urban: $r_p = 0.029$, $n = 12$, $p = 0.929$; NC rural: $r_p = -0.073$, $n = 12$, $p = 0.821$).

Discussion

Our study began with the qualitative observation that male song sparrows in an urban population exhibited high boldness, allowing close approach by human observers. This qualitative observation was confirmed using FID as a measure of boldness, as the urban birds had closer FID than either rural population. Numerous other studies have found bolder or less wary responses by wildlife to humans in urban or high human traffic environments (Fernández-Juricic et al. 2002; Vuorisalo et al. 2003; Bejder et al. 2006; Gonzalez et al. 2006; Moller 2008), similar to what we have found in urban song sparrows.

We demonstrate that in song sparrows, FID is a repeatable measure, with males showing consistent individual differences. Only a few studies have demonstrated repeatability in FID (Carrete & Tella 2009) and in fact, at least one study has concluded that individual identity is not an important predictor of FID (Runyan & Blumstein 2004). It should not be surprising to find individual variation in FID. Many studies have described species-specific differences in FID and have argued that natural selection has shaped these species-specific differences (Fernández-Juricic et al. 2002; Blumstein 2006; Blumstein et al. 2005; Heil et al. 2007), and have suggested that FID has evolved in birds in response to living in urban environments (Moller 2008). If FID measures a trait capable of evolving between species, there must be individual variation in the trait within a species.

We also found that males in the urban population were more aggressive than males in the rural populations. We initially hypothesized that if urban birds were bolder, they may also be more aggressive, if boldness and aggression are correlated parts of a behavioural syndrome. As mentioned above, such correlations of behaviours within a behavioural syndrome have been observed to result in surprising, or even maladaptive behavioural patterns (Arnqvist & Henriksson 1997; Sih et al. 2003). It has even been suggested that selection on FID helped drive the evolution of domestic dogs from their wild wolf ancestors, with many other traits we associate with domestication having arisen due to their correlation with FID (Coppinger & Coppinger 2002). We found that aggression and FID were correlated across all populations, as well as within the Pennsylvania population, which could be interpreted as support for the hypothesis FID and territorial aggression are part of a behavioural syndrome. However, we were unable to detect a within-population correlation in the two North Carolina populations, and thus, there is no evidence of a behavioural syndrome acting as a constraint, and the birds in the urban setting may be adaptively adjusting their behaviour and habituating to the presence of humans. For several reasons, we are limited in our ability to fully interpret the overall correlation that we observed. Though the correlation between aggression and boldness was significant in only the Pennsylvania population, there were no significant differences between populations in the strength of the correlation (NC urban vs. NC rural: $Z = 0.22$, $p = 0.828$, NC urban vs. PA: $Z = 1.175$, $p = 0.828$, NC rural vs. PA: $Z = 1.43$, $p = 0.153$). Also, we have low power to detect a correlation between aggression and boldness of the strength seen in the Pennsylvania population (Pearson Correlation: $r_p = 0.470$, $n = 21$, $p < 0.032$) with sample sizes of just 12 in the North Carolina populations (power < 0.33). More importantly, it may that the failure to detect a correlation in the urban population was a result of low variation in the urban population in aggression (variance in aggression: NC urban = 0.069, NC rural = 0.066, PA = 0.114) and boldness (variance in FID: NC urban = 3.242, NC rural = 27.187, PA = 28.472). Therefore, it is impossible for us to state conclusively that aggression and boldness are not correlated in the North Carolina populations. It remains possible that aggression and boldness are truly uncoupled in some populations, but not in others, and we must consider several hypotheses to explain this pattern.

It is worth noting that the Pennsylvania population was the only one in which birds were banded and through the past experience with being mist netted, these birds may have a particular aversion to humans. This experience could cause measures of aggression and FID to be correlated, as FID obviously measures an individual's aversion to a human observer, and responses to playback may measure aggression and also, in part, reflect the boldness of the individual in approaching a human observer of the playback. In this case, a correlation between aggression and boldness would be generated, but only in the banded birds of our rural population. In the future, it will be important to perform playback and FID trials before a population is banded to investigate the effects of mist netting on FID and playback responses.

Multiple studies in sticklebacks (*Gasterosteus* sp.) have found that aggression and boldness were correlated in some populations, but uncorrelated in populations that appeared to have lower predation risk (Bell 2005; Dingemanse et al. 2007), and exposure to predation caused the correlation between boldness and aggression to arise (Bell & Sih 2007). These studies on sticklebacks demonstrate that not all correlations between aggression and boldness reflect fixed behavioural syndromes, but that behavioural plasticity can play an important role in generating correlations between behaviours. If predation pressure is lower on the urban song sparrows, we may be observing a similar phenomenon. At present, however, it is unknown if predation pressure differs between our urban and rural populations.

If aggression and boldness are uncoupled in these song sparrow populations, we are left with the question of why the urban birds were strikingly more aggressive than birds from rural populations. One possibility is that the urban habitat is actually a better habitat for these song sparrows, resulting in higher competition for territories, and thus higher aggression. Urban habitats could be better for many songbirds due to lower abundance of predators (Gering & Blair 1999), warmer temperatures, or greater light levels resulting in an early dawn chorusing (Miller 2006), which could be preferred by females (Otter et al. 1997), and could also result in longer days with more available time for foraging. Studies examining endocrine correlates of stress have found that urban Common blackbirds show lower corticosterone stress response than rural birds, suggesting either that they find urban habitats less stressful, that they shifted their behaviour to avoid the urban stress, or adapted to have a lower stress response (Partecke et al. 2004). Similarly, suburban Florida scrub-jays (*Aphelocoma coerulescens*) have lower stress hormone levels than their rural counterparts (Schoech et al. 2004). Interestingly, studies of dark-eyed juncos have found that males in urban populations are less aggressive, and this reduced aggression was hypothesized to result from the milder climate and longer breeding season at the urban site (Newman et al. 2006).

Alternatively, one could argue that urban habitats are poorer habitats, leading to greater competition for more limited resources. Much recent research has demonstrated that birds in urban habitats experience unique stresses, such as high levels of light (Miller 2006), noise (Slabbekoorn & Peet 2003; Wood & Yezerinac 2006), chemical pollution (Burger et al. 2004; Chandler et al. 2004; Gorissen et al. 2005; Roux & Marra 2007), and higher abundances of predators (Jokimaki & Huhta 2000; Sorace 2002). Some studies of the endocrine correlates of stress support the idea of tough urban habitats as urban white-crowned sparrows (*Zonotrichia leucophrys*) show a higher baseline corticosterone levels than rural birds, suggesting that urban white-crowned sparrows find urban habitat particularly stressful (Bonier et al. 2007a,b). In the face of high predator abundance, the boldness that allows birds to persist in an urban area could also lead such birds to have higher mortality from predators. Such populations would experience high territory turnover and greater territorial boundary instability, which could lead to higher levels of aggression. As a result, boldness and aggression would be higher in urban habitats and correlated across populations even when the behaviours are not correlated in individuals, which essentially matches what we saw in our study. As of yet, however, we do not know if territory turnover differs between these urban and rural populations.

In our study, we demonstrated that birds in an urban population of song sparrows were both bolder and more aggressive than rural birds. It is important to note that this study is based on a comparison of just three populations. As noted above, urbanization does not appear to generally lead to higher aggression in birds (Newman et al. 2006) and further comparisons will be necessary to examine if these findings represent a general trend towards greater boldness and aggression in urban song sparrows. The lack of a correlation between boldness and aggression in the smaller study populations leaves us unable to support the hypothesis that high urban aggression occurred as part of a behavioural syndrome linked to high urban boldness. Increasing our sample size of urban birds may allow us to determine if the correlation between aggression and boldness differs for urban and rural birds. However, the lower variance in aggression and boldness scores for urban birds may continue to limit our ability to see a correlation, even with larger sample sizes. At present, we are unable to conclude if urban populations are bolder due to habituation or through differential settlement in urban and rural habitats. The 'differential settlement' hypothesis implies that there are inherent differences between the urban and rural birds. To investigate this issue further, one could perform behavioural tests on urban and rural birds in captivity where they would be isolated from their typical urban or rural environmental conditions. If behavioural differences persist, they would provide further evidence for the idea that the birds

settling in urban and rural habitats are different, though developmental effects could not be ruled out. Another possibility would be to perform longitudinal studies of birds in urban habitats to see if boldness and aggression increase with time, or to look for evidence of less bold birds disappearing earlier. Ultimately, a common garden experiment, as was done with European blackbirds (Partecke et al. 2004) could determine if the behavioural differences between urban and rural populations arise from inherent differences between the birds in these populations.

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