

**DISTANCE GRADIENT OF VOCALIZATION
DISCRIMINATION AND AGGRESSION IN
NEIGHBORHOODS OF RUFOUS-AND-WHITE WRENS
(*THRYOPHILUS RUFALBUS*)**

**By Andrew (Anders) Newgard
Department of Ecology and Evolutionary Biology (EBIO),
University of Colorado at Boulder**

**Thesis Defense Date:
April 9th, 2019**

**Thesis Advisor and Department: Dr. Andrew Martin
EBIO**

**Defense Committee Members and Departments:
Dr. Andrew Martin, EBIO**

**Dr. Barbara Demmig-Adams, EBIO & EBIO Honors Council
Representative**

Dr. Daniel Jones, Music & Honors Program

Abstract

Vocalization-based communication networks have been observed in multiple animal taxa. Many territorial animals in these communication networks tend to act differentially towards their neighbors compared to farther-removed strangers given competitive pressure in habitats. My study investigated communication among rufous-and-white wrens (*Thryophilus rufalbus*), and whether this involves greater aggression towards neighbors or towards strangers. *T. rufalbus* vocally defend territories year-round and have been shown to exhibit ability to discriminate between vocalizations of neighbors versus strangers (neighbor-stranger discrimination, NSD). I quantified whether *T. rufalbus* demonstrates different levels of aggression upon hearing played-back vocalizations from close-by neighbors, neighbors of adjacent neighbors, and most distant strangers. Multiple measured parameters exhibited such a gradient of aggression in a population of *T. rufalbus* in Monteverde, Costa Rica, particularly time spent vocalizing and number of songs performed while defending. Response intensity increased for both of the latter parameters from strangers to neighbor-neighbors and to direct neighbors. Other variables that increased, albeit less significantly, in the same direction (from strangers to neighbor-neighbors to neighbors), included bandwidth and range between minimum and maximum frequencies of vocalizations. My study thus demonstrates a gradient of aggression in defensive behaviors of *T. rufalbus* that is consistent with what has been termed the nasty neighbor effect of more aggressive responses to simulations of intrusions by neighbors compared to strangers. This gradient of aggression may involve eaves-dropping behavior (listening to the interactions of other individuals) as described in other species of wren that frequently listen to and identify vocalizations of individuals of the same species more than a territory away.

Introduction

Territoriality has been observed in a variety of species from multiple different taxa (Heinze *et al.* 1996, Leiser and Itzkowitz 1996, Bourne *et al.* 2005, Pratt and McLain 2006). Defending a territory containing mates or resources is highly beneficial. However, surveying a territory requires time, actively defending it requires energy, and physical altercations can be lethal (Huntingford and Turner 1987, Neat *et al.* 1998). If the benefits outweigh the costs of territory defense, territoriality will be implemented (Brown 1964). Vocalizations are consistently used by a variety of animal taxa to establish and defend territories (Briefer *et al.* 2007).

Being able to discriminate between signals from neighboring individuals and signals from strangers is valuable (Lovell and Lein 2004). Individuals that have a shared territory boundary are typically considered neighbors, whereas strangers are many territories away. In highly competitive habitats, individuals that consistently encounter each other have to choose between evading, tolerating, or fighting the competitor (Tanner and Alder 2009). Fights are costly to animals as they can result in serious injury to both the winner and loser, require time and energy, and increase the risk of predation (Huntingford and Turner 1987, Neat *et al.* 1998). Being able to recognize a neighbor's signal can increase the fitness of both individuals involved by lowering the chance and frequency of physical altercations because these signals are no longer perceived as threatening (Briefer *et al.* 2007). This phenomenon, described as "the dear enemy effect" (Fisher 1954), has been explored across multiple species and taxa (Heinze *et al.* 1996, Leiser and Itzkowitz 1996, Bourne *et al.* 2005, Pratt and McLain 2006). Many oscine passerines (songbirds), such as skylarks, sparrows, and wrens, display this behavior (Vehrencamp *et al.* 2014). The dear enemy effect reflects an established mutualism between two individuals of the same species capable of neighbor stranger discrimination (NSD). The two

individuals in question will no longer expend energy on defensive behavior, for they no longer recognize their neighbors' signals as threatening. Conversely, there are other situations in which neighbors represent a greater threat than strangers. For example, fluctuating food levels in patchy feeding territories can encourage quick usurpation by neighbors and losses to neighbors that may be more significant than potential losses to strangers. In such cases, a greater, and more aggressive, response to neighbors is expected. This phenomenon is referred to as the "nasty neighbor" effect (Christensen and Radford 2018).

Territorial interactions arise because any territorial individual is equidistant from multiple neighbors and is capable of receiving signals from more distant individuals up to a certain distance (McGregor 1993, 2005). Groups of territory holders can therefore be considered an interacting network of signalers and receivers, in which many combinations of signalers and receivers are possible (McGregor 1993). In such networks, individuals can obtain information on the quality and motivation of neighboring individuals by eavesdropping on their signaling interactions (Naguib *et al.* 2004). It has been shown in a variety of species that birds learn their songs from eavesdropping on the interactions of other individuals (Beecher *et al.* 2007). The capacity to learn another individual's song could be beneficial in the context of territory defense. Individuals capable of recognizing signalers from more than one territory away will gain an inherent benefit in knowing the location of another individual's territory. Moreover, territory holders with the capacity to determine if a signaler is within their territory will gain multiple benefits. First, they would reduce the amount of energy required in detecting the position of the signaler. Second, they would minimize the potential injury associated with closely approaching the signaler (McGregor 1993). The term *range* is often used to refer to the distance between signaler and signal receiver. Increasing the range of bird and insect songs results in decreases in

signaling amplitude and increases in signal degradation or distortion (McGregor 1993). Either decreases in amplitude or increases in distortion can be used as determinants for range (McGregor 1993). This ability assists multiple avian species with signal discrimination (McGregor 2005).

Birds consistently live in communication networks in which NSD occurs. This idea has been tested across multiple species of songbirds in the tropics (Battiston *et al.* 2015, Vehrencamp *et al.* 2014, Wei *et al.* 2011). However, the extent to which eavesdropping and information gathering comes into play alongside NSD has not been tested thoroughly. Naguib *et al.* (2014) demonstrated that territorial birds pay attention to responses of neighbors to other birds, and that they respond according to what their neighbors do in those interactions with other birds. Hence, if they can estimate distance range and eavesdropping, birds that exhibit NSD should also be able to discriminate between neighbors, strangers, and neighbors of neighbors at least. To our knowledge, this has not been tested in any species within the context of NSD.

The rufous-and-white wren (*Thryophilus rufalbus*) is a neotropical bird species that occur up to elevations of approximately 1300 meters (Stiles and Skutch 1989). Other species of wren demonstrate the ability to estimate signal range (McGregor 1993) and eavesdrop on heterospecifics (individuals of a different species) (Fallow and Magrath 2010, Magrath *et al.* 2009). The population of *T. rufalbus* in Monteverde, Puntarenas, Costa Rica exists at the maximum of its elevational range and has been shown to demonstrate NSD (Dunn 2006). Dunn (2006) showed that rufous-and-white wrens in Monteverde respond for longer to simulated intrusions of strangers compared to neighbors and that they sing more songs overall. This behavior illustrates that rufous-and-white wrens in this area exhibit the dear enemy effect.

This study aimed to evaluate whether *T. rufalbus* can discriminate between neighbors located at different distances and strangers. Calls from multiple individuals in a neighborhood were recorded and played back to simulate territorial intrusions to focal individuals. This was done with the goal to evaluate whether focal territory holders responded differentially to invasion by adjacent neighbors, neighbors of adjacent neighbors, and strangers. *T. rufalbus* is a great candidate study species because it exhibits NSD, and wrens show territoriality year-round (Hyman 2002). On the basis of the results of Dunn (2006), which found evidence for the dear enemy effect in *T. rufalbus*, rufous-and-white wrens should exhibit less aggression towards simulated neighbor intrusions as compared to neighbors located at further distances and strangers. A gradient of aggression from the three different simulated intrusions is predicted across the measured variables.

Methods

Study Site

Research was conducted at Bajo del Tigre Reserve in Monteverde, Puntarenas, Costa Rica (10° 19' 31.5" N, 84° 48' 58.1" W) at an elevation of approximately 1300 meters. This reserve is dominated by a thick secondary forest and is classified as a tropical premontane moist forest (Holdridge 1966). Research was conducted in October and November of 2018.

Study Species

Rufous-and-white wrens are distributed widely throughout the neotropics. They can be found from southernmost Mexico to Panama's canal zone, then through northern and eastern Columbia, to north east Venezuela (Stiles and Skutch 1989). The Rufous-and-white wren is a year-round resident of the mature humid and late-succession forests on the pacific slope of Costa Rica, and it prefers sunny edge habitat (Douglas *et al.* 2012). This species of wren is socially monogamous.

Typically, one male and one female defend a territory together (Mennill 2006, Osmun and Mennill 2011) and build a globular nest (Mennill and Vehrencamp 2008). Rufous-and-white wrens inhabit their territories year-round and begin nesting at the onset of the rainy season in May (Battiston *et al.* 2015). My study was conducted outside of the breeding season, which extends from April to August (Stiles and Skutch 1989).



Figure 1: Photographs of the rufous-and-white wren. Photos taken from neotropical.birds.cornell.edu, accessed February 4th, 2019.



Territory Location

Rufous-and-white wren territories were discovered by walking along the trails of the Bajo del Tigre reserve as well as on the roads adjacent to this reserve. A generic conspecific song from xeno-canto.org was played from a small Bluetooth speaker every 100m for 3 minutes in order to determine if a responsive individual was present. The generic song form [xeno-canto](http://xeno-canto.org) was

recorded in Santa Rosa, Costa Rica. Territory confirmation was made if an individual responded with a song to the generic playback. If visual confirmation of an individual was made, then the generic playback sequence would be repeated again in order to provoke a response from the individual. This was done over the course of several days. Upon confirmation of a territory, GPS coordinates of the site of response were generated by using a GarminX60c model GPS system. Neighbors shared a territory boundary, neighbor-neighbors were two territories away, and strangers were three or more territories away (Fig. 2). The average Rufous-and-white wren territory is $1.35 \text{ Ha} \pm 0.10$ (Battiston *et al.* 2015). Neighbor boundaries are usually 50m in width and can span into neighboring territories (Battiston *et al.* 2015).



Figure 2: Territories used in the study of rufous-and-white wren in Monteverde, Puntarenas, Costa Rica. Neighbors were one territory away; neighbor-neighbors were two territories away, and strangers were three or more territories away. For instance, Individual 4 would be a neighbor to 3, a neighbor-neighbor to 5, and a stranger to 11. Photograph of the map retrieved from maps.google.com. Yellow dots on the map are GPS coordinates of known territories.

Initial Recording of Individuals

Confirmed territorial individuals were presented with the generic Rufous-and-white wren again to record its response. After reaching a confirmed territory, the portable speaker was hung roughly 1 meter off the ground from a perch that was off-trail. I watched the perch from approximately 5 to 10 meters away. Upon the response of an individual or pair, the playback was immediately stopped, and their full song was recorded using an Olympus LS-12 Linear PCM Recorder, which produces uncompressed waveform recordings.

Preparation of Recorded Songs for Intrusion Simulations

The recorded songs of the 12 individuals were edited in Audacity 2.3.0 to isolate the song portion from each recording and to filter out background noise. The isolated song stimulus was repeated once every five seconds for three minutes. The prepared 3-minute recordings for the 12 confirmed individuals were then downloaded onto an iPhone 6.

Simulated Intrusion of Adjacent neighbors, Neighbors of Neighbors, and Strangers

Each of the 12 confirmed territories (Fig. 2) were then assigned a playback from an adjacent neighbor (hereafter called “neighbor”), a neighbor of a neighbor (hereafter called “neighbor-neighbor”), and a stranger. Each territory received all three treatments sequentially in randomized order using a random number generator. The protocol stated above for initial response recording was then followed. After the individual sang its last song or call, a 7-minute grace period was given before stopping the recording in order to ensure the individual finished its defense. There was a 10-minute waiting period between treatments to reduce the chance of aggravating the individual because of rapid, sequential playbacks.

Quantifying Subjects' Responses

Behavioral and acoustic responses were recorded for each of the 36 trials from the 12 territories. Measured behavioral parameters included distance of closest approach to the playback speaker

within 10m (cm), latency from the start of the playback to the subjects first song (seconds), and time spent vocalizing (seconds). Acoustic parameters measured were bandwidth (Hz), lowest and highest frequencies (Hz) across all songs produced during the response, and number of song types used during response (Fig. 2). Before initiating playback trials, a perch 10m away from the speaker was marked. If the individual responded without being seen and was outside of the 10m boundary, then it was assigned a distance value of 20m. If the bird did not respond during the treatment, then a value of 420 seconds was assigned for the latency value (the amount of time for the grace period). The acoustic response measurements were taken by using Audacity 2.3.0 and Ravenlite 2.0.

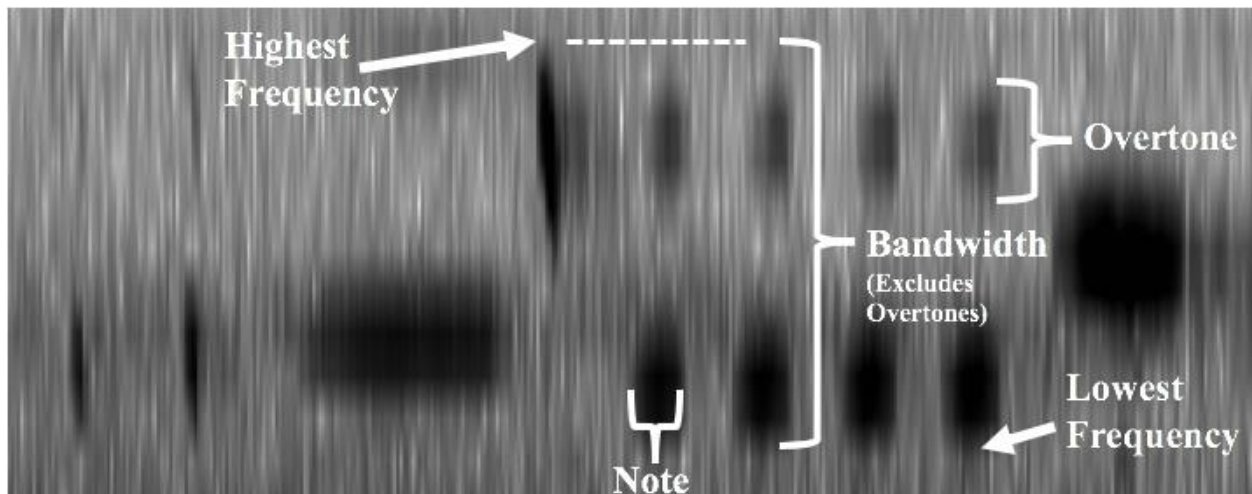


Figure 3: Sonogram of a Rufous-and-white wren song (individual 5 from Fig. 1) created in Ravenlite 2.0. Highest frequency (Hz), lowest frequency (Hz), and bandwidth (Hz) were measured from sonograms as shown here. Only the fundamental frequencies were measured. Overtones were ignored because they would convolute frequency measurements.

Statistical Analysis

Linear mixed models (LMMs) were used to compare variables individually between treatments while acknowledging the dependency between responses produced by a given individual (e.g. individual was included as a random effect in the model). Simply put, LMMs attempt to factor in randomness that can be attributed to an individual. Different birds will most likely have different

responses to the same stimulant. This is why LMMs were used for analysis. When necessary, variables were log transformed to meet the assumption of normality. P-values correspond to an analysis of deviance conducted with the function “Anova” of the R package “car”. Pairwise post-hoc comparisons of means were conducted by using Tukey tests with the R package “emmeans”. All analyses were conducted in R 3.4.3.

Results

In general, rufous-and-white wrens demonstrated marked differences between behavioral and acoustic responses to the neighbor, neighbor-neighbor, and stranger treatments. In the case of bandwidth, responses to strangers showed reduced bandwidths compared to neighbors and neighbor-neighbors (LMM: chi-square = 17.463; df = 2; p = 0.0001; Fig.3). A similar trend was observed in number of songs, with less songs being performed for simulated strangers compared with neighbor-neighbors and neighbors (LMM: chi-square = 11.064; df = 2; p = 0.0040; Fig. 4). As for latency from start of playback to first response, focal individuals responded much more quickly to simulated intrusions of neighbors compared with neighbor-neighbors and strangers (LMM: chi-square = 6.1715; df = 2; p = 0.0457; Fig. 5). Largely significant differences between time spent responding to the three different simulated intrusions were observed (LMM: chi-square = 42.487; df = 2; p < 0.0001; Fig. 6). *T. rufalbus* tended to approach the playback speaker more closely during simulations of neighbor intrusions compared with neighbor-neighbor and stranger intrusions (LMM: chi-square = 7.1573; df = 2; p = 0.02791; Fig. 7). Response time and number of songs displayed the predicted gradient. The lack of significance is likely due to small sample size.

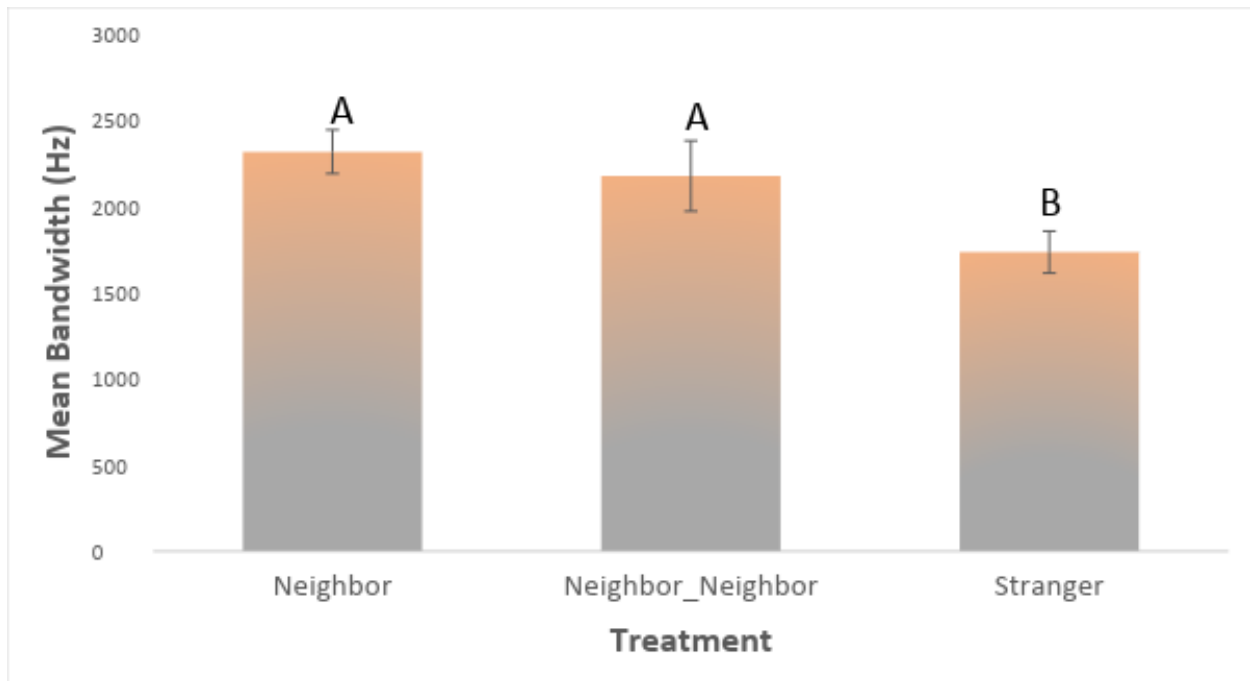


Figure 4: Bandwidth change in responses from *T. rufalbus* in Monteverde, Puntarenas, Costa Rica to simulated intrusions of conspecific adjacent neighbors, neighbor of neighbors, and strangers. Bars with differing letters indicate a significant difference in post-hoc pairwise comparisons between means according to Tukey tests ($p < 0.05$) following the detection of significant differences between treatments using a linear mixed model.

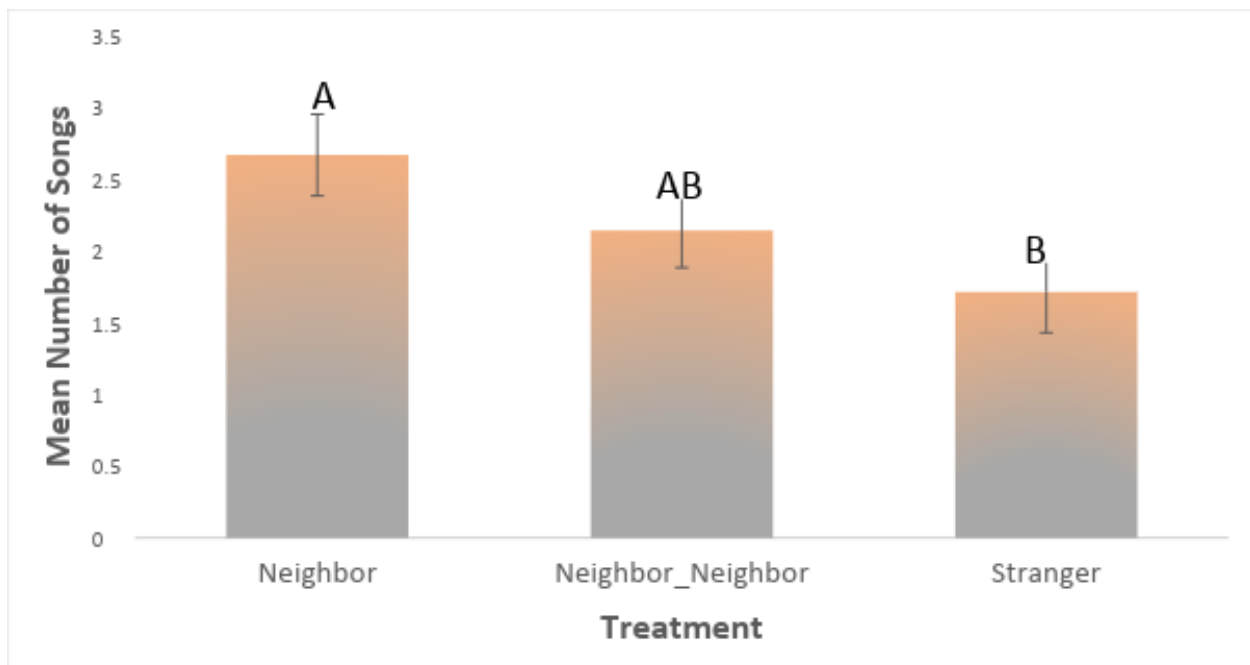


Figure 5: Change in number of songs in responses from *T. rufalbus* in Monteverde, Puntarenas, Costa Rica to simulated intrusions of conspecifics to adjacent neighbors, neighbor of neighbors, and strangers. Bars with differing letters indicate a significant difference in post-hoc pairwise

comparisons between means according to Tukey tests ($p < 0.05$) following the detection of significant differences between treatments using a linear mixed model.

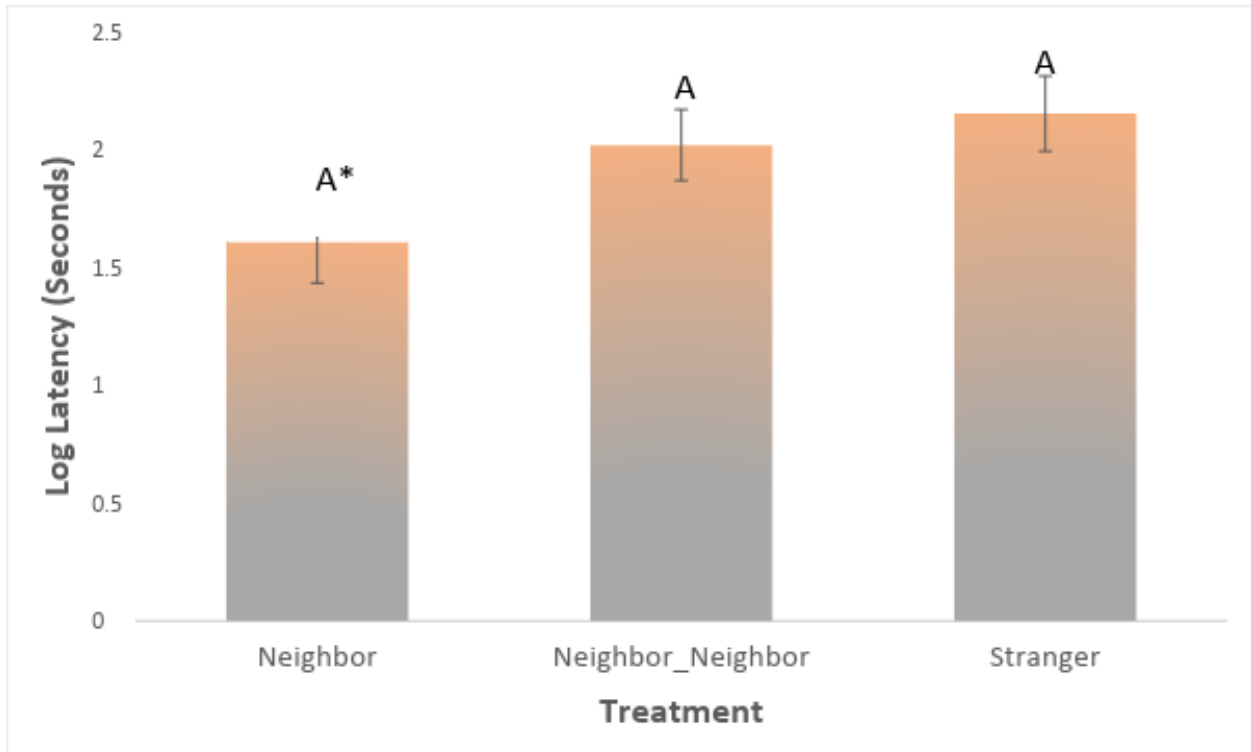


Figure 6: Changes in log of latency from start of playback to subjects first response by *T. rufalbus* in Monteverde, Puntarenas, Costa Rica to simulated intrusions of conspecific adjacent neighbors, neighbor of neighbors, and strangers. Bars with differing letters indicate a significant difference in post-hoc pairwise comparisons between means according to Tukey tests ($p < 0.05$) following the detection of significant differences between treatments using a linear mixed model. Post hoc p -values between 0.05 and 0.10 are marked with different letters followed by an asterisk.

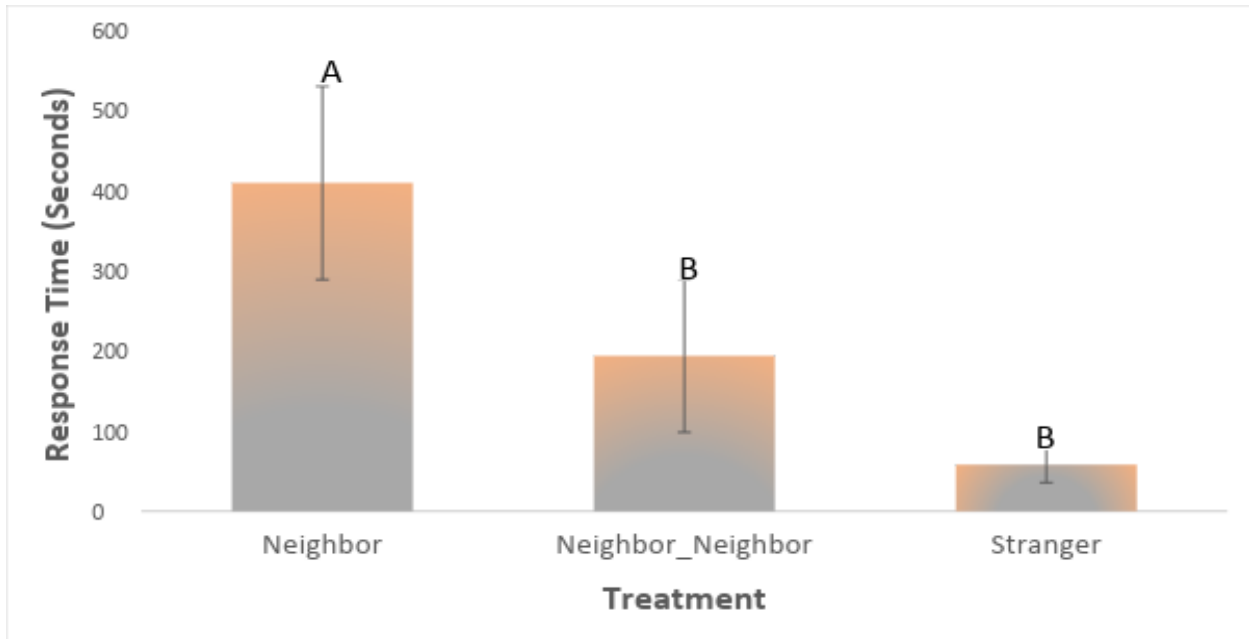


Figure 7: Time spent responding by *T. Rufalbus* in Puntarenas, Monteverde, Costa Rica to simulated intrusions of conspecific adjacent neighbors, neighbor of neighbors, and strangers. Bars with differing letters indicate a significant difference in post-hoc pairwise comparisons between means according to Tukey tests ($p < 0.05$) following the detection of significant differences between treatments using a linear mixed model.

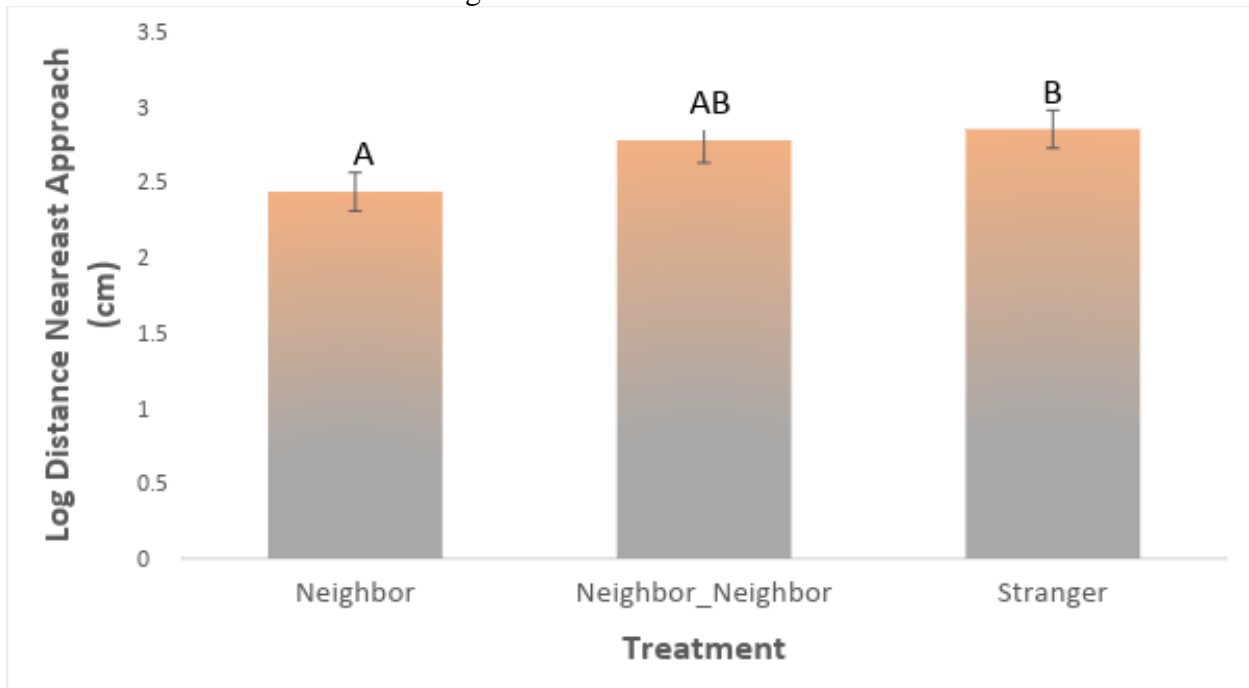


Figure 8: Log of nearest approach distance by *T. rufalbus* in Puntarenas, Monteverde, Costa Rica to simulated intrusions of conspecific adjacent neighbors, neighbor of neighbors, and strangers. Bars with differing letters indicate a significant difference in post-hoc pairwise comparisons between means according to Tukey tests ($p < 0.05$) following the detection of significant differences between treatments using a linear mixed model.

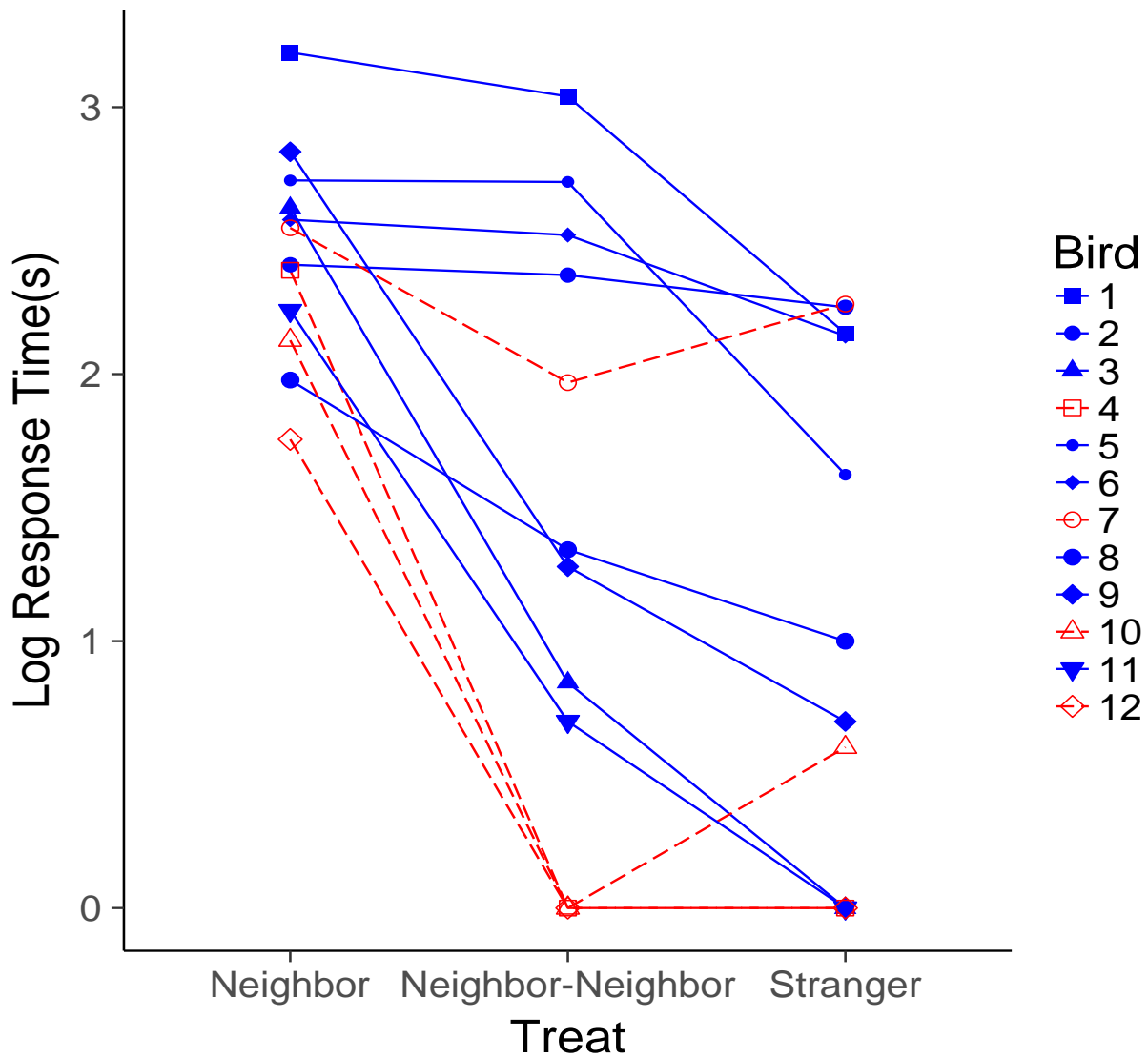


Figure 9: Log transformed time spent responding for each individual *T. Rufalbus* sampled in Puntarenas, Monteverde, Costa Rica to simulated intrusions of conspecific adjacent neighbors, neighbor of neighbors, and strangers. Each line corresponds to an individual. In descending order, most individuals responded for much longer to neighbors, then neighbor-neighbors, then strangers.

Discussion

The individuals tested in this study displayed traits contradicting the results of Dunn (2006).

Individuals responded for longer and at closer distances and with more songs, to simulated intrusions of neighbors and neighbor-neighbors compared with strangers. More songs in

response to neighbor intrusions explain the broader bandwidths observed. While Dunn (2006) found evidence for the dear enemy effect in *T. rufalbus*, the variables tested in my study reflect more aggressive behavior towards neighbors, which would be consistent with the nasty neighbor effect. *T. rufalbus* vocalized for longer, responded at a closer distance, and with lower latency between start of simulated intrusion and response. Godard (1993) demonstrated that these behaviors reflect aggression. Individuals demonstrating these aggressive traits were seeking out the source of the playback in an attempt to potentially initiate a physical altercation with the competitor. A variety of factors can potentially describe this behavior. Life history theory predicts that males with more opportunities for reproduction should avoid risk-taking behavior in order to minimize the cost of current reproduction, whereas competitive environments should favor higher aggression to defend limited resources. Aggression in males (the more vocal sex in *T. rufalbus*) can be modulated by familiarity with competitors to be either lower (dear enemies) or higher (nasty neighbors) towards neighbors. Competitive environments as indicated by breeding density rather than life history shape geographical variation in levels of aggression (Yoon *et al.* 2012). The differences in the results between my study and Dunn's (2006) may arise from differences in competition between sampling sites. Although both studies were conducted in Monteverde, they were conducted at different places within the area. Differences in roosting or nesting site availability could lead to different intraspecific competition levels. Gustafsson (1988) demonstrated that a lack of nesting sites results in increased intraspecific competition, which could then lead to increased aggression towards neighbors. Since species are not always most abundant at the center of their ranges, species-abundance trends (amount of birds per area) are difficult to predict (Dallas *et al.* 2017). It is possible that *T. rufalbus* is more abundant at the sampling site of my study versus Dunn's (2006). Since the study by Dunn (2006) and my study

were conducted both in late October and early November, differences in behavior cannot be explained by presence or absence of the breeding season (from April to August; Stiles and Skutch 1989). In highly competitive environments, neighbors pose a higher threat to males' paternity, partnership, and territorial resources, such as nesting sites and feeding sites (Battiston *et al.* 2015). The population of *T. rufalbus* in my study potentially responds more aggressively to neighbors, which reflects "nasty neighbor" behaviors.

My results suggest that rufous-and-white wrens learn the calls of their neighbor-neighbors, presumably through eavesdropping behavior that may help *T. rufalbus* to learn to discriminate between adjacent neighbors and neighbors of neighbors. However, my study did not directly collect data on eavesdropping behavior. In simulations of neighbor-neighbor intrusions into the territories of the individuals sampled, the behavioral and acoustic measurements frequently matched the responses of individuals to the neighbor, and in some cases were less aggressive than the response to the neighbor. Being able to discriminate between neighbors, neighbors of neighbors, and strangers potentially bolsters an individual's territorial defense ability (Naguib *et al.* 2004). If involved, eavesdropping may confer an advantage (McGregor 2005) by helping a bird decide whether or not to invest in defensive behaviors. Knowing whether a signal was sent from a neighbor, a neighbor-neighbor, or a stranger will help the bird in making these decisions. Naguib *et al.* (2004) demonstrated that birds respond to neighbors of neighbors on the basis of how the latter interacted with other birds. This behavior may introduce experimental variation, thus complicating detection of a gradient in aggression, due to latency between start of playback and response of focal individual as birds may be waiting to hear a response from another bird.

Ultimately, my findings suggest that *T. rufalbus* is capable of discriminating between adjacent neighbors, neighbors of their adjacent neighbors, and strangers. This may suggest that other species exhibiting NSD are also capable of this level of discrimination. My study also suggests that eavesdropping may play a prominent role between conspecifics in territorial avian communication networks.

Limitations of my study

In future iterations of this experiment, the potential territories of each individual sampled should be better defined. Previous studies showed that other species of wren respond slightly more intensely to a neighbor on the wrong side of the subject's territory than to the same song on the correct side of the territory. Birds tend to identify the source of a signal that comes from a particular direction and associate that signal with another bird's territory depending on how consistently it hears the same signal from that particular direction (Wiley and Wiley 1977). This finding indicates that wrens have the capability of differentiating neighboring songs by direction. By effectively mapping out the territory of each individual, researchers can ensure they are playing back the appropriate individuals on the correct sides of the territory. My study should also be repeated over a longer time frame because both duetting and individual singing strategies change significantly with time of year and breeding stage (Topp and Mennill 2008). Responses of rufous-and-white wrens to duets can be much stronger and more aggressive than to vocalizations by individuals (Mennill 2006). The latter author suggested that duets play a role in territory defense against conspecific rivals and an additional role in mate guarding and paternity guarding. Therefore, studies should also attempt to measure change in responsiveness from males to duets versus individual songs.

Acknowledgements

I would like to give a massive thanks to my thesis advisor Dr. Andrew Martin. This work and presentation would not have come together if not for his exceptional statistical advice and helpful suggestions. I would also like to thank Dr. Barbara Demmig-Adams, who helped me tremendously with the anxiety of defending a thesis. In times of need, she guided me through the process of preparing a thesis while I was abroad, and for that I am eternally grateful. Another big thanks to Dr. Daniel Jones for being my outside committee member, and for being the cool jazz master that he is. I would also like to thank my research Advisor, Dr. Johel Chaves-Campos, for his incredible statistical knowledge and wonderful guidance. I would also like to thank Kalina “Karla” Barboza, Dr. Alan Masters, Jose-Carlos “Moncho” Calderón, and all of my classmates who helped me along every step of the way. A massive thanks to the Monteverde Conservation League for access to Bajo del Tigre, and to Frank Joyce for allowing me to record the wrens on his property.

References

- Battiston, M.M., Wilson, D.R., Graham, B.A., Kovach, K.A. and Mennill, D.J., 2015. Rufous-and-white wrens *Thryophilus rufalbus* do not exhibit a dear enemy effects towards conspecific or heterospecific competitors. *Current Zoology* 61: 23-33.
- Beecher, M.D., Burt, J.M., O’Loughlen, A.L., Templeton, C.N. and Campbell, S.E., 2007. Bird song learning in an eavesdropping context. *Animal Behaviour* 73: 929-935.
- Bourne, G.R., Collins, A.C., Holder, A.M. and McCarthy, C.L., 2001. Vocal communication and reproductive behavior of the frog *Colostethus beebei* in Guyana. *Journal of Herpetology* 49: 272-281.
- Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull* 76: 160-169.
- Briefer, E., T. Aubin, K. Lehongre, and F. Rybak. 2007. How to identify dear enemies: the group signature in the complex song of the skylark *Alauda arvensis*. *Journal of Experimental Biology* 211: 317-326.

- Christensen, C. and Radford, A.N., 2018. Dear enemies or nasty neighbors? Causes and consequences of variation in the responses of group-living species to territorial intrusions. *Behavioral Ecology* 29: 1004-1013.
- Dallas, T., Decker, R.R. and Hastings, A., 2017. Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters* 20: 1526-1533.
- Douglas, S.B., Heath, D.D. and Mennill, D.J., 2012. Low levels of extra-pair paternity in a neotropical duetting songbird, the Rufous-and-white wren (*Thryothorus rufalbus*). *The Condor* 114: 393-400.
- Fallow, P.M. and Magrath, R.D., 2010. Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. *Animal Behaviour* 79: 411-417.
- Fisher, J. 1954. Evolution and bird sociality. In *Evolution as a Process* (ed. J. Huxley, A.C. Hardy, and E. B. Ford). pp. 71-83. London: Allen and Unwin.
- Godard, R., 1993. Tit for tat among neighboring hooded warblers. *Behavioral Ecology and Sociobiology* 33: 45-50.
- Gustafsson, L., 1988. Inter-and intraspecific competition for nest holes in a population of the Collared Flycatcher *Ficedula albicollis*. *Ibis* 130: 11-16.
- Heinze, J., Foitzik, S., Hippert, A. and Hölldobler, B., 1996. Apparent dear-enemy phenomenon and environment-based recognition cues in the ant *Leptothorax nylanderi*. *Ethology* 102: 510-522.
- Holdridge, L.R., 1966. The life zone system. *Adansonia* 6: 199-203.
- Huntingford, F.A. and Turner, A.K., 1987. *Animal conflict. Animal Behavior Series. Chapman & Hall Ltd.*
- Hyman, J., 2002. Conditional strategies in territorial defense: do Carolina wrens play tit-for-tat? *Behavioral Ecology*, 13: 664-669.
- Leiser, J.K. and Itzkowitz, M., 1999. The benefits of dear enemy recognition in three-contender convict cichlid (*Cichlasoma nigrofasciatum*) contests. *Behaviour* 136: 983-1003.
- Lovell, S.F. and Lein, M.R., 2004. Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. *Behavioral Ecology*, 15: 799-804.
- Magrath, R.D., Pitcher, B.J. and Gardner, J.L., 2009. An avian eavesdropping network: alarm signal reliability and heterospecific response. *Behavioral Ecology* 20: 745-752.
- McGregor, P.K. ed., 2005. *Animal communication networks*. Cambridge University Press.
- McGregor, P.K., 1993. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society London B*, 340: 237-244.

- Mennill, D. J. 2006. Aggressive responses of male and female Rufous-and-white Wrens to stereo duet playback. *Animal Behaviour* 17: 219–226.
- Mennill, D. J., and S. L. Vehrencamp. 2008. Context-dependent functions of avian duets revealed through microphone array recordings and multi-speaker playback. *Current Biology* 18: 1314–1319.
- Naguib, M., V. Amrhein, and H. P. Kunc. 2004. Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales. *Behavioral Ecology* 15: 1011–1015.
- Neat, F.C., Taylor, A.C. and Huntingford, F.A., 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. *Animal Behaviour* 55: 875-882.
- Osmun, A. E., and D. J. Mennill. 2011. Congruent patterns of territoriality in male and female neotropical songbirds. *Ethology* 117:385–394
- Pratt, A.E. and McLain, D.K., 2006. How dear is my enemy: intruder-resident and resident-resident encounters in male sand fiddler crabs (*Uca pugilator*), *Behaviour* 143: 597-617.
- Stiles, F.G. & Skutch, A.F., 1989. *A Guide to the Birds of Costa Rica*, Ithaca, New York: Comstock Publishing Associates.
- Tanner, C.J. and Adler, F.R., 2009. To fight or not to fight: context-dependent interspecific aggression in competing ants. *Animal Behaviour* 77: 297-305.
- Topp, S.M. and Mennill, D.J., 2008. Seasonal variation in the duetting behaviour of rufous-and-white wrens (*Thryothorus rufalbus*). *Behavioral Ecology and Sociobiology* 62: 1107-1117.
- Vehrencamp, S. L., J. M. Ellis, B. F. Cropp, And J. M. Koltz. 2014. Negotiation of territorial boundaries in a songbird. *Behavioral Ecology* 25: 1436–1450.
- Wei, M., Lloyd, H. and Zhang, Y., 2011. Neighbour–stranger discrimination by Yellow-bellied Tit Parus venustus: evidence for the “dear-enemy” effect. *Journal of Ornithology*, 152: .431-438.
- Wiley, R.H. and Wiley, M.S., 1977. Recognition of neighbors' duets by stripe-backed wrens *Campylorhynchus nuchalis*. *Behaviour*, 62: 10-34.
- Yoon, J., Sillett, T.S., Morrison, S.A. and Ghalambor, C.K., 2012. Breeding density, not life history, predicts interpopulation differences in territorial aggression in a passerine bird. *Animal Behaviour* 84: 515-521.