View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by Scholarship at UWindsor

University of Windsor

Scholarship at UWindsor

Electronic Theses and Dissertations

Theses, Dissertations, and Major Papers

2008

The form and function of coordinated vocal signalling in a cooperatively breeding Neotropical songbird, the Rufous-naped Wren (Campylorhynchus rufinucha)

David William Bradley
University of Windsor

Follow this and additional works at: https://scholar.uwindsor.ca/etd

Recommended Citation

Bradley, David William, "The form and function of coordinated vocal signalling in a cooperatively breeding Neotropical songbird, the Rufous-naped Wren (Campylorhynchus rufinucha)" (2008). *Electronic Theses and Dissertations*. 8193.
https://scholar.uwindsor.ca/etd/8193

This online database contains the full-text of PhD dissertations and Masters' theses of University of Windsor students from 1954 forward. These documents are made available for personal study and research purposes only, in accordance with the Canadian Copyright Act and the Creative Commons license—CC BY-NC-ND (Attribution, Non-Commercial, No Derivative Works). Under this license, works must always be attributed to the copyright holder (original author), cannot be used for any commercial purposes, and may not be altered. Any other use would require the permission of the copyright holder. Students may inquire about withdrawing their dissertation and/or thesis from this database. For additional inquiries, please contact the repository administrator via email (scholarship@uwindsor.ca) or by telephone at 519-253-3000ext. 3208.

THE FORM AND FUNCTION OF COORDINATED VOCAL SIGNALLING IN A COOPERATIVELY BREEDING NEOTROPICAL SONGBIRD, THE RUFOUS-NAPED WREN (*CAMPYLORHYNCHUS RUFINUCHA*)

by

DAVID WILLIAM BRADLEY

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

2008

© David William Bradley

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 978-0-494-47008-4
Our file Notre référence
ISBN: 978-0-494-47008-4

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Declaration of Co-Authorship

I hereby declare that this thesis incorporates material that is result of joint research. Both data chapters are co-authored with my supervisor, Dr. Daniel Mennill, who supported my research, shared in the research design, provided feedback, and provided editorial input during the writing of both manuscripts. The first data chapter, Chapter 2, is written in the style of the journal The Auk, and was submitted for review on 10 May 2008. The second data chapter, Chapter 3, is written in the style of the journal Animal Behaviour, and will be submitted for review in the coming months.

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.

I declare that, to the best of my knowledge, my thesis does not infringe upon anyone's copyright nor violate any proprietary rights and that any ideas, techniques, quotations, or any other material from the work of other people included in my thesis, published or otherwise, are fully acknowledged in accordance with the standard referencing practices. Furthermore, to the extent that I have included copyrighted material that surpasses the bounds of fair dealing within the meaning of the Canada Copyright Act, I certify that I have obtained a written permission from the copyright owner(s) to include such material(s) in my thesis.

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.

Abstract

Coordinated vocal signals produced by birds, such as duets and choruses, present a compelling opportunity to investigate the adaptive significance of cooperation and conflict-based behaviours. I studied the form and function of coordinated vocal signals in cooperatively breeding Neotropical Rufous-naped Wrens (*Campylorhynchus rufinucha*). I examined variation in daily and seasonal vocal output and found that solo and duet songs peak at dawn and decrease thereafter, and that solo song rate, but not duet or chorus song rate, varied across breeding stages. Both sexes have song repertoires, and song sharing decreases with distance between territorial groups. To examine the function of coordinated vocalizations, I played back solos, duets, and choruses to territorial birds to represent varying degrees of threat. Groups responded strongly and similarly to all playback treatments. This study suggests that song may be an important indicator of group identity and that coordinated vocalizations function in cooperative territory defence.

Acknowledgements

Firstly, I would like to thank the birds that I came to know so well during my work on this thesis. You and your friends (and enemies) in Santa Rosa kept me wide-eyed and open-mouthed during field work, where every day I 'discovered' something new. For making field work in Costa Rica possible I would like to thank the staff at Santa Rosa, in particular Roger Blanco and Maria Marta Chavarria.

For academic guidance, mentorship, and infectious enthusiasm, I am sincerely indebted to my thesis advisor, Dan Mennill. Dan has been so helpful in teaching me how to turn what I know in the field into something scientifically meaningful, and in showing me how to best put pen to paper. Stéphanie Doucet and my fellow lab members, in particular Nicole Barker, were very helpful in their academic guidance. Nicole was also a great help in the field while I was banding nestlings.

For warmth, kindness, laughter, and love that continues to motivate and inspire me while keeping a smile on my face, I would like to thank Sandra Valderrama. The best part of my time in Windsor was meeting her. For friendship and support I am indebted to my fellow 'bird nerds' in Windsor: Nicole Barker, Celia Chui, Jessica Cuthbert, Daniel Hanley, Allison Mistakitis, and Karan Odom. For laughs and grimaces in the field; Celia, Jess, and Nicole were invaluable.

Lastly, I would like to express my deep affection and appreciation to my wonderful family, to whom I dedicate this thesis. The example they have set for me has been my guide throughout my life, and I would not be here if it wasn't for their love and adventurous spirit. In particular, I would like to thank my older brother James, with

whom I have experienced so many avian wonders. His passion for ornithology from a young age provided the light that I continue to follow to this day.

Table of Contents

List of Tables

List of Figures

Chapter 1

General introduction

Communication in birds

Communication plays a central role in the ecology and evolution of animal social behaviour. All animals must survive and reproduce, and communication facilitates these basic life processes by allowing individuals to locate conspecific individuals, attract breeding partners, and mediate social interactions. Communication is the intentional production and transmission of sensory information from a sender to a receiver, which is conveyed in the form of signal (Bradbury and Vehrencamp 1998). When we think of communication in birds, bright colours and melodious songs first come to mind. In fact, these two ways of transferring information are the most developed sensory modalities in birds; visual communication (Hill and McGraw 1996, 1997) and auditory communication (Catchpole and Slater 1995). Understanding the ways in which animals communicate and the specific functions of different animal signals is important for understanding an animal's ecology, and enhances our appreciation of both the ecological and evolutionary processes that govern behaviour.

In this thesis I focus on the form and function of acoustic communication in birds. Specifically, I investigate the form of auditory signals produced by birds and the ways in which birds use those signals to communicate, using a chorusing, cooperatively breeding, Neotropical songbird as a model system. The tremendous diversity of vocal signals produced by birds reflects the diversity of the approximately ten thousand avian species on earth (Clements 2007). Owing to this diversity, avian bioacoustics has received considerable attention from the scientific community (e.g. Catchpole and Slater 1995, Kroodsma and Miller 1996, Marler and Slabberkoorn 2004). Although some birds also produce non-vocal sounds to communicate (e.g. woodpecker drumming, Stark et al.

1998), vocal signals are a more common and better studied form of acoustic communication.

Avian vocal signals have been divided into two broad categories; songs and calls. This categorization is based on several characteristics, but one important feature of a song is that it is a learned behaviour while calls are innate. Songs are therefore influenced by the social environment that a young bird experiences while learning, whereas calls are genetically predetermined. Songs have been classically defined as a being "long, complex vocalizations produced by males in the breeding season", and calls have been defined as being "shorter, simpler, and produced by both sexes throughout the year" (Catchpole and Slater 1995). These definitions have been challenged in a number of commentaries that object to the omission of female song (e.g. Langmore 1998, Slater and Mann 2004) and birds that produce song outside the breeding season (e.g. Morton 1996, Terborgh 1996). As a result of these criticisms, much research has been recently conducted to examine avian vocal communication from the perspective of both sexes (e.g. Mennill and Rogers 2006, Topp and Mennill 2008). In this thesis I take a holistic approach to studying avian communication whereby I examine bird song as a multifunctional signal produced both by males and females.

In this introductory chapter, I briefly summarize several topics that will provide the reader of this thesis with the information necessary to appreciate the following data chapters. I begin by summarizing bird song in general, and then discuss female song and the differences between temperate and tropical birds. I then describe duets and choruses, two forms of coordinated vocal behaviour that are common in tropical animals, and I briefly describe cooperative breeding. I conclude with a brief description and a summary of what is known, to date, of my study species.

Bird song as a model system for investigating animal communication

Bird song varies in both form and function between taxa. Given that song is a learned behaviour, it follows that variation exists due to different social and physical environments that young birds experience in the formative song learning period (Hultsch and Todt 2004). The learning process can involve mistakes, innovations, and improvisations that can lead to changes in song structure between individuals. The function of song also varies. Research in temperate environments demonstrates that male birds use song in two main ways; in order to attract females, and to defend territories (Catchpole 1989). Experimental support for these two functions of bird song can be found in many published studies. In a groundbreaking study of Pied Flycatchers (*Ficedula hypoleuca*) and Collared Flycatchers (*Ficedula albicollis*) in Sweden, Eriksson and Wallin (1986) showed that female flycatchers choose nest boxes that contain a loudspeaker broadcasting male song over silent nest boxes. In a similar study on European Starlings (*Sturnus vulgaris*), Mountjoy and Lemon (1991) showed that females are more attracted to nest boxes broadcasting male song. These examples highlight the importance of song in mate attraction. The territory defence role of bird song was first explicitly tested by Goransson et al. (1974), who showed that Thrush Nightingales (*Luscinia luscinia*) frequently invaded neighbour's territories after the neighbour had been experimentally removed, but rarely invaded territories where the neighbour was replaced with speakers broadcasting male song. Krebs (1977) later used a more sophisticated approach to show the same effect of song on territory invasions in the Great Tit (*Parus major*). Taken together, these field studies clearly demonstrated the two major functions of bird song, eloquently illustrating the two components of sexual selection in birds; mate attraction and territory defence (reviewed in Andersson 1994). Given its importance in the fundamental life history processes of reproduction and resource acquisition, bird song is an excellent system to investigate the ecology and evolution of animal communication.

Differences between temperate and tropical birds

There are many differences in the life histories and behaviour of birds in temperate and tropical latitudes. For example, many of the birds that inhabit North America have distinct, synchronous, predictable, and short breeding seasons, and defend territories only during that period (Morton 1996). In contrast, many tropical species breed over extended periods – often throughout the entire year – and defend a territory continuously (Morton 1996). This variation can be attributed to differences in climate and seasonality, and consequently resource supply, influencing the length of territory tenure. Many temperate birds also migrate over very long distances to take advantage of seasonally abundant resources, whereas tropical birds are largely sedentary (Stutchbury and Morton 2001). Temperate birds also tend to live shorter lives and only form breeding partnerships for short periods while breeding, while tropical birds live for longer and tend to form long-term pair bonds (Morton 1996).

Unfortunately, the fundamental differences in the ecology of temperate and tropical birds have been underexplored for many years (Slater and Mann 2004), and have led to a bias in our understanding of bird biology. The reason for this research bias has been attributed to the fact that the majority of wealth, and therefore research potential, is concentrated in northern temperate latitudes (Morton 1996, Slater and Mann 2004). Bird song research is no exception to this pattern of a heavy focus on temperate ecosystems. Research into the form and function of tropical bird song therefore has the potential to greatly expand our understanding of the proximate and ultimate causes of vocal behaviour in birds.

Female song in birds

A longstanding oversight in bird song research is the study of female song. With few exceptions (e.g. Black-headed Grosbeaks, *Pheucticus melanocephalus*, Ritchison 1983; Northern Cardinals, *Cardinalis cardinalis*, Ritchison 1986; European Robins, *Erithacus rubecula*, Hoelzel 1986), female birds in the temperate zone rarely sing (Riebel 2003), whereas females of tropical bird species often do (Langmore 1998, Slater and Mann 2004). The prevalence of female song in the tropics is thought to be linked to a convergence of gender roles in tropical birds (Slater and Mann 2004), possibly resulting from extended breeding periods without a clearly defined external cue to stimulate reproduction (Dilger 1953). It has also been suggested that low annual fecundity, resulting from the high prevalence of nest predation (Ricklefs 1969) and lower clutch sizes in the tropics (Martin et al. 2000), requires high reproductive investment by both sexes (Slater and Mann 2004). Consequently, these factors may have contributed to the evolution of female song in the tropics. In this way, male and female birds in the tropics are more alike than they are in the temperate zone, with both sexes producing complex and learned songs.

One way in which female song provides a compelling avenue of research is in the occurrence of joint acoustic displays produced together by males and females. Duets are defined as temporally coordinated vocal signals produced by two birds, usually members of a mated pair (Farabaugh 1982). Duetting is known to occur in at least 222 species of largely tropical birds (Farabaugh 1982). Duetting has been the focus of much research in recent years (reviewed by Hall 2004), in part due to the interest in the motivation of both males and females in coordinating their songs, and the functional significance of duetting. This has led to the formulation of several hypotheses for duet function (reviewed in Hall 2004). The hypotheses that have found the most empirical support fall into two categories; those which argue that duets arise out of conflicting interests between the duetting partners, and conversely those which argue that duets arise out of cooperation between the duetting partners. As a behaviour representing conflict, duetting has been hypothesized to function in mate guarding (i.e. a bird sings a duet to advertise its partner's mated status to same-sex rivals; Stokes and Williams 1968), or paternity guarding (i.e. a bird sings a duet to advertise its mated status and prevent rivals from seeking extra-pair copulations; Sonnenschein and Reyer 1983). As a cooperative behaviour, duetting has been hypothesized to function in joint territory defence (i.e. a bird sings a duet to advertise to intruders a united and coordinated territorial defensive unit; Seibt and Wickler 1977), or as pair bond maintenance behaviour that either ensures reproductive synchrony (i.e. a bird sings a duet to convey its readiness to breed with its partner; Dilger 1953) or serves to maintain contact in dense vegetation (i.e. a bird sings a duet to convey its location to its partner; Cobb 1897). However, recent findings have established that duetting is rarely a mutually exclusive, single-function behaviour, and likely serves multiple functions simultaneously (Hall 2004, Topp and Mennill 2008).

Cooperative breeding

Cooperative breeding is a social reproductive system in which more than two individuals of the same species rear a single brood of young (Stacy and Koenig 1990, Cockburn 1998). Within this definition there is a broad range of breeding strategies that differ in the size, composition, and structure of cooperative groups. The number of breeding individuals in a group varies from exclusively the principal dominant pair (e.g. Laughing Kookaburras, *Dacelo novaeguineae*, Reyer and Schmidl 1988) to cases involving multiple breeding males and females (e.g. Groove-billed Anis, *Crotophaga sulcirostris*, Koford et al. 1990). In addition, the level of reproductive access allocated to the extra-pair individuals (also known as 'helpers'; Skutch 1935) and the level of investment made by those helpers is diverse (Koenig and Dickinson 2004). Cooperative breeding systems are relatively uncommon in the avian world, occurring in approximately 2.2 % of bird species (Stacy and Koenig 1990). In particular, it has been noted that cooperative breeding systems are more abundant in the ground-foraging insectivorous birds of Australasia, where cooperative breeding is 'very common' (Ford et al. 1988), in New World Jays (family Corvidae, Hardy 1969), and in Old World Babblers (family Timaliidae, Gaston 1978). Among and within different species of cooperatively breeding birds the composition of groups varies, with helpers being either breeding or non-breeding, and either related kin or unrelated birds that have dispersed from their natal site (Koenig and Dickinson 2004). Despite these differences, a common theme seen in cooperative breeding birds is the delayed dispersal of young and retention in the natal territory to assist in the rearing of subsequent siblings.

Cooperative breeding behaviour was long considered a paradox in nature (Cockburn 1998). What do non-breeding helpers have to gain from investing their energy in rearing offspring that are not their direct descendents? This paradox has been explained through extensive research by behavioural ecologists (reviewed in Kokko et al. 2002) which found that under certain biological conditions, individuals find increased genetic benefit by helping to rear kin rather than reproducing themselves. This idea is known as kin selection (Hamilton 1964). It is also likely that when territories are saturated, a juvenile bird is more likely to inherit its natal territory in future years than it is to find one by dispersing. Delayed dispersal is common in cooperatively breeding birds, and it appears that the benefits to remaining on a natal territory and assisting in the care of kin outweigh the fitness costs of delayed or sacrificed breeding opportunities.

Chorusing

Cooperatively breeding birds are the only avian taxa known to produce coordinated group vocalizations, known as a chorus. This form of song is defined as a coordinated vocal display produced by more than two individuals (Reyer and Schmidl 1988, Brown and Farabaugh 1991, Baker 2004, Hale 2006). Choruses are sung with varying levels of coordination between the vocalizations of the contributing animals, both between and within species. For example, individual Black-breasted Wood-quails (*Odontophorus leucolaemus*) sing alternating sets of paired elements to produce a distinctive and repetitive chorus (Hale 2006). In contrast, the Green Woodhoopoe (*Phoeniculus purpureus*) 'rally' chorus is produced by group members contributing entire songs simultaneously (Radford 2003). In other species, the level of coordination of the chorus varies, such as the Subdesert Mesite (*Monias benschi*) that sings some choruses with a very precise alternation of syllables and others in a more haphazard manner (Seddon et al. 2003). The most extreme form of coordinated chorus may be found in the Plain-tailed Wren (*Thryothorus euophrys*), where multiple males and females produce alternating vocal contributions to create a highly synchronized chorus (Mann et al. 2006). It has been argued that the chorus of this species is the most coordinated animal vocal behaviour ever recorded (Mann et al. 2006).

In all chorusing species studied in detail to date, choruses contain sex-specific vocal parts, thereby containing information about the presence or absence of each sex in a group. However, it may be possible that other species that sing choruses that do not contain sex-specific vocal parts have not yet been investigated. Sex-specificity in a chorus may be important in conveying information to dispersing juveniles about group vacancies or potential extra-group copulations (Seddon 2002). The diversity of chorus structure and the costs and benefits to helpers of cooperative breeding leads to the obvious scientific question of why groups chorus, and what role(s) the chorus plays in complex social systems.

Much like the seemingly paradoxical nature of cooperative breeding, chorusing represents a balance between conflict and cooperation within and between groups. Current hypotheses for the function of chorusing behaviour can be broadly categorised based on the intended signal receiver (Table 1.1). Within these categories, the function of the chorus can further by classified based on whether it represents conflict or cooperation between the sender and receiver. As a form of between-group communication, the chorus may represent conflict between groups as an advertisement of territory ownership (Brown and Farabaugh 1991). Alternatively, chorusing may represent cooperation between groups as an advertisement of group-size and composition and thus potential for dispersal and mating opportunities (Seddon and Tobias 2003). As a form of within-group communication, the chorus may play a role in conflict between individuals and maintain dominance hierarchies among group members (Reyer and Schmidl 1988), or the chorus may play a cooperative role allowing groups to coordinate activities and maintain contact in dense vegetation (Thorpe 1972). However, it should be noted that the hypotheses are not mutually exclusive and may occur concurrently (Brown and Farabaugh 1991, Seddon 2002).

Study species and study site

In order to investigate the form and function of coordinated avian acoustic displays, in this thesis I focus on the Rufous-naped Wren (*Campylorhynchus rufinucha*; Fig.1.1.), a highly vocal Neotropical songbird. Rufous-naped Wrens are abundant inhabitants of the tropical dry forest of western Central America from the Mexican states of Colima and Michoacan, to Guanacaste Province in Costa Rica (Stiles and Skutch 1989, Howell and Webb 1995; Fig.1.2.). I chose to study this species in sector Santa Rosa of the Area Conservación Guanacaste, due to its high abundance there and the presence of nearby research facilities. Santa Rosa is a predominantly regenerating tropical dry forest, with some remnant old growth stands of mature trees. Within this conservation area, Rufous-naped Wrens are commonly encountered throughout the year as they produce conspicuous vocalizations and defend year-round territories. They build bulky, fibrous nests (Fig.1.3.) to coincide with the marked onset of the wet season in early May and breed until the onset of the dry season in December (Skutch 1940).

Despite the fact that Rufous-naped Wrens are frequently observed in groups of more than two individuals (Skutch 1935, 1960), the extent to which this species breeds cooperatively is controversial. In his seminal work on Central American birds, Skutch (1960) described family groups of Rufous-naped Wrens together outside the breeding season and extra-pair individuals aiding in the provisioning of other birds' offspring. Nevertheless, Selander (1964) argued that cooperative breeding does not occur in Rufous-naped Wrens, based on several anecdotal observations. This is surprising in that observers witnessed groups of more than two birds and juveniles delayed dispersal for several months after fledging. Furthermore, there are well documented examples of cooperative breeding in some congeners. Wiley (1983) accepted Selander's conclusion, writing that fledged young remain in the family group for most of their first year, yet leave before the following breeding season. However, in a study of Rufous-naped Wren nest placement, Joyce (1993) documented examples of cooperative breeding, although this occurred in fewer than 10% of nests. Given Skutch's early observations (Skutch 1960) and Joyce's more recent and comprehensive study (Joyce 1993), it is evident that cooperative breeding does in fact occur in this species, though perhaps in low numbers. Despite this, the level of access to reproductive opportunities given to extra-pair birds, and the genetic mating system of this species is unknown. The prevalence of cooperative breeding and the degree to which helpers participate in reproduction have yet to be carefully quantified, and merit investigation. This is especially true in light of the presence of chorusing behaviour in this species.

The vocal behaviour of the Rufous-naped Wren has only been anecdotally described in the literature, and has never been given a thorough description. In one account, Skutch (1954) writes:

> "...the wrens all too often mix their harsh and liquid notes together in a manner which exasperates one who wishes to hear them at their best. For a bird capable of such glorious music to mar its performance with an admixture of harsh and trivial notes seems a perverse waste of natural talent."

Other authors have written similar descriptions (Skutch 1940, 1960, Selander 1964), yet little attempt has been made to quantify the characteristics of their vocal behaviour in any rigorous way. To date in particular, no studies have quantified the fine-scale structural features of Rufous-naped Wren vocalizations, no studies have applied sound spectrography to evaluate this species' songs, and no studies have attempted to quantify song output as a function of daily or seasonal rhythms. Additionally, no studies have so far assessed the diversity of vocalizations on an individual or population level, or used a playback approach to understand how territorial Rufous-naped Wrens respond to conspecific solos, duets, or choruses. The combination of an extended breeding season, year round territoriality, the possibility of cooperative breeding, and the fact that both sexes produce songs make the Rufous-naped Wren an ideal species in which to investigate the form and function of vocal behaviour.

Summary

Bird song is an ideal model system in which to study the evolution of complex signals and the functional significance of conspicuous behaviour. This is particularly true when both females and males produce complex, learned acoustic signals that they combine into coordinated displays such as duets and choruses. Convergence of gender roles and long-term territory tenure in the tropics promote these behaviours, and as such the examination of tropical birds is especially valuable in this field of research. Cooperative breeding systems add a further level of complexity to coordinated vocalizations by introducing additional contributors with potentially opposing motivations for cooperation or conflict. This thesis investigates the form and function of acoustic communication in the Rufous-naped Wren. In the first data chapter of this thesis, Chapter 2, I characterise the fine scale acoustic structure of vocal signals produced by this species and assess variation in this structure both between males and females, and across my study population. I also describe temporal variation in vocal production both at daily and seasonal scales. In the second data chapter, Chapter 3, I assess the function of vocal behaviour in this species by reporting the results of a playback experiment in which I evaluate the responses of territorial groups to broadcast of solos, duets, and choruses.

References

ANDERSSON, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

BAKER, M. C. 2004. The chorus song of cooperatively breeding laughing kookaburras (Coraciiformes, Halcyonidae: *Dacelo novaeguineae*): Characterization and comparison among groups. Ethology 110:21-34.

BRADBURY, J. W., AND S. L. VEHRENCAMP. 1998. Principles of Animal Communication. Sinauer Associates, Sunderland, Massachusetts.

BROWN, E. D., AND S. M. FARABAUGH. 1991. Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. Part III. Sex specificity and individual specificity of vocal parts in communal chorus and duet songs. Behaviour 118:244-274.

CATCHPOLE, C. K. 1989. Responses of male sedge warblers to playback of different repertoire sizes. Animal Behaviour 37:1046-1048.

CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. Bird Song - Biological Themes and Variations. Cambridge University Press, Cambridge, UK.

CLEMENTS, J. F. 2007. The Clements Checklist of Birds of the World. 6th edition. Cornell University Press, Ithaca, New York.

COBB, N. A. 1897. The sheep-fluke. Agricultural Gazette of NSW 8:470-480.

COCKBURN, A. 1998. Evolution of helping behavior in cooperatively breeding birds. Annual Review of Ecology and Systematics 29:141-171.

DILGER, W. C. 1953. Duetting in the crimson-breasted barbet. Condor 55:220-221.

ERIKSSON, D., AND L. WALLIN. 1986. Male bird song attracts females - a field experiment. Behavioral Ecology and Sociobiology 19:297-299.

FARABAUGH, S. M. 1982. The ecological and social significance of duetting. Pages 85-124 in Acoustic Communication in Birds (D. E. Kroodsma and E. H. Miller, Eds.) vol. 2. Academic Press, New York.

FORD, H. A.,H. BELL , R. NIAS, AND R. NOSKE. 1988. The relationship between ecology and the incidence of cooperative breeding in Australian birds. Behavioral Ecology and Sociobiology 22:239-249.

GASTON, A.J. 1978. Evolution of group territorial behavior and cooperative breeding. American Naturalist 112:1091-1100.

GORANSSON, G., G. HOGTEDT, J. KARLSSON, H. KALLANDER, AND F. ULFSTRAND. 1974. Sangenstroll fur revirhallandet hos naktergal *Luscinda luscinia* – nagra experiment med playback-teknik. Var Fagelvarld 33:201-209.

HALE, A. H. 2006. The structure, context and functions of group singing in black-breasted wood-quail (*Odontophorus leucolaemus*). Behaviour 143:511-533.

HALL, M. L. 2004. A review of hypotheses for the functions of avian duetting. Behavioral Ecology and Sociobiology 55:415-430.

HAMILTON, W. D. 1964. The genetical evolution of social behaviour, I, II. Journal of Theoretical Biology 7:1-51.

HARDY, J. W. 1969. A taxonomic revision of new world jays. Condor 71:360-375.

HILL, G. E., AND K. J. MCGRAW. 2006. Bird coloration. vol I. Mechanisms and Measurements. Harvard University Press, Cambridge, Massachusetts.

HILL, G. E., AND K. J. MCGRAW. 2007. Bird coloration. vol II. Function and Evolution. Harvard University Press, Cambridge, Massachusetts.

HOELZEL, A. R. 1986. Song characteristics and response to playback of male and female robins Erithacus rubecula. Ibis 128:115-127.

HOWELL, S. N. G., AND S. WEBB. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford University Press, Oxford.

HULTSCH, H., AND D. TODT. 2004. Learning to sing. Pages 80-106 in Nature's Music (P. Marler and H. Slabbekoorn, Eds.). Elsevier Academic, London.

JOYCE, F. J. 1993. Nesting success of Rufous-naped Wrens (*Campylorhynchus rufinucha*) is greater near wasp nests. Behavioral Ecology and Sociobiology 32:71-77.

KOENIG, D.K., AND J. L. DICKINSON. 2004. Ecology and Evolution of Cooperative Breeding in Birds. Cambridge University Press, Cambridge, UK

KOFORD, R. R., B. S. BOWEN, AND S. L. VEHRENCAMP . 1990. Groove-billed Anis: joint-nesting in a tropical cuckoo. Pages 335-355 in Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behaviour (P. B. Stacy and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, UK.

KOKKO, H., R. A. JOHNSTONE, AND J. WRITE. 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? Behavioral Ecology 13:291-300.

KREBS, J. R. 1977. Song and territory in the great tit *Parus major*. Pages 47-62 in Evolutionary Biology (B. Stonehouse and C. Perrins, Eds). Macmillan, London.

KROODSMA, D. 2004. The diversity and plasticity of birdsong. Page 108-130 in Nature's Music: The Science of Birdsong (P. Marler and H. Slabbekoorn, eds). Elsevier Academic Press, San Diego, CA.

KROODSMA, D., AND E. H. MILLER, EDS. 1996. Ecology and Evolution of Acoustic Communication in Birds. Cornell University Press, Ithaca, New York.

LANGMORE, N. E. 1998. Functions of duet and solo songs of female birds. Trends in Ecology and Evolution 13:136-140.

MANN, N. I. , K. A. DINGESS, AND P. J. B. SLATER. 2006. Antiphonal four-part synchronized chorusing in a Neotropical wren. Biology Letters 2:1-4.

MARLER, P., AND H. SLABBERKOORN, EDS. 2004. Nature's Music: The Science of Birdsong. Elsevier Academic Press, London.

MARTIN, T. E., P. R. MARTIN, C. R. OLSON, B. J. HEIDINGER, AND J. J. FONTAINE. 2000. Parental care and clutch sizes in north and south American birds. Science 287:1482-1485.

MENNILL, D. J. AND A. C. ROGERS. 2006. Whip it good! Geographic consistency in male songs and variability in female songs of the duetting Eastern Whipbird (*Psophodes olivaceus*). Journal of Avian Biology 37:93-100.

MORTON, E. S. 1996. A comparison of vocal behavior among tropical and temperate passerine birds. Pages 258-268 in Ecology and Evolution of Acoustic Communication in Birds (D. E. Kroodsma and E. H. Miller, Eds.). Comstock Publishing Associates, Ithaca and London.

MOUNTJOY, D. J., AND R. E. LEMON. 1991. Song as an attractant for male and female European starlings, and the influence of song complexity on their response. Behavioral Ecology and Sociobiology 28:97-100.

RADFORD, A. N. 2003. Territorial vocal rallying in the Green Woodhoopoe: influence of rival group size and composition. Animal Behaviour 66:1035-1044.

REYER, H.-U., AND D. SCHMIDL. 1988. Helpers have little to laugh about: group structure and vocalization in the Laughing Kookaburra *Dacelo novaeguineae*. Emu 88:150-160.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

RIEBEL, K. 2003. The 'mute' sex revisited: vocal production and perception learning in female songbirds. Advance in the Study of Behaviour 33: 49-86.

RITCHISON, G. 1983. The function of singing in female black-headed grosbeaks (*Pheucticus melanocephalus*): family-group maintenance. Auk 100:105-116.

RITCHISON, G. 1986. The singing behaviour of female northern cardinals. Condor 88:156-159.

SARANATHAN, V., D. HAMILTON, G. V. N. POWELL, D. E. KROODSMA, AND R. O. PRUM. 2007. Genetic evidence supports song learning in the three-wattled bellbird Procnias tricarunculata (Cotingidae). Molecular Ecology 16:3689-3702.

SEDDON, N. 2002. The structure, context and possible functions of solos, duets and choruses in the Subdesert Mesite (*Monias benschi*). Behaviour 139:645-676.

SEDDON, N., AND J. A. TOBIAS. 2003. Communal singing in the cooperatively breeding subdesert mesite *Monias benschi*: evidence of numerical assessment? Journal of Avian Biology 34: 72-80.

SEDDON, N., J. A. TOBIAS, AND S. H. M. BUTCHART. 2003. Group living, breeding behaviour and territoriality in the subdesert mesite *Monias benschi*. Ibis 145:277-294.

SEIBT, U., W. AND H.-U. WICKLER. 1977. Duettieren als Revier-Anzeige bei Vogeln. Zeitschrift für Tierpsycholgie, 43:180-187.

SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. University California Publications in Zoology 74:1-279.

SKUTCH, A. F. 1935. Helpers at the nest. Auk 52:257-273.

SKUTCH, A. F. 1940. Social and sleeping habits of central American wrens. Auk 57:293-312.

SKUTCH, A. F. 1960. Life histories of Central American birds. Pacific Coast Avifauna No.34:293-312.

SLATER, P. J. B., AND N. I. MANN. 2004. Why do females of many bird species sing in the tropics? Journal of Avian Biology 35:289-294.

SONNENSCHEIN, E., AND H.-U. REYER. 1983. Mate-guarding and other functions of antiphonal duets in the Slate-coloured Boubou (*Laniarius funebris*). Zeitschrift für Tierpsychologie 63:112-140.

STACY, P. B. AND W. D. KOENIG, EDS. 1990. Cooperative Breeding in Birds: Long-Term studies of Ecology and Behaviour. Cambridge University Press, Cambridge, UK

STARK, R. D., D. J. DODENHOFF, AND E. V. JOHNSON. 1998. A quantitative analysis of woodpecker drumming. Condor 100:350-356.

STILES, F. G., AND A. F. SKUTCH. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, New York.

STOKES, A. W., AND H. W. WILLIAMS. 1968. Antiphonal calling in quail. Auk 85:83-89

STUTCHBURY, B. J. M., AND E. S. MORTON. 2001. Behavioral ecology of tropical birds. Academic Press, London.

TERBORGH, J. 1996. Bird song. Biological themes and variations. In: Catchpole, C. K. and Slater, P. J. B. (book review) New York Rev. Books 43:40.

THORPE, W. H. 1958. The learning of song patterns by birds, with especial reference to the song of the chaffinch, *Fingilla coelebs*. Ibis 100:535–570.

THORPE, W. H. 1972. Duetting and antiphonal song in birds. Behaviour 18:1-193.

TOPP, S. M., AND D. J. MENNILL. 2008. Seasonal variation in the duetting behavior of rufous-and-white wrens (*Thryothorus rufalbus*). Behavioral Ecology and Sociobiology 62:1107-1117.

WILEY, R. H. 1983. Pages 558-560 *in* Costa Rican Natural History (D. H. Janzen, Ed.). University of Chicago Press, Chicago.

WINGFIELD, J. C., AND D. M. LEWIS. 1993. Hormonal and behavioural responses to simulated territorial intrusion in the cooperatively breeding white-browed sparrow-weaver, *Plocepasser mahali*. Animal Behaviour 45:1-11.

Table 1.1. Functions of avian chorusing, categorised by intended signal receiver, type of information conveyed, and whether it represents conflict between the sender and receiver.

Primary Function	Intended Signal Receiver	Information Conveyed	Within-group Conflict?	Between-group Conflict?
Territory defence[1]	Intruders	Territory ownership	No	Yes
Membership advertisement[2]	Intruders	Group size and composition	No	No
Group dynamics[3]	Within-group individuals	Social dominance	Yes	No
Coordination and contact[4]	Within-group individuals	Location/willingness to cooperate	No	No

[1] Brown and Farabaugh 1991, [2] Seddon and Tobias 2003, [3] Reyer and Schmidl 1988, [4] Thorpe 1972

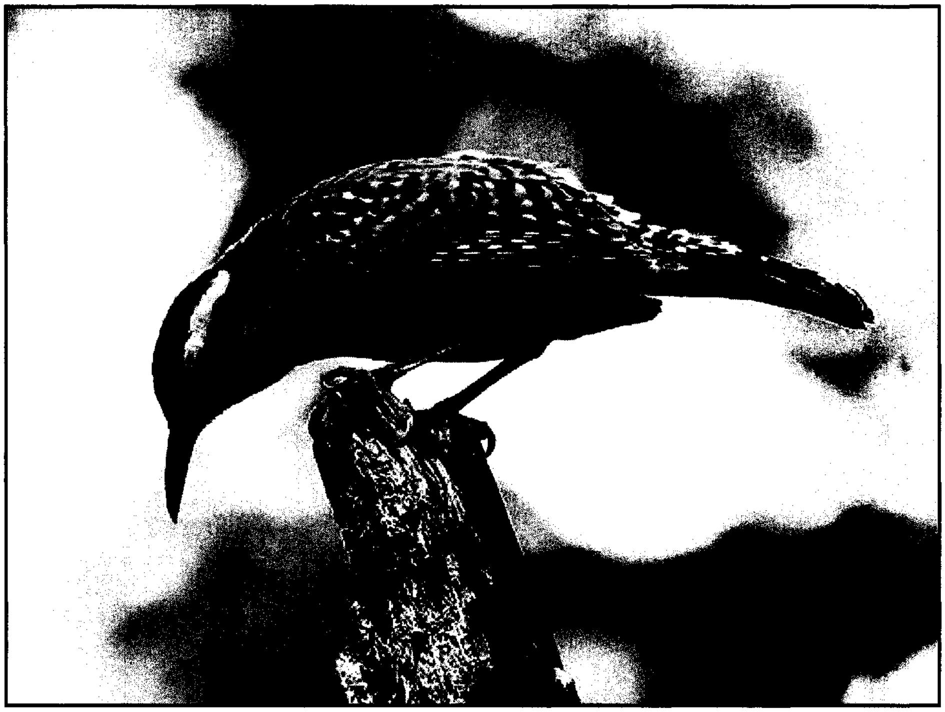

Figure 1.1. An adult Rufous-naped Wren (*Campylorhynchus rufinucha*; photo by B. Lyon, University of California, Santa Cruz).

Figure 1.2. Range map of the Rufous-naped Wren (*Campylorhynchus rufinucha*; map modified from Google Earth and InfoNatura: Animals and Ecosystems of Latin America [web application]. 2007. Version 5.0. Arlington, Virginia, USA).

Figure 1.3. An adult Rufous-naped Wren (*Campylorhynchus rufinucha*) at a nest in a Bullhorn Acacia (*Acacia collinsii*; photo by D. Bradley).

Chapter 2

Solos, duets, and choruses: Vocal behaviour of the Rufous-naped Wren, a cooperatively breeding Neotropical songbird

This chapter is co-authored with my supervisor, Dr. Daniel Mennill, who supported my research, shared in the research design, provided feedback, and provided editorial input.

Synopsis

Vocal communication in duetting and chorusing birds is a growing area of study in avian ecology, yet much remains unknown about temporal and population-level variation in these complex vocal signals. In this study we describe the acoustic structure and temporal variation in solos, duets, and choruses in the Rufous-naped Wren (*Campylorhynchus rufinucha*), a cooperatively breeding Neotropical passerine. We collected focal recordings of 20 groups to assess both diel and seasonal variation in vocal output, as well as population-wide sharing of vocal signals. We found that birds produce a complex array of vocalizations, including tonal, frequency-modulated syllables grouped into phrases, as well as stereotyped, atonal sounds. Songs are produced as solos, or combined into duets and choruses. Solo and duet songs show a dawn chorus effect. Solo song rate, but not duet or chorus rate, varied across breeding stages. The majority of phrases are shared among groups, significantly more so among groups in nearby territories. The findings of this study suggest that songs may be an important indicator of group identity and may play a role in group territorial defence. The degree of population-wide phrase-sharing suggests either short distance dispersal or delayed song learning. This paper is the first fine-scale description of vocal behaviour in this species and enhances our understanding of group-singing in a complex social environment.

Introduction

Avian vocal duets are coordinated acoustic signals produced by two individuals, usually a mated pair, in a long-term pair bond (Farabaugh 1982). Several non-mutually exclusive hypotheses have been proposed for the function of duetting, the most widely supported of which are joint resource defence, mate defence, paternity defence, and a signal of partner commitment (reviewed in Hall 2004). These hypothesized functions represent varying levels of cooperation and conflict between the sexes and help explain the adaptive value of coordinated singing from the perspective of both the male and the female. Although avian duetting has received modest attention, we have less understanding of the adaptive value of avian chorusing, which occurs when more than two birds combine their vocalizations into a coordinated acoustic display (e.g. Seddon 2002, Baker 2004, Hale 2006). Choruses are necessarily more complex than duets because more individuals are involved, each with a different degree of motivation for conflict or cooperation. It has been suggested that choruses may function similarly to duets, either cooperatively in joint resource defence (Reyer and Schmidl 1988, Brown and Farabaugh 1991, Wingfield and Lewis 1993, Seddon 2002, Baker 2004, Hale 2006) and in maintaining social bonds within the group (Brown et al. 1988), or in conflict between group members by mediating social hierarchies (Reyer and Schmidl 1988). Despite these findings, much remains unknown about avian choruses, in particular the influence of the type of social breeding system on the structure and function of both duetting and chorusing.

We studied solos, duets, and choruses in the Rufous-naped Wren (*Campylorhynchus rufinucha*), a Neotropical passerine that lives in groups of two or more (Skutch 1935, 1960). One of the more controversial aspects of this species' behaviour is the extent to which non-reproducing individuals assist in rearing other birds' offspring. In his seminal work on Central American birds, Skutch (1960) described family groups together outside the breeding season and extra-pair individuals aiding in the provisioning of other birds' offspring. However, in a later review of several anecdotal observations of the species, Selander (1964) concluded that cooperative breeding does not occur in this species. This is surprising in the light of several facts: observers witnessed groups of more than two birds, juveniles delayed dispersal for several months after fledging, and there are well documented examples of cooperative breeding in some congeners. Selander's conclusion is accepted by Wiley (1983), who also writes that fledged young remain in the family group for most of their first year, yet leave before the following breeding season. Joyce (1993) examined Rufous-naped Wren nesting success in relation to nest placement and found examples of cooperative breeding, although this occurred in fewer than 10% of nests. Given Joyce's more recent and exhaustive study, it is clear that cooperative breeding does occur in this species. However, its prevalence and the degree to which helpers participate have yet to be systematically quantified.

Long-term territory tenure and the convergence of gender roles are common characteristics of tropical birds (Stutchbury and Morton 2001). As a result, communication between tropical songbirds is necessarily different from those in temperate regions where, in general, males sing to defend territories and attract mates, while females do not sing (Langmore 1998). The genus *Campylorhynchus* is a particularly interesting taxon in this regard, because it is commonplace for both males and females to sing, for mated pairs to perform duets, and for groups to sing choruses while cooperating to rear a single brood of young (reviewed in Barker 1999). Despite this, little research has been conducted on the role of vocal communication in mediating territoriality and maintaining social bonds within groups in this genus, including Rufous-naped Wrens. Although their vocalizations have been anecdotally characterised in several onomatopoeic descriptions (Skutch 1935, 1940, 1960, Selander 1964), little attempt has been made to quantify their vocal behaviour in any rigorous way. In particular, no studies to date have quantified fine-scale structural features of Rufous-naped Wren vocalizations, or attempted to quantify song output as a function of daily or seasonal rhythms. Additionally, no studies have assessed the diversity of vocalizations at either an individual, or a population level. These behavioural features are likely to shed light on the functional significance and adaptive value of vocal communication on the ecology and evolution of this species and of tropical, group-living birds in general.

In this study we present the first formal fine-scale description of the complex vocal behaviour of Rufous-naped Wrens, based on recordings collected in the seasonal dry forests of Guanacaste, Costa Rica. We discuss the temporal structure of vocal behaviour in the context of daily and seasonal rhythms in this species. We also assess population-level variation in the acoustic structure of vocalizations, and the degree to which vocal characteristics are shared within the population. We discuss our findings in light of the functional significance of duetting and chorusing, and the process of song learning in this species.

Methods

Field techniques

Rufous-naped Wrens inhabit the tropical dry forest of western Central America from the Mexican states of Colima and Michoacan, to Guanacaste Province in Costa Rica (Howell and Webb 1995, Stiles and Skutch 1989). We conducted this study in the deciduous tropical dry forest of sector Santa Rosa of the Area de Conservación Guanacaste, Costa Rica (10°40′N, 85°30′W). In early May 2007, we located and mapped 20 contiguous Rufous-naped Wren territories by following birds within their territory (Fig. 2.1). When birds began to construct their bulky, domed nests in mid-May, nest sites were marked with a GPS and monitored every two to four days. Rufous-naped Wrens are sexually monomorphic in plumage yet dimorphic in body measurements. Although we did not collect adequate data to verify this, Selander (1964) measured multiple specimens of the Costa Rican *capistratus* subspecies of the Rufous-naped Wren and found that males were larger than females across all body regions measured. We attempted to capture and colour band birds, but they proved to be very difficult to capture in the mature dry forest of Santa Rosa where they remain in the canopy high above the forest floor. We were successful in capturing four birds from two different pairs and to those we applied unique combinations of three plastic colour bands and one numbered metal band. We distinguished males from females based on a combination of body size measurements and whether or not the bird was seen incubating eggs; females generally perform all incubation in duties this taxonomic family. Observations of these birds, as well as other colour-banded birds that were not part of the present study, confirmed that birds remained within the same space throughout the study period, and showed season-long territory tenure. Consequently, we are confident that we could reliably return to the same individuals in the same territories for the unbanded birds that constituted the rest of our study population.

We collected focal audio recordings of birds in 20 territories between 5 May 2007 and 20 July 2007. We used a directional microphone (Sennheiser ME66) and a solid state digital recorder (Marantz PMD 660) and saved digital recordings as uncompressed single-channel WAV files (16-bit, 44 kHz). Recording sessions lasted approximately two hours and took place in one of two time periods; between 0500 and 0700 hours CST (early morning) or between 0730 and 1030 hours (late morning). Whenever possible, we recorded each territorial group during two early morning sessions and two late morning sessions. During recordings we dictated the following details into the microphone: the number of birds contributing to each vocalization; the physical distance between the birds; any visual displays performed during vocalizing; and any nesting behaviour witnessed. When possible, we determined the breeding stage of the focal group into one of the following categories: pre-egg laying stage (before the female laid eggs and the pair were nest building); incubation stage (when the female was seen visiting and incubating eggs in the nest); nestling stage (after eggs had hatched and parents were either brooding or feeding chicks); or fledgling stage (when chicks had left the nest and were accompanying the pair around the territory). In total we collected 153 hours of recordings from 19 groups (one territory was abandoned part way through the study after being recorded only twice and was not included in analyses of vocal behaviour). On average, we recorded each group for a total of 8.06 ± 0.31 h.

Analysis of vocalizations

We analyzed audio recordings by visualizing sounds as spectrograms using SYRINX-PC (J. Burt, Seattle, Washington). We characterised all vocalizations based on the number of contributors, as either a solo (one bird vocalizing), a duet (two birds vocalizing), or a chorus (more than two birds vocalizing). Each vocalization was deemed distinct when separated from other vocalizations by at least 1 second. We subdivided vocalizations into two categories based on the type of sound being produced: 1) those consisting of lengthy, repeated phrases of tonal syllables which showed a high degree of variability and that most resemble song; and 2) several shorter, stereotyped, atonal vocalizations that most resemble calls (*sensu* Catchpole and Slater 1995). We characterised duets based on the combination of these vocalization categories (i.e. whether the two birds were producing tonal or atonal vocalizations). Choruses were considerably harder to separate into different vocal parts and so were termed choruses whenever three birds took part in the vocalization. We categorised and numbered each of the distinct vocalizations and stored them as separate sound files in a population-level phrase dictionary.

To describe the fine-scale structure of the songs, we performed detailed measurements of frequency and temporal characteristics of the component song phrases. We determined the 10 most commonly produced phrases in the population and isolated 10 examples of each from 10 different individuals, each in different territories. We ensured that we pooled examples from measurements of the same individuals by only using recordings from the same territory, whereby successive songs in a single recording were analysed. On each of the resulting 100 phrases we performed fine-scale measurements using the time and frequency cursors in SYRINX-PC. We measured the number of distinct syllables in each phrase (defined as continuous traces on a sound spectrogram; Catchpole and Slater 1995), the length of the entire phrase, and the maximum and minimum frequencies produced in each phrase. Spectrograms were generated with an FFT length of 1,024 points and viewed as a Blackman window, allowing a frequency resolution of 4.8 Hz and a temporal resolution of 1.6×10^{-3} s. When comparing male and female phrases, we measured the maximum and minimum frequencies, and the frequency of maximum amplitude (FMA) of each syllable in each phrase using AUDITION (Adobe Systems Inc., San Jose, California). We then calculated the average syllable FMA measurements within phrases to produce a value representing the overall phrase FMA.

We determined song output in relation to time of day by assessing the number of times each type of vocalization (solo, duet, and chorus) was produced by a group in each of the hourly periods after sunrise (sunrise occurred consistently at approximately 0500 hours). As we recorded each group several times, we calculated the average song rate for each group in each hourly time period, and then determined the average song rate for all pairs in those time periods. Solo song rates and duet song rates were calculated for all groups, and chorus song rates were only calculated for groups of more than two birds. We performed a similar analysis to determine song output across the four breeding stages outlined above.

We examined phrase sharing in the population by comparing phrase repertoires among groups. We categorised tonal phrases into different phrase types by visually comparing the sound spectrograms. We considered two phrases to be of the same phrase type when they shared at least half of the component syllables (following Hill et al. 1999 and Burt et al. 2001). For each territory, we calculated group repertoire size as the number of different phrase types produced by any bird in the group. When possible, we determined the individual phrase repertoires of both male and female birds in a mated pair ($n = 2$ pairs where one or both of the pair was colour-banded). To assess whether our sampling of phrase repertoires was complete, we plotted the cumulative number of novel phrase types detected against the cumulative number of phrases. We report phrase repertoires of Rufous-naped Wren groups where sampling was deemed complete based on whether this curve reached an asymptote. Consistent with other studies (e.g. Byers 1996, Hill et al. 1999, Molles and Vehrencamp 1999, Wilson et al. 2000, Molles et al. 2006, Nicholson et al. 2007), we determined the proportion of shared phrase types between groups in the population using the formula developed by McGregor and Krebs (1982) to account for comparisons between groups with different repertoire sizes: $2N_s / (R_1 + R_2)$, where N_s is the number of shared phrases, and R_1 and R_2 are the repertoire sizes of the two groups. We then related the proportion of shared repertoires between each of the groups to the physical separation of their territories, measured in terms of the number of intervening territories.

Statistical analysis

We analyzed song output in relation to breeding stage and time of day by performing mixed-model ANOVA. We used this analysis because including both random and fixed factors allowed us to account for non-independence of data collected from the same group (random factor) while assessing variation in the dependent variables (fixed factors). In these models, we estimated variance in the random factor using the residual maximum likelihood technique and in the fixed factors using standard least squares. We assessed phrase-sharing in the population using a Mantel test, creating two matrices; one of the number of shared phrases of all the groups in relation to each other; and another of the number of intervening territories between each territory as a proxy of physical separation. We used POPTOOLS 3.0 (G. Hood, Canberra, Australia), performing 999 iterations of random matrices per run to compare correlations with the observed matrices. Additionally, to assess how phrase-sharing between groups varied as a function of the distance between groups, we calculated the mean number of shared phrases for each of the territory separation categories, and ran a regression on these values in JMP 5.0 (SAS Institute, Cary, North Carolina). All tests are two-tailed and all values are reported as means ± SE.

Results

Among twenty Rufous-naped Wren territories in the Neotropical dry forest of Costa Rica, we found that 18 territories (90%) were occupied by a breeding pair, and two territories (10%) were occupied by a breeding pair plus an additional individual. Individuals of the three-bird groups regularly moved around their territories and foraged together, often counter-singing with neighbouring groups by performing three-part choruses. Observations of the three-bird groups around the nest suggested that all three birds were involved in bringing food to the nestlings, although as the birds were not banded this could not be definitively confirmed.

Solo vocalizations

Rufous-naped Wrens produce melodic, frequency-modulated syllables that they combine into tonal phrases (Fig. 2.2A). On average, phrases are 1.70 ± 0.07 s long, are composed of 4.7 ± 0.5 syllables, and range in frequency from a minimum of 861 ± 31 Hz to a maximum of 2,635 ± 85 Hz. Both sexes produce tonal phrases, with both members of a mated pair often capable of producing the same phrase type (Fig. 2.2A). Rufous-naped Wrens also produce a variety of stereotyped, atonal vocalizations in various contexts (Fig. 2.2B): *waahs* are comprised of loosely spaced harmonic stacks; *barks* are comprised of harsh bursts of broadband noise; nasal *snarls* consist of tightly spaced harmonic stacks; and *rattles* are longer vocalizations comprised of a series of chattering broadband notes.

In addition to isolated tonal phrases and atonal vocalizations, Rufous-naped Wrens often produce solo songs by repeating phrases several times in succession (Fig. 2.2C). Birds most often repeat the same phrase type in succession during these solo songs (92.7 ± 0.6% of recorded solos), although they occasionally switch phrase type partway through the song (7.3 ± 2.0% of recorded solos). Songs are also occasionally preceded or terminated by atonal vocalizations (6.9 ± 1.7% of recorded solos).

Duet and chorus vocalizations

Rufous-naped Wrens create duets when members of a pair simultaneously vocalize: either when both produce tonal phrases (“2-tonal duets”), when one bird produces tonal phrases and a second bird produces atonal vocalizations (“1-tonal duets”), or when both birds produce atonal vocalizations (“atonal duets”). When producing 2-

tonal duets, mated pairs often match their phrase types (Fig. 2.3A; 51.4 ± 1.7% of recorded 2-tonal duets), but sometimes do not match their phrase types (Fig. 2.3B; 48.6 ± 1.8% of recorded 2-tonal duets). Because we could assign phrase repertoires only to territories, and not to individuals, we cannot calculate a specific chance level of phrase-type matching in 2-tonal duets. However, since we know that individual birds possess moderately large phrase repertoires (see below), the observed level of phrase matching must be substantially higher than chance. In the groups of three birds, we found that tonal phrases and atonal vocalizations are combined in different ways to produce choruses, including all three birds singing tonal phrases (Fig. 2.3C), some birds singing tonal and others singing atonal phrases, or all three birds producing atonal phrases.

Male versus female vocalizations

Frequency components of Rufous-naped Wren songs varied with sex. Males sing phrases with significantly lower FMA (1380 ± 35 Hz) than females (1770 ± 35 KHz; ANOVA $F_{1,2} = 35.8$, $P = 0.03$), and with a significantly lower maximum frequency (2190 ± 55 KHz) than females (2900 ± 55 KHz; ANOVA $F_{1,2} = 82.6$, $P = 0.01$). Our repertoire sampling of four individuals of known sex was complete for one male and one female, and incomplete for another male and female (Fig. 2.4A), yet suggests that males and females possess similarly sized repertoires.

Song output

Solo song output varied with time of day for tonal phrases, but not for atonal phrases. Solo tonal vocalization rates varied significantly throughout the morning, with the highest levels in the first hour after dawn and declining thereafter (Fig. 2.5A; $F_{4,67}$ = 7.3, $P < 0.0001$). Atonal solo vocalization rates did not vary with time of day ($F_{4,67}$ = 0.4, P = 0.81). Duets where both birds sang tonal phrases (2-tonal duets) varied significantly with time of day, with the highest levels in the first hour after dawn (Fig. 2.5B; $F_{4,67}$ = 4.7, P = 0.002). Duets where one or both birds contributed atonal vocalizations did not vary significantly with time of day ($F_{4,67}$ = 1.4, P = 0.25). Chorus rate did not appear to vary with time of day (Fig. 2.5C; $F_{4,4}$ = 0.34, P = 0.84), although we had only two groups with more than two individuals.

Song output also varied significantly with breeding stage for solo tonal vocalizations (Fig. 2.6; $F_{3,32}$ = 3.6, P = 0.02); tonal solos were given more often during the nestling stage than during the nest building and incubation stages. There was no significant variation with breeding stage for 2-tonal duets ($F_{3,36}$ = 1.5, P = 0.22), duets where one or both birds contributed atonal vocalizations ($F_{3,28}$ = 0.6, P = 0.64), or choruses ($F_{3,1}$ = 0.5, P = 0.75), although we had only two groups with more than two individuals.

Repertoires and phrase-sharing

Territorial groups of Rufous-naped Wrens showed variable repertoire sizes (Fig. 2.4B), with an average repertoire size of 20.8 ± 1.1 songs per group (n = 16 groups where the repertoire curve reached a stable asymptote). Repertoire sizes were significantly smaller (20.1 ± 1.0) for pairs than for groups of three (27.0 ± 0.5; ANOVA $F_{1,17}$ = 4.4, P = 0.05). Groups on average shared 11.5 ± 0.28 phrases (58.0 ± 1.39% of their repertoire) with other groups in the study population. Birds were more likely to share phrase types with groups occupying territories closer than groups farther away (Mantel test: $R^2 = -0.26$, $P = 0.005$). A quadratic regression of phrase-sharing and distance of territory separation revealed a highly significant correlation ($R^2 = 0.79$, $P < 0.0001$).

Of the 88 phrase types identified in this study, most phrase types (42) were unique to a single group and not shared with any other. At the other extreme, six phrases were shared across all 19 groups. Different numbers of phrases were shared between fewer numbers of groups to a maximum of seven phrases shared between just two groups.

Discussion

Rufous-naped Wrens produce an extraordinary array of complex vocalizations including solos, duets, and choruses by combining repeated phrases of tonal syllables and/or atonal vocalizations. Males and females produce similar tonal phrases, although male songs have lower frequency components than female songs. Rufous-naped Wrens produce tonal vocalizations at different rates depending on time of day and breeding stage. In contrast, vocalization rates where one or both birds produce atonal sounds, either as solos or in a duet, did not vary with time of day. Chorus rates also did not vary with time of day or breeding stage, although the power of this analysis was low. Although groups shared most of their tonal phrases with at least one other group, and several phrases are shared throughout the whole population, the majority of phrases are unique to single groups. We also found that phrase-sharing is higher between groups occupying territories closer together than between more distant groups. These findings are the first formal description of the vocal behaviour of the Rufous-naped Wren.

Our quantitative descriptions of the vocalizations of Rufous-naped Wrens in this study agree with the early qualitative descriptions provided by Skutch (1940, 1960) and Selander (1964). Skutch (1960) notes that the birds produce a song that is "clear and liquid" and calls that are "loud and harsh", no doubt referring to the tonal and atonal vocalizations respectively, as described in the present study. Skutch also notes that both sexes are "equally gifted" (Skutch 1940) or "equally endowed" (Skutch 1960) with the ability to produce tonal phrases. These statements reflect our findings that both males and females produce tonal phrases and possibly have similarly sized repertoires. The variation we found in the acoustic structure of phases, represented by the large number of phrases in the study population, is echoed by Selander (1964), who found that "there is considerable variation in song pattern". The duets we describe in this study also agree with the qualitative descriptions by Skutch (1940, 1960) who writes that birds "sing in unison" and "raise their voices together". The difference we observed in frequency characteristics between male and female phrases has not been observed in previous studies of this species. This difference may relate to the greater body size of males, which results in the production of lower frequency songs (Podos and Nowicki 2004). For Rufous-naped Wrens, size dimorphism is so pronounced that we could visually detect subtle differences in body size between the sexes when a pair was perched close together.

Typical of most birds, diurnal variation in Rufous-naped Wren song output is consistent with the production of a dawn chorus, both in terms of tonal solos and 2-tonal duets. The dawn chorus in many bird species is thought to play several roles: in mate attraction (e.g. McNamara et al. 1987), in guarding paternity (e.g. Welling 1995), or in territorial defence (e.g. Kacelnik and Krebs 1983). These functions are thought to be best achieved at dawn due to a number of factors (reviewed in Staicer et al. 1996): environmental conditions for optimal sound transmission peak shortly after dawn when air temperatures are cooler, humidity is higher, and there is less wind compared to later in the day (Henwood and Fabrick 1979). Dawn singing is also thought to be favoured in territorial defence since mortality is most frequent during the night and territory invasions occur in the early morning (Amrhein et al. 2004), although daily patterns of variation in predation in tropical environments have not been studied in detail. Increased dawn singing in males has been hypothesized to occur as a paternity-guard (Staicer et al. 1996), since extra-pair copulations occur at a high rate during pre-dawn forays by females (e.g. Superb Fairy-wrens; Dalziell and Cockburn 2008), though the extent to which extra-pair fertilizations occurs in Rufous-naped Wrens is unknown. Because Rufous-naped Wrens are insectivorous and dependent on suitable light conditions for foraging, the semi-darkness of dawn is probably a suboptimal foraging time for wrens. It is therefore possible that dawn singing occurs as an alternative behaviour (Kacelnik and Krebs 1983). Our findings that Rufous-naped Wrens exhibit a dawn chorus are compelling in light of the fact that they are a duetting, cooperatively breeding tropical species. Staicer et al. (1996) note that diel variation in song production in tropical species has not been studied in detail. In this study both solo and duet song output peaked at dawn, demonstrating that females as well as males exhibit a dawn chorus effect. Interestingly, we found that chorus rates do not show a similar trend to those of solos and duets, and are produced at a similarly low rate throughout the morning. This suggests that choruses may serve distinct functions from solos and duets, although we make this interpretation with caution due to the low sample size of chorusing groups in the present study.

We also assessed variation in individual vocal production across different breeding stages. We found that solo vocalization rates were highest during the nestling stage when adults were bringing food to the nest. This is unlike many other species, which show a peak in male vocal activity during the female fertile period (e.g. Cuthill and MacDonald 1990, Pinxten and Eens 1998, Topp and Mennill 2008). In this study we included the female fertile period in the nest building stage, which exhibited the lowest solo vocalization rate of all breeding stages. Increased vocal production during the nestling stage may be important in allowing group members to maintain contact while foraging and as a way to assess the location of partners and the effort they are dedicating to the provision of young.

Duet rates did not vary significantly across breeding stages. If duets function as a signal of the pairs' mated status so as to deter potential rivals attracted to solo songs (Sonnenschein and Reyer 1983, Levin 1996), then we would predict that pairs produce more duets during the nest building stage when the female is fertile than at other times. Alternatively, males may duet with females as a way of preventing paternity loss (Komdeur et al. 1999, Topp and Mennill 2008). Again, under this hypothesis we would predict that duet rates peak in the nest building stage, when females are fertile. Neither of the above predictions were met in this study, suggesting that duets are not used as a mate-guard or paternity-guard for Rufous-naped Wrens. It is more likely that duets represent cooperation between males and females in maintaining contact (Thorpe 1963), or in joint territory defence (Hall 2004, Mennill 2006). Under both of these hypotheses we would predict duet rates to be relatively stable across breeding stages, and this prediction is not refuted by the data in this study. We also found that chorus rates did not differ across breeding stages. Hypotheses for the function of chorusing are similar to those of duetting (Hale 2006), one of the most compelling of which is an inter-group signal in the collaborative maintenance of territories (Reyer and Schmidl 1988, Brown and Farabaugh 1991, Wingfield and Lewis 1993, Seddon 2002, Baker 2004, Hale 2006). This hypothesis predicts that chorus rates will be higher during nesting and fledgling stages when resource demand is highest. This prediction is not met in this study, although this may be due to a low sample size. Additionally, chorusing may function as a cooperative intra-group signal in maintaining group cohesion (Brown et al. 1988), or serve a conflicting role in establishing and maintaining social hierarchies within the group (Reyer and Schmidl 1988). Predictions generated by these hypotheses are unclear based on song rates obtained from passive recordings, such as those made in this study. More intensive sampling of family groups in manipulated contexts may provide more evidence with which to assess these hypotheses. In addition, future studies could focus on investigating whether sex-specific patterns in song production across breeding stages exists, especially in light of the fact that this has been shown in other species (e.g. Rufous-and-white Wrens, Mennill & Topp 2008).

The majority of Rufous-naped Wren tonal phrases are shared between territorial groups, and especially between groups occupying nearby territories. Communication between neighbouring territorial groups has been shown in other studies to occur most effectively when song types are shared (Kroodsma 2004), as this gives birds the ability to produce graded responses to territorial threats (Krebs et al. 1981). For example, song matching has been shown to be an honest signal of aggression (Vehrencamp 2001), so sharing song types allows a bird to match a neighbour's song and escalate a conflict, or not to match it and thereby de-escalate a conflict (Krebs et al. 1981). The ability to reply to a neighbour's song in a variety of different ways reduces unnecessary and costly physical conflict, and confers advantages either through mate attraction or territorial defence (Beecher et al. 2000). Increased phrase-sharing between neighbouring groups in the present study population is expected under this model. Interestingly, we often heard groups matching phrase types when counter-singing occurred between neighbouring groups. That nearby groups share more phrase types than distant groups raises questions concerning the mechanism of song learning in this species. Does the pattern of increased sharing between nearby birds arise because Rufous-naped Wrens learn songs from their parents and then disperse over short distances, by dispersing birds acquiring songs over an extended period that encompasses the duration of dispersal, or by birds learning many phrase types and undergoing selective attrition after dispersal (Marler and Peters 1982)? We witnessed fledglings producing subsong within weeks of leaving the nest, which we could often identify as phrase types possessed by their parents, and fledglings regularly attempted to match phrase types and duet with other adults in the group (D. Bradley, pers. obs.). The fact that we found a highly significant quadratic relationship between phrase-sharing and territory separation distance raises the possibility of a dual dispersal strategy. We suggest the possibility that Rufous-naped Wrens exhibit sex-biased dispersal, whereby one sex remains on the natal territory to queue for breeding opportunities while the other sex disperses to fill vacant breeding opportunities in nearby groups. This pattern of dispersal has been shown in the congeneric Stripe-backed Wren (Zack and Rabenold 1989), where males remain on the natal territory and females disperse. We also found that although most phrases in any group's repertoire were shared with other groups, the majority of phrases in the population were unique to specific groups. This result is highly suggestive of the existence of group-specific vocal signatures, which has been shown to be important in recognition of group membership in other species (Brown et al. 1988, Price 1999, Hopp et al. 2001, Radford 2005). We suggest that large phrase repertoires in Rufous-naped Wrens permits groups to communicate effectively with neighbours and mediate territoriality, and to maintain social bonds with the existence of group specific vocal signatures.

The general observations of group social behaviour of Rufous-naped Wrens in this study support the observations of Joyce (1993), who reports cooperative breeding in approximately 10% of nests. Although we did not definitively document extra-pair birds assisting in incubation or nestling provisioning, we did find groups of three birds that regularly took part in joint territorial defence in 10% of territories, and our observations suggested extra-pair birds provisioned nestlings in those territories. This type of cooperative breeding, characterised by group territoriality and singular breeding, is similar to other congeners (reviewed in Brown 1987, Barker 1999).

The Neotropical genus *Campylorhynchus* ranges widely from the southern U.S.A. to southern Amazonia (Brewer 1999). The singing styles of the majority of species in this genus have been described only anecdotally, with the exception of the Stripe-backed Wren (*C. nuchalis*; Wiley and Wiley 1977; Price 1998, 1999, 2003; Zack and Rabenold 1989) and the Cactus Wren (*C. brunneicapillus*; Anderson and Anderson 1977), which have received more thorough treatment. Within this genus there are 13 currently recognised species: 12 species are known to produce female song, 12 species produce duets, and 12 species are thought to breed cooperatively. We found that female

Rufous-naped Wrens sing, pairs produce duets, and groups produce choruses. A comparative assessment of vocal behaviour in this genus by Barker (1999), showed that all duetting species produce simultaneous (overlapping) duet contributions. We also found that pair repertoire size was high when compared to other *Campylorhynchus*. It has been suggested that social and environmental circumstances leading to intense competition for resources favours the evolution of large repertoires (Kroodsma 2004). This study therefore suggests that competition for both mates and territories is potentially higher in this species than in its congeners. Skutch (1940) makes a broad comparison of duet structure to heterogeneric, confamilial species. He states that vocal parts of Rufous-naped Wren duets are "delivered simultaneously", and yet the duets of the Rufous-breasted Wren (*Pheugopedius rutilus*) and the Plain Wren (*Cantorchilus modestus*) are produced antiphonally.

We found that Rufous-naped Wrens sing choruses consisting of simultaneously produced vocal parts. Although Skutch (1935, 1940, 1960), does not mention chorusing in this species, Selander (1964) briefly states that "groups of three or more birds sing choruses in unison". This style of chorusing is similar to that of some other cooperatively breeding birds. Laughing Kookaburras (*Dacelo novaeguineae*; Reyer and Schmidl 1988, Baker 2004) produce a 'laugh' chorus and Green Woodhoopoes (*Phoeniculus purpureus*; Radford 2003, 2005; Radford and Du Plessis 2004) produce a 'rally' chorus consisting of structurally similar vocal parts produced by multiple group members simultaneously. In contrast, the Plain-tailed Wren (*Pheugopedius euophrys*; Mann et al. 2006), the Black-breasted Wood-Quail (*Odontophorus leucolaemus*; Hale 2006), and possibly the White-browed Sparrow Weaver (*Plocepasser mahali*; Wingfield and Lewis 1993) produce precise, highly synchronized antiphonal choruses. Intermediate to the above two chorus styles are those produced by the Subdesert Mesite (*Monias benschi*), which vary in the amount of overlap between component vocal parts, from precise alternation to complete overlap (Seddon 2002). Varying degrees of synchronization and complexity of vocal choruses may reflect the stability and tenure of social units, as the investment required to learn complex vocal performances must be offset by the benefits to cooperative breeding. A more detailed comparative study of the type of cooperative breeding system, including the level of effort of non-reproducing individuals, and the complexity of chorusing behaviour may elucidate the relationship between vocal investment and fitness benefits in cooperatively breeding birds.

Acknowledgements

We thank the staff of sector Santa Rosa of the Area de Conservación Guanacaste, Costa Rica for logistical support, particularly R. Blanco and M. M. Chavarria. This work was funded by the Natural Science and Engineering Research Council (NSERC), the Canadian Foundation for Innovation (CFI), the Government of Ontario, and the University of Windsor.

References

AMRHEIN, V., H. P. KUNC, AND M. NAGUIB. 2004. Non-territorial nightingales prospect territories during the dawn chorus. Proceedings of the Royal Society of London, Series B (Suppl.), 271:S167-S169.

ANDERSON, A. H., AND A. ANDERSON. 1973. The Cactus Wren. The University of Arizona Press, Tuscon.

BAKER, M. C. 2004. The chorus song of cooperatively breeding Laughing Kookaburras (Coraciiformes, Halcyonidae: *Dacelo novaeguineae*): characterization and comparison among groups. Ethology 110:21-35.

BARKER, F. K. 1999. The evolution of cooperative breeding in *Campylorhynchus* wrens: a comparative approach. Ph.D. Dissertation, University of Chicago.

BEECHER, M. D., S. E. CAMPBELL, J. M. BURT, C. E. HILL, AND J. C. NORDBY. 2000. Song-type matching between neighboring Song Sparrows. Animal Behaviour 59:21-27.

BREWER, D. 2001. Wrens, Dippers and Thrashers. Yale University Press, New Haven, Connecticut.

BROWN, E. D., S. M. FARABAUGH, AND C. J. VELTMAN. 1988. Song sharing in a group-living songbird, the Australian Magpie, *Gymnorhina tibicen.* Part I. Vocal sharing within and among social groups. Behaviour 104:1-28.

BROWN, E. D., S. M. FARABAUGH. 1991. Song sharing in a group-living songbird, the Australian Magpie, *Gymnorhina tibicen.* Part III. Sex specificity and individual specificity of vocal parts in communal chorus and duet songs. Behaviour 118:244-274.

BROWN, J. L. 1987. Helping and Communal Breeding in Birds. Princeton University Press, Princeton, New Jersey.

BURT, J. M., M. D. BEECHER, AND S. E. CAMPBELL. 2001. Song type matching as threat: a test using interactive playback. Animal Behaviour 62:1163-1170.

BYERS, B. E. 1996. Geographic variation of song form within and among Chestnut-sided Warbler populations. Auk 113:288-299.

CUTHILL, I. C., AND W. A. MACDONALD. 1990. Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. Behavioral Ecology and Sociobiology 26:209-216.

DALZIELL, A .H., AND A. COCKBURN. 2008. Dawn song in superb fairy-wrens: a bird that seeks extrapair copulations during the dawn chorus. Animal Behaviour 75:489-500.

FARABAUGH, S. M. 1982. The ecological and social significance of duetting. Pages 85-125 in Acoustic Communication in Birds, vol. 2 (D.E.Kroodsma and E.H.Miller, Eds.). Academic Press, New York.

HALE, A. H. 2006. The structure, context and functions of group singing in Black-breasted Wood-Quail (*Odontophorus leucolaemus*). Behaviour 143:511-533.

HALL, M. L. 2004. A review of hypotheses for the functions of avian duetting. Behavioral Ecology and Sociobiology 55:415-430.

HENWOOD, K., AND A. FABRICK. 1979. A quantitative analysis of the dawn chorus: Temporal selection for communicatory optimization. American Naturalist 114:260-274.

HILL, C. E., S. E. CAMPBELL, J. C. NORDBY, J. M. BURT, AND M. D. BEECHER. 1999. Song sharing in two populations of Song Sparrows. Behavioral Ecology and Sociobiology 46:341-349.

HOPP, S. L., P. G. JABLONSKI AND J. R. BROWN. 2001. Recognition of group membership by voice in Mexican Jays, *Aphelocoma ultramarina*. Animal Behaviour 62:297-303.

HOWELL, S. N. G., AND S. WEBB. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford University Press, Oxford.

JOYCE, F. J. 1993. Nesting success of Rufous-naped Wrens (*Campylorhynchus rufinucha*) is greater near wasp nests. Behavioral Ecology and Sociobiology 32:71-77.

KACELNIK, A., AND J. R. KREBS. 1983. The dawn chorus in the Great Tit (*Parus major*): proximate and ultimate causes. Behaviour 83:287-309.

KOMDEUR, J., F. KRAAIJEVELD-SMIT, K. KRAAIJEVELD, AND P. EDELAAR. 1999. Explicit experimental evidence for the role of mate guarding in minimizing loss of paternity in the Seychelles warbler. Proceedings of the Royal Society B Biological Sciences 266:2075-2081.

KREBS, J. R., R. ASHCROFT, AND K. VAN ORSDOL. 1981. Song matching in the Great Tit *Parus major*. Animal Behaviour 29: 918-923.

KROODSMA, D. E. 2004. The diversity and plasticity of bird song. Pages 108-130 in Nature's Music (P. Marler and H. Slabbekoorn, Eds.). Elsevier Academic, London.

LANGMORE, N. E. 1998. Functions of duet and solo songs of female birds. Trends in Ecology and Evolution 13:136-140.

LEVIN, R. N. 1996. Song behavior and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. II. Playback experiments. Animal Behaviour 52:1107-1117.

MANN, N. I., K. A. DINGESS, AND P. J. B. SLATER. 2006. Antiphonal four-part synchronized chorusing in a Neotropical wren. Biology Letters 2:1-4.

MARLER, P., AND S. PETERS. 1982. Development overproduction and selective attrition: new processes in the epigenesis of birdsong. Developmental Psychobiology 15:369-378.

MCGREGOR, P. K., AND J. R. KREBS. 1982. Song types in a population of Great Tits (*Parus major*): their distribution, abundance and acquisition by individuals. Behaviour 79:126-152.

MCNAMARA, J. M., R. H. MACE, AND A. I. HOUSTON. 1987. Optimal routines of singing and foraging in a bird singing to attract a mate. Behavioral Ecology and Sociobiology 20:399-405.

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., J. D. HUDSON, AND J. R. WAAS. 2006. The mechanics of duetting in a New Zealand endemic, the Kokako (*Callaeas cinerea wilsoni*): song at a snail's pace. Ethology 112:424-436.

MOLLES, L. E., AND S. L. VEHRENCAMP. 1999. Repertoire size, repertoire overlap, and singing modes in the Banded Wren (*Thryothorus pleurostictus*). Auk 116:677-689.

NICHOLSON, J. S., K. L. BUCHANAN, R. C. MARSHALL, AND S. K. CATCHPOLE. 2007. Song sharing and repertoire size in the Sedge Warbler, *Acrocephalus schoenobaenus*: changes within and between years. Animal Behaviour 74:1585-1592.

PODOS, J., AND S. NOWICKI. 2004. Performance limits on birdsong. Pages 316-342 in Nature's Music (P. Marler and H. Slabberkoorn, Eds.). Elsevier Academic Press, London.

PINXTEN, R., AND M. ENS. 1998. Male starlings sing most in the late morning, following egg-laying: a strategy to protect their paternity? Behaviour 135:1197-1211.

PRICE, J. J. 1998. Family- and sex-specific vocal traditions in a cooperatively breeding songbird. Proceedings of the Royal Society of London, Series B, 265:497-502.

PRICE, J. J. 1999. Recognition of family-specific calls in Stripe-backed Wrens. Animal Behaviour 57:483-492.

PRICE, J. J. 2003. Communication with shared call repertoires in the cooperatively breeding Stripe-backed Wren. Journal of Field Ornithology 74(2):166-171.

RADFORD, A. N. 2003. Territorial vocal rallying in the Green Woodhoopoe: influence of rival group size and composition. Animal Behaviour 66:1035-1044.

RADFORD, A. N. 2005. Group-specific vocal signatures and neighbor-stranger discrimination in the cooperatively breeding Green Woodhoopoe. Animal Behaviour 70:1227-1234.

RADFORD, A. N., AND M. A. DU PLESSIS. 2004. Territorial vocal rallying in the Green Woodhoopoe: factors affecting contest length and outcome. Animal Behaviour 68:803-810.

REYER, H.-U., AND D. SCHMIDL. 1988. Helpers have little to laugh about: group structure and vocalisation in the Laughing Kookaburra *Dacelo novaeguineae*. Emu 88:150-160.

SEDDON, N. 2002. The structure, context and possible functions of solos, duets and choruses in the Subdesert Mesite (*Monias benschi*). Behaviour 139:645-676.

SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. University California Publications in Zoology 74:1-279.

SONNENSCHEIN, E., AND H.-U. REYER. 1983. Mate-guarding and other functions of antiphonal duets in the Slate-coloured Boubou (*Laniarius funebris*). Zeitschrift für Tierpsychologie 63:112-140.

STILES, F. G., AND A. F. SKUTCH. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, New York.

SKUTCH, A. F. 1935. Helpers at the nest. Auk 52:257-273.

SKUTCH, A. F. 1940. Social and sleeping habits of central American wrens. Auk 57:293-312.

SKUTCH, A. F. 1960. Life histories of Central American birds. Pacific Coast Avifauna No.34:293-312.

STAICER, C. A., D. A. SPECTOR, AND A. G. HORN. 1996. The dawn chorus and other diel patterns in acoustics signaling. Pages 426-453 in Ecology and Evolution of Acoustic Communication in Birds (D. E. Kroodsma and E. H. Miller. Eds.). Cornell University Press, Ithaca, New York.

STUTCHBURY, B. J. M., AND E. S. MORTON. 2001. Behavioral ecology of tropical birds. Academic Press, London.

THORPE, W. H. 1963. Antiphonal singing in birds as evidence for avian auditory reaction time. Nature 197:774-776.

TOPP, S. M., AND D. J. MENNILL. 2008. Seasonal variation in the duetting behavior of rufous-and-white wrens (*Thryothorus rufalbus*). Behavioral Ecology and Sociobiology 62:1107-1117.

VEHRENCAMP, S. L. 2001. Is song-type matching a conventional signal of aggressive intentions? Proceedings of the Royal Society of London B 268:1637-1642.

WELLING, P., K. KOIVULA, AND K. LAHTI.1995 The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. Journal of Avian Biology 26:241-246.

WILEY, R. H. 1983. Pages 558-560 *in* Costa Rican Natural History (D. H. Janzen, Ed.). University of Chicago Press, Chicago.

WILEY, R. H., AND M. S. WILEY. 1977. Recognition of neighbors' duets by Stripe-backed Wrens *Campylorhynchus nuchalis*. Behaviour 62:10-34.

WILSON, P. A., M. C. TOWNER, AND S. L. VEHRENCAMP. 2000. Survival and song-type sharing in a sedentary subspecies of the Song Sparrow. Condor 102:355-363.

WINGFIELD, J. C., AND D. M. LEWIS. 1993. Hormonal and behavioural responses to simulated territorial intrusion in the cooperatively breeding White-browed Sparrow-Weaver, *Plocepasser mahali*. Animal Behaviour 45:1-11.

ZACK, S., AND K. N. RABENOLD. 1989. Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. Animal Behaviour 38:235-247.

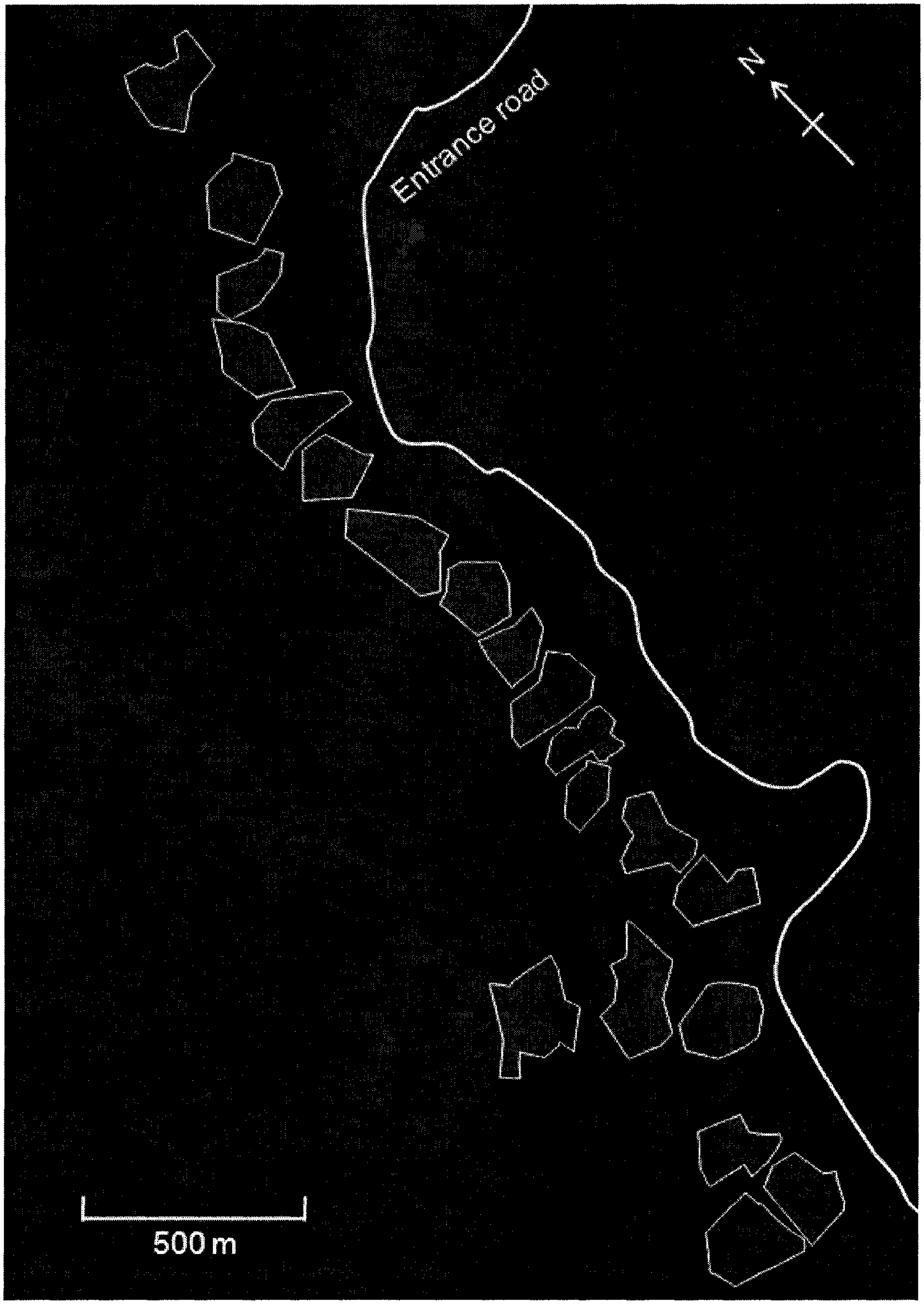

Figure 2.1. Map showing 20 Rufous-naped Wren territories in sector Santa Rosa, Area Conservación Guanacaste, Costa Rica (background image modified from Google Earth).

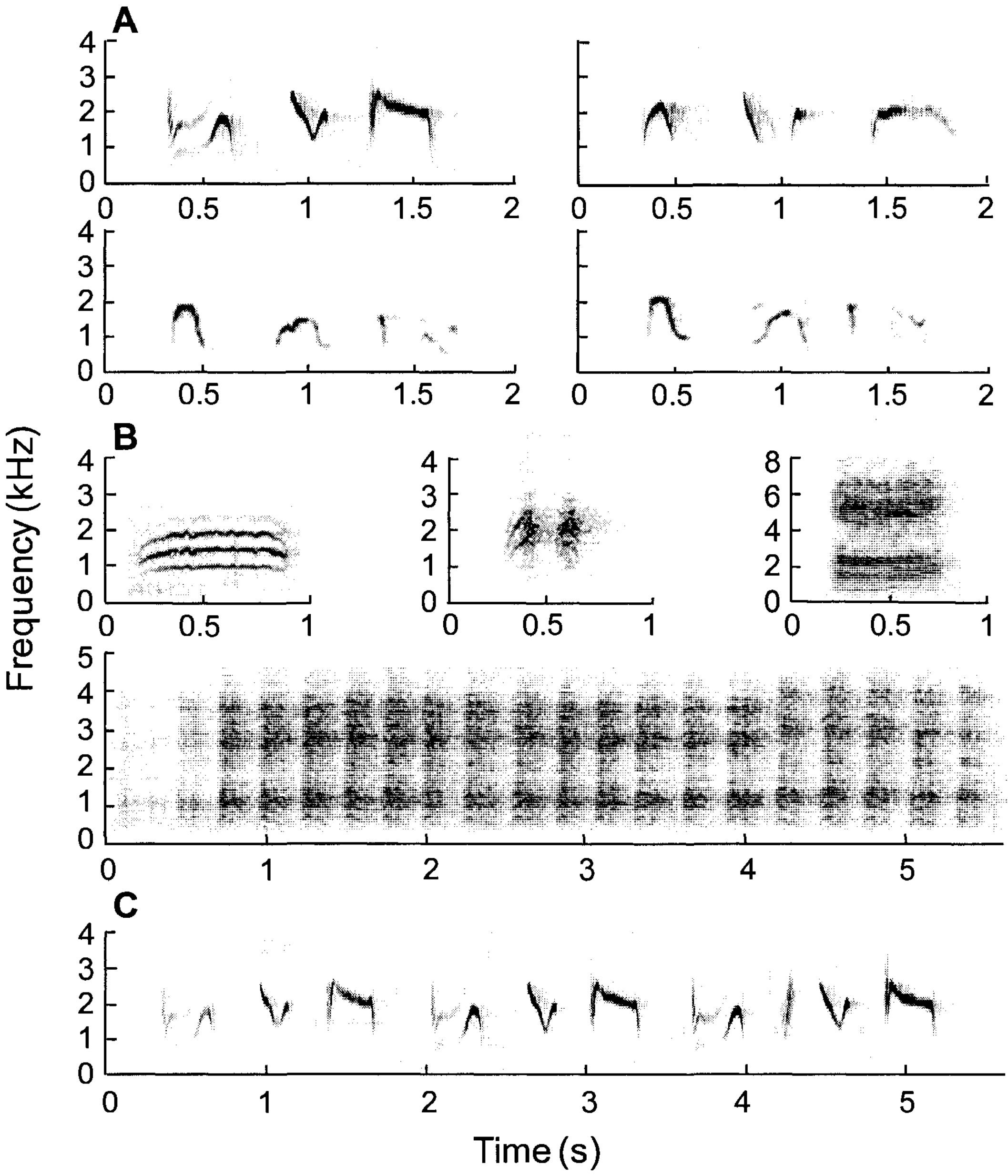

Figure 2.2. Sound spectrograms of Rufous-naped Wren solos. (A top) Examples of two different tonal syllable phrases, and (A bottom) tonal phrases of the same type produced by a male (left) and a female (right). (B) Examples of atonal vocalizations; *waah* (top left), *bark* (top centre), *snarl* (top right), and *rattle* (bottom). (C) A typical solo song comprised of repeated phrases of tonal syllables. Note different scale of vertical and horizontal axes in some spectrograms.

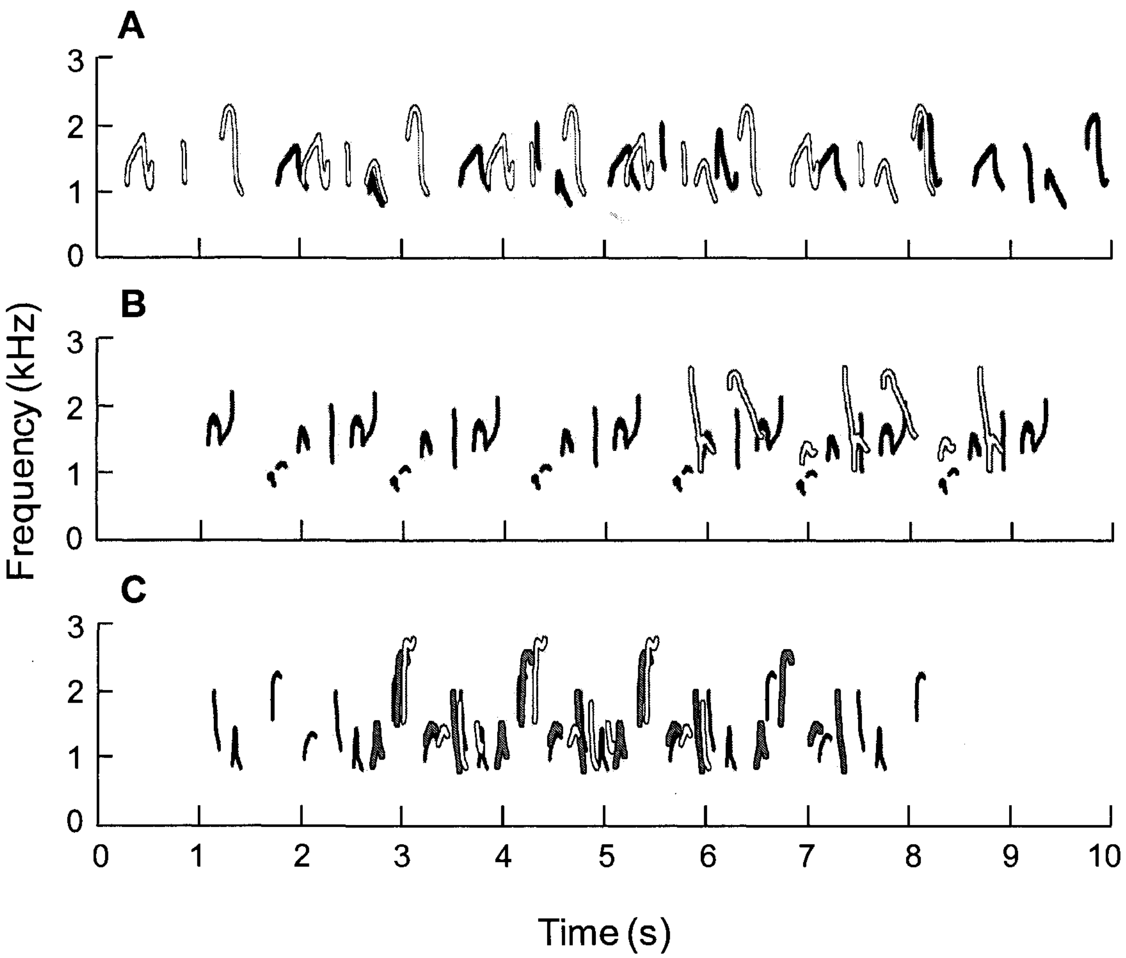

Figure 2.3. Stylized sound spectrograms of Rufous-naped Wren songs. (A) Example of a duet with the male and female both singing the same tonal phrase type, (B) a duet with two birds singing different tonal phrase types, and (C) a chorus with three birds all singing the same tonal phrase type.

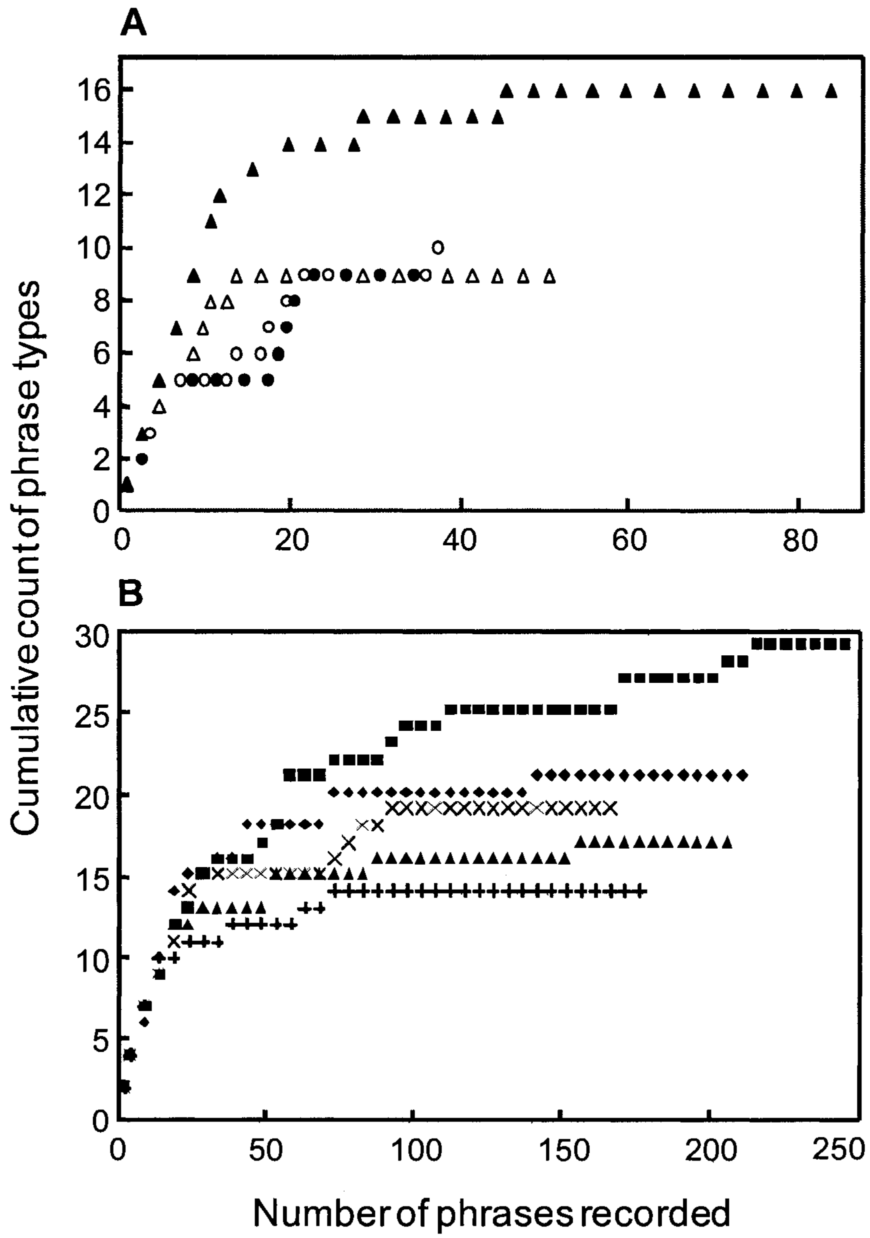

Figure 2.4. (A) Repertoire curves for four Rufous-naped Wrens from two mated pairs. One pair is depicted by triangles and the other by circles; males are depicted as solid symbols and females as open symbols. (B) Five example repertoire curves of territorial pairs of Rufous-naped Wrens. Complete repertoire sampling (indicated by a stable asymptote) was complete for four pairs and incomplete for one pair (the pair depicted by the solid squares).

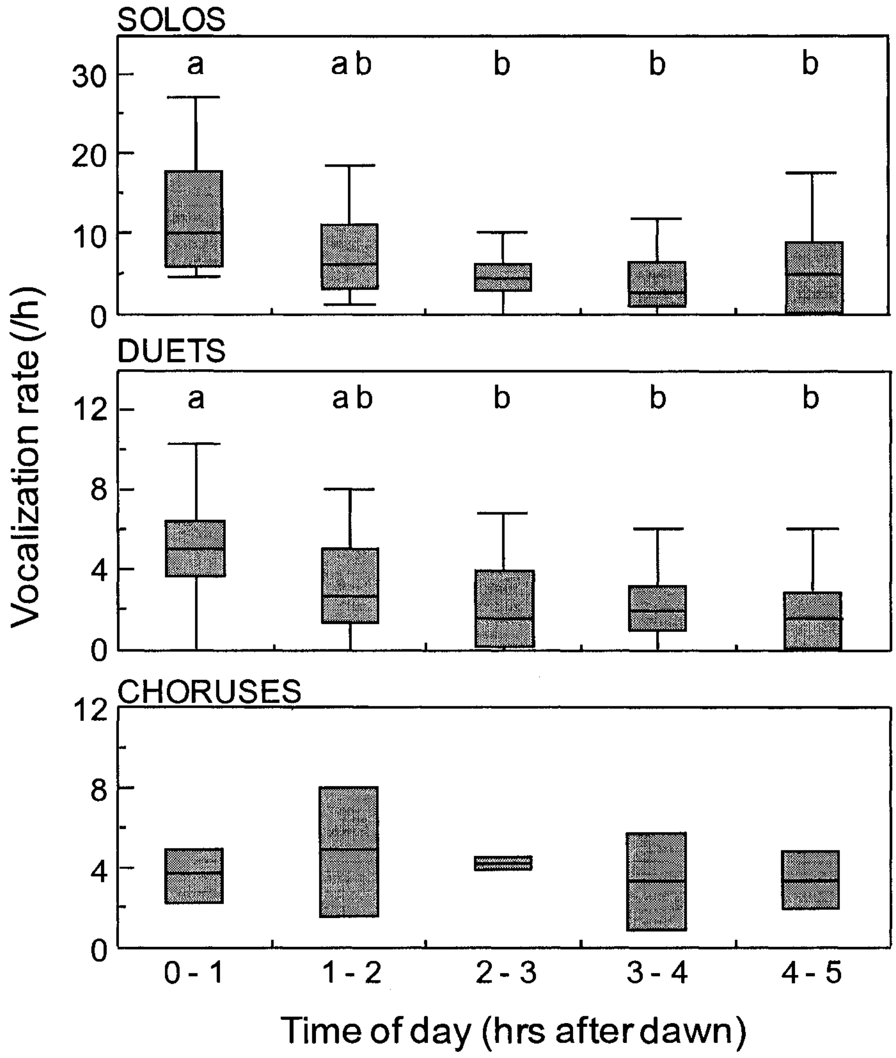

Figure 2.5. Variation in song output of Rufous-naped Wrens in relation to time of day (*n* =19 groups). Solo song rates were significantly higher in the first hour of the day (first light at ~0500 hours) than in the third, fourth and fifth hours. Duet output followed a similar pattern, with groups producing significantly more duets in the first hour of daylight than in the third, fourth and fifth hours. Chorus rates did not vary in relation to time of day. Note the different scales on the vertical axes of the top graph and the bottom two graphs. Columns sharing letters are not significantly different. Box plots show horizontal lines for 10th, 25th, 50th, 75th, and 90th percentiles.

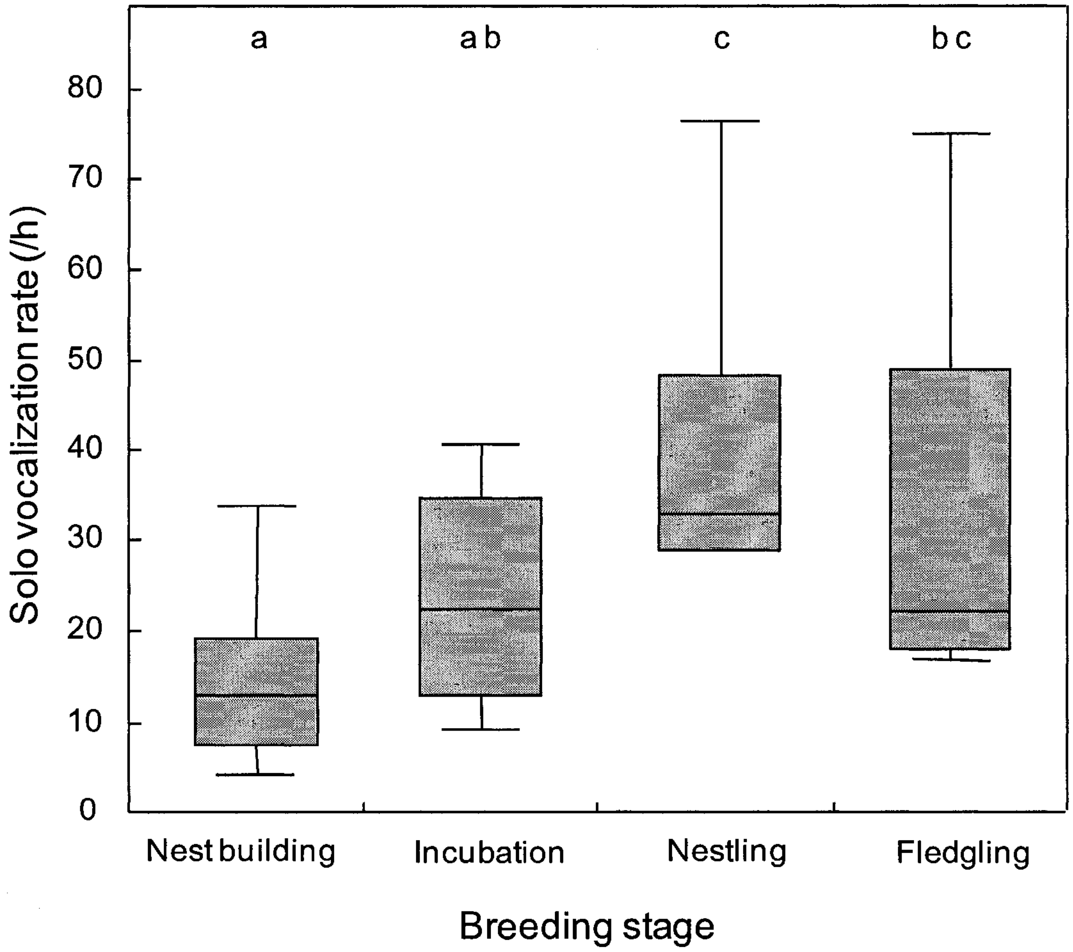

Figure 2.6. Variation in solo vocalization output of Rufous-naped Wrens in relation to breeding stage (n =19 groups). Solos include all tonal phrases and atonal vocalizations. Columns sharing letters are not significantly different. Box plots show horizontal lines for 10th, 25th, 50th, 75th, and 90th percentiles.

Chapter 3

A strong ungraded response to playback of solos, duets, and choruses in a cooperatively breeding passerine

This chapter is co-authored with my supervisor, Dr. Daniel Mennill, who supported my research, shared in the research design, provided feedback, and provided editorial input.

Synopsis

Coordinated vocal displays of cooperatively breeding birds provide a compelling model for investigating the opposing motivations for cooperative versus conflict-based behaviours. Hypotheses for the function of coordinated vocal displays differ with respect to these motivations, and have been traditionally investigated by using playback to simulate varying degrees of threat to individuals and groups. Here, we test functional hypotheses by presenting territorial groups of the cooperatively breeding rufous-naped wren (*Campylorhynchus rufinucha*) with three playback stimuli: (1) solos, (2) duets, and (3) choruses. We found that all groups responded strongly and consistently to playback by approaching the loudspeaker together, vocalising, and performing visual displays. The composite response measure to playback was significantly more aggressive to all playback treatments compared to a pre-playback control period, yet did not vary across treatments. This suggests that the playback stimuli we employed represented equally strong threats despite the varying numbers of contributors to each stimulus, and refutes the hypothesis that coordinated vocalisations are graded signals of threat in this species. The findings of this study are significant in that they stand in contrast to the majority of playback studies, which find either an increase in aggression with increasing simulated intruders, or an increase in coordinated vocalisations in response to solo playback. We interpret the results of this study as evidence that coordinated vocalisations function in the cooperative behaviour of joint territory defence in the rufous-naped wren.

Introduction

Cooperation and conflict are opposing behaviours that govern social interactions in animals. Much research has investigated the degree of individual motivation for engaging in cooperative versus conflict-based behaviours as an evolutionary consequence of the resulting fitness benefits. The cooperative behaviour of aiding a breeding partner in rearing offspring has direct fitness benefits (Maynard Smith 1977), while cooperating to assist related individuals to rear their offspring has indirect benefits in the form of kin selection (Hamilton 1964). In contrast, conflict can arise when partners have opposing motivations for parental investment, or when related individuals queue for breeding opportunities in social groups, and this can lead to aggressive signalling contests or outright physical fights (Wiley & Rabenold 1984). Cooperatively breeding animals often produce coordinated territorial displays, and this has been suggested as a way in which non-breeding helpers cooperate with breeders (e.g. Cockburn 1998), but has also been argued to reflect the conflicting interests of the members of the group (e.g. Reyer & Schmidl 1988). Decisions to cooperate or act in conflict may be influenced by assessing acoustic signals produced by members of an animal's own social group, or by assessing acoustic signals produced by competing groups during territorial encounters. Assessment of group size may be especially important in social animals because group size may outweigh inter-individual differences in resource holding potential between contestants (Parker 1974, McComb 1992, McComb et al. 1994, Seddon & Tobias 2003, Radford 2003). Consequently, the advertisement of group size and the assessment of rival group size through coordinated vocal displays may mediate social interactions in group-living animals. The degree to which animals participate in coordinated vocalisations presents an excellent opportunity to assess the adaptive significance of cooperative and conflict-based behaviours.

Few studies have tested the function of group vocalisations in animals using playback to simulate varying degrees of threat. McComb et al. (1994) compared the response to playback of single female lions (*Panthera leo*) to playback of both solo and group vocalisations. Females were less likely to approach groups than to approach single individuals. Similarly, Radford (2003) broadcast playbacks representing varying numbers of intruders to territorial groups of green woodhoopoes (*Phoeniculus purpureus*). Individuals and groups responded more aggressively to playback of larger groups than smaller groups by increasing the length of their vocal response. Seddon & Tobias (2003) performed playbacks of varying group sizes to territorial groups of subdesert mesites (*Monias benschi*). The number of simulated intruders significantly influenced group responses, where resident birds approached more cautiously and produced a more prolonged and communal response to playback simulating increasing numbers of intruders. Taken together, these studies have shown that groups were influenced by the composition of the defending focal group and the simulated intruding group, and reflects the possibility of recruiting additional group members (McComb et al. 1994), or attaining reproductive opportunities (Radford 2003, Seddon & Tobias 2003).

Bird species provide good model systems for investigating coordinated vocal signalling because they are conspicuous, show a variety of social mating systems, and vary dramatically in their modes of signal production and in the functional significance of their signals. The form and adaptive significance of bird song has generated much scientific interest, leading to numerous hypotheses for its function. It has been shown that the primary functions of bird song in many taxa are mate attraction and territory defence (Catchpole & Slater 1995). While this is true for species in which only males sing, more complex forms of acoustic signalling, such as coordinated vocalisations produced by both males and females in many tropical birds, have been hypothesized to function in a variety of additional ways that reflect the motivation of each individual. The coordinated production of vocalisations by two birds, know as a duet, has been studied in increasing detail in recent years (reviewed in Hall 2004). This increase in research has led to a series of hypotheses that explain the adaptive significance of the behaviour from the perspective of both individuals. In particular, these hypotheses investigate the degree to which duetting is a cooperative behaviour benefiting both birds, or alternatively representing conflict between the birds, benefiting only one of the duet partners. As a cooperative behaviour, duetting has been shown to function in joint territory defence (e.g. rufous-and-white wrens, *Thryothorus rufalbus*, Mennill 2006) and in maintaining the pair bond (e.g. magpie larks, *Grallina cyanoleuca*, Hall 2000). Alternatively, duetting has been shown to play a conflicting role between the pair, in mate guarding (e.g. bay wren, *Thryothorus nigricapillus*, Levin 1996) and paternity guarding (e.g. slate-coloured boubou, *Laniarius funebris*, Sonnenshein & Reyer 1983).

Birds that breed cooperatively also produce group vocalisations, whereby more than two birds combine their vocalisations into a coordinated vocal display, known as a chorus. Chorusing is especially interesting from an evolutionary perspective, because the motivation of extra-pair group members requires consideration. Hypotheses explaining the adaptive significance of chorusing are similar to those of duetting, and can be classified based on whether they propose conflict or cooperation among the group. There is strong evidence that chorusing functions as a cooperative behaviour in collaborative territory defence (e.g. laughing kookaburras, *Dacelo novaeguineae*, Reyer & Schmidl 1988, Baker 2004; Australian magpies, *Gymnorhina tibicen*, Brown & Farabaugh 1991; white-browed sparrow-weavers, *Plocepasser mahali*, Wingfield & Lewis 1993; subdesert mesites, Seddon 2002; black-breasted wood-quail, *Odontophorus leucolaemus*, Hale 2006) and in maintaining social bonds within the group (Australian magpies, Brown et al. 1988). Chorusing has also been suggested to function as a form of conflict between group members by mediating social hierarchies (e.g. laughing kookaburras, Reyer & Schmidl 1988).

In this study we investigate the function of duetting and chorusing behaviour in a cooperatively breeding bird, the rufous-naped wren (*Campylorhynchus rufinucha*). This species is a widespread and common passerine inhabiting the dry forests of western Central America from southwest Mexico to northwest Costa Rica. Birds live in groups of two or more individuals and produce duets and choruses composed of simultaneous contributions of repeated syllable phrases (Chapter 2). We used audio playback of solos, duets, and choruses to simulate increasing levels of threat to resident territorial birds. If duets and choruses provide groups with information with which to assess the ability of rival groups to defend resources, we predicted that territorial birds would show increased aggression in response to increasing numbers of simulated intruders, because threat to the defended territory should increase with the size of the rival group. Alternatively, if duets and choruses are important for pair or group cohesion (Thorpe 1972), we predicted that territorial birds would show increased aggression towards solo playback than duet or chorus playback because lone individuals likely represent rival individuals prospecting for new breeding opportunities. By assessing responses of territorial groups to varying degrees of threat to individuals and groups in this way, we investigate the functional significance of coordinated vocal behaviour in a complex social context.

Methods

Study population and study site

We presented a series of playback trials to 18 territorial groups of free-living rufous-naped wrens in sector Santa Rosa, Area Conservación Guanacaste, Costa Rica (10°40′N, 85°30′W). Sixteen territories were occupied by a breeding pair, while the remaining two territories were occupied by a breeding pair and an adult extra-pair individual. Our study site is predominantly regenerating deciduous dry forest with isolated remnant patches of mature evergreen forest. All 18 territorial groups were located along minor access roads, within second-growth forest with a canopy height of 15 to 20 m and an understory dominated by bull horn acacia (*Acacia collinsii*), the preferred nesting tree of the rufous-naped wren (Joyce 1993). We conducted the experiments from 28 July to 13 Aug 2007 after all pairs had commenced breeding activities, approximately 75 days after the start of the rainy season. During the experiment, we observed dependent juveniles in nine of the 18 territories; the remaining nine groups were assumed to have had a failed first breeding attempt. We did not conduct playback experiments on groups that were known to be incubating eggs because a pilot study showed that incubating females seldom respond to playback, whereas females in pre-nesting and fledgling periods regularly respond to playback. We conducted all playback trials during periods with low wind and without rain, when background noise was low.

Playback stimuli

To simulate territorial intrusion by one, two, or three rival conspecifics, we presented each territorial group with three different playback treatments: solos, duets, and choruses. We created playback stimuli using songs recorded from birds within the study population who were strangers to the playback subjects. To generate stimuli, we first isolated songs from field recordings collected in natural contexts, each with a high signal to noise ratio. We then selectively filtered background noise from the recordings by using the lasso selection tool followed by a frequency bandpass filter between 250 Hz and 21,000 Hz using Audition (Adobe, San Jose, CA). All recordings were then normalised to -1 dB using Audition. We created solo song playback stimuli (Fig. 3.1A) by looping a single song phrase six times in immediate succession, as is often found in naturally occurring solo songs (Chapter 2). We created duet playback stimuli (Fig. 3.1B) by combining the same solo song phrase type recorded from each member of a mated pair, such that the second bird's contribution started after the first bird's initial phrase, with an additional 0.15 sec offset. This offset is within the range of asynchrony of contributions to naturally occurring duets (Chapter 2). We created chorus playback stimuli (Fig. 3.1C) using the above duet in addition to a same solo phrase type of a third bird, incorporating an additional offset of 0.15 sec. Where possible, the third individual was a member of the same group that produced the components of the duet. Where not possible, a solo from the neighbour to the stimulus pair was used. For all three types of stimulus, the six-phrase playback stimulus was repeated four times at a rate of once every 30 sec, so that all playback stimuli were the same length. To minimise the effects of pseudoreplication (Kroodsma 1989), we created four different sets of playback stimuli from recordings obtained from four different groups. One of the four treatment sets was presented to each test group according to a factorial design, with the condition that no group received playback produced from birds closer than three territories distant (approximately 0.5 km).

Playback trials

We broadcast single-channel playback stimuli (16-bit WAV files) from an iPod (Apple Inc., Cupertino, CA) connected to a Minivox PB-25 loudspeaker (Anchor Audio, Inc., Torrance, CA). The speaker was mounted on a pole 1.5 m above the ground, facing upwards, and positioned near the edge of the subject group's territory (approximately 20 m from territory boundary; approximately one half of the distance from the territory edge to the territory centre). We held the volume of the speaker constant across all playback trials at a natural sound pressure level; 80 dB at 1 m horizontal distance from the forward oriented speaker using a sound level metre (Realistic 33-4050). Prior to broadcasting any playback stimuli, we monitored the focal group for 30 min to obtain baseline data to compare against behaviours observed following playback. The order of presentation of the three playback stimuli was chosen using a block factorial design, whereby each of the six possible orders of presentation was given to three different groups. Each stimulus presentation was followed by a 20 min silent period to allow the group to return to normal behaviour and singing rate. All stimuli were presented between 0600 and 1030 h because song rates are relatively consistent during this period (Chapter 2).

During each playback trial we made observations and recordings of the resident group from a partially concealed location 20 m from the speaker. All vocal responses were recorded with a directional microphone (Sennheiser ME66) and a solid state digital recorder (Marantz PMD-660). To quantify the response to each treatment we measured the following response variables: (1) latency to first vocalisation; (2) solo song rate; (3) duet song rate; (4) closeness of approach to loudspeaker; and (5) the proportion of the trial that any member of the subject group was within 10 m of the speaker. Because the majority of our playback groups were mated pairs, and only two subject groups included extra-pair birds, we did not assess chorus rate as a response variable. However, we describe the chorusing responses of these two groups anecdotally. For the pre-playback control period, we measured latency to first vocalisation from the arbitrary time of the start of our recording, whereas for playback treatments we measured latency from the start of the first playback stimulus. We considered the following signal variants to be consistent with aggressive responses: short latencies of response, high solo song rates, high duet rates, small distances of closest approach, and high proportions of the trial spent within 10 m of the speaker. Due to the thick vegetation at our study site, the rapid and often secretive movements of the playback subjects, and the fact that birds tended to stay in very close proximity to their group mates, it was difficult to track the responses of individuals; instead we evaluated the responses of the entire territorial group as a unit. We collated all vocal responses to playback trials by visualising the sounds as spectrograms and annotating them using SYRINX-PC (J. Burt, Seattle, WA).

Statistical analysis

To compare the behaviour of territorial rufous-naped wrens during the pre-playback control period and following the three playback treatments, we performed a principle components analysis to reduce the variables to a single composite response measure. Principal components analysis was conducted on all five response variables using Varimax rotation, and generated one principal component (PC1) with an Eigenvalue greater than 1.0. PC1 explained 53.6 % of the variance in the five response variables and showed strong positive loading from solo song rate, duet song rate, and the proportion of the trial that any member of the subject group was within 10 m of the speaker, and negative loading from latency to response and closeness of approach to the speaker. As such, we refer to PC1 as "intensity of response" where high PC1 scores are consistent with strong aggressive responses. We tested for differences in the responses of rufous-naped wrens to different playback treatments using repeated measures ANOVA. This approach allowed us to model the effects of a within-subject factor (the type of playback treatment), and two between-subject factors (the order of presentation of playback stimuli, and the presence or absence of dependent juveniles), on the response variable (the PC1 "intensity of response" measure). Principal components analysis was performed using JMP 6.0 (SAS Institute, Cary, NC) and ANOVA was performed using SPSS 16.0 (SPSS Inc., Chicago, IL). We present values as means ± S.E. and express effect sizes (E.S.) using Cohen's *d* (Cohen 1988). For factors that showed a significant effect, we conducted Tukey post-hoc analysis and present values with 95 % confidence intervals (Colegrave & Ruxton 2003).

Results

In all 18 trials, playback elicited strong aggressive responses from territorial rufous-naped wren groups. In response to playback, birds vocalised, approached the speaker, and produced visual displays such as tail fanning and erecting chest feathers (Fig. 3.2). Overall, birds showed a significant response to playback; the principal component summarising response (PC1) showed a significant effect of treatment (Fig. 3.3; $F_{3,24} = 43.0$, $P < 0.001$, E.S. = 0.84), but no effect of playback order ($F_{5,8} = 2.59$, $P = 0.11$, E.S. = 0.62), or the presence of fledglings in the responding group ($F_{1,8} = 1.00$, $P = 0.35$, E.S. = 0.11). To assess differences between responses to each of the treatment categories we performed a post-hoc Tukey test, which showed a significant difference between the behaviour of birds during the silent pre-playback period (-1.3 ± 0.10, 95% confidence interval: -1.52 – -1.11) compared to their responses to playback of solos (0.39 ± 0.19, 95% confidence interval: -0.01 – 0.78), duets (0.49 ± 0.15, 95% confidence interval: 0.16 – 0.81), and choruses (0.44 ± 0.17, 95% confidence interval: 0.08 – 0.80), but no significant difference between the responses to three playback treatments.

In order to assess specific individual response measures to playback of all three stimuli in comparison to the pre-playback control period, and given that we found no differences in the responses to solos, duets, and choruses, we pooled data from the three playback treatments. We found that all response measures differed significantly after playback compared to the pre-playback control period (Table 3.1), where responses to the three playback treatments were significantly more intense than pre-playback behaviour.

Sixteen of the groups receiving playback consisted only of a male and female breeding pair, whereas two groups consisted of a breeding pair and an extra-pair individual. These two groups rarely gave three-part choruses during the silent period (1.0 ± 1.0 songs/h) but often produced choruses in response to playback of solos (60.0 ± 30.0 songs/h), duets (90.0 ± 30.0 songs/h), and choruses (54.0 ± 6.0 songs/h). Choruses appeared to be given at similarly high rates across the three playback treatments, although the small number of groups with three individuals precludes statistical analysis.

Discussion

We found that rufous-naped wren groups reacted aggressively to playback simulating territorial intrusion of strangers producing solos, duets, and choruses. Resident birds showed elevated aggressive responses to the playback treatments, including a combination of vocal and physical behaviours. Compared to the natural, passive context represented by the pre-playback period, groups vocalised with little delay, produced solos and duets at a higher rate, approached the speaker more closely, and spent more time within close range of the speaker. Interestingly, we found that playback subjects responded with equal intensity across each of the playback treatments, suggesting that that all three treatments were perceived as similar levels of threat.

A strong reaction to playback simulating the vocalisations of a conspecific rival is not unexpected. Many classical studies of animal behaviour have used playback to test specific hypotheses regarding the function of bird song, showing that males use song to defend territories and react strongly to simulated intrusions represented by playback (McGregor 1992). Some studies have also shown that birds increase their rate of duetting in response to playback (e.g. Levin 1996, Hall 2000, Mennill 2006), indicating that duets may function in joint territorial defence (Seibt & Wickler 1977). Alternatively, duets may function as a form of acoustic mate guarding to deter intruding birds from usurping a partner (Stokes & Williams 1968), or as a paternity guard to deter males from seeking to copulate with the female (Sonnenschein & Reyer 1983). As we found that rufous-naped wrens produced more solos and duets in response to all three playback treatments compared to the pre-playback control period, this suggests that solo and duet songs are generally used in territorial defence. However we cannot be sure if the second bird creates the duet to further intimidate the perceived intruder and advertise a united defensive unit, or if it does so in a mate or paternity guarding role to advertise the first bird's paired status.

We found that rufous-naped wrens do not produce graded responses to different simulated threats levels. To assess this result, we consider the relative threat that each of the playback stimuli represents to the subject groups. Solo playback of a non-neighbouring 'stranger' is likely more of a threat to the pair-bond than the territory, and likely simulates a single individual that is prospecting to form a new partnership, to fill a vacant position on a territory, or to seek extra-pair mating opportunities. In contrast, duet and chorus playbacks of a non-neighbouring group likely pose more of a threat to the territorial tenure of the resident group than to a pair bond, and likely simulate a rival pair or trio attempting to assert themselves or obtain a new territory. The results of this study do not suggest that communal vocalizations function in pair or group cohesion; this hypothesis predicts that duet rate should be higher in response to solo playback compared to duet or chorus playback. Additionally, given that we found no clear difference in the level of aggression in response to the different playback treatments, we infer that communal vocalizations are not used to assess the ability of rival groups to defend resources.

The findings of this study stand in contrast to other playback studies involving duetting and chorusing birds. Hall (2000) used solo and duet playback to represent two levels of threat to magpie larks, and found that the proportion of individual songs that were joined and formed into duets increased in response to playback of duets compared to solos. Similarly, Seddon & Tobias (2003) found that the number of simulated intruders presented to subdesert mesites strongly influenced the strength of response to playback. As the number of vocal contributors in the playback increased, vocal responses became more protracted, groups became less likely to approach, and the number of vocal contributors increased (Seddon & Tobias 2003). They concluded that groups respond more collectively and with greater caution to threats from two or more intruders compared to single intruders. Radford (2003) investigated the effect of the number of simulated intruders on group responses in the green woodhoopoe. He found that subject groups vocalised for longer time periods in response to playback representing a group larger than the subject group than they did to a smaller playback group. The aforementioned studies demonstrated that coordinated vocalisations increase in aggression as more members of the focal group participate.

Despite a clear aggressive response to playback by rufous-naped wrens in this study, our predictions of a graded response to the varying threat levels represented by the different playback treatments were not met. To our knowledge, only one published study to date has reported similar results; Fedy & Stutchbury (2005) found that white-bellied antbirds (*Myrmeciza longipenis*) respond equally to male solo, female solo, and duet playback. From these findings the authors concluded that duetting does not function as a mate-guard in that species, and when viewed together with other data indicating that duetting rates do not vary seasonally, they exclude a territory function for duetting (Fedy & Stutchbury 2005). Similarly demonstrating a lack of a graded response to varying degrees of simulated threat, Mennill & Vehrencamp (in review) found that rufous-and-white wrens produced duets at similar rates across playback treatments. In combination with physical response data from subject pairs, they concluded that duetting is a multifunctional signal functioning in cooperative territorial defence and intrasexual aggression in the rufous-and-white wren (Mennill & Vehrencamp, in review).

In the present study we observed differences in response to playback compared to the pre-playback control period. Although these results could be attributed to an inability of the birds to distinguish between treatments, we deem this unlikely given the method by which we produced the stimuli, incorporating a slight offset in the component vocal parts. A more plausible interpretation of our results is that a group's perception of territory invasion in this species is not influenced by the number of intruders but is assessed in terms of the quality of the resource being defended and the resulting motivation of group members. It has been suggested that in contests between single competitors, resource holding potential is assessed based on individual size or body weight as an indication of fighting ability (Riechert 1998). However, when groups defend resources together as a unit, the number of individuals in a group may outweigh inter-individual differences in fighting ability in determining contest outcomes (e.g. female lions, McComb 1992; McComb et al. 1994; green woodhoopoes, Radford 2003; subdesert mesites, Seddon & Tobias 2003). Despite this, it has been demonstrated in other species that the outcome of naturally occurring territorial contests is not predicted by asymmetries between invading and defending group sizes (e.g. Tasmanian native hen, *Gallinula mortierii*, Putland & Goldizen 1998). Alternatively, variability in reward was shown to best predict contest outcomes (Putland & Goldizen 1998). In the present study, it is possible that the quality of the defending group's territory varied between subject groups, resulting in variation in the motivation for cooperative or conflict-based behaviours.

Resource demand and consequent aggression levels are often higher during breeding periods, when individuals must defend access to resources in order to feed developing nestlings and fledged juveniles, than during non-breeding periods. The contrast between the lack of graded response levels in the present study and the findings reported in others studies may be attributed to a variation in resource demand. For example, Hall (2000) conducted playback experiments on magpie larks in the non-breeding and pre-breeding seasons, and Radford (2003) studied green woodhoopoes after all breeding was complete. Both of these studies found an increase in response measures with an increasing number of simulated territorial intruders. In contrast, we presented playback while groups either had very recently fledged young or had failed an initial breeding attempt and were likely preparing to re-nest. As a result of the potentially elevated resource demand during this period, aggression levels may have been sufficiently high to produce a strong response to all playback treatments, regardless of the number of simulated intruders the treatment represented. Future studies of this species could perform a similar experimental procedure in the pre-breeding period between September and March, and would provide an interesting point of comparison.

Group composition and differential responses of group members to each playback treatment may explain the consistent responses to different playback treatments that we observed. In a study of group singing in subdesert mesites (Seddon & Tobias 2003), the likelihood of approach to the playback speaker was determined by the asymmetry of male group members between defending and simulated intruding groups, and in the ratio of males to females in the defending group. The authors suggest that a male-biased ratio increases the potential for conflict whereby non-breeding group members approach the speaker to assess the possibility of breeding opportunities and mated pairs approach the speaker to expel the invading group (Seddon & Tobias 2003). In the present study, the physical response by focal groups may have been determined by only a single group member acting to either repel an invader or seeking dispersal and breeding opportunities. Further studies to assess the function of coordinated vocal behaviour in this species could examine individual responses to playback by marking individuals prior to playback. In doing so, responses can be attributed to specific group members and the motivation of male and female, and breeding and non-breeding individuals can be compared. This will facilitate further studies to determine whether the strong, ungraded response we observed is common among different cooperatively breeding species.

Acknowledgements

We thank the staff of sector Santa Rosa of the Area de Conservación Guanacaste, Costa Rica for logistical support, particularly R. Blanco and M. M. Chavarria. This work was funded by the Natural Science and Engineering Research Council (NSERC), the Canadian Foundation for Innovation (CFI), the Government of Ontario, and the University of Windsor.

References

Baker, M. C. 2004. The chorus song of cooperatively breeding laughing kookaburras (Coraciiformes, Halcyonidae: *Dacelo novaeguineae*): Characterization and comparison among groups. *Ethology*, **110**, 21–34.

Brown, E. D. & Farabaugh, S. M. 1991. Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. Part III. Sex specificity and individual specificity of vocal parts in communal chorus and duet songs. *Behaviour*, **118**, 244–274.

Brown, E. D., Farabaugh, S. M. & Veltman, C. J. 1988. Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. Part I. Vocal sharing within and among social-groups. *Behaviour*. **104**, 1–28.

Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.

Clutton-Brock, T. H. & Albon, S. D. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour*, **69**, 145–169.

Cockburn, A. 1998. Evolution of helping behaviour in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, **29**, 141–177.

Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences.* 2nd edn. Hillsdale, New Jersey: Lawrence Erlbaum.

Colegrave, N & Ruxton, G, D. 2003. Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. *Behavioral Ecology*, **14**, 446–450.

Fedy, B. C. & Stutchbury, B. J. M. 2005. Territory defense in tropical birds: are females as aggressive as males? *Behavioral Ecology and Sociobiology*, **58**, 414–422.

Hale, A. H. 2006. The structure, context and functions of group singing in the black-breasted wood-quail (*Odontophorus leucolaemus*). *Behaviour*, **143**, 511–533.

Hall, M. L. 2000. The function of duetting in magpie larks: cooperation, conflict or commitment? *Animal Behaviour*, **60**, 667–677.

Hall, M. L. 2004. A review of hypotheses for the function of avian duetting. *Behavioral Ecology and Sociobiology*, **55**, 415–430.

Hamilton , W. D. 1964. The genetic evolution of social behavior. I. *Journal of Theoretical Biology*, **7**, 1–16.

Joyce, F. J. 1993. Nesting success of Rufous-naped Wrens (*Campylorhynchus rufinucha*) is greater near wasp nests. *Behavioral Ecology and Sociobiology*, **32**, 71–77.

Kroodsma, D. E. 1989. Suggested experimental designs for song playbacks. *Animal Behaviour*, **37**, 600–609.

Levin, R. N. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: II. Playback experiments. *Animal Behaviour*, **52**, 1107–1117.

McComb, K. 1992. Playback as a tool for studying contests between social groups. In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 111–119. New York: Plenum Press.

Maynard Smith, J. 1977. Parental investment: A prospective analysis. *Animal Behaviour*, **25**, 1–9.

McComb, K., Parker, C. & Pusey, A. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour*, **47**, 379–387.

McGregor, P. K. 1992. *Playback and Studies of Animal Communication*. Plenum Press, New York.

Mennill, D. J. 2006. Aggressive responses of male and female rufous-and-white wrens to stereo duet playback. *Animal Behaviour*, **71**, 219–226.

Parker, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, **47**, 223–243.

Putland, D. A. & Goldizen, A. W. 1998. Territorial behaviour in the Tasmanian native hen: group and individual performance. *Animal Behaviour*, **56**, 1455–1463.

Radford, A. N. 2003. Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition. *Animal Behaviour*, **66**, 1035–1044.

Reyer, HU. & Schmidl, D. 1988. Helpers have little to laugh about: group structure and vocalisation in the laughing kookaburra *Dacelo novaeguineae*. *Emu*, **88**, 150–160.

Riechert, S. E. 1998. Game theory and animal contests. In: *Game Theory and Animal Behaviour* (Ed. by L. A. Dugatkin & H. K. Reeve), pp. 64–93. Oxford: Oxford University Press.

Seddon, N. & Tobias, J. A. 2003. Communal singing in the cooperatively breeding subdesert mesite (*Monias benschi*): evidence of numerical assessment? *Journal of Avian Biology*, **34**, 72–80.

Seibt, U. & Wickler, W. 1977. Duettieren als Revier-Anzeige bei Vogeln. *Zeitschrift für Tierpsycholgie*, **43**, 180–187.

Sonnenschein, E. & Reyer, HU. 1983. Mate-guarding and other functions of antiphonal duets in the slate-coloured boubou (*Laniarius funebris*). *Zeitschrift für Tierpsycholgie*, **63**, 112–140.

Stokes, A. W. & Williams, H. W. 1968. Antiphonal calling in quail, *Auk*, **85**, 83–89.

Thorpe, W. H. 1972. Duetting and antiphonal song in birds. *Behaviour*, **18**, 1–193.

Wiley, R. H. & Rabenold, K. N. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution*, **38**, 609–621.

Wingfield, J. C. & Lewis, D. M. 1993. Hormonal and behavioural responses to simulated territorial intrusion in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. *Animal Behaviour*, **45**, 1–11.

Table 3.1. Pairwise comparisons of response measures of territorial rufous-naped wren groups to playback. All tests are significant to a bonferroni corrected α-value of 0.01. Significance between pre-playback and playback assessed using paired t-tests.

	Means				
Responses	Pre-playback	Playback	S.E.	t_{17}	P
Latency (s)	282.1	15.4	59.0	-4.5	< 0.001
Solo rate (per h)	5.8	18.1	3.4	3.7	< 0.01
Duet rate (per h)	4.4	67.3	9.7	6.5	0.0001
Closeness of approach (m)	16.9	5.2	1.6	-7.5	0.0001
Proportion of trial within 10m of speaker	0.01	0.4	0.05	8.2	0.0001

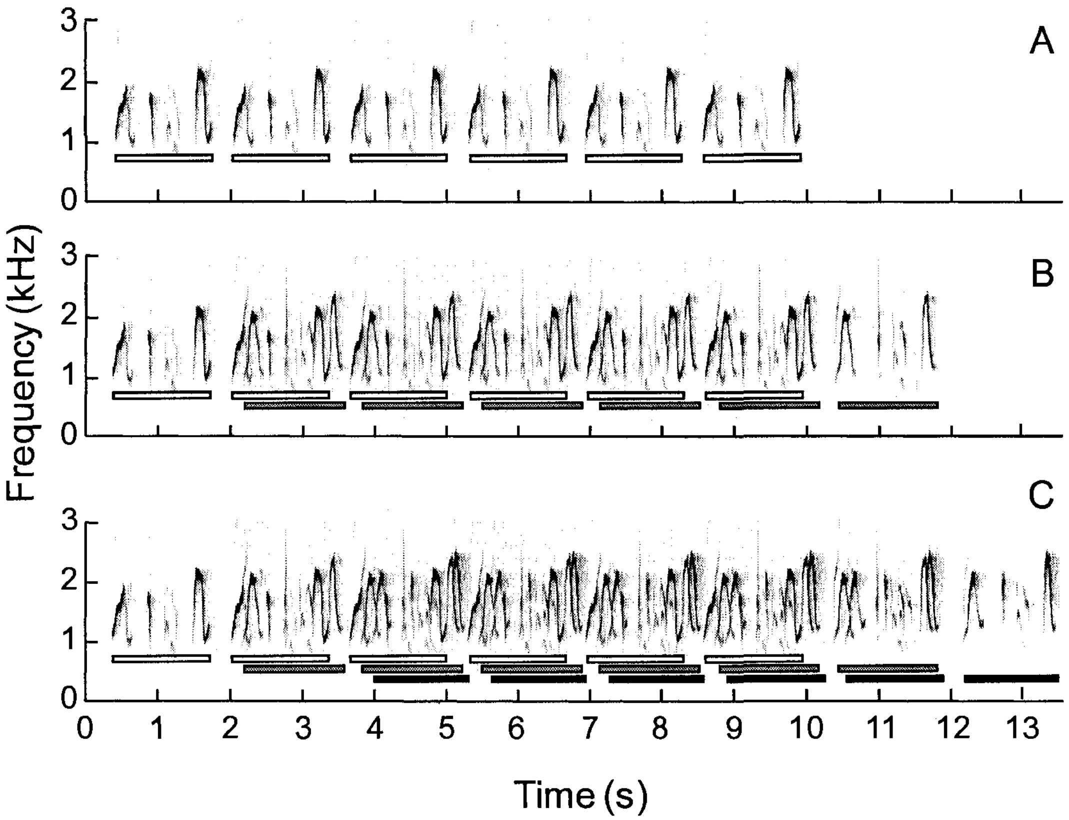

Figure 3.1. Sound spectrograms of one example set of playback stimuli used to simulate solos (A), duets (B), and choruses (C) of rufous-naped wrens. Four different stimulus sets were used according to a factorial design. Bars underscore the vocal contributions of different individuals.

Figure 3.2. Photo showing physical postures of a pair of rufous-naped wrens in response to playback. Note spreading of tail feathers and erecting of feathers on the chest by both birds (photo by D. Bradley).

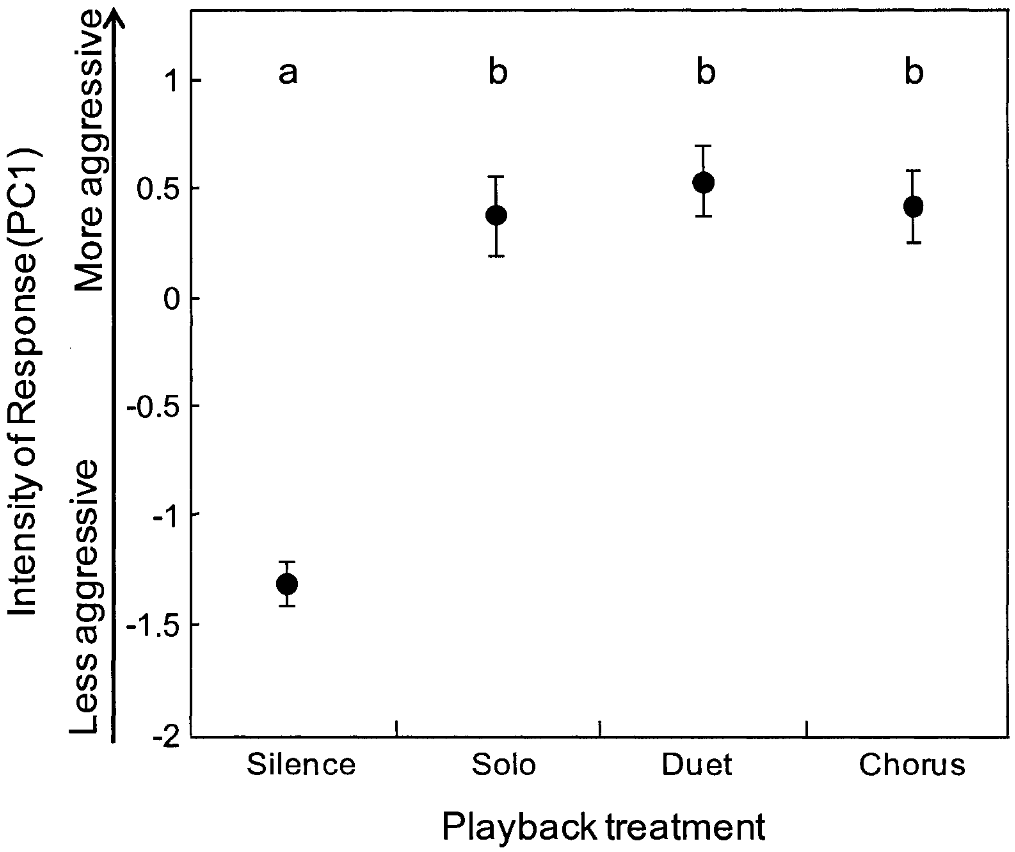

Figure 3.3. Responses of rufous-naped wrens to playback of solos, duets, and choruses compared to a pre-playback control period (silence). Intensity of response is a composite variable summarised through principal components analysis where positive values are consistent with aggressive responses (short latencies of response, high solo song rates, high duet rates, small distances of closest approach, and high proportions of the trial spent within 10 m of the speaker). Letters above bars show significant differences revealed through a post-hoc analysis; responses not connected by the same letter are significantly different.

Summary

Coordinated vocal signals are one way in which birds express their intent to cooperate or engage in conflict-based behaviours. In this thesis I investigated the form and function of coordinated vocal signals in a cooperatively breeding Neotropical songbird, the Rufous-naped Wren (*Campylorhynchus rufinucha*). In Chapter 2, I examined the acoustic structure and both diel and seasonal variation in vocal output by 19 pairs and groups of free-living birds in Costa Rica. I found that birds produce a complex array of vocalizations, including tonal, frequency-modulated syllables grouped into phrases, as well as stereotyped, atonal sounds. Songs are produced as solos, or combined into duets and choruses. Patterns of diel variation show that solo and duet songs show a dawn chorus effect. Patterns of seasonal variation reveal that solo song rate, but not duet or chorus rate, vary across breeding stages. I also assess the population-wide sharing of vocal signals and found that the majority of phrases are shared among groups, significantly more so among groups in nearby territories. These findings suggest that songs may be an important indicator of group identity and may play a role in group territorial defence. The degree of population-wide phrase-sharing suggests either short distance dispersal or delayed song learning. This study is the first fine-scale description of vocal behaviour in this species and enhances our understanding of group-singing in a complex social environment.

There are several hypotheses for the function of coordinated vocal displays in birds which differ with respect to whether they suggest a cooperative or conflicting role for the behaviour. I tested these hypotheses in Chapter 3 by presenting each of 18 groups

of Rufous-naped Wrens with three playback treatments: (1) solos, (2) duets, and (3) choruses to simulate varying degrees of threat to individuals and groups. I found that all groups responded strongly and consistently to playback by approaching the loudspeaker together, vocalizing, and performing visual displays. The composite response measure to playback was significantly more aggressive to all playback treatments compared to a pre-playback control period, yet did not vary across treatments. This suggests that all playback stimuli I employed represented equally strong threats despite the varying numbers of contributors to each stimulus, and stands in contrast to the idea that choruses represent a greater threat than duet or solo songs in this species. My findings contrast against the majority of playback studies that find either an increase in aggression with increasing simulated intruders, or an increase in coordinated vocalizations in response to solo playback. I therefore interpret these results as evidence that coordinated vocalizations in this species function in the cooperative behaviour of joint territory defence in this species.

Taken together, the findings of this thesis support the idea that coordinated vocalizations in the Rufous-naped Wren are cooperative behaviours. Duets and choruses likely function to maintain social bonds between partners and group members, and allow individuals to express their intent to participate in the cooperative behaviours of breeding and joint territory defence.

Vita Auctoris

Name: David William Bradley

Place and Year of Birth: Newcastle-upon-Tyne, England, 1981

Education:

Kelvin High School, 1996-1999

University of Winnipeg, 1999-2000

University of British Columbia, 2000-2004
Bachelor of Science, Biology

University of Windsor, 2006-2008
Masters of Science, Biological Sciences

Experience:

Teaching Assistant, Department of Biological Sciences, University of Windsor, 2006-2008

Niceforo's Wren field biologist, Colombia, 2008

Rufous-naped Wren field biologist, Costa Rica, 2007

Rufous-and-white Wren field biologist, Costa Rica, 2006

Species at Risk Consultant biologist, Parks Canada, 2005

Life History-Physiology Nexus field biologist, Panama, 2005

Fire Ecology field biologist, Oregon, USA, 2004

Behavioural Ecology of Antbirds field biologist, Panama, 2003

Field Biologist, Behavioural Ecology of *Catharus* thrushes, Mexico, 2003

NestWeb Project field biologist, British Columbia, Canada, 2001-2002

Awards:

American Ornithologists Union conference Travel Award, Portland, Oregon, 2008

University of Windsor Postgraduate Tuition Scholarship, 2007-2008

Runner-up Prize for Student Poster Presentation, Society of Canadian Ornithologists Annual meeting, 2007

University of Winnipeg Undergraduate Entrance Scholarship, 2000

Publications:

Bradley, D. 2008. Description of the nest and parental behaviour of the Bare-crowned Antbird (*Gymnocichla nudiceps*). Ornitologia Neotropical 19(1):153–157.