



## Behavioral Syndromes Break Down in Urban Song Sparrow Populations

Jennifer Scales\*, Jeremy Hyman† & Melissa Hughes\*

\* Department of Biology, College of Charleston, Charleston, SC, USA

† Department of Biology, Western Carolina University, Cullowhee, NC, USA

### Correspondence

Jeremy Hyman, Department of Biology,  
Western Carolina University, Cullowhee, NC  
28723, USA.  
E-mail: jhyman@email.wcu.edu

Received: March 1, 2011

Initial acceptance: May 21, 2011

Final acceptance: July 3, 2011

(D. Zeh)

doi: 10.1111/j.1439-0310.2011.01943.x

### Abstract

Animals in urban habitats face a number of unique stresses, including the necessity of dealing with high levels of human activity. Growing research suggests that: (1) inherent traits, as opposed to learned behavior, influence which species invade urban habitats, and (2) individuals exhibit behavioral syndromes that limit behavioral flexibility. As a result, perhaps only animals with inherently bold personalities successfully settle in areas of high human activity, and such animals may also exhibit correlated variation in other behavioral traits, such as territorial aggression. In this study, we examine boldness and aggression in several urban and rural populations of song sparrows (*Melospiza melodia*). We found that urban birds were both bolder toward humans and also showed higher levels of aggression. We found a correlation between boldness and aggression in all populations combined, but no correlation within urban populations. Our results agree with other recent studies of song sparrow behavior, suggesting that greater boldness and aggression are general features of urban song sparrow populations, and a lack of a correlation between boldness and aggression in urban habitats is a general phenomenon as well. Urban habitats may select for bold and aggressive birds, and yet the traits can vary independently. These results add to a small number of studies which find that behavioral syndromes break down in potentially high quality habitats.

### Introduction

Human disturbances present organisms with a variety of novel experiences, the impacts of which are not completely understood. Human disturbance can have morphological (Evans et al. 2009) or physiological (Partecke et al. 2006) effects on wildlife, and can result in a wide array of changes in behavior, such as changes in daily patterns of activity (McClennen et al. 2001; Tigas et al. 2002; Riley et al. 2003), changes in anti-predator behavior (McCleary 2009; Kitchen et al. 2010), the development of avoidance behavior along trails (Miller et al. 1998), shifting of nest site locations (Yeh et al. 2007), modification of vocalizations (Brumm 2004; Foote et al. 2004; Sun

& Narins 2005; Wood & Yezerinac 2006), and changes in female mate selection, such that females avoid nesting on the territories of males located near higher levels of human-created noise (Habib et al. 2007). Examining how different species of animals vary in their behavioral and evolutionary responses to human disturbance will be the key to understanding which species will be able to thrive in human-disturbed habitats and which will not (Sih et al. 2011).

The animals that are going to be most successful in colonizing urban habitats are likely to be those that are best able to deal with human disturbance. Living in urban areas would seem to require high levels of boldness, as boldness relates to an

individual's willingness to engage in risk taking behaviors, such as exploring novel situations (Wilson et al. 1994). Risk taking and exploration of novel environments correlate in great tits and this exploratory behavior is heritable (van Oers et al. 2003). Boldness varies between individuals such that some individuals are consistently bolder than others (van Oers et al. 2003; Carere & van Oers 2004; Reaney & Backwell 2007; Webster et al. 2009; Wilson & Godin 2009). Thus, some inherently bolder individuals may be better suited to actively seek out and use resources available in urban settings (Short & Petren 2008). If urban settings favor bolder individuals, the heritability of the behavior suggests that human disturbance may influence the evolution of boldness in urban populations. Indeed, it has been suggested that boldness toward humans has been evolving in urban populations of European birds, where boldness correlates with time since urbanization (Moller 2008). Changes in boldness of urban birds becomes more significant when we consider the possibility that as boldness evolves, other correlated traits may change as well. Boldness under predation risk has been found to be positively correlated with aggression toward conspecifics in sticklebacks (Bell 2005), great tits (Verbeek et al. 1996), fiddler crabs (Reaney & Backwell 2007), and a previous study of song sparrows found that males in highly disturbed urban habitat are significantly more aggressive and score higher on an assay of boldness than song sparrows in an undisturbed rural habitat (Evans et al. 2010).

Individual differences in boldness and aggression can have significant consequences for habitat selection (Bejder et al. 2006; Carrete & Tella 2010), and by extension, for species distribution. Duckworth (2008) found that new areas along the edges of existing populations are colonized by more aggressive individuals, but that shortly after (within a few generations) the highly aggressive trait disappears from the population. Increased aggression is costly to individuals (Wingfield et al. 2001; Duckworth 2006a). However, increased aggression can also be beneficial as aggressive individuals benefit from higher fitness levels in new populations than their less aggressive counterparts (Duckworth 2008). A correlation between aggression and exploratory or risk taking behavior, then, may result in more aggressive and bolder individuals being found in novel environments, such as human impacted habitats. However, Evans et al. (2010) found a correlation between aggression and boldness in song sparrows in some habitats but not others; specifi-

cally, aggression and boldness were correlated in a rural Pennsylvania population, but not in an urban North Carolina population. Thus, the relationship between an aggression–boldness syndrome and increases in these behaviors in human disturbed, urban habitats remains unclear.

This study expands on the Evans et al. (2010) study, comparing boldness and aggression in male song sparrows in the same rural population with nearby individuals found on human-disturbed urban sites, such as parking lots, roads and near buildings. Based on the results of previous studies on song sparrows (Evans et al. 2010), we predict that males holding urban territories will be both bolder and more aggressive than their undisturbed counterparts and that aggression and boldness will be correlated. This study adds to this previous work in three ways: (1) by adding additional urban populations, to determine whether increased aggression and boldness is a general phenomenon in urban song sparrows; (2) by increasing the sample size within urban populations, to ensure that the lack of correlation between aggression and boldness in the NC urban population (Evans et al. 2010) was not a sample size effect; and (3) to compare urban and rural populations on a smaller geographic scale – as neither the rural nor urban NC populations studied by Evans et al. (2010) had a correlation between aggression and boldness, it is possible that this lack of a correlation is due to differences between PA and NC, not urban vs. rural habitats.

## Methods

This study was conducted in Crawford County, Pennsylvania. The rural, minimally disturbed study site was located within a 11 ha section of State Game Land 214 (SGL) while disturbed, urban sites were located in and around the towns of Linesville and Conneaut Lake. These two towns are approx. 13 km from one another, and Linesville is approx. 14 km from the rural site, while Conneaut Lake is approx. 9 km from the rural site. All three sites share similar climate, elevation, and vegetative features, though the disturbed settings contain obvious human alterations (including buildings, ornamental plants, mown lawns, etc.).

## Rural Site

The rural study site is composed of old fields and hedgerows of trees, surrounded on most margins by wetlands. All territorial males in this population are

marked with a unique combination of leg bands including one permanent Fish & Wildlife band and a unique combination of three plastic color bands. All 2008 territories on the rural site were mapped. The area is not completely free of human disturbance as it is managed for white-tailed deer and Canada geese; however, management is limited to annual mowing and occasional planting of some fields with corn or seasonal grasses, neither of which occurred during the 2008 study season.

### Urban Sites

The two urban sites were the towns of Linesville and Conneaut Lake, PA (population of 1155 and 708 respectively, according to the 2000 census, US Census Bureau 2008c). Though these small towns might not fit political definitions of the word 'urban', we use the word 'urban' here in a more general sense, to denote the fact that the males on these sites were in towns, and surrounded by roads, parking lots and buildings in close proximity. Males in these sites were located on accessible private and public property in close proximity to roads or parking lots. Males were located opportunistically through observations during trips through both towns and through the use of brief playbacks along potentially suitable edge habitats, most of which were along the edge of parking lots and buildings. When a male was located, his location was noted and a GPS point was saved to allow for easy location on subsequent visits. Song sparrows outside State Game Lands were not banded; location of territory was used to recognize individual males. During the breeding season, males show high territory fidelity: in a 9-yr study of song sparrows in Pennsylvania, only 3.4% of males switched territories within season (Hughes & Hyman, in press). Thus, even without marked individuals, it is highly likely that males tested in the same location days apart were the same individual, though we cannot rule out a small number of misidentifications.

### Behavioral Assays

All behavioral assays were run between May 21 and June 20 2008 in the morning hours between 6 am and 10 am. The order of experiments, assaying boldness or aggression, was varied throughout so that different individuals received different assays first. In all cases, the boldness assay and aggression assay were conducted on separate days giving the subjects at least 1 d of rest between each experiment.

We quantified aggressive response using playback experiments. Subjects were tested with playback song from an unknown song sparrow, broadcast from within the subject's territory for 6 min. When playback began, the subject was not singing, and typically at an unknown location. The playback speakers would be set up along hedgerows, allowing the subjects to approach the speaker without venturing into open ground. The observer was located approx. 20–25 m from the playback speaker, and thus, in a location away from the path which the subject would use to approach. The subject's distance from the speaker during the playback was recorded at 5-s intervals for 9 min (6 min of song playback and 3 min of silence post-song); the average distance to the speaker was calculated for each territorial male (Nowicki et al. 2002; Hyman et al. 2004; Hyman & Hughes 2006; Evans et al. 2010). We interpret a closer approach to the speaker as increased aggressiveness. Searcy et al. (2006) found distance to the speaker during a playback experiment was a significant predictor of attack, and this measure of aggressive response is highly repeatable within males, both within seasons (Nowicki et al. 2002; Hyman et al. 2004) and across years (Hyman unpubl. data). The number of response songs sung by the subject during the 9 min was also recorded.

Aggression assays were distributed throughout the study sites to ensure that no individual male heard another playback (such as his neighbor's) on the day he would be tested. Individual males were played different playback tapes recorded from different males, ensuring that it was not a reaction to a specific song that influenced the aggressive reactions. We performed aggression assays with 22 males in Linesville, 12 at Conneaut Lake, and 26 males on the rural site.

Individual variation in boldness was measured with a flight-initiation distance experiment (FID). The FID is used to assess a male's reaction to a potential predator, in this case, a human observer. The assay was conducted when the subject was located on a singing perch no more than 10 m from the ground and 20 to 25 m from the observer, to minimize the FID's dependence on intruder starting distance (Blumstein 2003). The observer approached the male at a rate of 1 m/s until the subject left his perch and went into hiding. The observer's distance from the bird's perch was recorded and the FID was calculated following the methods of Blumstein (2006). A shorter FID is interpreted as being bolder. FID has been widely used as a measure of boldness, and while FID may to some degree represent habituation

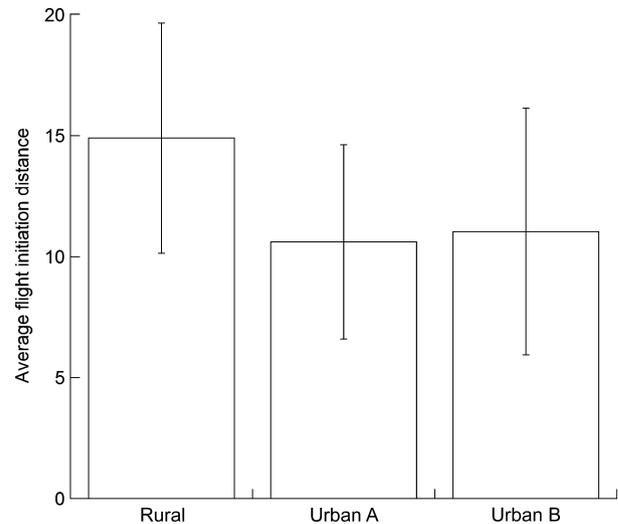
to humans, it has been proposed to be a trait that explains where individuals will settle in relation to human disturbance (Carrete & Tella 2010). FID is also highly repeatable in song sparrows (Evans et al. 2010). Furthermore, FID has been proposed to be a trait under selection, explaining why urban animals typically have lower FID scores than rural animals (Moller 2008). We performed FID assays with 21 males in Linesville, 12 at Conneaut Lake, and 23 males on the rural site. We also performed multiple trials, 1–4 d apart with 13 males to determine if FID is repeatable.

To determine whether behaviors differed between rural and urban habitats, a one-way ANOVA analysis was used. To obtain normality, approach distance to speaker was log transformed prior to analysis. To determine whether aggression and boldness were correlated, Pearson product moment correlations were run for approach to speaker, number of response songs, and FID both within each site and collectively for all sites. These analyses were performed using Minitab 15, provided by the College of Charleston, SC. To determine whether variance in aggression and boldness differed in the populations, variances were calculated and compared using SYSTAT 12 (Systat software, Inc., Chicago, IL, USA). To determine if the relationship between aggression and boldness differed between habitats, the strength of the correlations was compared using SYSTAT 12.

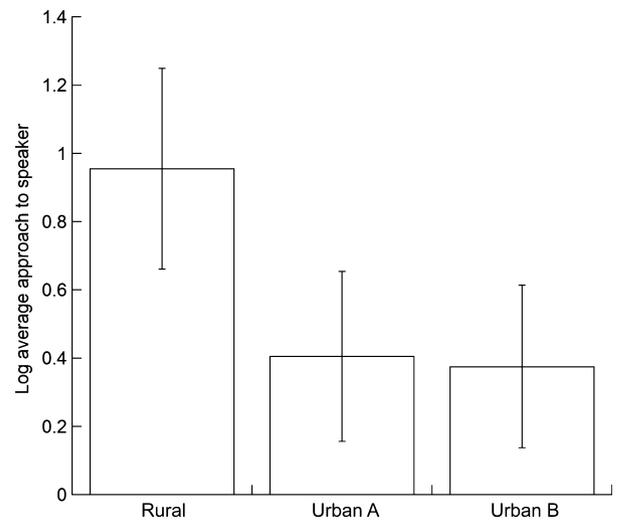
## Results

Males within the urban sites were significantly bolder than males in the rural site, allowing closer approach by the observer ( $F_{2,57} = 6.081$ ,  $p = 0.004$ , Fig. 1). Post hoc analysis reveals that boldness score for males in urban habitats (Linesville vs. Conneaut Lake) did not differ from each other (Tukey test =  $-0.424$ ,  $p = 0.965$ ), while males from both urban locations were significantly bolder than the males from rural locations (Linesville vs. SGL, Tukey test =  $-4.291$ ,  $p < 0.001$ , Conneaut Lake vs. SGL Tukey test =  $-3.868$ ,  $p < 0.047$ ). For individuals tested multiple times, there was a significant correlation between FID scores from one trial to the next, demonstrating consistent individual differences in FID (Pearson Correlation:  $r_p = 0.762$ ,  $n = 13$ ,  $p = 0.002$ ).

Males on urban sites are also significantly more aggressive than males located within the rural site, ( $F_{2,57} = 32.303$ ,  $p < 0.001$ , Fig. 2). Average aggressive responses to the simulated intrusion were three times stronger in the urban habitat than in the rural habitat (urban sites = 2.94 m, rural site = 10.51 m)

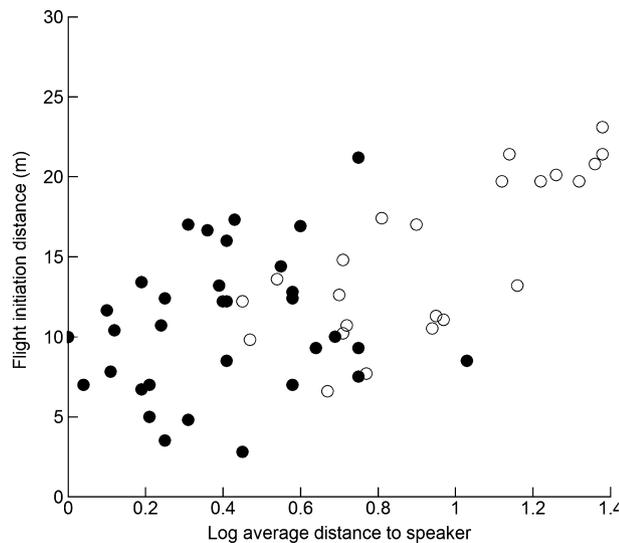


**Fig. 1:** Average flight-initiation distance in response to a human observer ( $\bar{x} \pm SD$ ) for birds at three study sites: Rural, Pennsylvania State Gamelands 214, near Hartstown, PA, Urban 1, the town of Linesville, PA, and Urban 2, the town of Conneaut Lake, PA. Birds in the urban populations have significantly smaller flight-initiation distance experiment than birds in the rural population.



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

with males on urban territories coming significantly closer to the speaker and at times even landing on it. Males on urban sites also sang significantly more in response to playback than males on the rural site ( $F_{2,31} = 8.516$ ,  $p < 0.001$ ). Post hoc analysis reveals that aggression scores for males in urban habitats (Linesville vs. Conneaut Lake) did not differ from



**Fig. 3:** Correlation between boldness (flight-initiation distance) and territorial aggression (log average distance to playback) for birds in urban (closed circles) and rural (open circles) habitats. Aggression and boldness were correlated in all populations combined. However, when separated by habitat, the correlation between aggression and boldness was maintained on the rural site but not on the urban sites.

each other in aggressive response (Tukey test = 0.030,  $p = 0.946$ ), while males from both urban locations were significantly more aggressive than the males from rural locations (Linesville vs. SGL, Tukey test =  $-0.550$ ,  $p < 0.001$ , Conneaut Lake vs. SGL Tukey test =  $-0.580$ ,  $p < 0.001$ ).

If all males from both rural and urban habitats are considered, aggression and boldness were correlated ( $r_p = 0.603$ ,  $n = 56$ ,  $p < 0.001$ , Fig. 3). Males who reacted more aggressively to the simulated intrusion, approached closer to the playback speaker, were also more likely to delay their flight from a potential predator, in this case the observer, and vice versa. However, when separated by habitat, the correlation between aggression and boldness was maintained on the rural site ( $r_p = 0.774$ ,  $n = 23$ ,  $p = 0.001$ ), but the relationship between aggression and boldness on the urban sites was not significant ( $r_p = 0.197$ ,  $n = 33$ ,  $p = 0.272$ ), and there was a significant difference in the strength of the correlations between the two habitats ( $Z = 2.875$ ,  $p = 0.004$ ). Our failure to find a correlation between aggression and boldness in urban habitats does not appear to have been due to reduced variance in either variable: there was no significant difference in variance between urban and rural habitats for either boldness (variance in FID: urban habitat = 19.064, rural habitat = 22.654,

$F_{27,33} = 1.188$ ,  $p = 0.637$ ), or aggression (variance in aggression: urban habitat = 0.059, rural habitat = 0.086,  $F_{26,34} = 1.477$ ,  $p = 0.292$ ), and for both aggression and boldness, the coefficient of variation in urban populations was greater than in rural (aggression:  $CV_{urban} = 0.613$ ,  $CV_{rural} = 0.308$ ; boldness:  $CV_{urban} = 0.405$ ,  $CV_{rural} = 0.319$ ).

## Discussion

Animals living in urban habitats show a variety of behavioral (Evans et al. 2010; morphological (Evans et al. 2009) and physiological (Partecke et al. 2006) differences from conspecifics living in undisturbed rural habitats. Here, we demonstrate that song sparrows in even minimally disturbed urban habitats, such as found in small towns, are bolder and show higher levels of territorial aggression than song sparrows in nearby rural habitats. Thus, even over small distances, low levels of human disturbance can have significant impacts on behavior. In addition, we find that while territorial aggression and boldness are correlated in the rural habitat, this syndrome is lost in the urban habitat. Human disturbance, then, not only affects the expression of individual behaviors, but can also alter the relationships among them.

Territorial song sparrows found within the urban habitats responded with significantly higher levels of boldness – allowing a potential predator to approach on average 4 m closer – and aggression – approaching the speaker simulating a territorial intrusion to one-third the distance – as compared to their counterparts on the rural site <13 km away. Evans et al. (2010) found similar differences in behavior when comparing rural song sparrows in Pennsylvania and Purchase Knob, NC, with those on the campus of Western Carolina University, Cullowhee, NC. The populations compared in Evans et al. (2010) were either quite distant from each other (Pennsylvania vs. North Carolina) or quite different in elevation (Purchase Knob, NC elevation c. 5000 ft vs. Cullowhee, NC, elevation c. 2200 ft), raising the possibility that habitat differences independent of proximity to human populations could be responsible for the observed differences in territorial male behavior. Given the relatively small spatial scales over which the present study was conducted, it is unlikely that habitat differences unrelated to human impacts (i.e., climate, elevation, major vegetative features, etc.) can account for the differences in male territorial behavior. The difference in behavior between these populations is all the more noteworthy, as the ‘urban’ sites used in this study were small towns

with populations of <1200 people, whereas the urban site in Evans et al. (2010) was a densely developed college campus. As such, the urban sites studied here are likely to be on the low end of possible human impacts in an area. Various studies have demonstrated that low levels of human activity can change bird behavior or even bird community structure (Miller et al. 1998; Heil et al. 2007) when certain species are unable to be flexible and adjust their response to humans in the landscape. Our results demonstrate that, within a species, proximity to even small human populations can have significant and substantial impacts on the behavior of territorial birds. When viewed in combination with Evans et al. (2010), these results suggest a strong general pattern for urban populations of song sparrows to be both bolder and more aggressive than rural populations. At this point, we cannot determine whether increased boldness in the urban birds is a result of evolutionary change, as suggested by Moller (2008) or individual habituation, but even a change via habituation reveals a level of behavioral plasticity apparently not found in all bird species (Miller et al. 1998; Heil et al. 2007), which may allow some species to invade urban habitats (Moller 2010).

We initially proposed that urban males would show higher aggression if it was correlated with boldness as part of a behavioral syndrome. Boldness and aggression have been connected in many other species (Verbeek et al. 1996; Bell 2005; Reaney & Backwell 2007), and we found an overall correlation between aggression and boldness within this population. However, boldness and aggression were correlated among territorial male song sparrows within the rural site, but not within the urban habitat. Evans et al. (2010) argued that low variation in boldness and aggression in the urban population made it difficult to observe a correlation due to a reduction in variation along both axes. In the present study, however, we found no significant differences between urban and rural populations in variance in boldness and aggression. Thus, the lack of correlation between boldness and aggression in urban populations of song sparrows, observed here and in Evans et al. (2010), is most likely not due to limited variation. While Evans et al. (2010) found a significant correlation between boldness and aggression in only one rural population, a significant correlation exists if the rural populations are pooled ( $r_p = 0.386$ ,  $n = 33$ ,  $p = 0.031$ ), and subsequent studies in yet other populations have found a correlation in rural, but not urban populations (J. Hyman, unpubl. data). Thus, a significant correlation

between boldness and aggression appears to be characteristic of rural populations, and the lack of a correlation appears to be characteristic of urban populations.

Understanding population differences in behavioral syndromes and when syndromes break down is considered to be an important next step in understanding the significance of behavioral syndromes (Sih & Bell 2008). Finding a behavioral syndrome in some populations but not in others has been noted in studies in sticklebacks (*Gasterosteus* sp., Bell 2005; Dingemanse et al. 2007), where exposure to predation causes the correlation between boldness and aggression to arise (Bell & Sih 2007), and in damselfish (*Stegastes leucostictus*) where a behavioral syndrome involving aggression and courtship behavior occurs in males in rural territories but not in males on artificial high quality territories (Snekser et al. 2009). For syndromes involving aggression and boldness, Sih & Bell (2008) argue that a correlation between aggression and boldness reflects a trade-off between the benefits of 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 and the syndrome disappears. Perhaps, it is informative that in both the stickleback and damselfish examples, though dealing with different behavioral syndromes, the syndromes disappear in high quality habitats. In our study, the difference between rural and urban sites in whether aggression and boldness are correlated in song sparrows suggests that human disturbance may affect habitat quality in such a way that changes the relationship between these behaviors; the human influenced urban habitats may represent high quality habitat, although the key variables which differ between the habitats remain unclear.

Given that aggression and boldness appear to be typically uncorrelated in urban song sparrow populations, the higher aggression of urban males is unlikely to be simply a consequence of urban habitats favoring bolder (and therefore more aggressive) males. High aggression in urban areas could occur if urban habitats represent high quality habitat, and either: (1) only the most inherently aggressive males obtain a high quality territory, or (2) males on high quality territories invest more highly in territorial defense, adjusting their behavior to become more aggressive. Support for either scenario can be found in the literature. Duckworth (2006b), for example, found that male bluebirds did not change their aggressive behavior if their territory quality

was manipulated after they had established their claim on an area, suggesting that in this species, individuals do not vary their aggressive response with territory quality. A large number of studies, however, have found that the behavior of the individual territory holder changes to reflect the quality of the territory after experimental manipulation (Ewald & Carpenter 1978; Camfield 2006; Snekser et al. 2009). These are not actually mutually exclusive hypotheses, as pointed out in a study by Kontiainen et al. (2009) which found that individual female Ural owls (*Strix uralensis*) showed individual variation in aggression in nest defense, and that intensity of nest defense changed to reflect resources. They argued, however, that individual variation in nest defense aggression accounted for a large proportion of the phenotypic variance in aggression seen, and that aggression was a trait under selection (Kontiainen et al. 2009). In song sparrows, evidence suggests that territorial aggression is a consistent individual trait (Nowicki et al. 2002; Hyman et al. 2004; Hyman & Hughes 2006); however, we do not know whether individuals also vary their aggressive responses according to territory quality.

Our comparison of rural vs. urban habitats demonstrates that seemingly small human disturbances, small towns or rural developments, can nonetheless have large impacts on the behavior of wild animals, changing not only the degree to which these behaviors are expressed, but the relationships between behaviors. Several other studies have noted that the mere presence of humans in primarily rural habitats can influence habitat settlement (Gutzwiller & Anderson 1999) and community structure (Skagen et al. 1991; Gutzwiller 1995; Fernandez-Juricic 2002; Heil et al. 2007), as shier species avoid hiking trails and other areas with human activity. Human disturbance has the potential to act as a selective force, quickly resulting in the evolution of phenotypic differences in urban and rural environments (Yeh 2004; Badyaev et al. 2008; Moller 2008), and as urbanization and human disturbance increases, humans may be influencing the evolution of wildlife around them in unpredictable ways. Understanding how human activities impact behavior and evolution may continue to be an important consideration for management and conservation strategies.

### Acknowledgements

We would like to thank Lindeke Mills and Ned Hettlinger for their comments on this manuscript. This work was supported by grants to JS from the Pyma-

tuning Laboratory of Ecology McKinley Grant, the College of Charleston Graduate School Research Grant and the Masters of Environmental Studies Research Grant. This is Pymatuning Laboratory of Ecology publication #302.

### Literature Cited

- Badyaev, A. V., Young, R. L., Oh, K. P. & Addison, C. 2008: Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution* **62**, 1951—1964.
- Bejder, L., Samuels, A., Whitehead, H. & Gales, N. 2006: Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Anim. Behav.* **72**, 1149—1158.
- Bell, A. M. 2005: Differences between individuals and populations of threespined stickleback. *J. Evol. Biol.* **18**, 464—473.
- Bell, A. M. & Sih, A. 2007: Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol. Lett.* **10**, 828—834.
- Blumstein, D. T. 2003: Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manage.* **67**, 852—857.
- Blumstein, D. T. 2006: Developing an evolutionary ecology of fear: how life history and natural history affect disturbance tolerance in birds. *Anim. Behav.* **71**, 389—399.
- Brumm, H. 2004: The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* **73**, 434—440.
- Camfield, A. F. 2006: Resource value affects territorial defense by Broad-tailed and Rufous hummingbirds. *J. Field Ornithol.* **77**, 120—125.
- Carere, C. & van Oers, K. 2004: Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. *Physiol. Behav.* **82**, 905—912.
- Carrete, M. & Tella, J. L. 2010: Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance induced habitat selection. *Biol. Lett.* **6**, 167—170.
- Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Koese, B., Hickling, R. & Dawney, M. 2007: Behavioural syndromes differ predictably between twelve populations of threespined stickleback. *J. Anim. Ecol.* **76**, 1128—1138.
- Duckworth, R. A. 2006a: Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behav. Ecol.* **17**, 1011—1019.
- Duckworth, R. A. 2006b: Aggressive behavior affects selection on morphology by determining the

- environment of breeding in a passerine bird. *Proc. Biol. Sci.* **273**, 1789–1795.
- Duckworth, R. A. 2008: Adaptive dispersal strategies and the dynamics of a range expansion. *Am. Nat.* **172**, S4–S17.
- Evans, K. L., Gaston, K. J., Sharp, S. P., McGowan, A. & Hatchwell, B. J. 2009: The effect of urbanization on avian morphology and latitudinal gradients in body size. *Oikos* **118**, 251–259.
- Evans, J., Boudreau, K. & Hyman, J. 2010: Behavioural syndromes in urban and rural populations of Song Sparrows. *Ethology* **116**, 588–595.
- Ewald, P. W. & Carpenter, F. L. 1978: Territorial responses to energy manipulations in the Anna hummingbird. *Oecologia* **31**, 277–292.
- Fernandez-Juricic, E. 2002: Can human disturbance promote nestedness? A case study with birds in an urban fragmented landscape *Oecologia* **131**, 269–278.
- Footo, A. D., Osborne, R. W. & Hoelzel, A. R. 2004: Whale-call response to masking boat noise. *Nature* **428**, 910.
- Gutzwiller, K. J. 1995: Recreational disturbance and wildlife communities. In: *Wildlife and Recreationists: Coexistence Through Management and Research* (Knight, R. L. & Gutzwiller, K. J., eds). Island Press, Washington DC, pp. 169–181.
- Gutzwiller, K. J. & Anderson, S. H. 1999: Spatial extent of human-intrusion effects on subalpine bird distributions. *Condor* **101**, 378–389.
- Habib, L., Bayne, E. M. & Boutin, S. 2007: Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *J. Appl. Ecol.* **44**, 176–184.
- Heil, L., Fernández-Juricic, E., Renison, D., Cingolani, A. & Blumstein, D. T. 2007: Avian responses to tourism in the biogeographically isolated high Córdoba Mountains, Argentina. *Biodivers. Conserv.* **16**, 1009–1026.
- Hughes, M. & Hyman, J. (in press): Should I stay or should I go now: late establishment and low site fidelity as alternative territorial behaviors. *Ethology*, in press.
- Hyman, J. & Hughes, M. 2006: Territory owners discriminate between aggressive and nonaggressive neighbours. *Anim. Behav.* **72**, 209–215.
- Hyman, J., Hughes, M., Searcy, W. A. & Nowicki, S. 2004: Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour* **141**, 15–27.
- Kitchen, K., Lill, A. & Price, M. 2010: Tolerance of human disturbance by urban Magpie-larks. *Aust. Field Ornithol.* **27**, 1–9.
- Kontianen, P., Pietiäinen, H., Huttunen, K., Karell, P., Kolunen, H. & Brommer, J. E. 2009: Aggressive Ural owl mothers recruit more offspring. *Behav. Ecol.* **20**, 789–796.
- McCleary, R. A. 2009: Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. *Landscape Ecol.* **24**, 483–493.
- McClennen, N., Wigglesworth, R. R. & Anderson, S. H. 2001: The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). *Am. Midl. Nat.* **146**, 27–36.
- Miller, S. G., Knight, R. L. & Miller, C. K. 1998: Influence of recreational trails on breeding bird communities. *Ecol. Appl.* **8**, 162–169.
- Moller, A. P. 2008: Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* **63**, 63–75.
- Moller, A. P. 2010: Interspecific variation in fear responses predicts urbanization in birds. *Behav. Ecol.* **21**, 365–371.
- Nowicki, S., Searcy, W., Krueger, T. & Hughes, M. 2002: Individual variation in response to simulated territorial challenge among territory-holding song sparrows. *J. Avian Biol.* **33**, 253–259.
- van Oers, K., Drent, P. J., de Goede, P. & van Noordwijk, A. J. 2003: Realized heritability and repeatability of risk-taking behavior in relation to avian personalities. *Proc. Biol. Sci.* **271**, 65–73.
- Partecke, J., Schwabl, I. & Gwinner, E. 2006: Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. *Ecology* **87**, 1945–1952.
- Reaney, L. T. & Backwell, P. R. Y. 2007: Risk-taking behavior predicts aggression and mating success in a fiddler crab. *Behav. Ecol.* **18**, 521–525.
- Riley, S. P. D., Sauvajot, R. M., Fuller, T. K., York, E. C., Kamradt, D. A., Bromley, C. & Wayne, R. K. 2003: Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conserv. Biol.* **17**, 566–576.
- Searcy, W. A., Anderson, R. C. & Nowicki, S. 2006: Bird song as a signal of aggressive intent. *Behav. Ecol. Sociobiol.* **60**, 234–241.
- Short, K. H. & Petren, K. 2008: Boldness underlies foraging success of invasive *Lepidodactylus lugubris* geckos in the human landscape. *Anim. Behav.* **76**, 429–437.
- Sih, A. & Bell, A. M. 2008: Insights from behavioral syndromes for behavioral ecology. *Adv. Study Behav.* **38**, 277–281.
- Sih, A., Ferrari, M. C. O. & Harris, D. J. 2011: Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* **4**, 367–387.
- Skagen, S. K., Knight, R. L. & Orians, G. H. 1991: Human disturbance of an avian scavenging guild. *Ecol. Appl.* **1**, 215–225.
- Snekser, J. L., Leese, J., Ganim, A. & Itzkowitz, M. 2009: Caribbean damselfish with varying territory quality:

- correlated behaviors but not a syndrome. *Behav. Ecol.* **20**, 124–130.
- Sun, J. W. C. & Narins, P. M. 2005: Anthropogenic sounds differentially affect amphibian call rate. *Biol. Conserv.* **121**, 419–427.
- Tigas, L. A., Van Vuren, D. H. & Sauvajot, R. M. 2002: Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biol. Conserv.* **108**, 299–306.
- Verbeek, M. E. M., Boon, A. & Drent, P. J. 1996: Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* **133**, 945–963.
- Webster, M. M., Ward, A. J. W. & Hart, P. J. B. 2009: Individual boldness affects interspecific interactions in sticklebacks. *Behav. Ecol. Sociobiol.* **63**, 511–520.
- Wilson, A. D. M. & Godin, J. J. 2009: Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behav. Ecol.* **20**, 231–237.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994: Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446.
- Wingfield, J. C., Lynn, S. E. & Soma, K. K. 2001: Avoiding the 'costs' of testosterone: ecological bases of hormone-behavior interactions. *Brain Behav. Evol.* **57**, 239–251.
- Wood, W. E. & Yezerinac, S. M. 2006: Song Sparrow (*Melospiza melodia*) song varies with urban noise. *Auk* **123**, 650–659.
- Yeh, P. J. 2004: Rapid evolution of a sexually selected trait following population establishment in a novel environment. *Evolution* **58**, 166–174.
- Yeh, P. J., Hauber, M. E. & Price, T. D. 2007: Alternative nesting behaviors following colonization of a novel environment by a passerine bird. *Oikos* **116**, 1473–1480.