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The vocal behaviour of a Neotropical suboscine songbird, the Barred Antshrike (*Thamnophilus doliatus*)

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**THE VOCAL BEHAVIOUR OF A NEOTROPICAL SUBOSCINE SONGBIRD,
THE BARRED ANTSHRIKE (*THAMNOPHILUS DOLIATUS*)**

by

JULIANNE KOLOFF

A Thesis
Submitted to the Faculty of Graduate Studies
through Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

2010

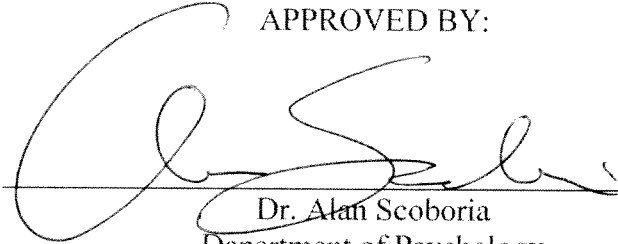
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(*Thamnophilus doliatus*)

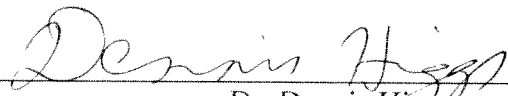
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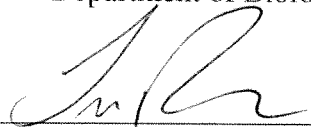
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DECLARATION OF CO-AUTHORSHIP

I hereby declare that this thesis incorporates material that is the result of joint research. I am the sole author of the first half of Chapter 1 (General Introduction Part 1). I am the primary author for the research in the General Introduction Part 2, and Chapters 2 and 3. The General Introduction Part 2 and Chapters 2 and 3 are co-authored with my thesis supervisor Dr. Daniel Mennill, who contributed financial assistance and logistical support, and provided guidance in research design, data analysis, and writing.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

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I declare that this is a true copy of my thesis, including any final revisions, as approved by my thesis committee and the Graduate Studies office, and that this thesis has not been submitted for a higher degree to any other University or Institution. The chapters are presented in manuscript format for peer-reviewed publication.

ABSTRACT

Despite the high biodiversity that characterizes the tropics relative to temperate latitudes, we know comparatively little about the ecology and behaviour of tropical animals. In many tropical birds, males and females coordinate their songs to form duets. My thesis quantitatively describes the vocal behaviour of Barred Antshrikes (*Thamnophilus doliatus*), Neotropical duetting songbirds. My thesis consists of two main components: a thorough description of vocal behaviour and a playback experiment testing two hypotheses for duet function. I found substantial sex differences in the fine structure of Barred Antshrike songs. Analysis of passive recordings revealed that song output is highest during the early morning and in the period prior to nesting. Playback results indicate that duets are important in territory defence and intrasexual aggression between females. Evaluating communication strategies of tropical species is important for understanding patterns of behavioural ecology and provides useful comparisons to patterns observed in north-temperate regions.

DEDICATION

For my parents Mark and Sue: who sparked my love of nature at an early age,
and for my siblings: Kristopher, Nicole, and Alexandra who share that love with me.

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*“For in the end, we will conserve only what we love;
we will love only what we understand;
and we will understand only what we are taught.”*

-Baba Dioum 1968

Chapter 1

General Introduction: Part 1

CHAPTER I

GENERAL INTRODUCTION PART I

Birds are remarkable singers and produce songs that largely function in mate attraction and territory defence (Catchpole and Slater 2008). Bird song has been well-studied in many north-temperate species; considerably less attention has been paid to birds that sing in tropical and south-temperate regions (Stutchbury and Morton 2001). As such, vocal behaviours that are prevalent in the tropics, such as duetting and female song, have received less attention in the literature (Slater and Mann 2004). In this general introduction, I provide an overview of important topics in bird song that are relevant to my study of Neotropical Barred Antshrikes including: the dawn chorus, seasonal variation in singing behaviour, vocal duetting and the hypotheses for why birds duet, acoustic playback and a summary of antbirds.

The Dawn Chorus

The dawn chorus is a phenomenon wherein the song output of many birds peaks in the earliest daylight hours (reviewed in Staicer *et al.* 1996, Kunc *et al.* 2005, Catchpole and Slater 2008). Across many species, individuals sing at high rates starting in the early morning twilight, and decrease their song output throughout the rest of the day. Although this behaviour has been observed in both tropical and temperate birds, it has been best studied in north-temperate regions (Staicer *et al.* 1996). The function of this widespread behaviour is poorly understood.

Many non-mutually exclusive hypotheses have been proposed to explain the early-morning increase in singing activity of birds. Hypotheses for why birds sing at dawn may be explained by proximate causes such as hormonal changes and circadian

rhythms (Kacelnik and Krebs 1982, Staicer *et al.* 1996). Heightened vocal output at dawn may serve social functions such as signalling individual quality, mate stimulation, mate attraction, mate guarding, or increased territoriality (e.g. mate attraction and territory defence in the chiffchaff, *Phylloscopus collybita*, Rodrigues 1996; Staicer *et al.* 1996). Lastly, environmental pressures such as increased sound transmission, low predation, or inefficient foraging at dawn may be functions of dawn chorus singing (e.g. increased sound transmission at dawn in the Swamp Sparrow, *Melospiza georgiana* and White-throated Sparrow, *Zonotrichia albicollis*, Brown and Handford 2003; Staicer *et al.* 1996).

Studies on both temperate and tropical species have provided evidence that early morning singing is related to eye size; birds with larger eyes sing earlier in the morning than birds with smaller eyes (Thomas *et al.* 2002, Berg *et al.* 2006). Thomas *et al.* (2002) suggests that individuals with larger eyes are able to detect lower light levels. They become active and sing earlier in the morning than birds with smaller eyes. In addition to eye size predicting time of first song, Berg *et al.* (2006) also found a strong relationship of dawn singing to foraging height in the tropics. Foraging height was found to be a primary factor determining the time songbirds begin to sing; birds that foraged higher in the canopy sang earlier in the morning compared to birds that routinely forage close to the ground (Berg *et al.* 2006).

There is some variation across species with respect to how close to dawn a bird begins to sing; some species sing at first light, while other species join the dawn chorus later in the morning twilight or even after the sun has risen (Staicer *et al.* 1996, Catchpole and Slater 2008). A study by Luther (2009) analyzed multiple features of the songs of 82 tropical species and compared them with the foraging strata of each species. Individuals

that foraged at similar heights in the forest had songs that were most different with respect to timing of singing during the dawn chorus. Luther's study demonstrates that birds may temporally partition their acoustic signals during the dawn chorus to minimize acoustic interference.

Seasonal Variation in Song Output

Patterns of singing activity in birds vary not only with time of day, but also with time of year. Studies on male songbirds in the north-temperate zone have demonstrated that there is a correlation between seasonality and breeding stage (Catchpole and Slater 2008). Many studies have found that an increase in male singing activity often precedes egg-laying (Catchpole 1973, Cuthill and MacDonald 1990, Amrhein *et al.* 2004a, Tremain *et al.* 2008). For example, a study of the Great Tit, *Parus major*, showed that males increased their song output prior to their partner's egg-laying stage and decreased singing activity after females had laid eggs. The seasonal variation in male vocal output observed related directly to female fertility (Mace 1987). More generally, a detailed study by Slagsvold (1977) on twenty European songbird species related song output to breeding activity. In each species, male song output increased a few days prior to egg-laying and decreased after the eggs were laid (Slagsvold 1977). Compared with tropical regions, the relationship between seasonality and breed stage is more conspicuous in temperate regions, where differences in season are more pronounced (Catchpole and Slater 2008).

Studies on several tropical bird species have revealed evidence of changes in vocal behaviour with changes in seasonality and breeding stage (e.g. Seychelles Warblers *Acrocephalus sechellensis*, Catchpole and Komdeur 1993, Rufous-and-White Wrens, *Thryothorus rufalbus*, Topp and Mennill 2008, Rufous-naped Wrens, *Campylorhynchus*

rufinucha, Bradley and Mennill 2009). In each of these studies, vocal output was low outside of the breeding season, but higher during the breeding season.

Seasonal patterns of male vocal activity in songbirds are coupled with seasonal shifts of gonadal steroid hormone levels (Marler *et al.* 1988, DeVoogd 1991). Production of song fluctuates with seasonal cycles of testosterone in the bloodstream, which has been related to photoperiod (Catchpole and Slater 2008). Two studies of male Great Tits measured monthly testosterone levels and found that testosterone levels were highest during seasonal peaks in male song output (Rost 1990, Van Duyse *et al.* 2003).

Compared to temperate birds, mean testosterone levels have been found to be lower in tropical birds (Goymann *et al.* 2004). A comparative study on testosterone levels in tropical birds found that testosterone levels were correlated with length of breeding season; birds with shorter breeding seasons, similar to those of temperate species, had higher levels of testosterone compared to birds that breed year-round (Goymann *et al.* 2004). Tropical birds with long breeding seasons may not be able to sustain the costs of maintaining testosterone levels over long periods of time (Wingfield *et al.* 2001).

Duetting Behaviour

Vocal duets occur when a male and female in a mated pair combine their songs in a temporally coordinated acoustic display (Farabaugh 1982; Hall 2004, 2009). Vocal duetting behaviour has been observed across many taxa including insects (Bailey and Hammond 2003), amphibians (Tobias *et al.* 1998), primates (Geissmann 2000) and birds (Farabaugh 1982). For birds, female song is rare in the north-temperate zone and so duets are rare north of the Tropic of Cancer. In the tropics and south-temperate zones, however, female song is more common and consequently, there is the possibility for vocal duetting

behaviour to occur in these regions (Morton 1996, Slater and Mann 2004). Although duetting has been studied for several decades (Thorpe 1963), we still know relatively little about the details of vocal duets; the vocal behaviour of most duetting species has never been described or studied in detail.

The form and function of vocal duets can vary both among species and within species (Hall 2004). Duetting can occur synchronously, when one bird temporally overlaps the song of their partner, as in the overlapping tones of African Forest Weavers (*Symplectes bicolour*) (Wickler and Seibt 1980). Other species perform duets antiphonally, where one individual sings and their partner responds immediately afterward (Hall 2004), as in the alternating male-female phrases in the duets of Plain Wrens, *Thryothorus modestus* (Mann *et al.* 2003, Cuthbert and Mennill 2007).

When studying avian duets, whether synchronous or antiphonal, it is useful to focus on the individual who sings second in the duet sequence. This individual actively creates the duet by combining their song with their partner's song. Had the second bird not sung, the song of the first bird would be produced as a solo (Hall 2004). By focusing on the second bird to perform in a vocal duet, we can gain insight into that individual's motivations to better elucidate duet function within a species. For example, in Topp and Mennill (2008) duetting Rufous-and-White Wrens were shown to have very different patterns of duet responsiveness in different contexts, where males were most responsive to their partner's songs during the breeding season.

Functions of Duetting

There are two schools of thought that attempt to explain why birds perform duets rather than sing alone. Hypotheses for duetting fall under cooperation or conflict between

the members of a duetting pair. Cooperation-based hypotheses suggest pairs perform duets for mutual benefit. Hypotheses that fall under this category include: the Maintaining Contact Hypothesis, the Ensuring Reproductive Synchrony Hypothesis, the Preventing a Partner Being Usurped Hypothesis and the Joint Resource Defence Hypothesis (reviewed in Hall 2004, 2009). The Maintaining Contact Hypothesis suggests that pairs duet to signal their location to their partner in dense vegetation (Thorpe 1963). The Ensuring Reproductive Synchrony Hypothesis suggests that duets signal a bird's reproductive state to their partner (Dilger 1953, Kunkel 1974). The Preventing a Partner Being Usurped Hypothesis suggests that birds duet to ward off intruders of the opposite sex that threaten their mate's position in the partnership (Appleby *et al.* 1999). The Joint Resource Defence Hypothesis suggests that pairs defend their territories and use duets to repel intruders (Wickler 1976).

Conversely, conflict-based hypotheses suggest individuals within a pair have separate agendas for duetting. Conflict-based hypotheses include: the Signalling Quality Hypothesis, the Signalling Commitment Hypothesis, the Guarding Paternity Hypothesis and the Mate Guarding Hypothesis (reviewed in Hall 2004, 2009). The Signalling Quality Hypothesis suggests that birds make assessments on an individual's quality based on the precision of their duets (Smith 1994). The Signalling Commitment Hypothesis suggests that pairs expend energy to coordinate their duets, thereby signalling their commitment to the pair bond (Wickler 1980). The Guarding Paternity Hypothesis suggests that males duet when their partner is fertile to repel intruders from seeking extra-pair copulations (Sonnenschein and Reyer 1983). The Mate Guarding Hypothesis suggests that

individuals advertise their partner's mated status by duetting and repel singing intruders that may attract their partner (Wickler 1980).

Of these many hypotheses, the Joint Resource Defence and the Mate Guarding Hypotheses are currently the most widely supported hypotheses for duet function. To date, experimental studies have shown support for both hypotheses (reviewed in Douglas and Mennill 2010). Under the Joint Resource Defence Hypothesis, both birds in a pair are predicted to readily defend a resource or territory together. Within this hypothesis, duets are considered cooperative endeavours and territorial pairs are expected to perceive duets as a greater threat than lone individuals (Hall 2004). The Joint Resource Defence Hypothesis has been supported empirically through many acoustic playback experiments (reviewed in Douglas and Mennill 2010). These studies have demonstrated that pairs respond more aggressively towards duet stimuli than solo song stimuli, without making distinctions between male or female stimuli (e.g. Hall 2000, Logue and Gammon 2004).

Under the Mate Guarding Hypothesis, both birds in a pair have separate agendas for duetting. Within this hypothesis, duets are considered conflictive endeavours and predict that a single bird poses a greater threat to a pair bond than to a territory (Hall 2004). The Mate Guarding Hypothesis has also been supported through a number of playback experiments (Douglas and Mennill 2010). Playback studies have demonstrated that pairs respond more aggressively towards same-sex solo stimuli than duet stimuli and pairs will duet more with their partners to acoustically guard their mate (e.g. Seddon and Tobias 2005, Rogers *et al.* 2007).

Previous studies have demonstrated that duet functions vary among species and, importantly, that duets can serve multiple functions for a variety of contexts within a

single species. In Tropical Boubous, *Laniarius aethiopicus*, for example, duets have been shown to function in both mate guarding and joint territory defence through a playback study (Grafe and Bitz 2004). Birds respond aggressively toward conspecific playback and approach the loudspeaker together to defend their territories; individuals also respond aggressively towards same-sex solo stimuli, indicating a mutual mate guarding function for duetting (Grafe and Bitz 2004). Similarly, in Rufous-and-White Wrens (*Thryothorus rufalbus*) duets have been shown to function in mate guarding and territory defence through playback studies where males responded strongly towards same-sex solos and pairs responded with great aggression towards duets (Mennill 2006).

Acoustic Playback Techniques

Acoustic playback is an experimental technique that has been used extensively to study animal communication. Acoustic playback involves broadcasting stimuli through loudspeakers and then measuring the responses of focal animals (Falls 1992). Acoustic playback experiments have been conducted on a variety of taxa including fish (e.g. plainfin midshipman, *Orichthys notatus*, McKibben and Bass 1998), insects (e.g. tarbush grasshoppers, *Ligurotettix planum*, Greenfield and Minckley 1993), mammals (e.g. marine mammals, reviewed in Deecke 2006), amphibians (concave-eared torrent frog, *Amolops tormotus*, Feng 2006) and birds (reviewed in McGregor 1992).

In studies of duetting birds, researchers have used acoustic playback to test duet function hypotheses such as the signalling quality, mate guarding, joint resource defence, identity, paternity guarding and pair-bond maintenance hypotheses (Hall 2004, 2009; Douglas and Mennill 2010). The vast majority of playback experiments that have tested duet function have employed non-interactive designs using a single loudspeaker. Such

experiments have produced evidence in support for the Joint Resource Defence Hypothesis (e.g. Bay Wrens, *Thryothorus nigricapillus*, Levin 1996), the Mate Guarding Hypothesis (e.g. Subdesert Mesites, *Monias benschi*, Seddon *et al.* 2002) and the Pair-bond Maintenance Hypothesis (e.g. Purple-crowned Fairy-wrens, *Malurus coronatus*, Hall and Peters 2008) as functions for duetting.

Some authors have argued that multi-speaker playback is more advantageous to study duet function because two-speaker designs provide a spatially realistic simulation of two birds duetting together from two distinct positions (Logue and Gammon 2004, Douglas and Mennill 2010). However, in some species, birds perform duets when breeding partners are very close together, so that single-speaker playback may still be an accurate simulation of the birds positions while singing. Multi-speaker playback should be especially important when studying species that perform duets when they are far apart, or when they perform duets at variable distances.

Depending on the way a stimulus is broadcast, playback stimuli may be either non-interactive or interactive with respect to the focal animals (Smith 1996). Non-interactive playback has been the most widely used design and involves broadcasting a fixed stimulus to focal animals that does not alter with respect to the behaviours of that animal. Non-interactive designs allow researchers to quantify an animal's behaviours towards a specific stimulus (Douglas and Mennill 2010).

Other studies have used interactive playback to test duet function and have found support for the Joint Resource Defence Hypothesis and the Mate Guarding Hypothesis (Grafe and Bitz 2004). In interactive playback designs, the researcher manipulates the stimuli being broadcast according to the behaviour of the focal animal while the

interaction is occurring (Smith 1996, McGregor 2000). Non-interactive playback, however, is advantageous because individuals receive the same type of stimuli allowing for easy replication and the experimenter has direct control over the output of each playback trial (Douglas and Mennill 2010).

Interactive vs. non-interactive, and single-speaker vs. dual speaker designs each have advantages and disadvantages. Choosing a suitable playback design to test duet function depends on the vocal behaviour of the focal species (e.g. How close do pairs duet? Can individuals in a pair produce both parts of a duet? Does the species have a repertoire?) and the predictions that a researcher wants to test (Douglas and Mennill 2010). Acoustic playback experiments are a useful tool for testing duet functions to explain why birds sing together rather than alone.

Antbirds

Typical Antbirds (Family: *Thamnophilidae*) are a group of songbirds, consisting of approximately 209 species, found almost exclusively in the Neotropics. Most antbirds form long-term monogamous pair bonds and hold year-round territories (Zimmer and Isler 2003). The plumage of many antbirds is cryptically coloured in shades of grey, black and brown. Sexual dimorphism is also a common feature of this family (Zimmer and Isler 2003). Antbirds are appropriately named, as many species habitually follow ant swarms through the forest and feed on insects that are disturbed by the ants.

Approximately 27 species actively follow ant swarms as a main food source and are known as obligate ant-followers. Many antbirds, however, only opportunistically follow ant swarms that move through their territories (Zimmer and Isler 2003, Willson 2004).

Interestingly, these birds do not eat the ants, but feed on other invertebrates that are

stirred up in the path of an ant swarm (Willson 2004). Most antbirds can often be found in areas of dense foliage such as scrubby, forest edge (Zimmer and Isler 2003). The density of their habitats results in low visibility, making acoustic signals a very important area of research.

Songbirds (order: Passeriformes) are a large and diverse group of birds collectively known as “song birds” or “perching birds”. The order is divided into two suborders: the suboscines and the oscines. Antbirds belong to the suboscines, a group with simple syrinxes and whose vocalizations are considered to be innate (Kroodsma 1984, Sibley and Monroe 1990, Kroodsma and Konishi 1991). The other group of songbirds are oscines, a group with more complex syrinxes and who learn their songs from conspecifics. Oscines comprise the vast majority of songbird species (Sibley and Monroe 1990). Within the family *Thamnophilidae*, there are many species where males and females temporally coordinate their songs to form duets, although this behaviour has been described only anecdotally for most species (Zimmer and Isler 2003).

My thesis focuses on the Barred Antshrike, *Thamnophilus doliatus*. In lieu of an introduction to my study species, I have written a second part of this general introduction in the format of a species account for the Neotropical Birds project coordinated through Cornell University’s Lab of Ornithology. The Neotropical Birds project attempts to produce detailed, peer-review species accounts for every species of bird in the Neotropics. The specific headings and subheadings used in the second part of this general introduction are a required formatting component of the Neotropical Birds project. The web address for this project is <http://neotropical.birds.cornell.edu/portal/home>.

Conclusion and Thesis Outline

By studying animal sounds, we can gain insight into the behavioural ecology and natural history of free-living organisms. Through exploring dawn chorus singing behaviour, seasonal variation in vocal output, and duetting behaviour we can understand how communication strategies influence the reproductive behaviours of animals. With further focus on the behaviour of tropical birds, we can increase our understanding of this understudied group of birds.

My thesis focuses on the vocal behaviour of the Barred Antshrike (*Thamnophilus doliatus*). In the General Introduction Part 2, I provide a detailed review of the life history of the Barred Antshrike. By reviewing previously published accounts, as well as observations and empirical data from three years of my own research, I have compiled information on Barred Antshrike life history traits, which may be used as a reference tool by ornithologists as well as bird enthusiasts.

In Chapter 2, I provide the first quantitative description of Barred Antshrike vocal behaviour. I describe the vocalizations of both sexes and I quantify singing rates for males and females. I describe patterns of variation in vocal output according to 24-hr and seasonal scales using passive recordings from an automated recording device. I provide a detailed description of duetting behaviour and analyses conducted on duet responsiveness, overlap and precision.

In Chapter 3, I investigate duet function in the Barred Antshrike through a rigorous acoustic playback experiment. I test two functions for duetting behaviour: the Joint Resource Defence Hypothesis and the Mate Guarding Hypothesis. I discuss my results in comparison to previous experimental work.

The General Introduction Part 2 has been formatted for submission for peer-review to Neotropical Birds online species accounts. Chapter 2 has been prepared in manuscript format for submission for peer-review to the journal *Auk*, the leading journal that specializes in ornithology. Chapter 3 has been prepared in manuscript format for submission for peer-review to the journal *Animal Behaviour*, one of the leading journals dealing with experimental studies of the behaviour of animals.

Literature Cited

- Appleby, B.M., Yamaguchi, N., Johnson, P.J., and D.W. MacDonald. 1999. Sex specific territorial responses in tawny owls *Strix aluco*. Ibis 141:91–99.
- Bailey, W.J., and T.J. Hammond 2003. Duetting in insects – does call length influence reply latency? J. Zool., Lond. 260: 267–274.
- Berg K.S, Brumfield R.T, and V. Apanius. 2006 Phylogenetic and ecological determinants of the neotropical dawn chorus. Proc. R. Soc. B. 273: 999–1005.
- Bradley, D.W., and D.J. Mennill. 2009b. Solos, duets and choruses: vocal behaviour of the Rufous-naped Wren (*Campylorhynchus rufinucha*), a cooperatively breeding Neotropical songbird. Journal of Ornithology 150: 743–753.
- Brown, T.J. and P. Handford. 2003. Why birds sing at dawn: the role of consistent song transmission. Ibis 145: 120–129.
- Catchpole, C.K. 1973. The function of advertising song in the sedge warbler (*Acrocephalus schoenobaenus*) and the reed warbler (*A. scirpaceus*). Behaviour 46:300–320.
- Catchpole, C.K., and J., Komdeur. 1993. The song of the Seychelles Warbler *Acrocephalus sechellensis*, an island endemic. Ibis 135:190-5.
- Catchpole, C.K., and P.J.B. Slater. 2008. Bird song: biological themes and variations: second edition. New York: Cambridge University Press.
- Cuthbert, J.L., and D.J., Mennill. 2007. The duetting behavior of Pacific Coast plain wrens. Condor 109: 686–692.
- Cuthill, I.C., and W.A. Macdonald.1990. Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. Behav Ecol Sociobiol 26:209–216.
- Deecke, V.B. 2006. Studying marine mammal cognition in the wild - a review of four decades of playback experiments. Aquatic Mammals 32:461-482.
- DeVoogd, T.J. 1991. Endocrine modulation of the development and adult function of the avian song system. Psychoneuroendocrinology 16:41–66.
- Dilger, W.C. 1953. Duetting in the crimson-breasted barbet. Condor 55:220-221.
- Falls, J.B. 1992. Playback: a historical perspective. In: Playback and studies of animal communication (P.K. McGregor, ed.), pp. 11–33. Plenum Press, New York, NY.
- Farabaugh, S.M. 1982. The ecological and social significance of duetting. In: Kroodsma DE, Miller EH (eds) Acoustic communication in birds, vol 2. Academic, New York, pp 85-124.
- Feng, A. S., Narins, P.M., Xu, C., Lin, W., Yu, Z., Qiu, Q., Xu, Z., and J. Shen. 2006. Ultrasonic communication in frogs. Nature 440:333–336.
- Geissmann, T. 2000. Duet songs of the siamang, *Hylobates syndactylus*: I. Structure and organisation. Primate Report 56: 33–60.
- Grafe, T.U., and J.H. Bitz. 2004. Functions of duetting in the Tropical Boubou, *Laniarius aethiopicus*: territorial defence and mutual mate guarding. Animal Behaviour 68: 193–201.
- Greenfield, M. D. and R.L. Minckley. 1993 Acoustic duelling in tarbush grasshoppers: settlement of territorial contests via alternation of reliable signals. Ethology 95:309-326.
- Hall, M. L. 2000. The function of duetting in Magpielarks: conflict, cooperation, or commitment? Animal Behaviour 60: 667–677.

- Hall, M.L. 2004. A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and Sociobiology* 55: 415–430.
- Hall, M.L. 2009. A review of vocal duetting in birds. In: *Advances in the study of behavior*, vol 40 (M.Naguib, AND V. M. Janik, eds.), pp. 67–121. Academic Press, Burlington, MA.
- Hall, M.L., and A. Peters. 2008. Coordination between the sexes for territorial defence in a duetting fairy-wren. *Animal Behaviour* 76: 65–73.
- Kacelnik, A. and J.R. Krebs. 1982. The dawn chorus in the great tit *Parus major*: proximate and ultimate causes. *Behaviour* 83:287–309.
- Kroodsma, D.E. 1984. Songs of the Alder flycatcher (*Empidonax alnorum*) and Willow flycatcher (*Empidonax traillii*) are innate. *Auk* 101: 13–24.
- Kroodsma, D.E., and M. Konishi. 1991. A subsong bird (eastern phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Animal Behavior* 42: 477–487.
- Kunc, H., Amrhein, V., and M. Naguib. 2005. Seasonal variation in dawn song characteristics in the common nightingale. *Animal Behaviour* 70:1265–1271.
- Kunkel, P., 1974. Mating systems of tropical birds: the effects of weakness or absence of external reproduction-timing factors with special reference to prolonged pair bonds. *Z. Tierpsychol.* 34: 265–307.
- Lanyon, W. E. 1978. Revision of the Myiarchus flycatchers of South America. *Bull. Amer. Mus. Nat. Hist.* 161: 429-627.
- Levin, R.N. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. II. Playback experiments. *Animal Behaviour* 52: 1007–1117.
- Logue, D.M., and D.E. Gammon. 2004. Duet song and sex roles during territory defence in a tropical bird, the Black-bellied Wren, *Thryothorus fasciatoventris*. *Animal Behaviour* 68: 721–731.
- Luther DA. 2009. The influence of the acoustic community on songs of birds in a neotropical rain forest. *Behavioral Ecology* 20:864-871.
- Mace, R. 1987. The dawn chorus in the great tit is directly related to female fertility. *Nature* 330:745–746.
- Mann, N.I., Marshall-ball, L., and P.J.B. Slater. 2003. The complex song duet of the Plain Wren. *Condor* 105: 672–682.
- Marler, P., Peters, S., Ball, G.F., Dufty, A.M., and J.C. Wingfield. 1988. The role of sex steroids in the acquisition and production of birdsong. *Nature* 336:770–772.
- McGregor, P.K., C.K. Catchpole, T. Dabelsteen, J.B. Falls, L. Fusani, H.C. Gerhardt, F. Gilbert, A.G. Horn, G.M. Klump, D.E. Kroodsma, M.M. Lambrechts, K.E. McComb, D.A. Nelson, I.M. Pepperberg, L. Ratcliffe, W.A. Searcy, and D M. Weary. 1992. Design of playback experiments: the Thornbridge Hall NATO ARW Consensus. In: *Playback and studies of animal communication* (P. K. McGregor, ed.), pp. 1–9. Plenum Press, New York, NY.
- McGregor, P.K. 2000. Playback experiments: design and analysis. *Acta Ethologica* 3:3–8.
- McKibben, J.R., and A.H. Bass. 1998. Behavioral assessment of acoustic parameters relevant to signal recognition and preference in a vocal fish. *J. Acoust. Soc. Am.* 104:3520–3533.

- Mennill, D.J. 2006. Aggressive responses of male and female Rufous-and-white Wrens to stereo duet playback. *Animal Behaviour* 71: 219–226.
- Morton, E.S. 1996. A comparison of vocal behavior among tropical and temperate passerine birds, in *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D.E. and Miller, E.H., eds), pp. 258–268, Cornell University Press.
- Rodrigues, M. 1996. Song activity in the Chiff chaff: Territorial defence or mate guarding? *Animal Behaviour* 51:709–716.
- Rogers, A. C., Langmore, N.E., and R.A. Mulder. 2007. Function of pair duets in the Eastern Whipbird: cooperative defense or sexual conflict? *Behavioral Ecology* 18: 182–188.
- Rost, R. 1990. Hormones and behaviour: a joint examination of studies on seasonal variation in song production and plasma levels of testosterone in the great tit *Parus major*. *J. Ornithol.* 131: 403–411.
- Seddon, N., Butchart, S.H.M., and L. Odling-Smee. 2002. Duetting in the Subdesert Mesite *Monias benschi*: evidence for acoustic mate defence? *Behavioral Ecology and Sociobiology* 52: 7–16.
- Seddon, N. and J.A. Tobias. 2005. Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*), *Behav. Ecol.* 17:73–83.
- Sedgwick, J. A. 2001. Geographic variation in the song of Willow Flycatchers: differentiation between *Empidonax traillii adastus* and *E. t. extimus*. *Auk* 118: 366–379.
- Sibley, C.G., and B.L. Monroe. 1990. *Distribution and taxonomy of birds of the world*. Yale University Press, New Haven, CT.
- Slagsvold, T. 1977. Bird song activity in relation to breeding cycle, spring weather and environmental phenology. *Ornis Scand* 8:197–222
- Slater, J. B. and N. I. Mann. 2004. Why do the females of many bird species sing in the tropics? *Journal of Avian Biology* 35:289–294.
- Smith, W.J. 1994. Animal duets: forcing a mate to be attentive. *J Theor Biol* 166:221–223.
- Smith, W.J. 1996. Using interactive playback to study how songs and singing contribute to communication about behavior. In: *Ecology and evolution of acoustic communication in birds* (D. E. Kroodsma and E. H. Miller, eds.), pp. 377–397. Cornell University Press, Ithaca, NY.
- Snow, D.W. 1977. Duetting and other synchronised displays of the blue-backed manakins, *Chiroxiphia* spp. In: Stonehouse B, Perrins CM (eds) *Evolutionary ecology*. Macmillan, London, pp 239–251.
- Sonnenschein, E., and H.U. Reyer. 1983. Mate-guarding and other functions of antiphonal duets in the slate-coloured boubou (*Laniarius funebris*). *Z Tierpsychol* 63:112–140.
- Staicer, C. A., Spector, D. A. & Horn, A. I. 1996. The dawn chorus and other diel patterns in acoustic signaling. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 426–453. Ithaca, New York: Cornell University Press.
- Stutchbury, B.J.M., and E.S. Morton. 2001. *Behavioral ecology of tropical birds*. Academic Press, London, UK.

- Thorpe, W.H. 1963. Antiphonal singing in birds as evidence for avian auditory reaction time. *Nature* 197: 774–776.
- Tobias, M. L., Viswanathan, S. S., and D.B. Kelley. 1998. Rapping, a female receptive call, initiates male–female duets in the South African clawed toad. *Proc. natl Acad. Sci. USA* 95:1870–1875.
- Topp, S.M., and D.J. Mennill. 2008. Seasonal variation in the duetting behaviour of Rufous-and-White Wrens (*Thryothorus rufalbus*). *Behavioral Ecology and Sociobiology* 62: 1107–1117.
- Thomas, R.J., Szekely, T., Cuthill, I.C., Harper, D.G.C., Newson, S.E., Frayling, T.D. and P.D. Wallis. 2002 Eye size in birds and the timing of song at dawn. *Proc. R. Soc. B* 269: 831–837.
- Tremain, S.B., Swiston, K.A., and D.J. Mennill. 2008. Seasonal Variation in Acoustic Signals of Pileated Woodpeckers (*Dryocopus pileatus*). *Wilson Journal of Ornithology* 120:499-504.
- Van Duyse, E., Pinxten, R., and M. Eens. 2003. Seasonal fluctuations in plasma testosterone levels and diurnal song activity in free-living male great tits. - *Gen. Comp. Endocrinol.*134:1-9.
- Westcott, D.A. 1997. Neighbours, strangers and male-male aggression as a determinant of lek size. *Behav Ecol Sociobiol* 40:235-242.
- Wickler, W., 1976. Duetting songs in birds: biological significance of stationary and non-stationary processes. *J. Theor. Biol.* 61: 493–497.
- Wickler, W. & Seibt, U. 1980. Vocal duetting and the pair bond. II. Unison duetting in the African forest weaver, *Symplectes bicolor*. *Zeitschrift für Tierpsychologie*, 52: 217–226.
- Wingfield, J.C., Lynn, S.E., and K.K. Soma. 2001. Avoiding the “costs” of testosterone: ecological bases of hormone behavior interactions. *Brain Behavior and Evolution* 57:239–251.
- Willson, S. K. Obligate Army-Ant-Following Birds: A Study of Ecology, Spatial Movement Patterns, and Behavior in Amazonian Peru. *Ornithological Monographs* 55: 1-67.
- Zimmer, K. J., and M. L. Isler. 2003. Family Thamnophilidae (Typical Antbirds). Pages 448-681 in J. del Hoyo, A. Elliott, and D. A. Christie (editors), *Handbook of the birds of the World. Volume 8 Broadbills to Tapaculos*. Lynx Edicions, Barcelona, Spain.

Chapter 1

General Introduction Part 2: Barred Antshrike Species Account

The General Introduction Part 2 is co-authored with my thesis supervisor Dr. Daniel Mennill, who contributed financial assistance and logistical support, and provided guidance in research design, data analysis, and writing.

CHAPTER I

GENERAL INTRODUCTION PART 2: BARRED ANTSHRIKE SPECIES ACCOUNT

Overview

The Barred Antshrike is a sexually dimorphic, medium-sized suboscine songbird that is abundant in its range from Mexico to Argentina. It is commonly found in dense thickets and forest edge habitat. These birds form long-term monogamous pair bonds and hold year-round territories. The striking male plumage consists of alternating black and white bars across all of the bird's feathered parts. The crown feathers form a black crest with a white patch near the back of the crown that is revealed only when crown feathers are erect. The upper plumage of the female is a cinnamon-rufous colour and the breast is lighter ochraceous-buff. Both sexes have a proportionally large bill compared to their body size, with a sharp hook at the tip.

Both male and female adult birds produce a 2-3 second long song which breeding partners often overlap to create duets. When males sing, they produce a characteristic stereotyped visual display consisting of head bobbing and tail wagging, often bending over to expose the bright white plumage patch on the back of their crown.

The Barred Antshrike is largely insectivorous and primarily captures prey by foliage gleaning. Although they are not obligate ant followers, Barred Antshrikes feed opportunistically at ant swarms that move through their territory.

I conducted a three-year study of a population of Barred Antshrikes in northwestern Costa Rica and include many observations from my field research.

Identification

Summary

Barred Antshrikes are medium-sized songbirds which possess a disproportionately large bill with a characteristic sharp hook at the tip. Male Barred Antshrike plumage consists of alternating black and white bars throughout the body. The head contains elongated black feathers which form a loose crest, under which is concealed a small patch of white feathers that is revealed when the male vocalizes (the white patch is located at the base of the erect crest feathers). Female plumage is drastically different from the male and is cinnamon-rufous coloured on the back and wings, with ochraceous-buff underparts. Females have slight black barring on their heads and cheeks. Elongated feathers on their heads also form a cinnamon-rufous coloured crest. Unlike the red irises of many antbirds, the iris of males and females are pale yellow.

Similar Species

Songs of the Barred Antshrike can easily be confused with those of the Western Slaty-Antshrike (*Thamnophilus atrinucha*) which overlap in range throughout most of Central America. The songs of both species have been described as having rapidly accelerating notes and ending with a rising inflection (Ridgely and Gwynne 1989). The Western Slaty-Antshrike can be distinguished as having a shorter song with all notes of roughly the same pitch; the Barred Antshrike's song accelerates quickly in the middle of the song and varies subtly in pitch (Slud 1964). Mnemonics for the songs have been described by Ridgely and Tudor (1994) as “anhanhanhanhanhanhanhánh” for the Western Slaty Antshrike and “hah-ha-ha-hahahahahahaha-hánh” for the Barred Antshrike.

The Bar-crested Antshrike (*Thamnophilus multistriatus*) has similar plumage characteristics to the Barred Antshrike. Upon closer inspection, unlike the male Barred Antshrike, the crest of the male Bar-crested Antshrike is heavily barred with black and white whereas the crest of the male Barred Antshrike is mainly black with white feathers underneath. Female plumage of the two species is more easily distinguished; the underparts of the female Bar-crested Antshrike are distinctly barred whereas the underparts of the female Barred Antshrike lack barring (Hilty and Brown 1986).

The male Barred Antshrike also resembles the male Fasciated Antshrike. Two characteristics can be used to distinguish between the males of these species. The male Fasciated Antshrike has a distinct red iris and plumage of very fine black and white bars, whereas the male Barred Antshrike has a pale yellow iris with much broader barring of black and white (Ridgely and Gwynne 1989).

In addition, the male Lined Antshrike (*Thamnophilus tenuipunctatus*) resembles the male Barred Antshrike; their ranges overlap at the base of the Andes. The white bars on the male Lined Antshrike are narrower, making the bird appear blacker than the Barred Antshrike. The female Lined Antshrike has distinct barring on her underparts whereas the female Barred Antshrike does not (Hilty and Brown 1986).

Vocalizations

The Barred Antshrike song is produced by both sexes and has been described as a long series of loud chuckling or cackling notes which rapidly ascend with increasing intensity, and then descend, ending with an emphatic final note (Young 1929, Slud 1964, Skutch 1969, Zimmer and Isler 2003). A detailed analysis of the Barred Antshrike song is lacking, and the species' singing behaviour had not been thoroughly described until a recent detailed study on a population in northwestern Costa Rica (Chapter 2). Ridgely

and Tudor (1994) describe the song as “hah-ha-ha-hahahahahahaha-hánh”. Of 38 pairs recorded in northwestern Costa Rica, the average male song was 3.06 ± 0.04 s and the average female song was 2.31 ± 0.04 s in length (Chapter 2). Males and females sing bouts of song interspersed between periods of silence. In the Costa Rica study, the average male song rate was one song every 88.16 ± 13.42 s and the average female song rate was one song every 226.83 ± 47.20 s. When periods of silence ≥ 60 s were removed, however, males and females had similar singing rates: males sang one song every 22.35 ± 0.69 s and females sang one song every 22.66 ± 2.18 s (Chapter 2).

Barred Antshrikes perform an interesting visual display while they sing. Birds stretch out their necks and bow forward – often far enough that their heads are below their feet. As the bowing display occurs, Barred Antshrikes rapidly pump their tails up and down causing their whole body to shake as they sing. This stereotyped display has been observed by both males and females. In addition to bowing and tail movements, males shake their outstretched necks, and lower their heads erecting their crests to reveal a bright white plumage patch underneath the back of their crest feathers (Skutch 1969). The function of this display is currently unknown.

Calls

Barred Antshrikes produce several types of calls in addition to their song. Call types may vary among the many different races of Barred Antshrike (Zimmer and Isler 2003). The “crow-like *caw*” seems to be a common call and has been noted as a possible warning call by some authors (Young 1929, Skutch, 1969). In northwestern Costa Rica, this call has often been observed by males and females in a variety of contexts. For example, males have been observed occasionally producing this call during the dawn chorus, interspersed among bouts of singing. Females have been observed producing this

call when close to their nests. A softer “*mew*” or “*whine*” call, which has previously been described, has also been observed by the authors during male-male territorial encounters. The functions of these calls are not fully understood. Playback of *caw* and *whine* calls to six pairs of Barred Antshrikes in northwestern Costa Rica in 2010 did not evoke any noticeable responses from territorial males or females, even though the birds were very close to the loudspeaker at the start of the playback (Chapter 2).

Additional calls have been described, including a low guttural “croak” (Skutch 1969), “*gnaar*” (Slud 1964), “*graaaaa*” (Hilty 2003), or “*growl, gurrr*” (Hilty and Brown 1986). Each of these descriptions may refer to the same call, which may be the *caw* call described above. Zimmer and Isler (2003) describe clear whistled notes which may be either long or short. Slud (1964) also reports a rare call made by both sexes which resemble “four or five trogon-like ‘*pyoo*’s”.

Duetting Behaviour

Males and females each possess one song type which can be sung as a solo or combined with the song of their breeding partner to form a duet. Both males and females create duets by responding to their partner with song before their partner’s song is complete. In a study of birds in northwestern Costa Rica, the females were found to create the majority of duets ($84 \pm 2\%$) by overlapping their partner’s song. Males and females sing with an average delay of 1.82 ± 0.05 seconds between the start of their song to the start of their partner’s song and Barred Antshrikes overlap approximately 31% of their partner’s song when creating duets (Chapter 2). As described above, Barred Antshrike duets are accompanied by a stereotyped visual display of head bobbing with an erect crest and simultaneous tail wagging (Young 1929, Haverschmidt 1947, Skutch 1969).

Diel variation in Vocal Output

In northwestern Costa Rica, male and female vocalizations were recorded throughout most daylight hours, but the highest vocal output occurred between 0500h and 0700h, indicating that Barred Antshrikes participate in dawn chorus singing. A detailed study of diel vocal patterns found no evidence of increased vocal activity at dusk to indicate a dusk chorus (Chapter 2).

Phenology –Seasonal Patterns of Vocal Output

The vocal output of the Barred Antshrike varies seasonally, with an increase in vocalizations at the onset of the breeding season, prior to nesting (Young 1929, Chapter 2). Keeler-Wolf (1986) noted a reduction of vocalizations occurring in the dry season in Tobago, compared to the rainy season.

Nonvocal Sounds

None described.

Detailed Description (Appearance)

Male: Upper body is covered in alternating thick black bars and thinner white bars. The underparts have wider white bars and thinner black bars. The sides of the head, throat and chin have thin black and white streaks. The head contains elongated black feathers forming a loose crest (Fig 1a). When viewed from the front, the crest is black when erect. When the male lowers his head, however, he reveals a bright white patch of feathers concealed underneath (Haverschmidt 1947, Skutch 1969). The white patch is created by crown feathers that are white at the base and black near the feather tips; when the head is lowered, the base of the crown feathers reveal the white portions. Wing and tail feathers are also distinctly barred with black and white colouration.

Female: Upper body is uniform cinnamon-rufous in colour, and the underparts are ochraceous-buff in colour. Similar to the male, the female has elongated feathers at the

top of the head forming a cinnamon-rufous coloured crest (Fig 1b). Female crest feathers lack the white colour at the base that male crest feathers have. Black and white streaks are found on the head, cheeks and sometimes on the buff-coloured chin (Haverschmidt 1947, Skutch 1969). Wing and tail feathers are also cinnamon-rufous.

Juveniles: Males have pale barring of light yellowish-brown white rather than white (Zimmer and Isler 2003). In northwestern Costa Rica, juvenile males have barred brown and yellowish plumage instead of the black and white barred plumage seen in adult males. Plumage of all observed fledglings resembled adult female plumage in colouration, although sex of the fledglings was unknown.

Bare Parts

Unlike many red-eyed antshrikes, the eyes of the Barred Antshrike are pale yellow. The upper mandibles of the bills of both sexes are black with a prominent hook at the tip, while the lower mandible is bluish gray (Young 1929, Skutch 1969). The legs and feet are both plumbeous (Skutch 1969).

Measurements

The body weight (g) of Barred Antshrikes ranges in northwestern Costa Rica from 24.0-29.1 for males (n=16) and 25.8-31.8 for females (n=6), matching previous descriptions (28g reported by Ricklefs 1976; Cody 2000; 30g by Reynaud 1998; 22.2-27.9g by Russell 1964; 24-30g by Zimmer and Isler 2003). Body length has been reported as 15.24 cm by Skutch (1969), 18.5 cm by Young (1929), and 15-16 cm by Zimmer and Isler (2003).

Culmen length (mm) of Barred Antshrikes ranges in northwestern Costa Rica from 11.5-13.2 for males (n=16) and 12.6-12.9 for females (n=5) measured from the front

of the nares to the tip of the bill. Young (1929) reported culmen length as 22mm for Barred Antshrikes in British Guiana.

Flattened wing chord length (mm) of Barred Antshrikes ranges in northwestern Costa Rica from 69.0-74.5 for males (n=16) and 57.1-71.0 for females (n=5). A measure of 80mm was reported by Young (1929) for birds in British Guiana.

Tarsus length (mm) of Barred Antshrikes ranges in northwestern Costa Rica from 25.9-28.3 for males (n=16) and 26.0-27.5 for females (n=5), similar to a previous report (27mm by Young 1929).

Tail center length (mm) of Barred Antshrikes ranges in northwestern Costa Rica from 56.0-64.0 for males (n=16) and 59.0-60.0 for females (n=5). Young (1929) reported a slightly higher value of 65mm for birds in British Guiana.

Molts

Molting of primary feathers has been observed in almost every month in Trinidad and Tobago, suggesting that molt occurs continuously year round. Irregularities in the sequence of wing molt were also observed (Keeler-Wolf 1986, Snow and Snow 1964). More research on patterns of molt is needed.

Geographic Variation

The Barred Antshrike is a polytypic species. Clements (2007) and the Handbook of the Birds of the World (Zimmer and Isler 2003) recognize 12 subspecies, although previous accounts have recognized as many as 17 (see Assis *et al.* 2007). For males, the subspecies vary in the amount of white in the crown and tail feathers, and in the width of the black and white bars. The females of the different subspecies vary in the relative darkness of plumage (Zimmer and Isler 2003).

- *Thamnophilus doliatus doliatus*, Linnaeus 1764. Range: northeastern Colombia, Venezuela (except in northwestern), the Guianas, Trinidad and North Amazonian Brazil (Zimmer and Isler 2003).
- *Thamnophilus doliatus intermedius*, Ridgway 1888. Range: eastern Mexico to southeastern Costa Rica (and probably adjacent Panama) (Slud 1964). In Mexico, this species is common throughout the evergreen forest in the Atlantic region and much less common in the semi-deciduous and swamp forests of the Pacific region (Binford 1989). This subspecies is often found in the humid Caribbean lowlands. The male plumage is much darker and is heavily barred with wide black bars (Monroe 1968).
- *Thamnophilus doliatus capistratus*, Lesson 1840. Range: Brazil (Zimmer 1933). This species inhabits threatened habitats, such as dry forest and caatinga woodland. Males and females have shorter, thicker bills and chestnut coloured eyes. Males have a black crown and tails have restricted white spots. Females have heavily streaked throats, bars on the breast and white bellies (Zimmer and Isler 2003).
- *Thamnophilus doliatus radiatus*, Vieillot 1816. Range: Paraguay (Zimmer 1933), southeastern Colombia (southern Amazonas), northeastern Ecuador (Napó), eastern Peru (except northern Amazonas and western Loreto), western & southcentral Brazil, northern & eastern Bolivia, Paraguay and northern & northeastern Argentina. Males have black crowns with white spots on the forecrown. Male underparts are whiter and black bars are reduced or absent on the belly (Zimmer and Isler 2003).

- *Thamnophilus doliatus difficilis*, Hellmayr 1903. Range: Brazil (Zimmer 1933). Birds resemble *radiatus* but the male's forecrown is whiter and their underparts are greyer. Females are darker in colour (Zimmer and Isler 2003).
- *Thamnophilus doliatus nigricristatus*, Lawrence 1865. Range: Panama (eastern Chiriqui and southern Veraguas eastern to western San Blas). The males in this subspecies have black crowns and their underparts are faintly barred or unbarred. The females lack black streaks on their throats (Zimmer and Isler 2003).
- *Thamnophilus doliatus eremnus*, Wetmore, 1957. Range: Coiba Island, southern Panama. This subspecies resembles *nigricristatus* but is more deeply coloured (Zimmer and Isler 2003).
- *Thamnophilus doliatus nesiotus*, Wetmore 1970. Range: Pearl Island, southern Panama. This subspecies also resembles *nigricristatus* but is more deeply coloured (Zimmer and Isler 2003).
- *Thamnophilus doliatus albicans*, Lafresnaye 1844. Range: northern & western Colombia (Caribbean slope from Antioquia and Cordoba o La Guajira, and southern in Magdalena Valley to Huila). The male has a black crown, white belly, and underparts that are sparingly barred. The female has pale underparts and a white throat. The plumage of both sexes becomes increasingly darker towards the Caribbean coast (Zimmer and Isler 2003).
- *Thamnophilus doliatus nigrescens*, Lawrence 1867. Range: northcentral Colombia east of Andes (Norte de Santander) and northwestern Venezuela north of Andes (Zuila, Tachira, western Merida). The male is very dark with a black crown and wider black bars than white bars (Zimmer and Isler 2003).

- *Thamnophilus doliatus tobagensis*, Hartert and Goodson 1917. Range: Tobago. In this species, the male is whiter below and the female is darker below (Zimmer and Isler 2003).
- *Thamnophilus doliatus cadwaladeri*, Bond and Meyer de Schauensee 1940. Range: southern Bolivia (Tarija). Male plumage is pale and the belly has very minimal barring. Female plumage is white below with buff-coloured sides and breast (Zimmer and Isler 2003).

Systematics

The Barred Antshrike, along with Chapman's Antshrike (*T. zarumae*), Bar-crested Antshrike (*T. multistriatus*), Lined Antshrike (*T. tenuipunctatus*), Chestnut-backed Antshrike (*T. palliatus*), Rufous-winged Antshrike (*T. torquatus*) and Rufous-capped Antshrike (*T. ruficapillus*) form a species group. Originally believed to be conspecific, Chapman's Antshrike and the Barred Antshrike are recognized as a superspecies, exhibiting differences in both morphology and vocal behaviour. Careful comparisons of plumage (shown to occur in a clinal pattern), morphology, vocalizations and molecular data may reveal multiple species among the different races. The taxonomy of the Barred Antshrike may undergo considerable revision upon further study, which is also needed to confirm existing races (Zimmer and Isler 2003). To date, the work of Assis *et al.* (2007) has confirmed the subspecies status of *T. d. capistratus* in eastern Brazil.

Distribution

The Americas

Barred Antshrikes have an extensive breeding range which is estimated to include 10,700,000 km² of land in Central and South America (BirdLife International 2009). The

range of the Barred Antshrike extends from northeastern Mexico to Bolivia and Northern Argentina (Slud 1964, Skutch 1969). Barred Antshrikes prefer regions with moderate rainfall and are more commonly found on the Pacific side of Central America, rather than the Caribbean side (Skutch 1969).

Outside the Americas

None reported or suspected.

Habitat

The Barred Antshrike is commonly found within 3m of the ground in dense undergrowth and in a variety of other habitats such as forest edge (Cody 2000), closed non-deciduous forest, dry scrub, gardens, deciduous woodland and second-growth forests (Keeler-Wolf 1986), second-growth thickets, and shrubs (Russell 1964, Slud 1964, Monroe 1968, Skutch 1969,). Barred Antshrikes are most abundant in areas with moderate rainfall (Skutch 1969).

Historical changes

No Information.

Fossil history

No Information.

Life History

Food

The Barred Antshrike is largely a leaf insectivore (Young 1929, dos Anjos 2001). Considered a foraging generalist, the Barred Antshrike feeds on fruit (11 types of fruit reported by Keeler-Wolf 1986), small lizards (Keeler-Wolf 1986), small seeds (Zimmer and Isler 2003), bread (Hundley and Mason 1965 in Skutch 1969) and a large variety of insects and invertebrates: terrestrial arthropods, mantids, phasmatids (Keeler-Wolf 1986),

gastropoda, araneae, ixodidae, diplopoda, (see Table 1, Poulin *et al.* 1994), orthoptera (locustidae and grillidae; Poulin *et al.* 1994, Ordano *et al.* 1999), coleoptera (alticinae, bruchidae, coccinelidae, cerambycidae, curculionidae, chrysomelidae, elateridae, staphylinidae; Ordano *et al.* 1999, Zimmer and Isler 2003), hemiptera (pentatomidae, reduviidae), homoptera, lepidoptera and lepidopteran larvae, hymenoptera (apidae, formicidae, meliponidae, myrmicinae, vespidae, vespoidea), isoptera (termites; Zimmer and Isler 2003).

Behaviour

Barred Antshrikes are found in dense areas with highly tangled foliage and consequently are heard more often than seen.

Locomotion

Barred Antshrikes spend most of their time hopping around within approximately 3m of the ground in thick, scrubby forest areas with dense shrubs and lianas. Males and females of a mated pair are typically found in close proximity to each other (Young 1929, Slud 1964). They tend to fly only short distances at a time. Their movements generally consist of heavy hops and “wing-assisted” leaps onto branches (Slud 1964, Zimmer and Isler 2003). Barred Antshrikes often climb up branches and vines by making many short hops, from side to side, as they ascend (Zimmer and Isler 2003).

Foraging

Barred Antshrikes are typically found feeding 0-3m from the ground on a variety of substrates. They may be observed as high as 10m from the ground, foraging and singing in the canopy. Birds actively forage individually and with their mates. Barred Antshrikes glean insects by probing around stems, leaves, branches and trunks with rapid

stabbing bill movements (Zimmer and Isler 2003). Barred Antshrikes also feed opportunistically at army ant swarms (Hilty and Brown 1986).

Self-Maintenance

No information available.

Agnostic Behaviour

The bowing display that accompanies male and female song has been observed by the authors during agonistic encounters with intruding individuals.

Territoriality

Barred Antshrike pairs hold relatively small, stable, year-round territories. Research on a population in northwestern Costa Rica, where many birds were individually marked, revealed that territories are small, numerous and in close proximity to each other. Male and female Barred Antshrikes both respond very aggressively towards playback of conspecific song. An experiment broadcasting male solos, female solos, duets where the male sang first, duets where the female sang first, and heterospecific song revealed interesting data about the role of song in territoriality. Males responded intensely to all conspecific stimuli compared with the control heterospecific playback without making distinctions between different playback types. Females also responded aggressively to conspecific playback, however, they responded with significantly more physical aggression towards same-sex solos than the other treatment types. This evidence suggests that the songs of both sexes may function in joint territorial defence and may serve an additional function of acoustic mate guarding in females (Chapter 3).

Sexual Behaviour

Mating System and sex ratios

The mating system of the Barred Antshrike is socially monogamous; the genetic mating system is unknown (Young 1929). In a population in northwestern Costa Rica, sex ratios were equal. Unpaired birds were never detected during three years of study in northwestern Costa Rica.

Pair bond

Males and females are thought to form long-term pair bonds (Young 1929, Skutch 1969), although a colour-banded population has not been observed over a long period of time to confirm this idea.

Courtship displays

Courtship displays have not been formally described. The description provided here includes vocal duets, a vibrating visual display, and a bowing posture that often accompanies song. Each of these behaviours may be important in courtship. One copulation was observed in early May in northwestern Costa Rica in 2010. This brief occurrence lasted approximately 10-15 seconds and involved the male hovering atop the female. No unusual behaviours were noted leading up to copulation or afterwards.

Extra-pair copulations

No information. The genetic mating system of this species is currently unknown.

Social and interspecific behaviour

Barred Antshrikes live in monogamous pairs, are highly territorial and hold year-round territories (Young 1929, Skutch 1969).

Predation

The largest predator threat for eggs, nestlings, and adults are snakes (Keeler-Wolf 1986). Some nests in Argentina have suffered brood parasitism from Shiny Cowbirds, *Molothrus bonariensis* (Zimmer and Isler 2003).

Reproduction

The breeding season for the Barred Antshrike varies by geographic area. In Guyana and central Costa Rica, the breeding season occurs from January to June (Young 1929, Skutch 1969). In the seasonal dry forests of northwestern Costa Rica, breeding coincides with the onset of the rainy season, which typically begins in mid-May and breeding is known to continue until at least July. The Barred Antshrike breeds from March to August in Panama, February to September in French Guiana, and September to December in Argentina and Brazil (Zimmer and Isler 2003). In Surinam, Trinidad and Tobago the Barred Antshrike breeds multiple times throughout the year. Breeding appears to be opportunistic and less dependent on seasonality (Zimmer and Isler 2003). In Trinidad and Tobago, the breeding season has been reported as being both variable and lengthy (Keeler-Wolf 1986).

Nests

Nests are small, deep, open cups with thin walls that are commonly found in densely tangled areas 0.5-3m off the ground between the forks of two branches (Young 1925, 1929; Skutch 1969). Nest materials include fine black and brown fibers, tendrils, vines and vegetable fibers, tightly woven into a cup (Skutch 1969), flowering grasses, rootlets, fine grasses (Young 1925, 1929). Nest diameter is approximately 8.9cm and nest depth is approximately 6.4cm (Young 1925, 1929).

In the most recent review of the Barred Antshrike, nest shape has been reported to vary by geographic region. The descriptions above match those observed in northwestern

Costa Rica, where nests are deep open cups made of fungal rhizomorphs, vines and tendrils and may have moss added to the outside. Nests are set in the forks of branches 1-9m from the ground (Zimmer and Isler 2003). In 11 nests observed in northwestern Costa Rica, the outside of each nest was largely made of fine black rhizome fibers, while a distinct inner layer was made of lighter brown coarse twigs. Similar to this description, Barred Antshrike nests in Trinidad are also deep cups made of weeds and grass stems with a distinct inner layer made of fine fibers (Fig. 1c). Nests in Trinidad are found 1-10m from the ground, secured in the fork of a branch (Zimmer and Isler 2003).

Nests in Guyana and Surinam lack the deep-cup shape. In Guyana, nests form a “hammock-like” shape made of fine grass-heads, rootlets, cow hair, and occasionally thread or string (when in close proximity to urban areas). These nests are secured in forked branches only 1m from the ground (Young 1925, 1929). In Surinam, the nests are made of dried grasses that form an open-basket shape and are found in low shrubs (Zimmer and Isler 2003).

Nest Building

Both males and females actively participate in nest-building (Young 1929). In four nests observed in northwestern Costa Rica, male and female building behaviour occurred in May.

Egg-laying

Barred Antshrikes have an average clutch size of two (Young 1925, 1929; Skutch 1969, Ricklefs 1976). In Trinidad, clutches containing three eggs have been reported (Skutch 1969). Eggs are white in colour with characteristic brown and purple markings (Young 1925, 1929; Skutch 1969). These markings vary in concentration and density. Egg colours have also been reported to range from rufous, chocolate brown or purplish-

brown blotches or speckles (Fig. 1d; Zimmer and Isler 2003). The average egg size is approximately 23.3mm by 17.2mm (calculated by raw observations in Skutch 1969). Four eggs were measured and average 22.7mm by 16.3 mm (Young 1925, 1929). In one nest in northwestern Costa Rica (2010), the first egg was laid approximately 24hrs after copulation was observed and the second egg was laid approximately 48hrs after copulation (24hrs after the first egg).

Incubation and Parental Care

Both sexes incubate (Young 1929, Skutch 1969, pers. obs.); however, the females incubate throughout the night (Skutch 1969). Both parents feed and provision nestlings (Willis 1983). The nestling stage lasts approximately 11-13 days in Argentina, Brazil and Surinam (Zimmer and Isler 2003). In northwestern Costa Rica (2010), the incubation period was observed to last at least 13 days after the second egg is laid.

Nestlings

Upon hatching, nestlings are featherless and blind. Nestling bodies and bare parts are dark black in colour with a yellow outline around the gapes and the interior of their mouths (Fig 1e; Skutch 1969, pers. ob.). Pin feathers grow rapidly and nestlings are usually covered with plumage within 10 days (Skutch 1969). Nestlings feed mainly on insects and fledge after approximately 12-13 days (Skutch 1969, Ricklefs 1976). In northwestern Costa Rica (2010), nestlings were found to fledge after approximately 10-12 days. Plumage of all observed fledglings resembled adult female plumage in colouration, although sex of the fledglings was unknown (Fig 1f). The upper parts of the plumage were rufous with dark barring and the underneath was a lighter, buffy-colour with dark bars (Koloff, pers ob). Skutch (1969) noted a difference in juvenile plumage between males and females, and also indicated that juveniles more closely resemble adult

male plumage. Cherrie (1916) found no difference in colour of male and female juveniles (Skutch 1969). A study on five nests in Argentina revealed that nestling success was 33.3% (Zimmer and Isler 2003).

Conservation

Populations and Demography

Population size is estimated to be 5,000,000-50,000,000 (BirdLife International 2009).

Conservation status

According to the IUCN Red List Status, the Barred Antshrike is listed as “Least Concern” due to their exceptionally large range (approximately 10,700,000 km²) and large population estimates of 5,000,000-50,000,000. Although Barred Antshrike populations seem to be decreasing, numbers are not declining at a rapid rate to categorize the population as “Vulnerable” (BirdLife International 2009).

Effects of human activity on populations

One of the largest challenges facing Barred Antshrike survival is deforestation, habitat destruction and habitat fragmentation. Although Barred Antshrikes inhabit scrub and edge forest, they also establish large populations in Neotropical dry forest, arguably the most threatened of all tropical habitats (Janzen 1988). A study using radio telemetry by Gilles and St. Clair (2009) in Costa Rica demonstrates Barred Antshrike sensitivity to forest fragmentation. Barred Antshrikes were trans-located from highly fragmented territories to an area containing riparian corridors, linear living fencerows and open pasture. Barred Antshrikes heavily relied on the riparian corridors and forested areas when returning to their initial territories (Gilles and St. Clair 2009). This information is

critical considering the large turnover of tropical habitats into pasture for agricultural purposes. Based on this account, Barred Antshrike conservation can be facilitated if conservation managers ensure the preservation of riparian and forested areas between habitat patches.

Priorities for Future Research

Many aspects of Barred Antshrike life history have yet to be fully understood. There are also many experimental avenues left unexplored in this species. Detailed accounts of Barred Antshrike vocal behaviour and song structure from many geographic regions, coupled with morphology and genetic measures, may elucidate the phylogeny of this species. Such studies are needed to confirm each of the subspecies that have been placed under the category of “Barred Antshrike”.

Long-term monitoring of colour-banded populations is needed to increase our understanding of the social mating system of the Barred Antshrike. The genetic mating system of Barred Antshrikes also remains unknown. Determining whether Barred Antshrikes have extra-pair copulations may explain why female aggression is so high towards same-sex intruders.

More field observations about the contexts in which male and female Barred Antshrikes call and perform visual displays may provide insight into the function of these interesting behaviours. Studies focused on individual variation in the characteristics of the white nape patch of males, such as patch size and brightness may provide information on individual quality. Observational data are needed to understand Barred Antshrike foraging activity as it relates to army ant swarms. How often do these birds follow ant swarms? Lastly, detailed information on life history traits such as self-maintenance,

agnostic displays, courtship displays, time of breeding, pair bonds and copulations are lacking in this species.

Barred Antshrikes have proved to be a fruitful species to study as they are abundant, ubiquitous, loud, sexually dimorphic and respond extremely well to playback. I encourage study on this species as Barred Antshrikes are relatively easy to work with in the field, making them an interesting subject for future studies of the ecology and behaviour of tropical birds.

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Literature Cited

- Assis, C. P., Raposo, M. A., Stopiglia, R., and R. Parrini. 2007. Validation of *Thamnophilus capistratus* Lesson, 1840 (Passeriformes, Thamnophilidae). *The Auk* 124: 665–676.
- Binford, L.C. 1989. A Distributional Survey of the Birds of the Mexican State of Oaxaca. *Ornithological Monographs* 43:1-418.
- BirdLife International (2009) Species factsheet: *Thamnophilus doliatus*. Downloaded from <http://www.birdlife.org> on 23/3/2010.
- Clements, J.F. 2007. *The Clements Checklist of Birds of the World*, 6th ed. Cornell University Press, Ithaca, New York.
- Cody, M.L. 2000. Antbird Guilds in the Lowland Caribbean Rainforest of Southeast Nicaragua. *The Condor* 102:784-794.
- dos Anjos, L. 2001. Bird communities in five Atlantic forest fragments in southern Brazil. *Ornitologia Neotropical* 12: 11–27.
- Farabaugh, S.M. 1982. The ecological and social significance of duetting. In: Kroodsma DE, Miller EH (eds) *Acoustic communication in birds*, vol 2. Academic, New York, pp 85-124.
- Gilles, C.S., and C.C. St. Clair. 2009. Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences* 105:19774-19779.
- Haverschmidt, F. 1947. Duetting in birds. *Ibis* 89: 357-358.
- Hilty, S.L. 2003. *Birds of Venezuela*. Princeton University Press, Princeton, New Jersey.
- Hilty, S.L., and W.L. Brown. 1986. *A Guide to the Birds of Columbia*. Princeton University Press, Princeton, New Jersey.
- Isler, M.L., Isler, P.R., and B.M Whitney. 1998. Use of Vocalizations to Establish Species Limits in Antbirds (Passeriformes: Thamnophilidae). *The Auk* 115:577-590.
- Janzen, D. H. 1988. Management of Habitat Fragments in a Tropical Dry Forest: Growth. *Annals of the Missouri Botanical Garden* 75:105-116.
- Keeler-Wolf, T. 1986. The Barred Antshrike (*Thamnophilus doliatus*) on Trinidad and Tobago: habitat niche expansion of a generalist forager. *Oecologia* 70:30-317.
- Monroe, B.L. 1968. A Distributional Survey of the Birds in Honduras. *Ornithological Monographs* 7. American Ornithologists' Union, Washington D.C. pp 458.
- Ordano, M., A. Bosisio, B. Boscarol, A. Beltzer, G. P. de Amsler. 1999. Stomach contents of thirty six bird species from Northern Argentina. *Revista Ceres* 46: 555-563.
- Poulin, B., G. Lefebvre, R. McNeil. 1994. Diets of Land Birds from North-eastern Venezuela. *The Condor* 96: 354-367.
- Ricklefs, R.E. 1976. Growth rates of birds in the humid new world tropics. *Ibis* 118:179-207.
- Ridgely, R.S., J.A. Gwynne. 1989. *A Guide of the Birds of Panama with Costa Rica, Nicaragua, and Honduras*. Princeton University Press, Princeton, New Jersey.
- Ridgely, R.S., and G. Tudor. 1994. *The Birds of South America, Volume 2, the Suboscine Passerines*. University of Texas Press & Oxford University Press, Texas.

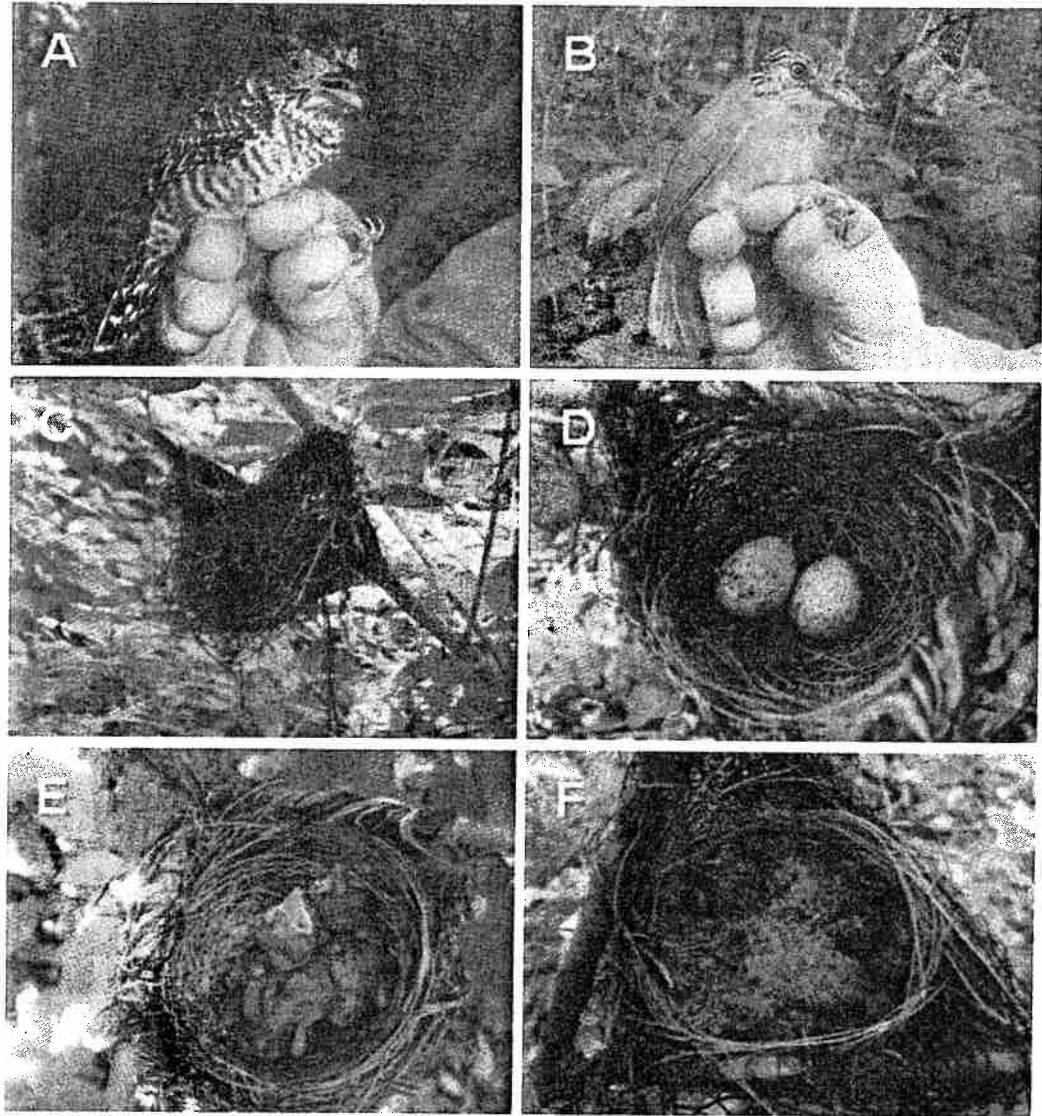
- Russell, S.M. 1964. A Distributional Study of the Birds of British Honduras. Ornithological Monographs 1. 96pp.
- Skutch, A.F. 1969. Life histories of Central American birds III. Pacific Coast Avifauna 35: 1-580.
- Slud, P. 1964. The birds of Costa Rica - Distribution and Ecology. Bulletin of the American Museum of Natural History 128:1-430.
- Snow, D.W., and B.K Snow 1964. Breeding seasons and annual cycles of Trinidad land-birds. Zoologica 49:1-39.
- Willis, E.O. 1983. *Thamnophilus doliatus* (Batara Barretrado, Barred Antshrike). Pp. 607-608 in Janzen, D.H. e.d. Costa Rican Natural History. University of Chicago Press, Chicago, Illinois.
- Young, C.G. 1925. Notes on the nests and eggs of some British Guiana Birds. Ibis 1:469.
- Young, C.G. 1929. A Contribution to the ornithology of the coastland of British Guiana. Part 2. Ibis 5:34.
- Zimmer, J.T. 1933. Studies of Peruvian birds. IX The Formicarian genus *Thamnophilus*. Part I. American Museum of Natural History 646:1-22.
- Zimmer, K. J., and M.L. Isler. 2003. Family *Thamnophilidae* (Typical Antbirds). Pages 448-681 in J. del Hoyo, A. Elliott, and D. A. Christie (editors), Handbook of the birds of the world. Volume 8 Broadbills to Tapaculos. Lynx Edicions, Barcelona, Spain.

Table 1. Emetic sample data for Barred Antshrikes sampled in North-eastern Venezuela
(taken from Poulin *et al.* 1994).

Percent of emetic samples containing:

Sample Size	Invertebrates	Fleshy Fruits	Seeds	Pollen
27	100	11	0	0

Figure 1: (A) an adult male Barred Antshrike, *Thamnophilus doliatus* (B) an adult female Barred Antshrike (c) a Barred Antshrike nest (D) two Barred Antshrike eggs (E) two day-old Barred Antshrike nestlings (F) two 10-day old Barred Antshrike nestlings (all photos taken by J. Koloff).



Chapter 2

The Vocal Behaviour of the Barred Antshrike, a Neotropical Duetting Suboscine Songbird

This chapter is the outcome of joint research and is co-authored with my supervisor Dr. Daniel Mennill, who contributed financial assistance and logistical support, and provided guidance in research design, data analysis, and writing.

CHAPTER II

THE VOCAL BEHAVIOUR OF THE BARRED ANTSHRIKE, A NEOTROPICAL DUETTING SUBOSCINE SONGBIRD

Chapter Summary

Despite the high biodiversity that characterizes the tropics relative to temperate latitudes, we know comparatively little about the behaviour of tropical birds. In the current study, I provide the first comprehensive description of the vocal behaviour of a Neotropical duetting suboscine songbird, the Barred Antshrike (*Thamnophilus doliatus*), which is found throughout most of Central and South America. Both males and females produce a similar song of rapidly repeated chuckling notes. Several characteristics of this song distinguish the sexes; male songs are longer, contain more syllables, and are lower in frequency than female songs. Males have higher song output than females, but within song bouts males and females sing at similar rates. Barred Antshrike songs vary diurnally with the highest levels of song output at dawn, indicating a dawn chorus pattern. Song output also varies seasonally with an increase in song prior to nesting, although this variation is not statistically significant. Males and females combine their songs to create duets, overlapping the terminal portion of their partner's song. The majority of duets are created by females responding to male song (84%), and the rest are created by males responding to female song. Duet response rate varies significantly between the sexes; males respond more quickly to their partner's song (1.6s) than females (2.0s). This detailed account of the Barred Antshrike's vocal behaviour provides insight into the life history of this little-studied species, creates a foundation for more advanced studies, and highlights new avenues for future research.

Introduction

The biology of many tropical birds is poorly understood when compared to temperate birds, despite the higher biodiversity that characterizes the tropics (Morton 1996). Suboscine songbirds, whose songs are generally understood to be innate rather than culturally inherited (Kroodsma 1984, Kroodsma and Konishi 1991), are a diverse and widespread suborder in the Neotropics that have received less attention than oscine songbirds in communication literature. Typical Antbirds (Family: Thamnophilidae) are suboscine songbirds that are numerous and found throughout the Neotropics, characterized by their cryptic behaviour and tendency to follow ant swarms (Zimmer and Isler 2003). Densely vegetated habitats reduce visibility, making acoustic signals important to antbird behaviour and ecology and are often the primary method by which antbirds are detected by ornithologists and wildlife biologists. Previous studies of suboscine acoustic signals have demonstrated the importance of using vocal characteristics to delineate species limits in thamnophilid antbirds (Isler *et al.* 1998, Seddon 2005), classify morphologically similar species (Lanyon 1978, Sedgwick 2001, Isler *et al.* 2002), study song divergence and reproductive isolation (Seddon and Tobias 2007), and distinguish among conspecific animals by recognizing individuals (Lovell and Lein 2004, 2005; Kirschel *et al.* 2009, Westcott 1997).

Vocal duets are temporally coordinated acoustic displays performed usually by members of a mated pair. Duets have been observed in many diverse species (Farabaugh 1982, Haimoff 1986, Tobias *et al.* 1998, Bailey and Hammond 2009). Duetting birds, particularly suboscine songbirds, are largely concentrated in the Neotropics (Morton 1996, Langmore 1998, Slater and Mann 2004). Slater and Mann (2004) suggest that the ecological characteristics and life histories of tropical birds promote the evolution of

females singing alone and with their mates. Breeding asynchrony, consistent food availability, low seasonality, stable territories, low rates of extra-pair fertilization and high nest predation may be factors that influence sex role convergence and cause females to participate in territory defence through song (Slater and Mann 2004). Duet function has only been experimentally investigated in two species of antbird to date (Warbling Antbirds, *Hypocnemis cantator*, and White-bellied Antbirds, *Myrmeciza longipes*; Seddon and Tobias 2006; Fedy and Stutchbury 2005), where duets appear to play a role in acoustic mate guarding and avoiding misdirected aggression from a mate. Anecdotal accounts suggest that duetting may be widespread in antbirds (Zimmer and Isler 2003).

Antbirds have a large range across Neotropical ecosystems, yet our knowledge of their vocal behaviour remains quite rudimentary. By studying acoustic communication in these birds we may gain greater insight into antbird behaviour, ecology, and evolution. My research focuses on Barred Antshrikes (*Thamnophilus doliatus*), a useful species to study suboscine vocalizations because they are widespread, produce loud and locatable songs and respond well to conspecific playback. To date, only brief anecdotal descriptions of Barred Antshrike vocalizations have been reported, and their communication has never been explored in detail.

In the current study, I provide the first thorough description of female and male vocalizations of the Barred Antshrike based on analyses of a large-scale, multi-year recording effort in northwestern Costa Rica. I had three primary research objectives in this study: (1) to quantitatively describe the vocalizations of the Barred Antshrike, including any sex-specific structural differences; (2) to describe the vocal patterns of

variation in Barred Antshrikes throughout the day and during the breeding season; and (3) to describe the vocal duetting behaviour of Barred Antshrikes.

Methods

GENERAL FIELD METHODS

Barred Antshrikes (*Thamnophilus doliatus*) are territorial, sexually dimorphic suboscine songbirds that are widespread throughout the Neotropics, ranging from Mexico to Argentina (Skutch 1969). Over a three year period, from the end of the dry season to the early months of the rainy season from 2008 to 2010, I studied a population of Barred Antshrikes in Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica (10°40'N, 85°30'W). This site protects Central America's largest remaining stand of Neotropical dry forest and provides a unique opportunity for understanding animals in what is arguably the most critically endangered Neotropical habitat (Janzen 1988). I recorded pairs of birds in 38 different territories. Males and females exhibit strong plumage dimorphism, making them easy to distinguish; males have prominent black and white stripes across their entire body, whereas females are cinnamon-rufous with ochraceous-buff underparts (Zimmer and Isler 2003). Most of the birds in my study population were unbanded, and I distinguished between territorial pairs on the basis of their territory position, noting the specific location of birds on detailed maps using a hand-held global positioning system (Garmin GPS60SCx). I captured and colour-banded 21 birds with mist nets and song playback; in 6 territories I captured both pair members, and in an additional 9 territories I captured the male only. For each bird captured, I measured mass (in g), as well as tarsus length, tail length, culmen length, and wing chord length (all in mm). My observations of colour-banded individuals demonstrated that birds were consistently found in the very

same small section of forest, even over extended time periods throughout the duration of each field season. Consequently, I am confident that the unbanded pairs that I monitored, based solely on location, can be readily distinguished as unique pairs.

I define a solo song as a vocalization that is produced by one individual and is not overlapped by songs from its partner. I define duets as songs sung from a mated pair, where one song temporally overlaps at least some part of the partner's song. I define male-created duets as duets where the female sings first and the male joins in to overlap his partner's song; female-created duets are duets where the male sings first and the female joins in to overlap her partner's song (Hall 2004). My definition of duets is more conservative than some previous papers that have required only that birds sing within 1.0 second of their partner, and provides a relatively strict definition of duets that matches with my understanding of this species' singing behaviour. I define a call as a short, simple vocalization produced by both sexes that have a particular function and occur under specific contexts (Catchpole and Slater 2008).

RECORDING TECHNIQUES

To analyze Barred Antshrike song structure, including quantification of sex differences in song structure, I collected recordings of banded and unbanded pairs of birds from 38 different territories between May and July 2009. I collected these recordings with a directional microphone (Audiotechnica AT815b) and a solid state digital recorder (Marantz PMD-660) between 0500h and 0800h. During each recording session, I stood as close as possible to the focal birds without disrupting their behaviour, and dictated into the microphone the sex and/or colour band combination of the singer after each vocalization whenever possible.

To analyze duet structure and duetting behaviour I sought to collect longer recordings in order to quantify how often Barred Antshrikes perform duets. I collected recordings of 34 banded and unbanded pairs of Barred Antshrikes between March and June 2008, May and July 2009, and February and March 2010. I collected recordings using automated recorders consisting of an omni-directional microphone (Sennheiser ME62/K6) connected to a solid-state digital recorder (Marantz PMD-670) powered by a sealed lead-acid battery. I attached the microphone to a 3m wooden pole and fastened it to a small tree within a pair's territory using two bungee cords (full details of the autonomous recorder setup are given in Hill *et al.* 2006). The automated recording setup allowed me to record birds continuously over a 24hr period. I moved the automated recorders to new territories approximately every 48hrs, whereas memory cards and batteries were changed every 24hrs. To distinguish male from female songs within the recorded duets, I used song length and peak frequency of songs to distinguish between male and female contributions (see results). In some of the recordings, male and female contributions to duets were assessed through observation at the time of recording.

To analyze song rate, I used the recordings of 34 banded and unbanded pairs of Barred Antshrikes collected between March and June 2008, May and July 2009, and February and March 2010. Recordings were collected using the automated recording setup described above.

To analyze diel variation in song output, I used 24-hr recordings of banded and unbanded pairs of birds from 16 different locations collected between March and June 2008. Recordings were collected using the automated recording setup described above. I annotated all songs recorded over one 24-hour period within each recording. No Barred

Antshrike vocalizations were ever detected before 0500h or after 1800h, so I restrict my analysis to this interval.

To analyze seasonal variation in song output, I used recordings of banded and unbanded pairs of birds from 25 different locations that were sampled one, two, or three times, between mid February and late June of 2008 through 2010. Recordings were collected using the automated recording setup described above. I annotated every song that occurred within a 60.0-minute time period starting with the first song of the morning (between 0500h and 0700h). If more than two birds were represented in the recording, the more distant songs were dismissed as being adjacent neighbours so that only one pair of birds were represented at each site.

SOUND ANALYSIS

I visualized all recordings as sound spectrograms using Syrinx-PC sound analysis software (J. Burt, Seattle, WA). To compare male and female songs from the 38 focal recordings, I selected 3 songs of known sex (based on observations during the recording) with a high signal-to-noise ratio and minimal heterospecific or ambient background noise. I exported songs into Avisoft SASLab Pro (R. Sprecht, Berlin, Germany) and used the automated parameter measurement feature to eliminate human bias in measuring song features. Within Avisoft, I used a threshold of -16 dB relative to maximum to standardize the amplitude of measured songs, and a hold time of 20 ms to determine when each syllable began and ended. From these automated measurements, I recorded 25 variables for every song: (a) length of entire song; (b) number of syllables in entire song; (c) average frequency of maximum amplitude (FMA) of the entire song; (d) FMA of the first syllable; (e) FMA of the second syllable; (f) FMA of the middle syllable; (g) FMA of the penultimate syllable; (h) FMA of the terminal syllable; (i) average bandwidth of the

entire song; (j) bandwidth of the first syllable; (k) bandwidth of the second syllable; (l) bandwidth of the middle syllable; (m) bandwidth of the penultimate syllable; (n) bandwidth of the terminal syllable; (o) average syllable length, (p) length of the first syllable; (q) length of the second syllable; (r) length of the middle syllable; (s) length of the penultimate syllable; (t) length of the terminal syllable; (u) average length of the inter-note interval; (v) length of interval between first and second syllables; (w) length of interval between second and third syllables; (x) length of interval between middle and following syllable; and (y) length of interval between penultimate and terminal syllables. To ensure I only measured characteristics of fundamental frequencies, I occasionally used the “eraser cursor” in AviSoft to avoid measuring harmonic stacks or background sounds that might have otherwise influenced automated measurements. For each individual, I used the mean measurements of the three songs in subsequent analyses.

STATISTICAL TECHNIQUES

All statistical analyses were conducted in JMP 6.0 (SAS Institute, Cary, North Carolina). I report all values as mean \pm SE.

In testing for differences between the sexes, I used discriminant function analysis with cross-validation based on the 25 fine structural characteristics. I randomly selected 70% of the data, constructed the canonical discriminant analysis, and then evaluated my ability to correctly identify sex in the remaining 30% of the data. I report accuracy as the percentage of the 30% of the data assigned to the correct sex in the cross-validation. I report the contributions of the original measurements to the discriminant functions for all song measures with factor loadings greater than 0.6 (Kline 1994).

I calculated male duet responsiveness as the number of male-created duets divided by the sum of the number of female solos and the number of male-created duets

(Hall 2009). I used similar calculations to quantify female duet responsiveness (Hall 2009). I assessed duet precision as the coefficient of variation between the delay from the start of the first song to the start of the second song in a duet, where the coefficient of variation is the quotient of the standard deviation and the mean multiplied by 100 (as in Levin 1996a, Mennill and Vehrencamp 2005). I quantified song rate as the time delay between the onset of consecutive vocalizations. Given that Barred Antshrikes often sing for a period of time and then take long pauses, I also reported song rate after removing periods of silence ≥ 60 seconds (following Mennill and Vehrencamp 2005) to gain a measure of how often birds sing without the influence of these long pauses.

I conducted a repeated measures ANOVA to analyze diel variation in the $n=16$ day-long recordings. For analysis of seasonal variation in the $n=57$ recordings collected between mid-February and late June, I conducted a linear mixed model with time-of-year as a fixed factor (recordings were grouped into the first or second half of each month), and pair as a random effect.

Results

Barred Antshrikes are vocal animals that sing repeated-note songs as solos and duets, as well as a variety of different types of calls.

DESCRIPTION OF CALLS

Several non-song vocalizations have been described in the literature (Zimmer and Isler 2003), and I collected recordings and observations of two of these calls. The first call is a soft “*mew*” or “*whine*” (Fig. 1a). I have observed this call during male-male encounters. It is unknown whether females also produce this call. The second call is a “crow-like *caw*” produced by both sexes (Fig. 1b). I have observed males producing this

call intermittently throughout the day and females producing this call while approaching their nests. Other authors have designated this call as a possible warning call (Young 1929, Slud 1964). I attempted playback of both the *caw* and the *whine* calls on six occasions to six different pairs; in all cases the birds did not respond vocally or with an approach towards the loudspeaker even though they were very near the loudspeaker at the start of playback.

Other authors report additional call types which I did not detect during this three-year study. A low, guttural “*gnaar*” (Slud 1964), a “*croak*” (Skutch 1969), “*graaaaa*” (Hilty 2003), and “*growl, gurrr*” (Hilty and Brown 1986) may be different authors’ accounts of the *caw* vocalization described above, or they may be additional vocalizations that are rare or absent from my study population. In addition, Zimmer and Isler (2003) describe long or short clear whistle notes, and Slud (1964) describes male and female calls reminiscent of “four or five trogon-like ‘*pyoo*’s”. The function of these calls is unknown.

SOLO SONG STRUCTURE

Male and female Barred Antshrikes produce similar songs, consisting of a series of rapidly repeated chuckling notes that subtly rise and then fall in pitch, concluding with an emphasized, higher-pitched terminal syllable (Fig. 1). Ridgely and Tudor (1994) provide a mnemonic for the song: “hah-ha-ha-hahahahahahaha-hánh”. The fine structure of songs reveals stereotyped sex-specific differences, which are often detectible by ear and easily detectible by spectral analysis. Male songs contain more syllables than female songs (males: 29.5 ± 0.45 ; females 22.4 ± 0.42 ; ANOVA: $F_{1,74} = 132.32$, $p < 0.0001$, $n = 76$ individuals) and consequently male songs are longer than female songs (males: $3.06 \pm 0.04s$; females: $2.31 \pm 0.04s$; ANOVA: $F_{1,74} = 167.96$, $p < 0.0001$). All five

measures of frequency of maximum amplitude (FMA) differed by sex. Male songs are significantly lower pitched than female songs in all cases (ANOVA: all $F > 13.84$; all $p \leq 0.0004$). All other measures did not differ between the sexes.

Canonical discriminant analysis based on 25 fine-scale measurements discriminated between the sexes. Vocalizations were assigned to the correct sex with 91% accuracy, well above the 50% accuracy expected by chance (chi-squared test: $\chi^2_{21} = 15.6$, $P < 0.0001$). Measurements that contributed most strongly to the sex discrimination were length of frequency measurements (particularly song length, number of syllables, and frequencies of maximum amplitude of the second syllable, the middle syllable, and average of all syllables).

DUET DESCRIPTION

Male and female Barred Antshrikes produce duets by combining their songs, using the same songs in duets that they sing as solos (Fig. 1a and 1b). Birds typically perform duets when perched at a distance of approximately 2m apart. Both sexes can create duets by overlapping their partner's song. The vast majority of Barred Antshrike duets ($84 \pm 2\%$) are created by females overlapping male songs (e.g. Fig. 1e), and the remainder are created by males overlapping female songs (e.g. Fig. 1f). Females produce $38 \pm 3.5\%$ of their songs as duets; males, in contrast, produce a significantly lower proportion of their songs as duets, $22.5 \pm 4.4\%$ (ANOVA: $F_{1,65} = 7.63$, $p = 0.0075$). I only observed duets performed by members of a mated pair.

DUET BEHAVIOUR

I quantified three characteristics of Barred Antshrike duetting behaviour: duet responsiveness, duet precision, and degree of duet overlap.

I define duet responsiveness as the proportion of a partner's songs that an individual joins to create duets (as in Levin 1996b; Hall 2004, 2009). Females were more responsive to their partner's song in creating duets, female duet responsiveness was $11.5 \pm 1.5\%$, significantly higher than male duet responsiveness at $8.3 \pm 1.3\%$ (matched pairs t-test: $t=2.5$, $n=34$, $p=0.009$).

I define duet precision as the variability in the time delay between the start of one bird's song to the start of their partner's song (as in Farabaugh 1982, Levin 1996a, Hall 2009). Barred Antshrikes responded fairly quickly to their partner's song. The average delay between the start of a bird's song to the start of their partner's song was 1.82 ± 0.05 seconds. This varied significantly by sex; for female-created duets, the delay was 2.01 ± 0.06 seconds from the male song to the female song, whereas in male-created duets, the delay was 1.6 ± 0.07 seconds from female song to the male song (ANOVA: $F_{1,53}=21.7$, $p<0.0001$). Barred Antshrikes had a moderate level of variation in duet precision; the delay between the first bird's song and their partner's song had a coefficient of variation of 30.4%. There was no difference in duet precision whether duets were created by females ($28.7 \pm 2.4\%$) or males ($30.0 \pm 2.7\%$; ANOVA: $F_{1,53}=0.13$, $p = 0.72$).

I found that similar ratios of male and female songs were overlapped by their partner to create duets. When males created duets, $31.1 \pm 1.9\%$ of the female's song was overlapped; when females created the duets, $30.8 \pm 2.6\%$ of the male's song was overlapped (ANOVA: $F_{1,53}=0.007$, $p=0.93$).

VOCAL BEHAVIOUR

Song rate

Males and females sing bouts of solos and duets that are punctuated by periods of silence. Males have higher song output than females; the average male song rate (one

song every 88.16 ± 13.42 s) is much higher than the average female song rate (one song every 226.83 ± 47.20 s). When silent periods longer than 60s are removed from song rate calculations, however, male and female song rates are quite similar: males sing consecutive songs every 22.35 ± 0.69 s and females sing consecutive songs every 22.66 ± 2.18 s (paired t-test: $t=0.35$, $p=0.72$, $n=48$ pairs where both sexes sang songs with <60 s inter-song intervals). Therefore, within each song bout, male and female song rates are very similar, but males spend more time singing than do females.

Diel Variation

Barred Antshrike singing behaviour varies throughout the day. Song output varied significantly with time of day both for males (Fig. 2a; repeated measures ANOVA: $F_{14}=7.5$, $p<0.0001$) and females (Fig. 2b; $F_{14}=8.9$, $p<0.0001$; $n=16$ pairs recorded for a 24-hour period). Vocal output also varied significantly with time of day for both solos (Fig. 2c; repeated measures ANOVA: $F_{14}=10.7$, $p<0.0001$) and duets (Fig. 2d; $F_{14}=3.8$, $p<0.0001$; $n=16$ pairs recorded for a 24-hour period). Barred Antshrike vocalizations were detected during all daylight hours, from 0500h until 1800h, but vocal output was highest during the early hours of the morning between 0500h and 0700h (Fig 2). Vocal activity was infrequent after 1100h, when the weather at the study site was very hot. The first vocalizations of the morning occurred between 0515 and 0530 h (first male song: $0518\text{h} \pm 3.3$ min; first female song: $0519\text{h} \pm 3.7$ min; $n=16$ day-long recordings) with solos occurring earlier than duets (first solo: 0516 ± 3.0 min; first duet: $0528\text{h} \pm 4.9$ min). The early-morning peak in song output demonstrates that Barred Antshrikes participate in dawn chorus singing behaviour. At this study site the sun rises at approximately 0500h (Bradley and Mennill 2009); Barred Antshrikes begin singing around 0518h which is later than most species in this site that begin singing at or just before sunrise (pers. obs.)

Seasonal Variation

Barred Antshrike vocal behaviour also varies with time of year. The frequency of Barred Antshrike songs were lowest before the start of the breeding season in late February, but rose to a higher level and remained at a consistently high level during the breeding season (Fig. 3). This pattern held true for both sexes, although the variation with time of year was not statistically significant for males (Fig. 3a; whole model: $F_{32,24}=2.0$, $p=0.05$; time of year: $F_8=0.9$ $p=0.54$; pair [random effect]: $F_{24}=1.9$, $p=0.07$) or females (Fig. 3b; whole model: $F_{32,24}=1.2$, $p=0.33$; time of year: $F_8=0.4$ $p=0.91$; pair [random effect]: $F_{24}=1.4$, $p=0.20$). The same pattern was observed for solos and duets but was not significant for either solos (Fig. 3c; whole model: $F_{32,24}=1.7$, $p=0.09$; time of year: $F_8=0.8$, $p=0.58$; pair [random]: $F_{24}=1.6$, $p=0.12$) or duets (Fig. 3d; whole model: $F_{32,24}=2.0$, $p=0.04$; time of year: $F_8=0.5$, $p=0.86$; pair [random]: $F_{24}=0.9$, $p=0.02$).

Discussion

This is the first quantitative description of Barred Antshrike vocal behaviour. Male and female Barred Antshrike songs each consist of a number of repeated chuckling notes which rapidly ascend and then descend, ending with an emphatic terminal note. Skutch (1969) described their songs as “unmelodious but not unpleasant”. The sexes show marked fine structural differences. Male songs contain more syllables and have longer duration and lower frequency components than female songs. Vocal output varies on both a diel and seasonal scale. Barred Antshrikes exhibit a pronounced increase in singing activity during the first two hours of morning, indicating that this species contributes to dawn chorus singing. Vocal output also increases from low levels in late February to higher levels in early April, and remained consistently high throughout the

breeding season. In addition to songs, Barred Antshrikes produce at least two types of call, although the function of these calls is unclear.

Male and female Barred Antshrikes have different rates of song output, with higher output from males than females. When long silences ≥ 60 s were removed from the analyses, however, the sexes showed similar singing rates during song bouts. Other studies of tropical species have shown that males have higher singing rates (e.g. Rufous-and-White Wrens, *Thryothorus rufalbus*, Mennill and Vehrencamp 2005) including other studies of antbirds (e.g. White-bellied Antbirds, Fedy and Stutchbury 2005; Chestnut-backed Antbirds, *Myrmeciza exsul*, Stutchbury *et al.* 2005). The similar singing rates within song bouts that we found for Barred Antshrikes may be related to heightened competition for territories in this species; their territories are small and densely packed, which may increase the importance of song for both males and females.

Barred Antshrike vocal output significantly varies with time of day. Vocal output was highest in the early morning between 0500 and 0700 hrs, indicating that Barred Antshrikes participate in dawn chorus singing. Singing activity dramatically decreases around 1100h and remains low throughout the hottest part of the day. At my study site, Barred Antshrikes tend to sing their first songs later than most species during the dawn chorus (pers. ob.). Luther (2008) looked at time of singing during the dawn chorus in four antbirds and found that the Chestnut-backed Antshrike, *Thamnophilus palliatus palliatus*, sang one to two hours after sunrise. The tendency to join in dawn chorus singing later than other species may be an effort to minimize acoustic competition with nearby species (Luther 2008, 2009).

The presence of dawn chorus singing in tropical duetting birds varies across species. In some species both sexes have heightened song output at dawn, in others only males have heightened song output at dawn (e.g. Rufous-and-white Wrens, Mennill and Vehrencamp 2005; Chestnut-backed Antbirds, Stutchbury *et al.* 2005) and in many species dawn chorus singing does not appear to occur at all (e.g. White-bellied Antbirds, *Myrmeciza longipes*, Fedy and Stutchbury 2005; see review Staicer *et al.* 1996). There are a number of non-mutually exclusive hypotheses used to explain why increased singing at dawn is important in many avian species. Studies have shown support for functions such as mate guarding, territory defence, mate attraction and acoustic transmission (for other hypotheses see review by Staicer *et al.* 1996, Catchpole and Slater 2008).

In my study site, Barred Antshrike territories are small and densely packed; increased song rates in the early hours of the morning may function in additional territorial defence against multiple neighbours. A study on male Common Nighthales (*Luscinia megarhynchos*) that were fitted with radio transmitters showed that new males arriving to the area made frequent visits to occupied territories at dawn, and did not seek out prospective territories throughout the rest of the day (Amrhein *et al.* 2004b). Similarly, this behaviour may also occur with lone or “floater” males in the tropics, although lone males have not been observed in my study population. Additionally, a playback study on Winter Wrens (*Troglodytes troglodytes*) showed that males who were subjected to simulated territorial intrusions at dawn had increased vocal output the following day at dawn (Amrhein and Erne 2006). Evidently, dawn chorus singing is

important for territory defence in many species and may be especially important in tropical species where both sexes sing and defend resources from intruders.

Barred Antshrike vocal behaviour also varied with time of year; although the variation was not statistically significant, there was a consistent pattern where song output increased just prior to the onset of nesting (nesting activity was first observed in early May in 2009 and 2010), and remained high throughout the breeding season. The lack of significant variation may be due to a low sample size, as there were only 5-6 pairs of birds recorded in many of the months. The pattern of increased singing activity I observed may result from a greater threat of intruders during nest building and consequently, a greater need for territory defence from both sexes. Barred Antshrikes hold stable territories and securing a territory prior to nesting may be a critical prerequisite for reproduction in this species. Alternatively, as the breeding season approaches, increased song output may be related to increased competition for mates. A concurrent playback study revealed that females, in particular, show high levels of intrasexual aggression during the breeding season which may be a contributing factor for higher song output for females.

Barred Antshrikes showed an interesting seasonal pattern of variation in vocal duets where duetting activity began to decrease later in the breeding season, although this pattern was not statistically significant. Later in the breeding season, many pairs had switched activities to rearing nestlings. Similar patterns of higher vocal output at the beginning of the breeding season followed by a decrease in duetting later in the breeding season have been demonstrated in other tropical passerines such as Rufous-and-White Wrens; the variation of vocal output in this species was highly correlated with the onset

of the rainy season and the female's fertile period (Topp and Mennill 2008). A playback study on White-bellied Antbirds demonstrated that birds displayed greater aggression to intruders during the dry season, prior to breeding, than the rainy season (Fedy and Stutchbury 2005). Heightened competition for resources early in the breeding season may place increased pressure on tropical birds to defend their territories against intruders.

Both male and female Barred Antshrikes create duets by overlapping their partner's song. Females in my population created the majority of duets (84%) by combining their song with their mate's song. This pattern has also been found in other antbird species such as the White-bellied Antbird (Fedy and Stutchbury 2005) and the Warbling Antbird (*Hypocnemis cantator*) (Seddon and Tobias 2006). Although this pattern holds for most species that have been studied, this is not the case for all tropical duetting birds (Hall 2009). Studies on a few species have shown that most duets are created by the male answering the female's song (e.g. Bay Wrens, *Thryothorus nigricapillus*, Levin 1996b; Stripe-headed Sparrow, *Aimophila r. ruficauda*, Illes and Yunes-Jimenez 2009). The sex bias shown in Barred Antshrike duets may be explained by inter-pair conflict, whereby females acoustically mate guard their partner by singing immediately after their partner's song. Although many hypotheses have been proposed for why birds duet rather than sing alone, the function(s) of Barred Antshrike duets has yet to be determined.

In addition to fine structural differences in male and female Barred Antshrike songs, I also found sex differences in patterns of duetting behaviour. Females are significantly more responsive to their partners and turn 11.5% of their partner's songs into duets. Interestingly, when males do create duets, they have a significantly shorter

delay in responding to their partners. When variability of duet response rate was assessed, however, males and females had similar levels of duet precision. Considering the relative differences in song lengths between males and females, both sexes overlap a similar proportion (31%) of their partner's songs when they create duets.

The vocal behaviour of many tropical bird species has yet to be described. Thorough accounts of vocal behaviour of suboscines may clarify or confirm many polytypic species (Kroodsma *et al.* 1996). My study on Barred Antshrikes has revealed both similarities and differences in vocal behaviour compared to other tropical birds. These findings contribute to our understanding of the behavioural patterns of tropical birds, as well as other duetting species. There is tremendous variation within and across species in regards to how birds form duets; describing duet structure is important for understanding duet function and patterns of duetting among species (Hall 2009).

Barred Antshrikes are emblematic of several aspects of research in animal communication that are poorly understood. As a tropical bird, the current study demonstrates similar patterns of diel and seasonal behaviour that has been shown in other tropical birds. As a duetting species, Barred Antshrikes possess both similarities and differences in duet structure to other species. As a suboscine songbird, the current study shows similar patterns of song use to that seen in oscines. As an antbird, Barred Antshrikes show some similarities but some important differences in vocal behaviour to other species that have been documented. Taken together, evaluating the vocal behaviour of tropical species is important for our understanding of patterns of behavioural ecology and provides useful comparisons to vocal patterns that have been observed in temperate regions. This research provides a foundation for continued research on this species and

other antbirds as well. Such studies will increase our understanding of a fascinating family of songbirds that are widespread in Neotropical ecosystems.

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Literature Cited

- Amrhein, V., and N., Erne. 2006. Dawn singing reflects past territorial challenges in the winter wren. *Animal Behaviour* 71: 1075–1080.
- Amrhein, V., Kunc, H. P. and M. Naguib. 2004a. Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk* 121: 110–117.
- Amrhein, V., Kunc, H.P., and M. Naguib. 2004b. Non-territorial nightingales prospect territories during the dawn chorus. *Proc R Soc Lond B (Suppl.)* 271:S167–S169.
- Bailey, W.J., and T.J. Hammond 2003. Duetting in insects – does call length influence reply latency? *J. Zool., Lond.* 260: 267–274.
- Bradley, D.W., and D.J. Mennill. 2009b. Solos, duets and choruses: vocal behaviour of the Rufous-naped Wren (*Campylorhynchus rufinucha*), a cooperatively breeding Neotropical songbird. *Journal of Ornithology* 150: 743–753.
- Catchpole, C.K., and P.J.B. Slater. 2008. Bird song: biological themes and variations: second edition. New York: Cambridge University Press.
- Farabaugh, S.M. 1982. The ecological and social significance of duetting. In: *Acoustic communication in birds*, vol. 2 (D. E. Kroodsma AND E. H. Miller, eds.), pp. 85–124. Academic Press, New York, NY.
- Fedy, B.C. and B.J.M. Stutchbury. 2005. Territory defence in tropical birds: are females as aggressive as males? *Behav. Ecol. and Sociobiology* 58:414-422.
- Haimoff, E. H. 1986. Convergence in the duetting of monogamous old world primates. *J. Hum. Evol.* 15: 51–60.
- Hall, M.L. 2004. A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and Sociobiology* 55:415-430.
- Hall, M.L. 2009. A review of vocal duetting in birds. In: *Advances in the study of behavior*, vol 40 (M. Naguib, and V M. Janik, eds.), pp. 67–121. Academic Press, Burlington, MA.
- Hill, G.E., Mennill, D.J., Rolek, B.W., Hicks, T.L. and K.A. Swiston. 2006. Evidence suggesting that Ivory-billed Woodpeckers (*Campephilus principalis*) exist in Florida. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* 1(3): 2.
- Hilty, S.L. 2003. *Birds of Venezuela*. Princeton University Press, Princeton, New Jersey.
- Hilty, S.L., and W.L. Brown. 1986. *A Guide to the Birds of Columbia*. Princeton University Press, Princeton, New Jersey.
- Illes, A.E., and L. Yunes-Jimenez. 2009. A female bird out-sings male conspecifics during simulated territorial intrusions. *Proc. R. Soc. Lond. B* 276: 981–986.
- Isler, M.L., Isler, P.R., and B.M. Whitney. 1998. Use of vocalisations to establish species limits in antbirds (Passeriformes: Thamnophilidae). *Auk* 115: 577–590.
- Isler, M.L., Alvarez, A., Isler P.R., Valqui, T., Begazo, A., and M. Whitney. 2002. Rediscovery of a cryptic species and description of a new subspecies in the *Myrmeciza hemimelaena* complex (Thamnophilidae) of the Neotropics. *Auk* 119:362–378.
- Janzen, D. H. 1988. Management of Habitat Fragments in a Tropical Dry Forest: Growth. *Annals of the Missouri Botanical Garden* 75:105-116.

- Kirschel, A.N.G., Earl, D.A., Yao, Y., Escobar, I., Vilches, E., Vallejo, E.E., and C.E. Taylor, 2009. Using songs to identify individual Mexican Antthrush (*Formicarius moniliger*): A comparison of four classification methods. *Bioacoustics* 19:1-20.
- Kline, P. 1994. An easy guide to factor analysis. London, New York: Routledge.
- Kroodsma, D.E. 1984. Songs of the Alder flycatcher (*Empidonax alnorum*) and Willow flycatcher (*Empidonax traillii*) are innate. *Auk* 101: 13–24.
- Kroodsma, D.E., Konishi M. 1991. A suboscine bird (eastern phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Animal Behavior* 42: 477–487.
- Kroodsma, D.E., Vielliard, J.M.E., and F.G., Stiles. 1996. Study of Bird Sounds in the Neotropics: Urgency and Opportunity. In: Kroodsma DH, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, pp 426–453.
- Langmore, N.E. 1998. Functions of duet and solo songs of female birds. *Trends Ecol. Evol.* 13:136- 140.
- Lanyon, W.E. 1978. Revision of the Myiarchus flycatchers of South America. *Bull. Amer. Mus. Nat. Hist.* 161: 429-627.
- Levin, R.N. 1996a. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. I. Removal experiments. *Anim Behav* 52:1093–1106
- Levin, R.N. 1996b. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. II. Playback experiments. *Animal Behaviour* 52: 1007–1117.
- Lovell, S.F., and M.R. Lein. 2004b. Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. *Behavioral Ecology* 15: 799–804.
- Lovell, S.F., and M.R. Lein. 2005. Individual recognition of neighbors by song in a suboscine bird, the alder flycatcher *Empidonax alnorum*. *Behav. Ecol. Sociobiol.* 57:623–630.
- Luther DA. 2008. Signaler-receiver coordination and the timing of communication in Amazonian birds. *Biol Lett.* 4:651–654.
- Luther DA. 2009. The influence of the acoustic community on songs of birds in a neotropical rain forest. *Behavioral Ecology* 20(4):864-871.
- Mennill, D.J., and S.L. Vehrencamp. 2005. Sex differences in the singing and duetting behaviour of neotropical rufous-and-white wrens (*Thryothorus rufalbus*). *Auk* 122:175–186.
- Morton, E.S. 1996. A comparison of vocal behavior among tropical and temperate passerine birds, in *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D.E. and Miller, E.H., eds), pp. 258–268, Cornell University Press.
- Ridgely, R.S., and G. Tudor. 1994. *The Birds of South America, Volume 2, the Suboscine Passerines*. University of Texas Press & Oxford University Press, Texas.
- Seddon, N. 2005. Ecological adaptation and species recognition drive vocal evolution in Neotropical suboscine birds. *Evolution* 59: 200–215.
- Seddon, N. and J.A. Tobias. 2006. Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). *Behav. Ecol.* 17:73–83.

- Seddon, N., and J.A Tobias. 2007. Song divergence at the edge of Amazonia: an empirical test of the peripatric speciation model. *Biological Journal of the Linnean Society* 90: 173-188.
- Sedgwick, J.A. 2001. Geographic variation in the song of willow flycatchers: differentiation between *Empidonax traillii adastus* and *E. t. extimus*. *Auk* 118:366–379.
- Skutch, A.F. 1969. Life histories of Central American birds III. *Pacific Coast Avifauna* 35: 1-580.
- Slater, J. B. and N. I. Mann. 2004. Why do the females of many bird species sing in the tropics? *Journal of Avian Biology* 35:289–294.
- Slud, P. 1964. The birds of Costa Rica - Distribution and Ecology. *Bulletin of the American Museum of Natural History* 128:1-430.
- Staicer, C.A., Spector, D.A., and A.G. Horn. 1996. The dawn chorus and other diel patterns in acoustics signaling. In: Kroodsma DH, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, pp 426–453.
- Stutchbury, B.J.M., Woolfenden, B.E., Fedy, B.C., and E. S. Morton. 2005b. Nonbreeding territorial behaviour of two congeneric antbirds, *Myrmeciza exsul* and *M. longipes*. *Ornithologia Neotropical* 16:397–404.
- Tobias, M.L., Viswanathan, S.S., and D.B. Kelley. 1998. Rapping, a female receptive call, initiates male–female duets in the South African clawed toad. *Proc. natl Acad. Sci. USA* 95:1870–1875.
- Westcott, D.A. 1997. Neighbours, strangers and male-male aggression as a determinant of lek size. *Behav Ecol Sociobiol* 40:235-242.
- Young, C.G. 1929. A Contribution to the ornithology of the coastland of British Guiana. Part 2. *Ibis* 5:34.
- Zimmer, K.J., and M.L. Isler. 2003. Family Thamnophilidae (Typical Antbirds). Pages 448-681 in J. del Hoyo, A. Elliott, and D. A. Christie (editors), *Handbook of the birds of the world. Volume 8 Broadbills to Tapaculos*. Lynx Edicions, Barcelona, Spain.

Figure 1: Sound spectrograms featuring (A) a male *whine* call, (B) a female *caw* call, (C) a male solo song, (D) a female solo song, (E) a female-created duet and (F) a male-created duet. Solid and open bars denote male and female vocalizations respectively.

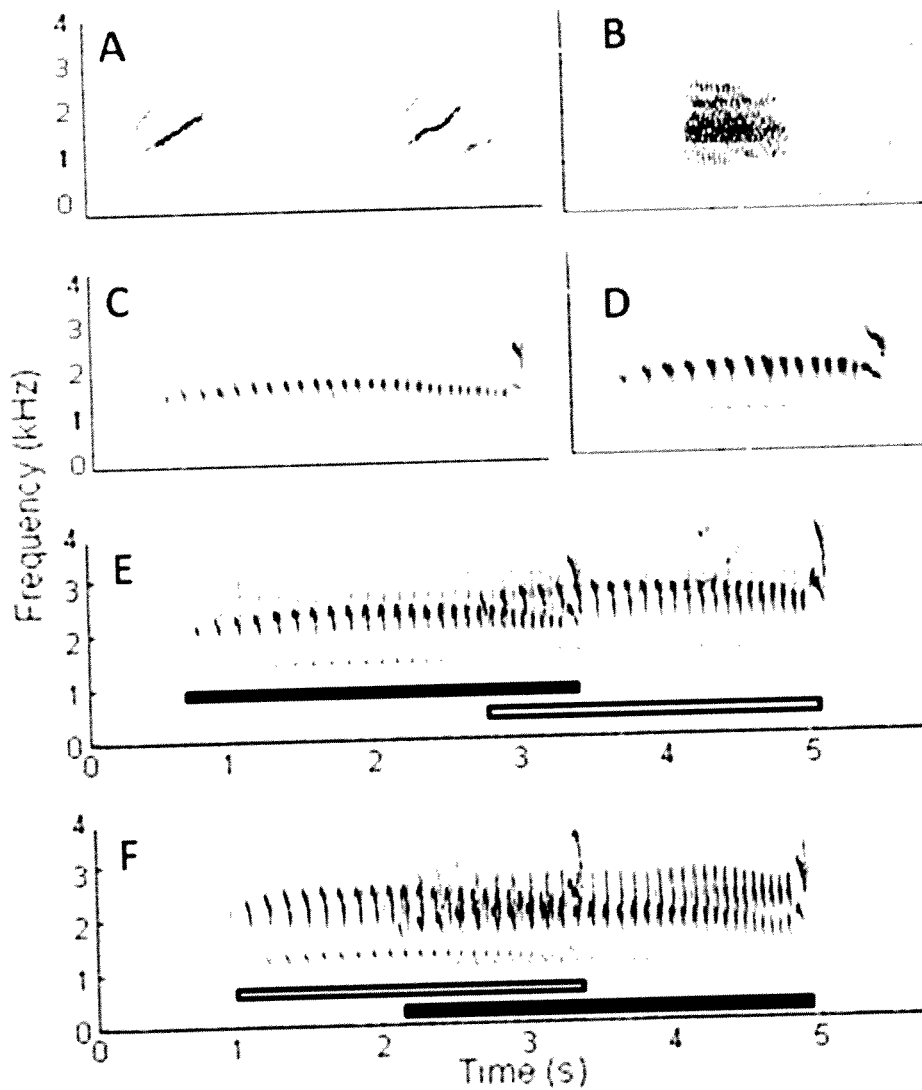


Figure 2: Diel variation in Barred Antshrike vocal output for (A) male songs/hour, (B) female songs/hour, (C) total solos/hour, (D) total duets/hour. Vocal output peaks at dawn and tapers off throughout the day.

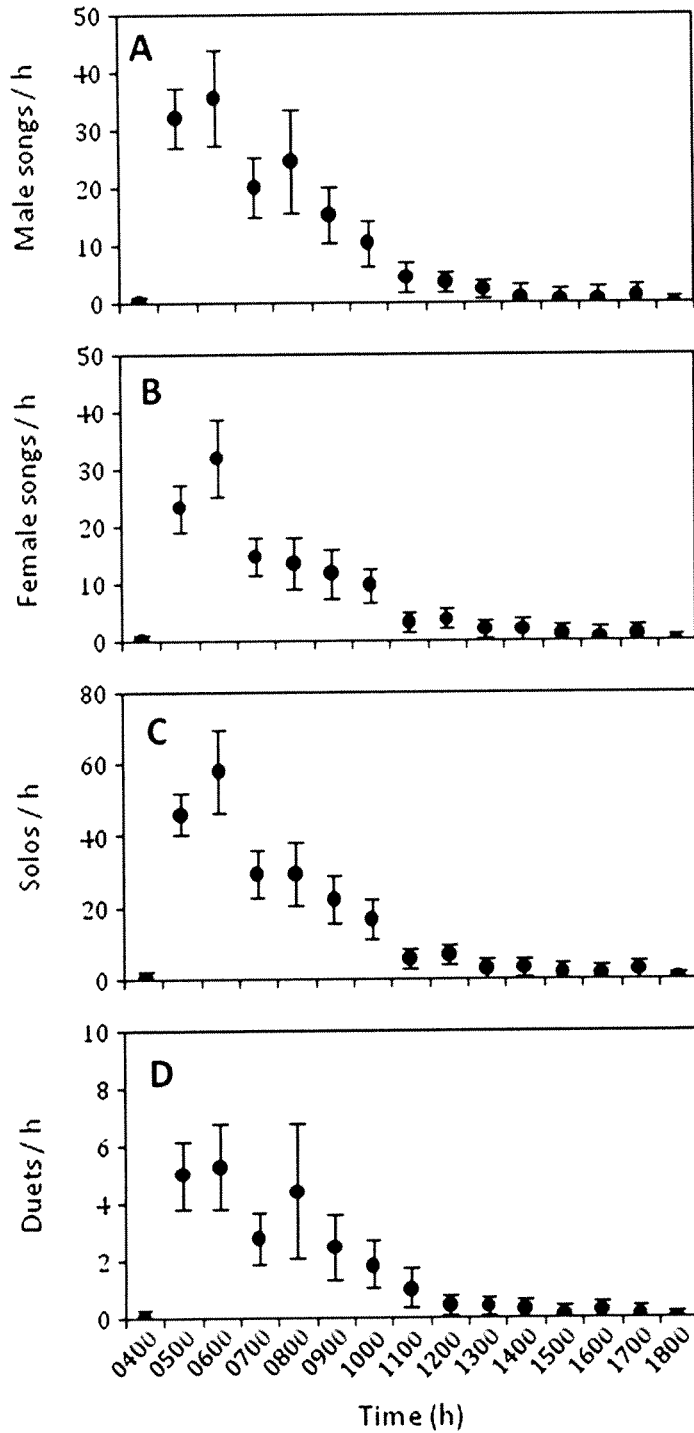
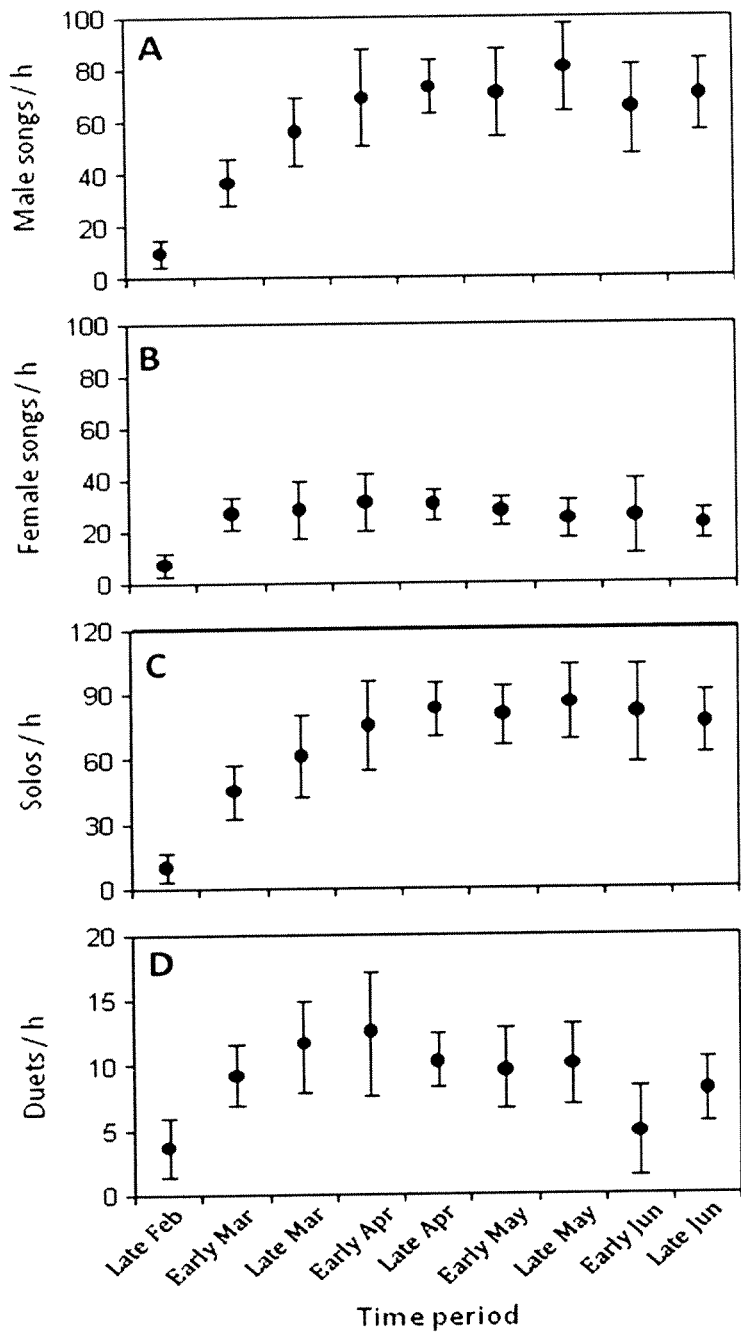


Figure 3: Seasonal variation in Barred Antshrike song output for the first hour of the morning for (A) male songs/hour, (B) female songs/hour, (C) total solos/hour, (D) total duets/hour. Vocal output begins to increase prior to the nesting period and remains high during the rainy season.



Chapter 3

Aggressive responses towards playback of solos and duets in Barred Antshrikes

This chapter is the outcome of joint research and is co-authored with my supervisor Dr. Daniel Mennill, who contributed financial assistance and logistical support, and provided guidance in research design, data analysis, and writing.

CHAPTER III

AGGRESSIVE RESPONSES TOWARDS PLAYBACK OF SOLOS AND DUETS IN BARRED ANTSHRIKES

Chapter Summary

Duetting behaviour is a unique form of animal communication that has been observed across many diverse taxa in the animal kingdom. In birds, hypotheses can be grouped into two broad categories to explain why individuals join their partner's songs to create duets: (1) duets are cooperative displays for purposes such as joint resource defence, or (2) duets are conflicting displays for purposes such as acoustically guarding a mate. In the current study, I conducted a playback experiment on 40 breeding pairs of Barred Antshrikes (*Thamnophilus doliatus*) in northwestern Costa Rica. I broadcast five different playback treatments to territorial pairs of antshrikes: male solos, female solos, male-created duets, female-created duets and a heterospecific control. I categorized responses from both the territorial male and female in terms of vocal and physical responses. Male vocal and physical responses were significantly higher towards conspecific stimuli than heterospecific stimuli. Males tended to increase their singing responses toward duet stimuli compared to solo stimuli, although this trend was not significant. A similar pattern was observed for female vocal responses. However, for physical responses, females show markedly more intense responses towards female solo stimuli than any other conspecific treatment, suggesting that other females are perceived as a greater threat toward resident females. My results provide some support for a joint resource defence function for duetting in this species, while the high intrasexual aggression observed between females may indicate acoustic mate-guarding.

Introduction

Duetting behaviour is a taxonomically widespread phenomenon that occurs when mated pairs combine their songs in a temporally coordinated acoustic display (Farabaugh 1982, Hall 2004). Many duetting species are restricted to tropical regions (Morton 1996, Langmore 1998); female song is rare in animals living in the north-temperate zone, but is more common in the tropics and south temperate ecosystems. Animal behaviourists have recently begun to focus on understanding the form and function of vocal duets, through both behavioural and experimental studies.

Several hypotheses have been proposed to explain why birds perform duets rather than sing alone (Hall 2004, 2009). Hypotheses for duet function fall into two broad categories, which either represent cooperation or conflict between the sexes. Cooperation-based hypotheses suggest mated pairs duet for mutual benefit, such as joint territory or resource defence (reviewed in Hall 2004, 2009). Conflict-based hypotheses suggest individuals within a pair have separate agendas for duetting, such as mate guarding (reviewed in Hall 2004, 2009). To date, experimental studies have shown support for both cooperation- and conflict-based hypotheses; a few studies have even shown evidence for cooperative and conflictive functions to occur within a single species (reviewed in Douglas and Mennill 2010). Such hypotheses are not mutually exclusive. Cooperative hypotheses for duetting, particularly the Joint Resource Hypothesis, are the most widely supported to date (see Douglas and Mennill 2010), however, research on several bird species have also revealed evidence for a mate guarding function for duetting (e.g. Warbling Antbirds, *Hypocnemis cantator*, Seddon and Tobias 2006; Eastern Whipbirds, *Psophodes olivaceus*, Rogers *et al.* 2007).

To investigate duet function, many researchers have employed acoustic playback experimental designs (e.g. Molles and Waas 2006, Bradley and Mennill 2009, Illes and Yunes-Jimenez 2009, Odom and Mennill 2010). Playback experiments are a versatile tool which allows researchers to create and broadcast realistic stimuli to test specific predictions for the various duet function hypotheses (Douglas and Mennill 2010). Assessing birds' responses to different stimuli may indicate how a duet is perceived by a resident pair. Heightened aggressive responses towards playback of duets may highlight the importance of duets in territory defence, whereas heightened responses to same-sex songs may reveal intra-sexual aggression.

The majority of acoustic playback experiments have been conducted on breeding pairs of oscine passerines, a monophyletic group of songbirds that learn their songs (Catchpole and Slater 2008). However, approximately 20% of passerine songbirds are suboscines, whose songs are understood to be inherited directly from parent to offspring without a period of vocal learning (Kroodsma 1984, Kroodsma and Konishi 1991). Suboscines are a diverse suborder that are largely concentrated in the Neotropics and contain many duetting species, yet the form and function of their vocal duets have only recently begun to be explored in this group (e.g. White-bellied Antbirds, *Myrmeciza longipes*, Fedy and Stutchbury 2005; Warbling Antbirds, Seddon and Tobias 2006).

Only two playback studies testing duet function have been conducted on suboscines to date -- with mixed results. A study on 18 pairs of Warbling Antbirds demonstrated evidence in favour of the Mate Guarding Hypothesis, in that birds responded more aggressively to same-sex solos than towards duets (Seddon and Tobias 2006). Conversely, a study on 15 pairs of White-bellied Antbirds found no evidence that

duets function in mate guarding or joint resource defence; males and females responded with low levels of aggression towards all conspecific stimuli regardless of the type (solos or duets) or sex of the singer (Fedy and Stutchbury 2005). Unlike playback experiments on oscine songbirds, neither of these antbird studies found support for the Joint Resource Defence Hypothesis for duet function. Considering the diversity of duetting suboscines in the tropics, suboscine duet function is an important and relatively unexplored avenue for understanding acoustic communication in birds.

In the current study, I investigate the function of duets in territorial pairs of Neotropical suboscines, Barred Antshrikes (*Thamnophilus doliatus*). Using acoustic playback to simulate territorial intrusions by individuals and pairs of birds, I assessed aggressive vocal and physical responses of territorial breeding pairs in northwestern Costa Rica. I predicted that if duet functions as a cooperative behaviour in this species, (a) duet stimuli would evoke a greater aggressive response than solo stimuli and (b) both sexes would display an equivalent level of aggression regardless of the sex of the stimulus. In this case, two birds would be perceived as a greater threat to a resource than a single bird. Conversely, if duets represent intersexual conflict as predicted by the mate guarding hypothesis, I predicted (a) birds would display greater levels of aggression toward same-sex solo stimuli than duet stimuli. In this case, a single bird would be perceived as a greater threat to the pair bond rather than a resource (Douglas and Mennill 2010).

Methods

GENERAL FIELD METHODS

I studied a population of Barred Antshrikes (*Thamnophilus doliatus*) in the Neotropical dry forest in Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica (10°40'N, 85°30'W) from 1 May to 16 July 2009. Barred Antshrikes are sexually dimorphic and live in socially monogamous pairs that hold year-round territories. I conducted a playback experiment on 40 breeding pairs of Barred Antshrikes from 21 May to 9 July 2009. For eight pairs, both birds were banded with unique colour band combinations, and for seven pairs only the male was banded. I routinely checked colour-banded individuals throughout the duration of the field season and found that the banded birds were reliably found on the same territory. Therefore, I am confident that unbanded pairs in this study were also site-faithful and represent unique pairs.

PLAYBACK STIMULI

Single-channel stimuli were created using AUDITION software (Adobe, San Jose, California) using recordings of birds of known sex collected from my population between 1 May and 20 May 2009. I chose songs from recordings with a high signal-to-noise ratio and minimal overlap from heterospecific birds. Recordings were highpass filtered to remove background noise below 200 Hz using AUDITION. I created stimuli for five treatments: male solos, female solos, male-created duets (a duet where a female song is overlapped by a male song), female-created duets (a duet where a male song is overlapped by a female song) and a control stimulus. I chose a heterospecific control stimulus of the male-male duet song of Long-tailed Manakins (*Chiroxiphia linearis*) which are commonly found in the same habitat. Long-tailed Manakin duet stimuli ensure that birds are responding to conspecific duet playback and not duetting birds of any species. I created eight unique stimulus sets to minimize the effect of pseudoreplication (Kroodsma 1989, Kroodsma *et al.* 2001). I cycled through the eight stimulus sets, so that

each stimulus set was used either four or five times over the course of the 40 trials. All stimuli were normalized to a standard amplitude of -1dB in AUDITION. The duet stimuli were created by overlapping male and female solos and the degree of overlap was varied for each stimulus to simulate natural singing behaviour. The average delay from the first song to the second song for all duet stimuli was 1.88s. Each stimulus was a total of 2 minutes in length with the same solo or duet repeated once every 10 seconds. Stimuli were stored as 16-bit WAV files with a sampling rate of 44.1 kHz.

PLAYBACK TECHNIQUE

I conducted playback trials between 21 May and 9 July 2009, corresponding to the early part of the rainy season, a time period when Barred Antshrikes are engaging in their first nesting activity of the year. I recorded pairs during the dawn chorus prior to playback treatments to estimate their territory boundaries and to inform loudspeaker placement. Loudspeaker positions were chosen in areas where focal pairs were often observed during a dawn chorus observation session, and were selected to maximize distance from neighbours thereby minimizing the influence of the behaviour of adjacent birds. All playback trials were carried out between 0700h and 1100h.

I broadcasted 5 treatments varying the order of presentation according to a sequential block factorial design. A loudspeaker (Califone VoiceSaver, model PA285AV) was set up within each territory attached to a 15m cable and a portable digital audio player (Apple iPod). Previous field observations (Chapter 2) confirm that Barred Antshrikes duet in very close proximity to each other, and therefore I considered a single-speaker design appropriate for playback in this species (Douglas & Mennill 2010). Flagging tape was used to mark horizontal distances of 1m, 2m, and 5m and vertical distances of 1m and 2m from the loudspeaker. The loudspeaker was set to a volume that

corresponded to natural levels based on comparison to singing birds in the field, and held at a constant level across all trials. Although I did not measure the amplitude of the stimuli with a sound level meter, volumes were held constant for all trials; the amplitude of the stimuli would not explain the aggressive responses I observed during the trials. I sat 15m away and dictated all observed behaviours of each bird into a microphone (Audiotechnica AT815b) mounted to a tripod and attached to a recording unit (Marantz PMD-660). The microphone setup allowed me to record both the vocalizations of the territorial birds and my description of their behaviours simultaneously.

Treatments consisted of 5 minutes of observation, including 2 minutes when the playback stimuli were being broadcast, and another 3 minutes of observation after the playback was complete. Each pair was allowed 10 minutes to recover before each subsequent treatment; this period was consistently enough time for birds to stop singing and leave the playback area. All five treatments were broadcast to each pair consecutively so that each playback trial lasted 80 minutes in total. The observer noted the identity and sex of the singer, distance from the loudspeaker and flights made over the loudspeaker into the microphone. Up to two playback trials were conducted per day. When selecting a playback stimulus I ensured that (1) the source of the playback stimuli came from >700m from the playback site to avoid any effects of familiarity, (2) the playback trials were conducted >500m from each other to avoid pairs being subjected to additional playback, and (3) trials were not conducted on adjacent territories at periods less than 48 hours.

RESPONSE MEASURES

To assess levels of aggression of the birds towards the loudspeaker I measured both vocal and physical responses. I measured three vocal responses for each sex which included: (1) latency to first song (in seconds), (2) number of independent songs, and (3)

number of created duets. I calculated the number of independent songs as the sum of the number of solos for each sex and the number of duets they initiated (whereby an individual sang and their partner overlapped their solo to create a duet). Calculations of independent songs provided an estimate of how much an individual sang without the influence of their mate singing. I calculated the number of created duets as the number of times a bird overlapped their partner's song, resulting in a duet. Together, number of independent songs and number of created duets sum to all of the songs produced by any playback subject.

For each sex I also measured three physical responses which included: (1) closest approach (in metres), (2) number of passes over the loudspeaker, and (3) latency to reaching within 5m from the loudspeaker (in seconds). If a bird never came within 5m during the treatment I recorded a value of 300s (5 min) for the response.

I used Syrinx-PC (J. Burt, Seattle, WA) to visualize field recordings of the playback trials, and annotated all songs from the birds and comments from the field observations in order to extract the three measures of vocal response and the three measures of physical response.

STATISTICAL TECHNIQUES

I conducted statistical analyses in JMP 6.0 (SAS Institute, Cary, North Carolina). I summarized birds' responses to playback using principle components analysis, based on the correlation matrix and using Varimax rotation, to condense the vocal and physical response measures for each sex. I report the contributions of the original measurements to the principal component scores for all measurements with factor loadings greater than 0.6 (Kline 1994).

I evaluated variation in responses to playback using a linear mixed model where playback treatment type and order of playback were two independent variables, pair was included as a random effect to account for the fact that some pairs may be more vocal than others, and the principal component response scores were the dependent variables. For analyses that revealed a significant effect of treatment, I used post-hoc Tukey's tests of honestly significant differences to explore which treatments were significantly different.

Results

Males and females showed strong aggressive responses towards all treatments of conspecific playback. Barred Antshrikes produced many vocalizations in response to the playback and both sexes readily approached the loudspeaker in many experiments.

PRINCIPLE COMPONENTS ANALYSIS

For males, principal components analysis yielded two factors, with eigen values greater than 1, which cumulatively explained 77.1% of the variation in male responses (Table 1). Factor 1 was influenced heavily by number of independent songs, number of male-created duets, and latency to first song, as well as delay to approach within 5m; I refer to this factor as "singing intensity". Males with high singing intensity scores displayed a high frequency of independent songs and duets and a short latency to sing after the onset of playback.

Factor 2 was heavily influenced by closest approach to the loudspeaker, number of passes over the loudspeaker, and delay to approach within 5m of the loudspeaker (Table 1); I refer to this factor as "physical intensity". Males with high physical intensity scores approached the loudspeaker closely, had a short latency to flight within 5m and passed over the loudspeaker many times.

Principal components analysis of female responses to playback also yielded two factors, with eigen values greater than 1, with nearly identical loadings to male factors, which cumulatively explained 78.7% of the variation in female responses. I interpreted female factors in the same way as males (Table 1).

SINGING INTENSITY OF MALES AND FEMALES

Male Barred Antshrikes showed significant variation in singing intensity (whole model: $F_{47, 152}=2.3$, $p<0.0001$), with a significant effect of playback treatment (Fig. 1a; $F_4=3.9$, $p=0.005$), no effect of playback order ($F_4=0.5$, $p=0.71$), and significant variation between individuals ($F_{39}=2.3$, $p=0.0001$). Male singing responses were strongest towards the two duet treatments, although the responses were not significantly higher than the responses towards the two solo treatments; a post-hoc Tukey's test revealed significant differences between the heterospecific control and the two conspecific duet treatments, with intermediate levels for the two conspecific solo treatments (Fig. 1a).

Female Barred Antshrikes also showed significant variation in singing intensity (whole model: $F_{47, 152}=3.2$, $p<0.0001$), with a significant effect of playback treatment (Fig. 1b; $F_4=13.0$, $p<0.0001$), no effect of playback order ($F_4=1.0$, $p=0.44$), and significant variation between individuals ($F_{39}=2.4$, $p<0.0001$). Female singing responses were strongest towards the two duet treatments and the male solo treatment, although the differences were not statistically higher than response to the female solo treatment; a post-hoc Tukey's test revealed significant differences between the heterospecific control treatment and male solos, male-created duets, and female created duets, with intermediate levels for female solos (Fig. 1b).

PHYSICAL INTENSITY OF MALES AND FEMALES

Male Barred Antshrikes showed significant variation in physical intensity (whole model: $F_{47, 152}=9.0$, $p<0.0001$), with a significant effect of playback treatment (Fig. 2a; $F_4=62.1$, $p<0.0001$), no effect of playback order ($F_4=1.7$, $p=0.16$), and significant variation between individuals ($F_{39}=4.3$, $p<0.0001$). Male physical intensity responses were equally strong across the four conspecific treatments; a post-hoc Tukey's test revealed significant differences only between the heterospecific control and the four treatments (Fig. 2a).

Female Barred Antshrikes also showed significant variation in physical intensity (whole model: $F_{47, 152}=3.2$, $p<0.0001$), with a significant effect of playback treatment (Fig. 2b; $F_4=28.2$, $p<0.0001$), no effect of playback order ($F_4=1.1$, $p=0.37$), and no significant variation between individuals ($F_{39}=2.4$, $p=0.11$). Interestingly, female physical intensity responses were much higher in response to playback of female solos than all other treatments; a post-hoc Tukey's test revealed significant differences between female solos and all the other treatments (Fig. 2b).

Discussion

Barred Antshrikes display high levels of aggression towards conspecific intruders simulated through playback. Both males and females responded with elevated vocal activity as well as close physical approaches toward the loudspeaker. Male vocal and physical responses toward conspecific stimuli were greater than responses toward heterospecific stimuli; males responded with similar intensities towards playback of male and female solos and male- and female-created duets. Females responded similarly to males in terms of their vocal responses. Female physical responses were significantly

higher towards female solos than any other conspecific stimuli, suggesting females are more aggressive towards intruding females. The current study is one of the few experimental studies to have tested duet function in suboscine songbirds or antbirds.

If duets serve a cooperative function within a pair, I predicted that when broadcast, duet stimuli would evoke greater aggressive responses than solo stimuli, and that birds would not show sex-specificity in regards to the stimuli presented. Based on the vocal responses of Barred Antshrikes to the playback treatments, my results reveal mixed support for the predictions of the Joint Resource Defence Hypothesis. Males and females had a tendency to display greater singing responses towards duet stimuli than solo stimuli, although this was not statistically significant. Additionally, males responded similarly to male- versus female-created duet stimuli, and male versus female solo stimuli, and therefore responded with equal levels of singing intensity regardless of the order or sex of the stimuli presented. Female vocal responses, however, differed in aggressive responses toward male and female solos, with greater aggression toward male solos. This difference was not statistically significant.

The physical responses of Barred Antshrikes showed different responses for male versus female playback subjects. Males responded with equal levels of physical aggression towards all conspecific stimuli, regardless of the sex of the stimulus presented or whether the stimuli featured solos or duets. The aggressive male and female responses I observed indicate that all conspecific intruders are perceived as a threat and will elicit territorial behaviour. Similar to my results for male and female singing responses, playback studies conducted across diverse avian species (including oscines, suboscines and non-passerines) also provide evidence to support a joint resource defence function for

duetting behaviour (e.g. Australian Magpie-larks, *Grallina cyanoleuca*, Hall 2000; Kokako, *Callaeas cinereus wilsoni*, Molles and Waas 2006; Purple-crowned Fairy-Wrens, *Malurus coronatus*, Hall and Peters 2008), that demonstrate greater aggressive responses toward duet stimuli than solo stimuli. The widespread occurrence of cooperative territorial behaviour among diverse bird taxa suggests that joint resource defence may be an important function of duetting behaviour.

If duets represent a conflict between the members of a pair, I predicted that same-sex solo stimuli would evoke greater aggressive responses than duet stimuli. I found some support for the mate guarding predictions in the physical responses of females; females responded with significantly higher levels of physical aggression towards female solo stimuli compared to all other stimuli types presented. Although differences between remaining treatments were not significant, females tended to respond with similar levels of aggression to both male- and female-created duet stimuli, and lowest levels of aggression towards male solo stimuli and the heterospecific control. Observed differences in female vocal and physical responses towards female solo stimuli may be a result of a constraint of simultaneously singing while flying back and forth over the loudspeaker.

Increased aggressive behaviour towards same-sex solo stimuli may be indicative of an additional mate-guarding strategy employed by females (Douglas and Mennill 2010); however, sex-specificity in response to intruders may still be possible under the Joint Resource Defence Hypothesis if there is a skewed sex ratio, or sexual size dimorphism within the population (Hall 2009). In the population I studied, pair bonds remained stable throughout the field season, and on no occasion was a Barred Antshrike observed unpaired (Koloff pers. ob.). To my knowledge, sex ratios are equal in my study

population. With regards to size dimorphism, male and female Barred Antshrikes are morphometrically similar, and so I have no reason to believe the birds are more aggressive to same-sex individuals as a result of attempts to size match intruders (Koloff and Mennill unpublished data).

A stereo playback study on duet function in Rufous-and-white Wrens (*Thryothorus rufalbus*) by Mennill (2006) demonstrated evidence for joint resource defence as well as an additional mate guarding function for males. Birds displayed high levels of aggression towards both loudspeakers; however, males were more aggressive toward male stimuli, while females showed no preference (Mennill 2006). Similar results were demonstrated in a related wren. Plain Wren (*Thryothorus modestus zeledoni*) duets also function in joint resource defence and mate guarding. Duets were shown to pose a greater threat to territory holders, however, both males and females responded to same-sex stimuli with elevated levels of aggression (Marshall-Ball *et al.* 2006).

Lastly, experimental evidence for joint resource defence and mate guarding within a species was also demonstrated by Grafe and Bitz (2004) in a playback study on Tropical Boubous (*Laniarius aethiopicus*). They broadcast solo and duet stimuli and found that pairs approached all intruders together and sang in close proximity to each other, which suggests that duets are a cooperative act in this species. Their findings also revealed, however, that individuals overlapped their partner's songs and created more duets when same-sex solos were broadcast, suggesting that duets may also function as an acoustic mate guard (Grafe and Bitz 2004). Taken together, these and the present study suggest that duets may be context-dependent, and reiterate that cooperative and conflict-based hypotheses for duet function are not mutually exclusive.

To further explore why female Barred Antshrikes display elevated physical aggressive responses towards same-sex intruders, future studies should focus on identifying the different selection pressures that are acting on males and females. Like many tropical species, the genetic mating system of Barred Antshrikes is unknown; a closer look may reveal why female competition is so important in this species.

The current study lends some support for a joint resource defence function for duetting. Joint territorial defence and intrasexual aggression between females are two findings that have not been shown in previous playback studies in suboscines. The diversity and variation in duet function that has been observed in only a handful of playback studies emphasizes the need for a focus on suboscine research. Future research on suboscine vocal behaviour will improve our understanding of communication strategies and behaviour in an underrepresented group of songbirds that are widespread throughout Central and South America.

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Literature Cited

- Bradley, D.W., and D.J. Mennill. 2009. Strong ungraded responses to playback of solos, duets and choruses in a cooperatively breeding Neotropical songbird. *Animal Behaviour* 77: 1321–1327.
- Catchpole, C.K., and P.J.B. Slater. 2008. Bird song: biological themes and variations. Cambridge University Press, Cambridge, UK.
- Douglas, S.B., and D.J. Mennill. 2010. A review of acoustic playback techniques for studying avian vocal duets. *J. Field Ornithol.* 81(2):115–129.
- Farabaugh, S.M. 1982. The ecological and social significance of duetting. In: *Acoustic communication in birds*, vol. 2 (D. E. Kroodsma AND E. H. Miller, eds.), pp. 85–124. Academic Press, New York, NY.
- Fedy, B.C. and B.J.M. Stutchbury. 2005. Territory defence in tropical birds: are females as aggressive as males? *Behav. Ecol. and Sociobiology* 58:414–422.
- Grafe, T.U., and J.H. Bitz. 2004. Functions of duetting in the Tropical Boubou, *Laniarius aethiopicus*: territorial defence and mutual mate guarding. *Animal Behaviour* 68: 193–201.
- Hall, M. L. 2000. The function of duetting in Magpielarks: conflict, cooperation, or commitment? *Animal Behaviour* 60: 667–677.
- Hall, M.L. 2004. A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and Sociobiology* 55: 415–430.
- Hall, M.L. 2009. A review of vocal duetting in birds. In: *Advances in the study of behavior*, vol 40 (M.Naguib, and V.M. Janik, eds.), pp. 67–121. Academic Press, Burlington, MA.
- Hall, M.L., and A. Peters. 2008. Coordination between the sexes for territorial defence in a duetting fairy-wren. *Animal Behaviour* 76: 65–73.
- Illes, A. E., and L. Yunes-Jimenez. 2009. A female songbird out-sings male conspecifics during simulated territorial intrusions. *Proceedings of the Royal Society B* 276: 981–986.
- Kline, P. 1994. *An easy guide to factor analysis*. London, New York: Routledge.
- Kroodsma, D.E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. *Auk* 101:13–24.
- Kroodsma, D.E. 1989. Suggested experimental designs for song playbacks. *Animal Behaviour* 37: 600–609.
- Kroodsma, D.E., and M. Konishi. 1991. A suboscine bird (eastern phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Animal Behavior* 42: 477–487.
- Kroodsma, D.E., Byers, B.E., Goodale, E., Johnson, S., and W-C Lui. 2001. Pseudoreplication in playback experiments, revisited a decade later. *61:1029-1033*.
- Langmore, N. E. 1998. Functions of duet and solo songs of female birds. *Trends Ecol. Evol.* 13: 136–140.
- Logue, D.M., and D.E. Gammon. 2004. Duet song and sex roles during territory defence in a tropical bird, the Black-bellied Wren, *Thryothorus fasciatoventris*. *Animal Behaviour* 68: 721–731.

- Marshall-Ball, L., Mann, N., and P.J.B. Slater. 2006. Multiple functions to duet singing: hidden conflicts and apparent cooperation. *Animal Behaviour* 71:823–831.
- Mennill, D.J. 2006. Aggressive responses of male and female Rufous-and-white Wrens to stereo duet playback. *Animal Behaviour* 71:219–226.
- Molles, L.E., and J.R. Waas. 2006. Are two heads better than one? Responses of the duetting Kokako to one- and two-speaker playback. *Animal Behaviour* 72: 131–138.
- Morton, E. S. 1996. A comparison of vocal behavior among tropical and temperate passerine birds. In: Kroodsma, D. E. and Miller, E. H. (eds), *Ecology and evolution of acoustic communication in birds*. Cornell University Press, N.Y., pp. 258–268.
- Odom, K.J., and D.J. Mennill. 2010. Vocal duets in a nonpasserine: an examination of territory defense and neighbour-stranger discrimination in a neighbourhood of Barred Owls. *Behaviour* 147: 619-639.
- Rogers, A.C., Langmore, N.E and R.A. Mulder. 2007. Function of pair duets in the Eastern Whipbird: cooperative defense or sexual conflict? *Behavioral Ecology* 18: 182–188.
- Seddon, N. and J.A. Tobias. 2006. Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). *Behav. Ecol.* 17:73–83.

Table 1. Factor loadings from principal components analysis of Barred Antshrike responses to playback; separate principal components analyses were conducted for males and females.

Variable	Male Factor 1	Male Factor 2	Female Factor 1	Female Factor 2
Number of independent songs	0.90	-0.14	0.83	-0.16
Number of created duets	0.62	-0.22	0.76	-0.13
Latency to first song	-0.93	0.06	-0.89	0.28
Closest Approach	-0.36	0.86	-0.57	0.73
Number of passes over speaker	-0.09	-0.84	0.01	-0.91
Delay to approach to within 5m of loudspeaker	0.87	0.88	-0.58	0.72
Eigen value	3.18	1.44	3.72	1.00
Percent of variance explained	53.0	24.1	62.2	16.5

Figure 1: Variation in the singing intensity in the responses of Barred Antshrikes to five playback treatments for males (left) and females (right). Singing intensity is a principal component score that reflects high song output and short latencies to sing. Circles show least square means \pm standard error for singing intensity when controlling for order effects and variation between individuals. Letters indicate post-hoc tests of honestly significant differences, where levels not connected by the same letter are significantly different.

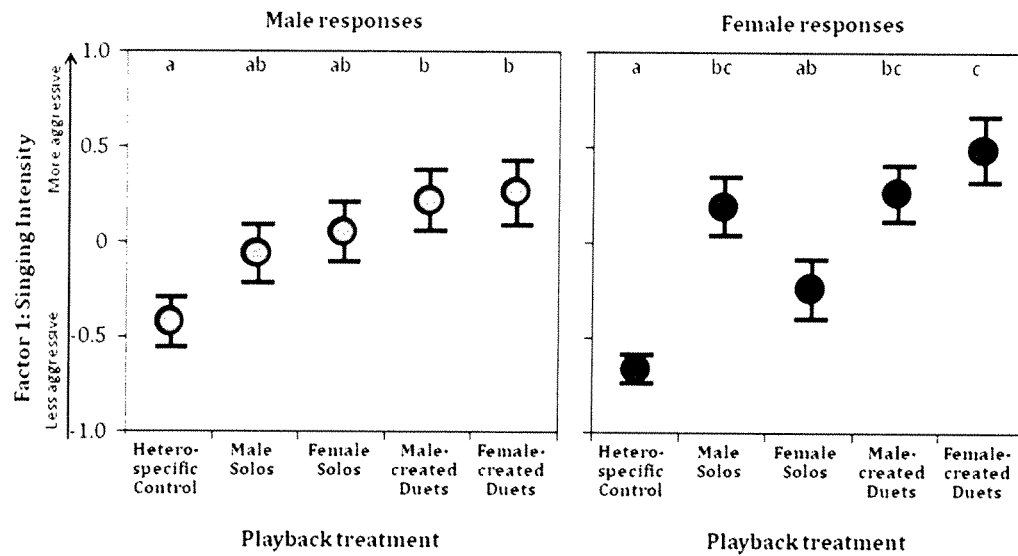
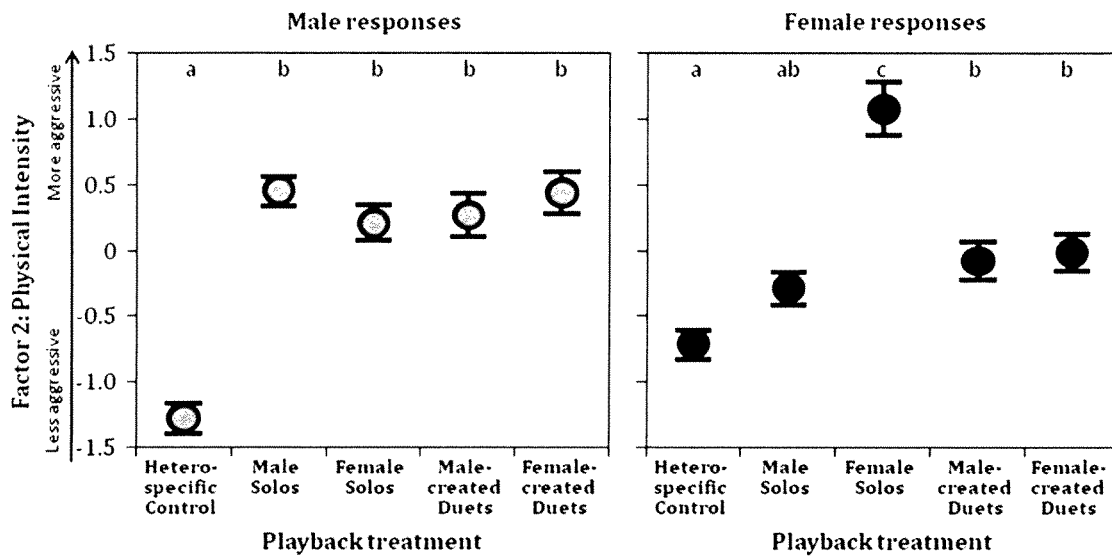


Figure 2: Variation in the physical intensity in the responses of Barred Antshrikes to five playback treatments for males (left) and females (right). Physical intensity is a principal component score that reflects rapid and close approaches to the loudspeaker with many passes over the loudspeaker. Circles show least square means \pm standard error for physical intensity when controlling for order effects and variation between individuals. Letters indicate post-hoc tests of honestly significant differences, where levels not connected by the same letter are significantly different.



THESIS SUMMARY

My thesis explores the communication behaviour and natural history of the Barred Antshrike (*Thamnophilus doliatus*). In the General Introduction Part 2, I provide a comprehensive species account of the natural history of this little-studied Neotropical bird by compiling observations documented by previous authors in addition to my own field research. The species account covers most aspects of Barred Antshrike life history including its habitat and distribution, appearance and vocal behaviour, reproductive behaviours, and feeding habits. I conclude the species account by discussing important avenues for future research, in light of the information that remains unknown for this species. In particular, I suggest combining vocal behaviour with genetic data to confirm the many subspecies, as well as a need for long-term monitoring of colour-banded populations to understand the social and genetic mating systems of Barred Antshrikes.

In chapter two, I present the first detailed and quantitative analysis of the vocalizations of Barred Antshrikes. I use fine structural analysis to describe the song structure for both males and females. I report significant structural differences between the sexes; male songs have lower frequency characteristics, contain more syllables, and are longer than female songs. I quantify variation in singing behaviour including song rates, diel variation, and seasonal variation in song output for both sexes. I show that male song output is higher than female song output, although song rate is similar between the sexes when silent pauses ≥ 60 s are removed from the analysis. I demonstrate significant diel variation in song output for males and females. Both sexes of Barred Antshrikes sing at high rates during the dawn chorus and song rate steadily decreases until it reaches very low levels after 1100h. I also show a pattern of variation in song

output on a seasonal scale, although this variation was not statistically significant. Song output was lowest in the season when Barred Antshrikes are not reproductive, and increase at the start of the rainy season when breeding begins, and remains at relatively constant levels until late June.

In chapter three, I use an experimental approach to test the Joint Resource Defence and Mate Guarding Hypotheses for duetting function. I broadcast five different playback treatments (male solos, female solos, male-created duets, female-created duets, and a heterospecific control treatment) to 40 territorial pairs of Barred Antshrikes. I assess both the vocal and physical responses of the male and female in each pair. For vocal responses, males and females show elevated vocal responses toward all conspecific treatments compared to the heterospecific control treatment. Birds show a non-significant tendency to respond more aggressively towards duets than solos. These results lend some support to the idea that duets have a joint resource defence function, whereby individuals defend their territories against intruders by performing duets and solos, without regard for the sex of the intruder. For physical responses, the sexes diverge in their responses towards conspecific playback; males respond similarly towards all conspecific treatments while females are significantly more aggressive towards playback of female solos. The high intrasexual aggression observed in this study suggests that female Barred Antshrikes perceive rival solo-singing females as a greater threat than all other types of territorial intruder.

VITA AUCTORIS

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Education

Master of Science

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Bachelor of Science (Honours)

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Teaching Experience

Biological Diversity Teaching Assistant

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Research Experience

Barred Antshrike field research, field project leader

University of Windsor, Santa Rosa National Park, Costa Rica, 2008-2010

Rufous-and-white Wren field research assistant

University of Windsor, Santa Rosa National Park, Costa Rica, 2008

Sound Analysis Technician on the Ivory-billed Woodpecker Project

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Research Technician, Department of Biological Sciences

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Research Assistant for Learning Outcomes Project

Faculty of Science Office, University of Windsor, 2006

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Conferences Presentations

Koloff, J., Mennill, D. J. July 2010. Playback reveals conflict and cooperation in the duets of tropical antbirds. 47th Annual Meeting of the Animal Behavior Society in Williamsburg, Virginia. International conference, oral presentation.

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Society Memberships

Two-year honorary student membership, Cooper Ornithological Society, 2010-2012

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Animal Behaviour Society, 2009-2010

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Frank M. Chapman Memorial Grant - American Museum of Natural History, 2009

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