5-2013

Ecology and Flock-Following Behavior of the Wedge-Billed Woodcreeper in Eastern Ecuador

Abigail Darrah
University of Arkansas, Fayetteville

Recommended Citation

Darrah, Abigail, "Ecology and Flock-Following Behavior of the Wedge-Billed Woodcreeper in Eastern Ecuador" (2013). *Theses and Dissertations*. 807.
http://scholarworks.uark.edu/etd/807

ECOLOGY AND FLOCK-FOLLOWING BEHAVIOR OF THE WEDGE-BILLED WOODCREEPER IN EASTERN ECUADOR

ECOLOGY AND FLOCK-FOLLOWING BEHAVIOR OF THE WEDGE-BILLED WOODCREEPER IN EASTERN ECUADOR

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

by

Abigail Darrah
Ohio University
Bachelor of Science in Biology, 2003
University of Arkansas
Master of Science in Biology, 2006

May 2013
University of Arkansas

ABSTRACT

The wedge-billed woodcreeper (*Glyphorynchus spirurus*) is a common understory suboscine passerine of lowland Neotropical rainforests. It frequently joins mixed-species understory flocks but also regularly forages alone, and thus is an excellent model species on which to conduct comparative behavioral observations to examine the hypothesized costs and benefits of flock-following. Individuals exhibit variable flocking propensities (proportion of time spent with flocks), and thus observing the correlations between flocking propensity and physical and environmental factors can provide further insight into the importance of flock-following to the ecology of this species. Despite its abundance at many sites and its wide geographic range, surprisingly few studies have focused on the ecology and behavior of this species; previous observations suggested that this species occupies large, overlapping home ranges, which has important implications for intraspecific interactions and flock-following behavior. This study had three primary objectives: 1) to compare the foraging behavior and movement patterns of the wedge-billed woodcreeper in and out of flocks to examine the importance of hypothesized costs and benefits of flock-following for this species; 2) to determine which physical and environmental factors have the greatest influence on individual flocking propensity; and 3) to quantify the extent of home range overlap among individuals and to examine the influence of this overlap on space use and flock-following behavior. Wedge-billed woodcreepers used more open microhabitats in flocks than alone, supporting an anti-predator hypothesis for the benefit of flocking behavior. A decrease in time spent per trunk in flocks than alone, and a decrease in time spent with a flock with increasing movement rate, suggests an energetic cost associated with following flocks. Average flocking propensity was 32% in 2011 and 20% in 2012, considerably lower than previously reported in the literature and predicted under the assumption that individuals always join a flock when one is present in the home range. Body mass was the strongest predictor of individual flocking propensity, with larger individuals spending more time in flocks, and the correlation between the differences in body mass and flocking propensities of overlapping neighbors suggests that larger individuals may exclude smaller individuals from flocks. The distribution of flock-following locations was not influenced by the space use of larger neighbors, although a rigorous examination of simultaneous space use, coupled with a genetic analysis to determine if any overlapping neighbors are genetically related, would be necessary to provide a robust test of this hypothesis. Home ranges overlapped extensively in this study, thus the wedge-billed woodcreeper does not appear to defend exclusive home ranges at this site, unlike most other understory insectivores including other woodcreepers. Finally, in order to provide additional information about the behavior and natural history of this species, this dissertation includes a chapter that describes a previously known display behavior and provides notes about incubation and fledgling care.

This dissertation is approved for recommendation
to the Graduate Council.

Dissertation Director:

Dr. Kimberly Smith

Dissertation Committee:

Dr. Bette Loiselle

Dr. Gary Huxel

Dr. Douglas James

DISSERTATION DUPLICATION RELEASE

I hereby authorize the University of Arkansas Libraries to duplicate this dissertation when needed for research and/or scholarship.

Agreed ____
Abigail Darrah

Refused ____
Abigail Darrah

ACKNOWLEDGMENTS

I would like to thank Drs. Bette Loiselle and John Blake for their invaluable comments and logistical assistance in the field, and for permitting me to use their plots for this study. They graciously allowed me to accompany them during their yearly mist-netting efforts on their plots, which greatly facilitated my ability to capture enough wedge-billed woodcreepers for this study. I thank them for continuing to color-band the woodcreepers after my departure from the field in 2010. I am grateful for their efforts to teach me how to extract difficult birds from the nets and for allowing me to practice extraction techniques.

I thank the staff of Tiputini Biodiversity Station for their support during my stays at the station, particularly on-site managers Diego Mosquera and Eduardo Mora. I am especially grateful for their efforts to provide comfort and transportation to a doctor when my husband and I were ill. I thank Consuelo de Romo for arranging transportation to and from the field station every year, and I thank David Romo Vallejo and María José Rendón for their assistance in obtaining research permits from the Ecuadorian Ministry of Environment. I thank Noah Strycker and Rebekah Rylander for volunteering their time to travel to Tiputini and help with field data collection.

I thank the current and former students of the Smith Lab for their support and advice, particularly Jeff Kimmons, Maureen McClung, Jason Luscier, and Thea Kristensen. I am grateful to my committee members, Drs. Gary Huxel, Doug James, and Bette Loiselle, and to my advisor, Dr. Kimberly Smith, for their support. I thank three anonymous reviewers of a manuscript based on chapter 2 of this dissertation, whose comments were useful in improving that chapter.

I thank the University of Arkansas Graduate School and the Arkansas Audubon Society Trust for providing funding for this project. Finally I thank my husband Tom Millican for his love and support throughout my endeavors.

DEDICATION

I dedicate this dissertation to my mother, Beverly Craig, whose hard work and achievements inspired me to test my limits and strive to excel in academia.

TABLE OF CONTENTS

LIST OF TABLES AND FIGURES

CHAPTER 1: INTRODUCTION

Mixed-species flocks of birds are a prevalent feature of avian communities throughout the world (Powell 1985, Greenberg 2000). Mixed-species flocks are generally defined as a group of two or more species interacting and traveling together (Morse 1970, Greenberg 2000), as distinguished from other types of mixed-species groups that result from mutual attraction to a food resource (e.g. frugivores attracted to a fruiting tree [Leck 1971], insectivores following an ant swarm [Willson 2004]), from which individual species arrive and depart independently. The composition or prevalence of flocks may vary seasonally (McClure 1967, Powell 1979, Alves and Cavalcanti 1996), and in temperate environments, mixed-species flocks disappear entirely during the breeding season (Morse 1970). However, in many lowland rainforests throughout the world, mixed-species flocks defend stable territories and participate in flocks year-round (Moynihan 1962, Munn and Terborgh 1979, Partridge and Ashcroft 1976, Diamond 1987, Goodale and Kotagama 2004).

Most hypothesized benefits of flocking fall under two categories: increased foraging efficiency and protection from predators. These types of benefits are not mutually exclusive, particularly when decreased time spent in vigilance allows for more time spent feeding (Dolby and Grubb 1998, Fernandez-Juricic et al. 2004b, Sridhar et al. 2009). Flock members may gain foraging benefits by copying information from other flock members about successful patches or by taking prey flushed by others (Powell 1985, Terborgh 1990, Veena and Lokesha 1993, Greenberg 2000). Members of winter woodland flocks in the North Temperate Zone have been shown to benefit by copying behaviors of successful individuals (Krebs 1973, Waite and Grubb 1988). However, many members of tropical mixed-species insectivore flocks engage in stereotyped,species-specific behaviors that are not conducive to social learning (Henderson 1989, Hutto 1994). With the exception of the bluish-slate and cinereousantshrikes

(*Thamnomanesschistogynus* and *T. caesius* respectively), there is little evidence that Neotropical understory flock members frequently take flushed prey (Munn 1986, English 1998).

Anti-predator benefits are generally believed to be a more important function than foraging enhancement for tropical mixed-species insectivore flocks. This is supported in part by the reduced prevalence of flocks on predator-free islands (Beauchamp 2004) and the increased survival rate for obligate flock-followers in the Neotropics (Jullien and Clobert 2000). Flock-following may incur anti-predator benefits via a number of mechanisms, including improving vigilance, decreasing the probability of the individual being selected during an attack, and creating confusion for an attacking predator (Powell 1985, Terborgh 1990, Greenberg 2000).Improved vigilancehas been cited as the most likely benefit operating in mixed-species forest flocks (Terborgh 1990, Greenberg 2000), with reduced scanning rates in individuals foraging in flocks compared to individuals foraging alone (Alves and Cavalcanti 1996, Dolby and Grubb 1998, Fernandez-Juricicet al. 2004, Sridhar et al. 2009).Furthermore, some species have been recorded foraging in more exposed situations in flocks than alone (Munn 1984, Dolby and Grubb 2000, Tubelis et al. 2006).

In some flocks, certain species appear to act as sentinels, such as greater racket-tailed drongos (*Dicrurus paradiseus*) in Sri Lanka (Goodale and Kotagama 2005), chalk-browed mockingbirds (*Mimus saturninus*) and shrike-like tanagers (*Neothraupis fasciata*) in the Brazilian Cerrado (Tubelis 2007), and *Thamnomanes* antshrikes in Amazonia (Munn and Terborgh 1979, English 1998); these species engage in sit-and-wait foraging tactics that allow them to maintain a high level of vigilance while foraging, and they are generally the first to produce alarm calls in the presence of a predator. Small- to medium-sized passerines that engage in active foraging maneuvers are believed to be more vulnerable to predatory attack by raptors than ground-dwellers or species that engage in sit-and-wait tactics (Thiollay 1999, Sridhar et al. 2009). Experimental evidence on guppies demonstrated that some foraging behaviors diverted the forager's attention from the surroundings and increased response time during a predatory attack; additionally foragers engaged in these "vulnerable" maneuvers were preferentially attacked by predators (Krause and Godin 1996). Sharp-shinned hawks (*Accipiter striatus*) also preferentially attacked foraging over vigilant birds and solitary over grouped individuals (Roth et al. 2006).A number of vulnerability attributes are correlated with the propensity of a species to join flocks (Buskirk 1976, Thiollay 1999, Sridhar et al. 2009), and such species may benefit from the vigilance and sentinel behaviorof the antshrikes in Amazonian flocks.

There are a number of possible costs associated with joining a mixed-species flock, and the cost-benefit balance likely influences how frequently a given species associates with flocks. Several studies on North Temperate woodland flocks have demonstrated both intraspecific and interspecific competition within flocks, with subordinate individuals or species restricting their foraging niches in the presence of dominants (Morse 1970, Alatalo 1981, Schneider 1984, Crimprich and Grubb 1994). However, it has been suggested that, due to the presence of species-specific foraging niches, members of mixed-species flocks experience reduced competition costs compared to similar-sized single-species flocks (Gradwohl and Greenberg 1980). In fact, several recent studies have document significant positive associations among species pairs within mixed-species flocks (Arbeláez-Cortés et al. 2011, Sridhar et al. 2012). Another potential cost is kleptoparasitism, where one species steals prey from another species in the same flock (McClure 1967, Munn 1986, King and Rappole 2001). Sentinel species, including fork-tailed drongos (*Dicrurus adsimilis*) in Botswana (Herremans and Herremans-Tonnoeyr 1997) and *Thamnomanes* anthrikes in Amazonia (Munn 1986, English 1998), have been documented to give apparently false alarm calls that cause other flock members to drop their prey, which is then snatched by the sentinel.One possible cost that remains largely untested is that species must conform to the movement rate of the flock, which could result in the use of suboptimal movement patterns and reduced foraging efficiency for some species (Partridge and Ashcroft 1976, Hutto 1988). For instance, babblers (Timaliidae) in Ceylon frequently lagged behind the other flocking species and had to interrupt foraging to catch back up (Partridge and Ashcroft 1976).

Mixed-species flocks of Amazonian rainforests are among the most diverse and seasonally stable in the world (Greenberg 2000). Two mixed-species flock types are recognized, with canopy and understory flocks consisting mostly of separate species and generally moving independently of one another (Munn 1985, Terborgh et al. 1990, English 1998). Canopy flocks appear to occupy larger territories than understory species, perhaps in part due to the tendency of many canopy species to consume fruit in addition to insects; conversely, understory flock species are strictly insectivorous (Munn 1985). Understory flocks contain 6-10 “core” species, called such because they defend a common flock territory from conspecifics and rarely forage away from the flock (Munn and Terborgh 1979, Jullien and Thiollay 1998, English 1998). Exact species composition varies regionally, but core species typically include one or two species of *Thamnomanes* spp. antshrikes, up to four species of antwrens (*Myrmotherula* and *Epinecrophylla*), one or two foliage-gleaners (*Automolus* and *Phylidor*), and one or more woodcreepers (usually *Xiphorhychus* spp.; Munn and Terborgh 1979, Jullien and Thiollay 1998, English 1998). In addition, there are seven or more species, termed “regular flock species” by Munn and Terborgh (1979), which forage almost exclusively with flocks but occupy territories that encompass more than one understory flock; these species include *Automolus infuscatus*, *Xenops minutus*, *Hylophilus ochraceiceps*, *Habia rubica*, and some woodcreepers (Munn and Terborgh 1979, Jullien and Thiollay 1998, English 1998). An additional 25 or more species, variously termed "frequent" or "occasional" flock members depending on the regularity with which they are found in flocks, follow mixed-species flocks but are also regularly seen foraging alone (Munn and Terborgh 1979, Jullien and Thiollay 1998, English 1998). These may include additional woodcreepers, foliage-gleaners, and antbirds (Thamnophilidae), as well as flycatchers (Tyrannidae), small woodpeckers (Picidae), tanagers (Thraupidae), trogons (Trogonidae), and nunbirds (*Monasa* spp.).

The wedge-billedwoodcreeper (*Glyphorynchusspirurus*) is a facultative flock-follower of the lowland Neotropics, frequently joining mixed-species understory flocks but also regularly foraging alone (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998). Previous comparisons of foraging behavior of species in and out of Amazonian flocks tended to rely on obligate species (e.g. Munn 1984), which by definition are rarely found away from flocks and therefore such foraging behaviorsare irregular and may be influenced by other factors. The Wedge-billedWoodcreeperis thus a good model species on which toconduct comparative behavioral observations.

The wedge-billed woodcreeper is a widespread suboscine passerine of the Neotropics, found in most lowland forests including mature rainforest and secondary forest (Marantz et al. 2003). Despite its wide geographic range and abundance at many locations, relatively few studies have focused on the ecology or behavior of this species. Gradwohl and Greenburg (1980) offered evidence, based on several color-marked individuals, that this species occupies extensively overlapping home ranges on Barro Colorado Island in Panama; however, home range overlap was not mentioned for this species as part of similar understory mixed-species flock studies in French Guiana (Jullien and Thiollay 1998) or central Brazil (described as a “typical territorial species", Johnson et al. 2011), and Marantz et al. (2003) suggest that home range overlap may vary across this species' range. The existence and extent of home range overlap is an important factor that may influence the probability that an individual joins a flock. In Neotropical understory flocks, most species aggressively exclude conspecifics from the flock territory, such that each species in the flock is represented by a single individual, pair, or family group (Munn and Terborgh 1979, Jullien and Thiollay 1998, English 1998). However, if the wedge-billed woodcreeper occupies extensively overlapping home ranges, they either must tolerate other conspecifics in flocks, unlike other flock members, or actively exclude conspecifics in these overlapping areas, with one individual or pair exhibiting a form of social dominance within this shared space.

The primary goals of this study were to use the wedge-billed woodcreeper as a model species for which to examine hypothesized costs and benefits of joining mixed-species flocks, and to examine the influence of intraspecific interactions on individual space use and flock-joining behavior. In Chapter 2 I compare the foraging behavior of the wedge-billed woodcreeper in and out of flocks and discuss the differences in the context of proposed costs and benefits of flocking behavior. In Chapter 3 I examine the effects of body mass, body condition, and environmental characteristics of the home range on individual flocking propensity. In Chapter 4 I discuss the influence of habitat characteristics and overlapping neighbor space on flock-following locations, and I provide details on the phenomenon of home range overlap among individuals at this study site. In Chapter 5 I provide the first description of a display behavior used in multiple contexts including courtship, along with notes about the timing and behaviors associated with incubation and fledgling care.

Literature Cited

Alatalo, R. V. 1981. Interspecific competition in tits *Parus* spp. and the goldcrest *Regulus regulus*: Foraging shifts in multi-specific flocks. Oikos 37:335–44.

Alves, M. A. S., and R. B. Cavalcanti. 1996. Sentinel behavior, seasonality, and the structure of bird flocks in a Brazilian savanna. Ornitologia Neotropical 7:43–51.

Arbeláez-Cortés, E., H. A. Rodríguez-Correa, and M. Restrepo-Chica. 2011. Mixed bird flocks: patterns of activity and species composition in a region of the Central Andes of Colombia. Revista Mexicana de Biodiversidad 82:19–31.

Beauchamp, G. 2004. Reduced flocking by birds on islands with relaxed predation.Proceedings of the Royal Society of London B 271:1039–1042.

Buskirk, W. H. 1976. Social systems in a tropical forest avifauna. The American Naturalist 110:293–310.

Cimprich, D. A., and T. C. Grubb. 1994. Consequences for Carolina chickadees of foraging with tufted titmice in winter. Ecology 75:1615–1625.

Diamond, J. 1987. Flocks of brown and black New Guinean birds: a bicoloured mixed-species foraging association. Emu 87:201–211.

Dolby, A. S., and T. C. Grubb, Jr. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Animal Behaviour 56:501–509.

Dolby, A. S., and T. C. Grubb, Jr. 2000. Social context affects risk taking by a satellite species in a mixed-species foraging group. Behavioral Ecology 11:110–114.

English, P. H. 1998. Ecology of mixed-species understory flocks in Amazonian Ecuador. Ph.D. Dissertation, University of Texas, Austin.

Fernandez-Juricic, E., J. T. Erichsen, and A. Kacelnik. 2004. Flock density, social foraging, and scanning: an experiment with starlings. Behavioral Ecology 15:371–379.

Goodale, E. and S. W. Kotagama. 2005. Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. Journal of Tropical Ecology 21:669–676.

Gradwohl, J., and R. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. Auk 97:385–395.

Greenberg, R. 2000. Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. Pages 521–558 in On the Move: How and Why Animals Travel in Groups (S. Boinski, and P. A. Garber, Eds). The University of Chicago Press, Chicago.

Henderson, I. G. 1989. The exploitation of tits *Parus* species, long-tailed tits *Aegithos caudatus* and goldcrests *Regulus regulus* by treecreepers *Certhia familiaris*: A behavioural study. Bird Study 36:99–104.

Herremans, M, and D. Herremans-Tonnoeyr. 1997. Social foraging of the forktailed drongo *Dicrurus adsimilis*: beater effect or kleptoparasitism? Bird Behavior 12:41–45.

Hutto, R. L. 1988. Foraging behavior patterns suggest a possible cost associated with mixed-species bird flocks. Oikos 51:79–83.

Hutto, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in western Mexico. Condor 96:105–118.

Johnson, E. I., P. C. Stouffer, and C. F. Vargas. 2011. Diversity, biomass, and trophic structure of a central Amazonian rainforest community. Revista Brasileira de Ornitologia 19: 1-16.

Jullien, M., and J. Clobert. 2000. The survival value of flocking in Neotropical birds: Reality or fiction? Ecology 81:3416–3430.

Jullien, M., and J.-M.Thiollay. 1998. Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. Journal of Animal Ecology 67:227–252.

King, D. I. and J. H. Rappole. 2001. Kleptoparasitism of laughingthrushes *Garrulax* by greater racket-tailed drongos *Dicrurus paradiseus* in Myanmar. Forktail 17:121–122.

Kotagama, S. W. and E. Goodale. 2004. The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. Forktail 20:63–70.

Krause, J., and J.-G.Godin. 1996. Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. Behavioral Ecology 7:264–271.

Krebs, J. R. 1973. Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). Canadian Journal of Zoology 51:1275–1288.

Leck, C. F. 1971. Measurement of social attractions between tropical passerine birds. Wilson Bulletin 86:278-283.

Marantz, C. A., A. Aleixo, L. R. Bevier, and M. A. Patten. 2003. Family Dendrocolaptidae (Woodcreepers). Pages 358–447 inHandbook of the Birds of the World, vol. 8: Broadbills to Tapaculos (J. del Hoyo, A. Elliott, and D. Christie, Eds). Lynx Edicions, Barcelona.

McClure, H. E. 1967. The composition of mixed species flocks in lowland and sub-montane forests of Malaya. Wilson Bulletin 79:131–154.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecological Monographs 40:119–168.

Moynihan, M. 1962. The organization and probable evolution of some mixed species flocks of Neotropical birds. Smithsonian Miscellaneous Collections 143:1–140.

Munn, C. A. 1984. The behavioral ecology of mixed-species bird flocks in Amazonian Peru. Ph.D. Dissertation, Princeton University, Princeton.

Munn, C. A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. Ornithological Monographs 36:683–712.

Munn, C. A. 1986. Birds that ‘cry wolf’. Nature 319:143–145.

Munn, C. A., and J. W.Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. Condor 81:338–347.

Partridge, L., and R. Ashcroft. 1976. Mixed-species flocks of birds in hill forest in Ceylon. Condor 78:449–453.

Powell, G. V. N. 1979. Structure and dynamics of interspecific flocks in a Neotropical mid-elevation forest. Auk 96:375-390.

Powell, G. V. N. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. Ornithological Monographs 36:713–732.

Roth, T. C. II, S. L. Lima, and W. E. Vetter. 2006. Determinants of predation risk in small wintering birds: the hawk’s perspective. Behavioral Ecology and Sociobiology 60:195–204.

Schneider, K. J. 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. Ecology 65:1820–1827.

Sridhar, H., G. Beauchamp, and K. Shanker. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Animal Behaviour 78:337–347.

Sridhar, H., U. Srinivasan, R. A. Askins, J. C. Canales-Delgadillo, C.-C. Chen, D. N. Ewert, G. A. Gale, E. Goodale, W. K. Gram, P. J. Hart, K. A. Hobson, R. L. Hutto, S. W. Kotagama, J. L. Knowlton, T. M. Lee, C. A Munn, S. Nimnuan, B. Z. Nizam, G. Péron, V. V. Robin, A. D. Rodewald, P. G. Rodewald, R. L. Thomson, P. Trivedi, S. L. Van Wilgenburg, and K. Shanker. 2012. Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. The American Naturalist 180:777–790.

Terborgh, J. 1990. Mixed flocks and polyspecific associations: Costs and benefits of mixed groups of birds and monkeys. American Journal of Primatology 21:87–100.

Terborgh, J., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. Ecological Monographs 60:213-238.

Thiollay, J.-M. 1999. Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: An intertropical comparison. Journal of Avian Biology 30:282–294.

Tubelis, D. P. 2007. Mixed-species flocks of birds in the Cerrado, South America: a review. Ornitologia Neotropical 18:75–97.

Tubelis, D. P., A. Cowling, and C. Donnelly. 2006. Role of mixed-species flocks in the use of adjacent savannas by forest birds in the central Cerrado, Brazil. Austral Ecology 31:38–45.

Veena, T. and R. Lokesha. 1993. Association of drongos with myna flocks: are drongos benefitted? Journal of Biosciences 18:111–119.

Waite, T. A., and T. C. Grubb, Jr. 1988.Copying of foraging locations in mixed-species flocks of temperate-deciduous woodland birds: an experimental study. Condor 90:132–140.

Willson, S. K. 2004. Obligate army-ant-following birds: a study of ecology, spatial movement patterns, and behavior in Amazonian Peru. Ornithological Monographs 55:1–67.

CHAPTER 2: COMPARISON OF FORAGING BEHAVIORS AND MOVEMENT PATTERNS OF THE WEDGE-BILLED WOODCREEPER (*GLYPHORYNCHUS SPIRURUS*) TRAVELING ALONE AND IN MIXED-SPECIES FLOCKS IN AMAZONIAN ECUADOR

Abstract

Flocking propensity in any given species is probably determined by the balance of costs and benefits of joining a flock. The wedge-billed woodcreeper (*Glyphorynchusspirurus*) frequently joins mixed-species understory bird flocks but also often forages alone. In this study, I compared the foraging behavior and microhabitat use of Wedge-billed woodcreepers foraging in and out of flocks, and I examined the differences in the context of severalhypothesized costs and benefits of flocking. I observed wedge-billed woodcreepers in two forest plots at Tiputini Biodiversity Station, Orellana Province, Ecuador during Jan-Mar of 2010-2012. I measured foraging height range, time spent per trunk, vertical movement rate, distance flown between trunks, extent of foliage cover around the foraging bird, hitch (search movement) rate, peck (prey attack) rate, and scan rate. I tracked woodcreepersin 2012 using radio telemetry to measure movement rates and to record the locations of flock-joining and -leaving. Woodcreepers in flocks foraged in more exposed microhabitats, spent less time per trunk, and exhibited greater hitch rates and vertical movement rates, and foraged in a narrower height range than woodcreepers foraging alone. Scanning rates, peck rates, and distance flown between trunks did not differ between flock situations. Horizontal movement rate did not differ in and out of flocks, but the length of individual flock-following sessions was negatively correlated with movement rate. These observations support an anti-predator benefit of flocking for this species. Conversely, woodcreepers may experience an energetic cost or decreased foraging efficiency associated with conforming to flock movement patterns.

Introduction

Mixed-species bird flocks are prevalent year-round throughout much of the world's lowland rainforests,and they are particularly diverse in the Neotropics (Powell 1985). Mixed-species flocks of understory insectivores in the Amazon Basin generally consist of one or two antshrike (*Thamnomanes*)species and 10-12 "core" species that share a common territory that is defended against other conspecifics (Munn and Terborgh 1979, Wiley 1980, English 1998, Jullien and Thiollay 1998). The core species are considered to be obligate flock-followers, rarely or never seen foraging away from flocks. In addition, 30 or more species are facultative flock-followers, joining these flocks for varying lengths of time but also regularly foraging away from them (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998).

Most hypothesized benefits of flocking fall under two categories: increased foraging efficiency and protection from predators. These types of benefits are not mutually exclusive, particularly when decreased time spent in vigilance allows for more time spent feeding (Dolby and Grubb 1998, Fernandez-Juricic et al. 2004b, Sridhar et al. 2009). Flock members may gain foraging benefits by copying information from other flock members about successful patches or by taking prey flushed by others (Powell 1985, Terborgh 1990, Greenberg 2000). However, many members of tropical mixed-species insectivore flocks engage in stereotyped,species-specific behaviors that are not conducive to social learning (Henderson 1989, Hutto 1994), and furthermore, typically only one individual or family group per species is present in a flock (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998). With the exception of the bluish-slate and cinereousantshrikes (*Thamnomanesschistogynus* and *T. caesius* respectively), there is little evidence that Neotropical understory flock members frequently take flushed prey (Munn 1986, English 1998).

Anti-predator benefits are generally believed to be a more important function than foraging enhancement for tropical mixed-species insectivore flocks. This is supported in part by the reduced prevalence of flocks on predator-free islands (Beauchamp 2004) and the increased survival rate for obligate flock-followers in the Neotropics (Jullien and Clobert 2000). Flock-following may incur anti-predator benefits via a number of mechanisms, including improving vigilance, decreasing the probability of the individual being selected during an attack, and creating confusion for an attacking predator (Powell 1985, Terborgh 1990, Greenberg 2000).Improved vigilance, either by the actions of sentinel species or the presence of many individuals, has been cited as the most likely benefit operating in mixed-species forest flocks (Terborgh 1990, Greenberg 2000). Evidence for this hypothesis comes from numerous studies that document reduced scanning rates in individuals foraging in flocks compared to individuals foraging alone (Alves and Cavalcanti 1996, Dolby and Grubb 1998, Fernandez-Juricicet al. 2004b, Sridhar et al. 2009). Furthermore, some species have been recorded foraging in more exposed situations in flocks than alone (Munn 1984, Dolby and Grubb 2000, Tubelis et al. 2006).

Small- to medium-sized passerines that engage in active foraging maneuvers are believed to be more vulnerable to predatory attack by raptors than ground-dwellers or species that engage in sit-and-wait tactics (Thiollay 1999, Sridhar et al. 2009). Experimental evidence on guppies demonstrated that some foraging behaviors diverted the forager’s attention from the surroundings and increased response time during a predatory attack; additionally foragers engaged in these “vulnerable” maneuvers were preferentially attacked by predators (Krause and Godin 1996). Sharp-shinned hawks (*Accipiter striatus*) also preferentially attacked foraging over vigilant birds and solitary over grouped individuals (Roth et al. 2006).A number of vulnerability attributes are correlated with the propensity of a species to join flocks (Buskirk 1976, Thiollay

1999, Sridhar et al. 2009), and such "vulnerable" species may benefit from the detection afforded by the vigilance of sentinel species or the presence of many individuals in flocks.

Relatively few studies have examined the possible costs associated with joining a mixed-species flock, and the cost-benefit balance likely influences how frequently a given species associates with flocks. Due to the presence of species-specific foraging niches, competition costs are likely reduced for members of mixed-species flocks compared to similar-sized single-species flocks (Gradwohl and Greenberg 1980). In fact, several recent studies have documented significant positive associations among species pairs within mixed-species flocks (Arbeláez-Cortés et al. 2011, Sridhar et al. 2012).A likely cost for members of mixed-species flocks is that species must conform to the movement rate of the flock, which could result in the use of suboptimal movement patterns and reduced foraging efficiency for some species (Partridge and Ashcroft 1976, Hutto 1988). For instance, babblers (Timaliidae) in Ceylon frequently lagged behind the other flocking species and had to interrupt foraging to catch back up (Partridge and Ashcroft 1976).

The wedge-billed woodcreeper (*Glyphorynchusspirurus*) is a facultative flock-follower of the lowland Neotropics, frequently joining mixed-species understory flocks but also regularly foraging alone (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998).The wedge-billed woodcreeperis thus a good model species on which toconduct comparative behavioral observations. Like most other woodcreepers, it forages by moving vertically along trunks and gleaning arthropods from the bark (Marantz et al. 2003). This behavior confers a large vertical component to its movement patterns that is lacking in the majority of core flock species, most of which glean insects from leaves (Munn and Terborgh 1979, English 1998). Therefore, in order to keep up with a moving flock, a wedge-billed woodcreeper might make one or more of the following behavioral modifications: reduce the height range searched per trunk, increase vertical movement rate, or increase the distance flown between trunks. Any of these modifications might manifest as a cost if they result in decreased foraging efficiency, or if an increase in movement rate is not compensated by an increase in energetic intake.

The purpose of this study was to compare the foraging behavior of wedge-billed woodcreepers in and out of flocks to determine the most likely costs and benefits derived by this facultative flock-follower. If the main benefit gained from flock-following is anti-predator vigilance, then we hypothesize that thewedge-billed woodcreepers would forage in more dense cover and spend more time in vigilant behavior away from flocks than in flocks. I hypothesized that the primary cost to flock-following is an increase in movement rate that compromises foraging efficiency. Therefore I expected one or more of the following behavioral changes: 1) an increase in either horizontal or vertical movement rates, or both, while following flocks; 2) a decrease in attack to search maneuver ratio in flocks than alone; and 3) a decrease in time spent with a flock as a function of flock movement rate.

Methods

Study area

This study was conducted atTiputini Biodiversity Station (0°38’15”S, 76°08’59”W) in Orellana Province, Ecuador. The station encompasses 638 ha of rainforest within the 1,682,000-ha UNESCO Yasuni Biosphere Reserve. The forest is composed mainly of undisturbed terra firme rainforest, with a strip of varzea bordering theTiputini River. The mean elevation at the station is ~220m above sea level, and the region receives roughly 3200mm of rainfall annually with a relatively dry period from January to February. The current project was conducted on two ~100-

ha plots within the reserve, separated by ~1.5 km (Blake 2007). Both plots consisted primarily of mature terra firme forest, with one plot characterized by a more dissected topography and the other plot flatter overall (although with a similar mean elevation; Blake 2007) with relatively more treefalls and swampy depressions. Abundance of wedge-billed woodcreepers and the flock-leading cinereous and dusky-throated antshrikes (T. *ardesiacus*) are similar in both plots (Blake 2007).

Field methods

I conducted foraging observations during all daylight hours from 12 Janto 5 Mar 2010, 17 Jan to 7 Feb 2011, and 14 Jan to 27 Mar 2012. In 2010 I systematically searched the plot trails for wedge-billed woodcreepers (hereafter "woodcreepers"). When I encountered a flock, I conducted observations on the first woodcreeper spotted in the flock. Only one individual per flock was observed unless other individuals were identifiable by color bands. In 2011 and 2012, I conducted observations opportunistically on unmarked and radio-tagged individuals (see below). I averaged repeated observations of five marked individuals in 2010, six in 2011, and ninein 2012, separately for flocking and non-flocking situations, for the current analysis.

Each foraging observation was categorized as “no flock” or “flock”. I considered a woodcreeper to be in a flock if it was actively foraging inside a flock or ≤10 m of a flock edge (maximum nearest-neighbor distance in Wiley [1980]).I began the observation when the focal individual flew to a new tree and continued until I lost track of the bird. For observations that included a complete bout on a trunk (bird was seen both alighting on and departing from that trunk), I visually estimatedstart height and end height to the nearest 0.5 m, and I measurd the time spent on that trunk (2010, 2012). I estimated the distance flown between trunks to the nearest 1 m in 2010. I categorized cover within a 1-m-radius sphere of the foraging individual as open (<25% cover), medium (25-75%), or dense (>75%). In 2010, I dictated foraging maneuvers continuously into a digital voice recorder. Maneuvers were categorized as pecks (any movement where the bill struck the surface of the trunk), hitches (one hitch = single hop resulting in an upward movement along the trunk), and scans (or head cocks as in Sullivan [1984]; twisting the head to the side in apparent attempt to scan the environment). The peck, hitch, and scan counts were then divided by the observation time to measure peck, hitch, and scan rates (no./min).

I captured wedge-billed woodcreepers in both study plots in 2012 using 2.6-m mist nets as part of a long-term demographic study of understory birds (see Blake and Loiselle 2012 for additional details). Twenty-three individuals were captured between 10 Jan and 17 Mar 2012 and fitted with a radio transmitter (0.45g BD-2, Holohil Systems Ltd., Carp, Ontario) using a thigh harness (Rappole and Tipton 1991) made from either cotton or elastic thread. Individuals were released at the site of capture.

I tracked woodcreepers during all daylight hours using Advanced Telemetry Systems Field Master receivers and hand-held three-element Yagi antennas for 2-3 h per day, beginning at least 24 hafter capture. I randomized the order of tracking each day such that all individuals had an equal proportion of tracking sessions among daily time periods. I determined the location of the woodcreeper by homing, in which the woodcreeper was approached until it was either seen, or until the lack of directionality in the signal indicated close proximity (~10m; technicians were trained with the transmitters prior to tracking in order to calibrate their abilities to judge distances using the equipment).I recorded location using a GPS unit every 15 min during the tracking sessions, along with the time and location of any flock-joining or flock-leaving.I occasionally recorded location at shorter time intervals if the focal individual changed direction multiple times while traveling a long distance (e.g. > 100m), or if a focal individual moved away and then returned to the same spot.

Statistical analysis

I compared flight distance between trunks, hitch rate, peck rate, scan rate, peck:hitch ratio, height range, time spent per trunk, cover use, horizontal movement rate, and vertical movement rate of woodcreepers foraging in and out of flocks. I pooled data from multiple years and from both plots. I used the Shapiro-Wilk test to determine if data were normally distributed and ln-transformed if necessary and re-tested the data for normality. I used at-test or Mann-Whitney U-test to compare each variable between flocking and non-flocking situations.I used log-linear regression to model the effect of flocking situation on the frequency of cover category use. I performed all statistical analyses in program R 2.15.1 (R Development Core Team 2012) at $\alpha<0.05$.

I formed two subsets of the data to investigate the effects of an unknown level of pseudoreplication present in the behavioral data set due to repeated observations of unmarked individuals. One set, termed the “independent set”, included single randomly selected observations from marked individuals and randomly selected observations from unmarked individuals spaced 400m apart in both plots from all years. I chose this distance because the likelihood that observations spaced 400m apart were from the same individual is very small, given the high density (Blake and Loiselle 2012) and the average home range size of this species at this site (~4 ha, Darrah, unpubl. data). The second subset, termed the “pseudoreplication set”, contained only repeated observations of 20 marked individuals from all years. Due to the small sample size of many behavior data, I generated these subsets using cover data only. In both subsets, I modeled the effect of flocking situation on cover use using log-linear regression.

I measured distances and times between consecutive locations within tracking sessions for each individual using the Movement Path Metrics feature in Geospatial Modeling Environment (GME; Beyer 2009) and categorized each location as "in flock" or "no flock". I used the distances and times to calculate the movement rate (m/min) between points. To test the hypothesis that movement rates differ in flocks and out of flocks, I conducted an ANOVA on movement rates with factors flock, individual, and flock-individual interaction. To explore the relationship between flock-following behavior and movement rates, I grouped the data for each individual into flock sessions (single events of joining and then leaving a flock), with the time spent in the flock and the average movement rate calculated for each session. I fit a linear mixed-effects model of the effect of movement rate on flock session length using residual maximum likelihood methods in program R, with individual included as a random effect.

To consider the possibility that any high movement rates in flocks simply resulted in reaching the woodcreeper’s home range boundary sooner, I explored the relationships among flock-joining locations, flock-leaving locations, and session length. I estimated the utilization distribution (UD) for each individual in 2012 in GME using fixed-kernel density estimation, with the smoothing parameter chosen using the least squares cross-validation method (Seaman and Powell 1996). For each individual, I measured the volume of the UD at each cell of the kernel density raster by generating percent volume contours (1-99%; Kertson and Marzluff 2010) using the Contour tool in GME. I converted the contours to a raster of volume measurements in ArcMAP (ESRI, Redlands, California) using the Feature to Raster tool in ArcTool Box. I plotted the locations of flock-joining and flock-leaving for each individual onto that individual’s UD volume raster, and I measured the volume of the UD at each flock-joining or -leaving point as an index of proximity to the edge of the home range. I used linear mixed-effects regression with individual as a random effect in program R to investigate the effects of flock-joining location and session length on flock-leaving location.

Results

Foraging Behavior

Woodcreepers spent less time per trunk while foraging in flocks than when foraging alone (F = 18.83, df = 1 and 3, p< 0.001; Table 1), and this pattern did not differ between years (F = 1.83, df = 1 and 3, p = 0.18). In 2010, hitch rate was significantly greater in flocks (U = 59, p = 0.03), while peck rate (U = -19, p = 0.43) and scan rate (U = -20.5, p = 0.28) differences were non-significant (Table 1). Woodcreepers used a smaller height range per trunk while foraging in flocks than alone (U = -2194.5, p = 0.046), as a result of a significant decrease in end height (t = 2.31, df = 74, p = 0.02) in flocks, but no change in start height (t = -1.70, df = 75.6, p = 0.093). Vertical movement rate was greater in flocks than alone (t = 2.4, df = 61.8, p = 0.016). There was no difference in flight distance between trunks (U = -9.5, p = 0.70) between flocking situations (Table 1). Woodcreepers used significantly less cover when foraging in flocks compared to foraging alone (χ^2 = 12.75, df = 2, p = 0.002; Fig. 1).

Effects of pseudoreplication

Wedge-billed woodcreepers used areas of less dense cover more frequency in flocks than alone in the independent set (χ^2 = 6.99, df = 2, p = 0.03), while this was marginally non-significant in the pseudoreplication set (χ^2 = 5.31, df = 2, p = 0.07; Table 2).

Movement rates and flock sessions

Movement rates of wedge-billed woodcreepers did not differ in and out of flocks (F = 1.68, df = 1 and 24, p = 0.19), although there was significant variation in average movement rate among individuals (F = 3.06, df = 22 and 24, $p < 0.001$). Mean individual movement rates varied from 1.35 m/min (0.22 SE) to 2.9 m/min (0.27 SE), with an overall mean of 2.2 m/min (0.55 SE) out of flocks and 2.36 m/min (0.11 SE) in flocks. Overall mean flock-following session length was 36.1 min (2.32 SE; range 5-210 min) with a mean of 91.7 m (5.6 SE; range 0-377 m) traveled per session. Session length was inversely related to movement rate (t = -2.33, df = 150, p = 0.02; Fig. 2). Location of flock-leaving was positively correlated with location of flock-joining (t = 12.12, df = 150, $p < 0.001$; Fig. 3) and unrelated to the length of the session (t = -3.45, df = 150, p = 0.12).

Discussion

Woodcreeper vertical movement rate was greater in flocks than alone, despite a concurrent decrease in height range utilized in flocks. The increased search movement (hitch) rate without a concurrent increase in prey attack (peck) rate, suggests that woodcreepers may incur an energetic cost while following flocks. Woodcreepers may have reduced the time spent per trunk in order to keep up with flock movements, given that they did not increase the distance flown between trunks while following flocks in this study. In a study on mixed-species flocks in Panama, Pomaraet al. (2003) also found that slate-throated redstarts (*Myioborusminiatus*) increased movement rates but not attack rates when foraging in flocks. They attributed this change to a shift from sit-and-wait flycatchingto a more active foraging strategy suitable for keeping up with a moving flock. If the time spent per trunk by woodcreepersis constrained by the need to keep up with the flock, this may or may not represent a cost of flock-following. On the one hand, increased search rate without a concurrent increase in attack rate suggests a reduction in foraging efficiency while in flocks. On the other hand, it is possible thatwoodcreeperscould compensate by taking only larger, more profitable prey items (Giraldeau and Caraco 2000). To further complicate matters, it is probable that some proportion of "pecks" constitutes search behavior rather than prey attack. Unfortunately it was not possible to measure prey capture rate in this species due to its rapid movements and often tiny prey consumed (English 1998, Marantz et al. 2003), although an increased search rate would be expected to yield a greater capture rate (Norberg 1977, Robinson and Holmes 1982). Thus it appears that woodcreepers increased search rates while in flocks, but it is not clear how this may have affected foraging efficiency.

Despite the decreased time spent per trunk in flocks, movement rates (m/min, generally measured over a 15-min period) did not differ in flocks or without. This may be due in part to the different time scales over which these variables were measured; the movement rate data reveals broader-scale movements that would not capture finer-scale variation due to visiting consecutive trunks in a non-linear pattern. However, movement rate was negatively correlated with flock session length, suggesting that woodcreepers may drop out of flocks sooner if they are moving faster. While flock movement rates were not measured in this study, examination of Figure 3 in Jullien and Thiollay (1998) reveals that *Thamnomanes*-led understory flocks (composition similar at the genus level to those in western Amazonia) moved at rates ranging from 1-11 m/min in lowland rainforest of French Guiana. If western Amazonian flocks move at similar rates, then flocks may regular move at a rate well above the average movement rate of wedge-billed woodcreepers at this site. There may be an energetic cost associated with keeping up with a rapidly moving flock, such that after a certain threshold is reached, the costs of following outweigh the benefits and the woodcreeper leaves the flock.

The negative relationship between movement rate and flock-following session lengthwas notresult of reaching the edge of the woodcreeper's home range more quickly; the relative positions of flock-joining and flock-leaving locations were positively correlated, which suggests that woodcreepers did not always travel from one edge of their home range to the other in a flock and regularly left flocks that were present in the core of their home range (>50% volume; Fig. 4). This differs from the observations of Pomara et al. (2007) for four passerine species in Panama, which were observed to join flocks for as long as the flock was present within the follower's home range. This has often been assumed to be the case for flock-followers in Amazonia (Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Marantz et al. 2003, Jullien and Thiollay 1998), but this study demonstrates that, for the wedge-billed woodcreeper, additional factors (such as flock movement rate) besides flock presence within the home range may influence an individual's decision to join a flock.

Wedge-billedWoodcreepers foraged in more exposed microhabitats when in flocks than when alone, which is consistent with the anti-predator hypothesis of flock function. Similarly, Munn (1984) reported several species that used less exposed microhabitats in the absence of the sentinel antshrikes, and Dolby and Grubb (2000) found that white-breasted nuthatches (*Sittacarolinensis*) were more reluctant to visit exposed feeders in the absence of tufted titmice (*Baeolophus bicolor*). Many animals respond to increases in predation risk by foraging in more protected areas, even if these areas are less profitable (Sih 1982, Lima and Dill 1990, Suhonen 1993). The reduced predation risk associated with flocking may release the Wedge-billedWoodcreeper from such constraints, allowing individuals to forage on a wider range of trunk surfaces. Such an explanation would mirror the observations of Tubelis et al. (2006), who suggested that participation in mixed-species flocks allowed some forest species to use more open habitats away from forest that they avoided while foraging alone. An alternative explanation is that the wedge-billed woodcreeper is subordinate to other flock members and thus is competitively excluded from more protected sites, as has been demonstrated in white-throated sparrows (*Zonotrichiaalbicollis*; Schneider 1984) and parid flocks (Morse 1970, Alatalo 1981,Cimprich and Grubb 1994). However, direct interspecific competition is likely to be minimal in the present case due to niche separation between the wedge-billed woodcreeper and other flock members, including other woodcreepers (Marantz et al.2003). The wedge-billed woodcreeper was never observed being supplanted by larger woodcreeper species in this study.

There was no significant reduction in scanning rate in woodcreepers foraging in flocks compared to foraging alone. This is contrary to the many studies that have demonstrated reduced scanning rates in individuals in flocks (Sullivan 1984, Fernandez-Juricicet al. 2004b, Sridhar et al. 2009).Foraging theories have historically assumed that vigilance and foraging maneuvers are mutually exclusive (e.g. Pulliam et al. 1982, Lima 1987), but more recent studies have suggested that many species can maintain some level of vigilance during feeding(Lima and Bednekoff 1999, Dukas and Kamil 2000, Cresswell et al. 2003). Due to the vertical body orientation of a foraging woodcreeper and the wide view afforded by laterally-positioned eyes (Fernandez-Juricicet al. 2004a), it is likely that woodcreepers can simultaneously search for food and predators. Indeed, few (n=12) unequivocal scans were observed in this study regardless of the social situation. Focusing attention on a foraging substrate, however, can result in a delayed reaction to dangerous stimuli perceived in the peripheral vision (Dukas and Kamil 2000),therefore foraging birds can still receive vigilance benefits by joining a flock even if they are able to maintain some level of personal vigilance.

In this study, social behavior was categorized as “with flock” or “without flock”. Although this ignores variation in flock size and composition, for the purposes of this study this dichotomy is adequate. First, the presence and number of core species varied little over spatial or temporal scales (pers. obs.; see English 1998 for additional details on flock composition in the area); all flocks contained both species of *Thamnomanes*antshrikes, three or more *Myrmotherula* and*Epinocrophylla*antwrens (generally including long-winged antwren [*M. longipennis*], white-flanked antwren [*M. axillaris*], and gray antwren [*M. menetriesii*]), one or more foliage-gleaners (*Automolus* and *Phylidor* spp.), and one or two *Xyphorynchus*spp. woodcreepers. A large source of variation in flock size and composition that may be of interest for future investigation is the concurrent presence or absence of a canopy flock (Munn and Terborgh 1979, English 1998), which would affect the average height of flock members and thus possibly the height range used by attendant wedge-billed woodcreepers. On one hand, if the primary benefit of joining a flock is to gain an anti-predator benefit in terms of improved vigilance, the exact composition of the flock should have little effect on most behaviors of an attendant wedge-billed woodcreeper as long as the sentinel antshrikes are present; on the other hand, several studies have documented that the movement rate of flocks increases with total flock size (Powell 1985, Greenberg 2000), and thus the total size of the flock may affect the length of time a wedge-billed woodcreeper can remain with the flock.

In the comparison between data subsets with extensive pseudoreplication and little to no pseudoreplication, the patterns of foraging behavior were broadly similar.Analysis of flocking status on the use of different vegetation densities revealed a significant tendency to use more open microhabitats in flocks and denser microhabitats away from flocks in the independent subset only, although this effect was only marginally non-significant in the pseudoreplication subset and exhibited the same overall pattern. The similarity of these results to each other and to those of the entire data set, despite the smaller sample size of the pseudoreplication subset and the extensive pseudoreplication that that likely far exceeds any hidden in the entire data set, suggests that analyses on the remainder of the behavior dataset were robust to some violation of statistical independence between observations.

Wedge-billed woodcreepers appear to join flocks to benefit from the additional vigilance provided by other flock members, freeing them to foraging in more exposed areas.At present, the hypothesized cost is an increased energetic demand, reduced foraging efficiency, or both, associated with the need to modify movement rates to keep up with the flock. Future studies could employ video of foraging behavior, which could be examined at slow speed, to allow a robust measurement of prey attack and capture rates to test this hypothesis.

Acknowledgments

I would like to thank B. Loiselle and J. Blake for their invaluable comments and logistical assistance in the field, and for permitting us to use their plots for this study. I thank the staff of Tiputini Biodiversity Station for their support and C. de Romo for arranging transportation to and from the field station. I thank N. Strycker and R. Rylander for volunteering their time to aid in data collection. B. Loiselle, G. Huxel, and three anonymous reviewers kindly provided comments on an earlier draft of this manuscript. Financial support was provided by the University of Arkansas Graduate School and the Arkansas Audubon Society Trust.

Literature Cited

Alatalo, R. V. 1981. Interspecific competition in tits *Parus* spp. and the goldcrest*Regulusregulus*: Foraging shifts in multi-specific flocks. Oikos 37:335–44.

Alves, M. A. S., and R. B. Cavalcanti. 1996. Sentinel behavior, seasonality, and the structure of bird flocks in a Brazilian savanna. Ornitologia Neotropical 7:43–51.

Arbeláez-Cortés, E., H. A. Rodríguez-Correa, and M. Restrepo-Chica. 2011. Mixed bird flocks: patterns of activity and species composition in a region of the Central Andes of Colombia. Revista Mexicana de Biodiversidad 82:19–31.

Beauchamp, G. 2004. Reduced flocking by birds on islands with relaxed predation.Proceedings of the Royal Society of London B 271:1039–1042.

Beyer, H. L. 2009.Geospatial Modelling Environment. http://www.spatialecology.com/gme/.

Blake, J. G. 2007. Neotropical forest bird communities: a comparison of species richness and composition at local and regional scales. Condor 109:237–255.

Blake, J. G., and B. A. Loiselle. 2012. Temporal and spatial patterns in abundance of the wedge-billed woodcreeper (*Glyphorynchus spirurus*) in lowland Ecuador. The Wilson Journal of Ornithology 124:436-445.

Buskirk, W. H. 1976. Social systems in a tropical forest avifauna. The American Naturalist 110:293–310.

Cimprich, D. A., and T. C. Grubb. 1994. Consequences for Carolina chickadees of foraging with tufted titmice in winter. Ecology 75:1615–1625.

Cresswell, W., J. L. Quinn, M. J. Whittingham, and S. Butler. 2003. Good foragers can also be good at detecting predators. Proceedings of the Royal Society of London, Series B 270:1069–1076.

Dolby, A. S., and T. C. Grubb, Jr. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Animal Behaviour 56:501–509.

Dolby, A. S., and T. C. Grubb, Jr. 2000. Social context affects risk taking by a satellite species in a mixed-species foraging group. Behavioral Ecology 11:110–114.

Dukas, R., and A. C. Kamil. 2000. The cost of limited attention in Blue Jays. Behavioral Ecology 11:502–506.

English, P. H. 1998. Ecology of mixed-species understory flocks in Amazonian Ecuador. Ph.D. Dissertation, University of Texas, Austin.

Fernandez-Juricic, E., J. T. Erichsen, and A. Kacelnik.2004a. Visual perception and social foraging in birds. Trends in Ecology and Evolution 19:25–31.

Fernandez-Juricic, E., J. T. Erichsen, and A. Kacelnik. 2004b. Flock density, social foraging, and scanning: an experiment with starlings. Behavioral Ecology 15:371–379.

Giraldeau, L.-A., and T. Caraco. 2000. Social Foraging Theory. Princeton University Press, Princeton.

Gradwohl, J., and R. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. Auk 97:385–395.

Greenberg, R. 2000. Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. Pages 521–558 inOn the Move: How and Why Animals Travel in Groups (S. Boinski, and P. A. Garber, Eds). The University of Chicago Press, Chicago.

Hutto, R. L. 1988. Foraging behavior patterns suggest a possible cost associated with mixed-species bird flocks. Oikos 51:79–83.

Hutto, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in western Mexico. Condor 96:105–118.

Jullien, M., and J.-M.Thiollay. 1998. Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. Journal of Animal Ecology 67:227–252.

Jullien, M., and J. Clobert. 2000. The survival value of flocking in Neotropical birds: Reality or fiction? Ecology 81:3416–3430.

Kertson, B. N., and J. M. Marzluff. 2010. Improving studies of resource selection by understanding resource use. Environmental Conservation 38:18–27.

Krause, J., and J.-G.Godin. 1996. Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. Behavioral Ecology 7:264–271.

Lima, S. L. 1987. Vigilance while feeding and its relation to the risk of predation. Journal of Theoretical Biology 124:303–316.

Lima, S. L., and P. A. Bednekoff. 1999. Back to the basics of antipredatory vigilance: Can nonvigilant animals detect attack? Animal Behaviour 58:537–543.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Marantz, C. A., A. Aleixo, L. R. Bevier, and M. A. Patten. 2003. Family Dendrocolaptidae (Woodcreepers). Pages 358-447 inHandbook of the Birds of the World, vol. 8: Broadbills to Tapaculos (J. del Hoyo, A. Elliott, and D. Christie, Eds). Lynx Edicions, Barcelona.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecological Monographs 40:119–168.

Munn, C. A. 1984. The behavioral ecology of mixed-species bird flocks in Amazonian Peru. Ph.D. Dissertation, Princeton University, Princeton.

Munn, C. A. 1986. Birds that ‘cry wolf’. Nature 319:143–145.

Munn, C. A., and J. W.Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. Condor 81:338–347.

Norberg, R. A. 1977. An ecological theory on foraging time and energetic and choice of optimal food-searching method. Journal of Animal Ecology 45:511–529.

Partridge, L., and R. Ashcroft. 1976. Mixed-species flocks of birds in hill forest in Ceylon. Condor 78:449–453.

Pomara, L. Y., R. J. Cooper, and L. J. Petit. 2003. Mixed-species flocking and foraging behavior of four Neotropical warblers in Panamanian shade coffee fields and forests. Auk 120:1000–1012.

Pomara, L. Y., R. J. Cooper, and L. J. Petit. 2007. Modeling the flocking propensity of passerine birds in two Neotropical habitats. Oecologia 153:121–133.

Powell, G. V. N. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. Ornithological Monographs 36:713–732.

Pulliam, H. R., G. H. Pyke, and T. Caraco. 1982. The scanning behavior of juncos: a game-theoretical approach. Journal of Theoretical Biology 95:89–103.

R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing.

Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Robinson, S. K., and R. T. Holmes.1982.Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918–1931.

Roth, T. C. II, S. L. Lima, and W. E. Vetter. 2006. Determinants of predation risk in small wintering birds: the hawk’s perspective. Behavioral Ecology and Sociobiology 60:195–204.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Sih, A. 1982.Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. Ecology 63:786–796.

Sridhar, H., G. Beauchamp, and K. Shanker. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Animal Behaviour 78:337–347.

Sridhar, H., U. Srinivasan, R. A. Askins, J. C. Canales-Delgadillo, C.-C. Chen, D. N. Ewert, G. A. Gale, E. Goodale, W. K. Gram, P. J. Hart, K. A. Hobson, R. L. Hutto, S. W. Kotagama, J. L. Knowlton, T. M. Lee, C. A Munn, S. Nimnuan, B. Z. Nizam, G. Péron, V. V. Robin, A. D. Rodewald, P. G. Rodewald, R. L. Thomson, P. Trivedi, S. L. Van Wilgenburg, and K. Shanker. 2012. Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. The American Naturalist 180:777–790.

Suhonen, J. 1993. Predation risk influences the use of foraging sites by tits. Ecology 74:1197–1203.

Sullivan, K. 1984. The advantages of social foraging in downy woodpeckers *Picoides pubescens*. Animal Behaviour 32:16–22.

Terborgh, J. 1990. Mixed flocks and polyspecific associations: Costs and benefits of mixed groups of birds and monkeys. American Journal of Primatology 21:87–100.

Thiollay, J.-M. 1999. Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: An intertropical comparison. Journal of Avian Biology 30:282–294.

Tubelis, D. P., A. Cowling, and C. Donnelly. 2006. Role of mixed-species flocks in the use of adjacent savannas by forest birds in the central Cerrado, Brazil. Austral Ecology 31:38–45.

Wiley, R. H. 1980. Multispecies antbird societies in lowland forests of Surinam and Ecuador: stable membership and foraging differences. Journal of Zoology 191:127–145.

Table 1. Means (±SE) of foraging and habitat variables recorded for wedge-billed woodcreepers (*Glyphorynchusspirurus*)foraging in and out of flocks from Jan-Mar 2010-2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

	Alone	Flock
Height Range (m)	2.6 (0.4) n=32	1.5 (0.2) n=44
Start Height (m)	1.1 (0.5) n=32	1.4 (0.5) n=44
End Height (m)	1.9 (0.6) n=32	1.6 (0.5) n=44
Time on Trunk (s)	112.9 (15.9) n=35	48.6 (6.3) n=44)
Vertical Movment Rate (s/m)	74.1 (10.7) n=32	46.4 (9.5) n=44
Peck Rate (n/min)	16.4 (5.7) n=13	10.6 (3.5) n=17
Hitch Rate (n/min)	14.8 (2.5) n=13	26.1 (4.1) n=17
Scan Rate (n/min)	0.9 (0.4) n=13	0.6 (0.3) n=17
Flight Distance (m)	5.6 (4.6) n=10	5.5 (1.1) n=21

Table 2.A comparison from two data subsets of the frequency of cover category use (density of vegetation within a 1-m radius of foraging individual; dense > 75%, medium= 25-75%, open < 25%) of wedge-billed woodcreepers (*Glyphorynchusspirurus*) observed foraging in and out of flocks from Jan-Mar 2010-2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

Cover Category	Independent Data Set[a] Category Frequency		Pseudoreplication Data Set[b] Category Frequency	
	No Flock	With Flock	No Flock	With Flock
Dense	5	3	3	0
Medium	17	12	12	7
Open	9	23	12	15

[a] Single observations of known individuals and randomly-selected observations of unmarked individuals spaced >400 m apart

[b] Repeated observationsof 20 marked individuals

Figure 1.Frequency of cover category use (density of vegetation within a 1-m radius of foraging individual; dense > 75%, medium= 25-75%, open < 25%) of wedge-billed woodcreepers (*Glyphorynchusspirurus*) observed foraging in (“Y”) and out (“N”) of flocks from Jan-Mar 2010-2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

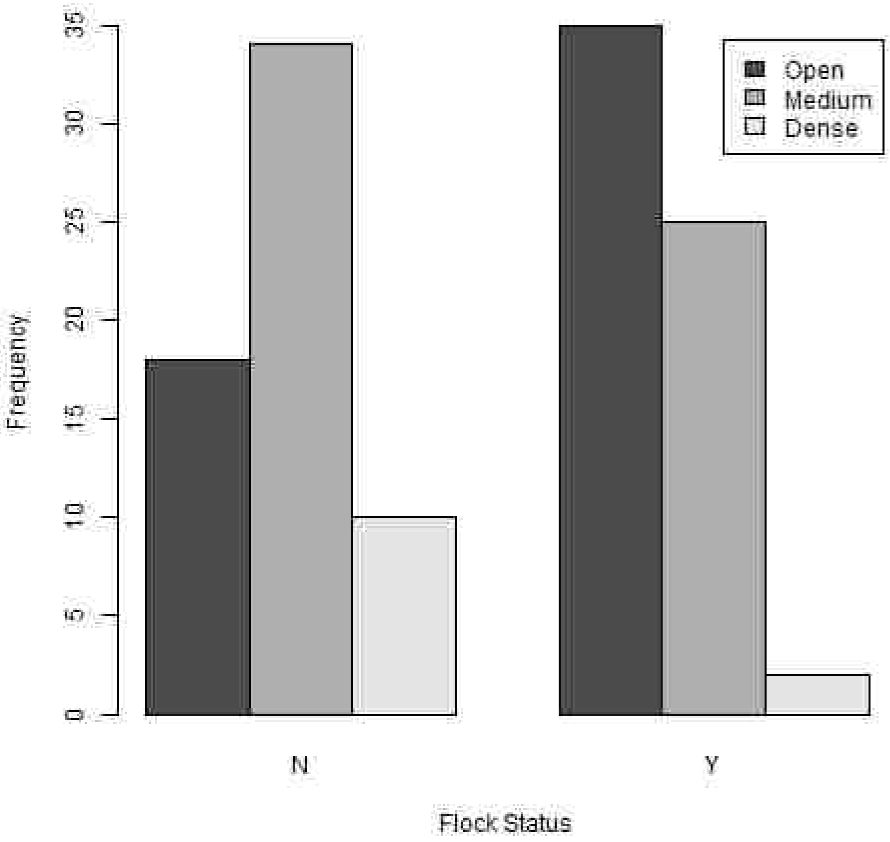


Figure 2.The relationship between movement rates (m/min) and flock-following session lengths (min) of 23 individual wedge-billed woodcreepers (*Glyphorynchusspirurus*) tracked using radio-telemetry from Jan-Mar 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

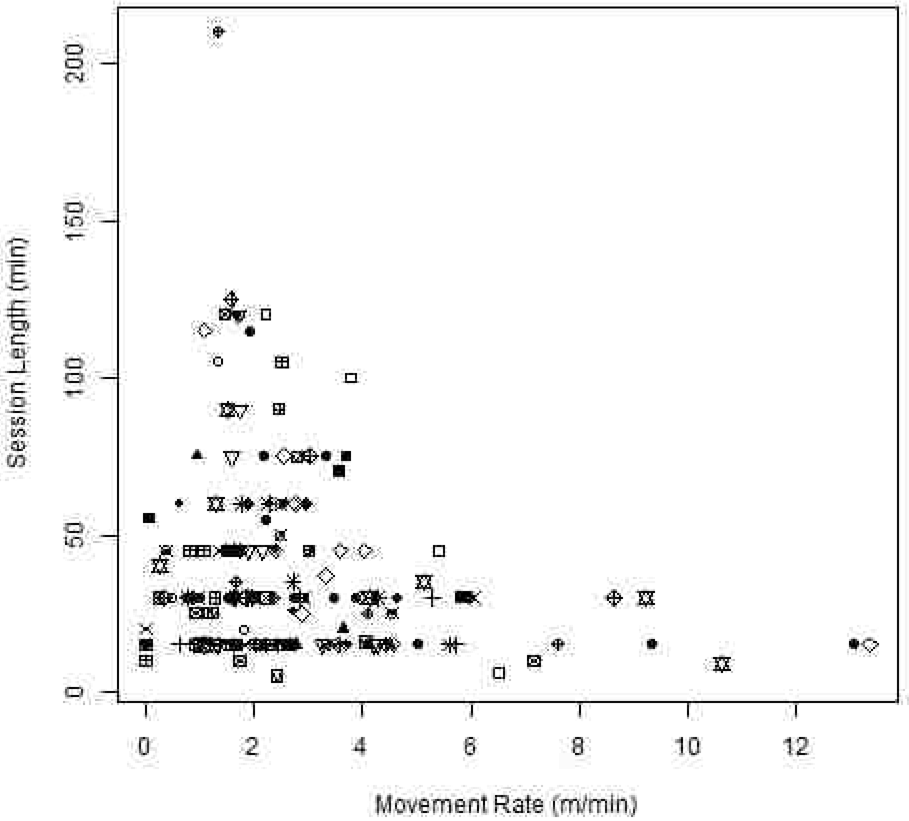
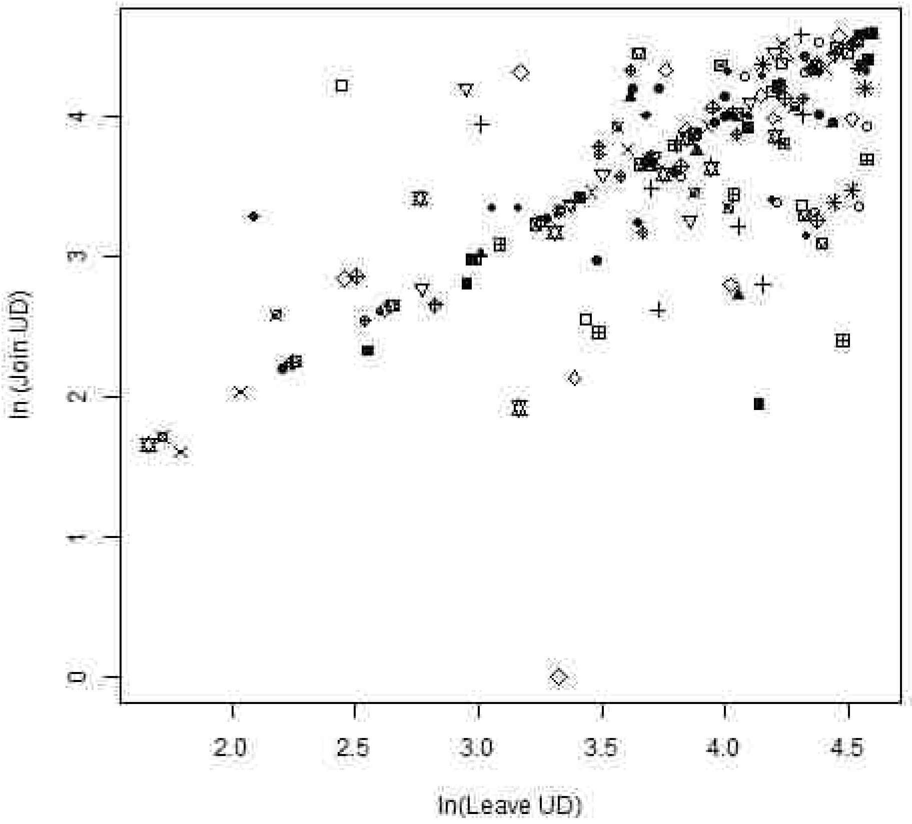


Figure 3.Relationship between relative flock-joining and -leaving locations (measured as the utilization distribution [UD] volume within home ranges) of 23 individual wedge-billed woodcreepers (*Glyphorynchusspirurus*) tracked using radio-telemetry from Jan-Mar 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.



CHAPTER 3: ECOLOGICAL CORRELATES OF FLOCKING PROPENSITY IN THE WEDGE-BILLED WOODCREEPER (*GLYPHORYNCHUS SPIRURUS*) IN EASTERN ECUADOR

Abstract

Wedge-billed woodcreeper (*Glyphorynchus spirurus*) is a common understory bird of lowland rainforests throughout the Neotropics. It frequently follows mixed-species understory flocks but also often forages alone. Physical and environmental factors that may affect the time an individual spends with flocks (flocking propensity) include frequency of flock-following opportunities, intraspecific interactions due to overlapping home ranges, body condition, and habitat characteristics. Individual wedge-billed woodcreepers were tracked using radio telemetry from Jan-Feb 2011 and Jan-Mar 2012. Home range size, estimated using a fixed-kernel density function, averaged 4.0 (2011) to 4.1 (2012) ha and ranged from 2.0-8.8 ha, with significant overlap among individuals. Flocking propensity was measured directly for the first time in this species by continuously following individuals and measuring percent time each individual spent in a flock. It was 30% in 2011 and 20% in 2012, which is considerably lower than reported in previous studies that simply counted birds in and out of flocks. This was also lower than the expected value of 47% based on home range size and number of flocks in the study area, indicating that wedge-billed woodcreepers do not always join flocks when one is present. Body mass was the strongest predictor of flocking propensity, with larger individuals spending more time in flocks; there was a weak effect of habitat composition and no effects of frequency of flock-joining opportunities or body condition. A comparison of the difference in body mass with the difference in flocking propensity among overlapping individuals revealed a significant positive relationship, and the effect was significantly stronger than a body mass-only effect generated in a bootstrap procedure comparing subsamples of all possible pairings. This suggests that larger individuals may be able to exclude smaller individuals from flocks.

Introduction

Mixed-species bird flocks are a prevalent feature of many lowland rainforests throughout the world (Partridge and Ashcroft 1976, Munn and Terborgh 1979, Greenberg 2000, Goodale and Kotagama 2004). Anti-predator benefits are generally believed to be the most important function for tropical mixed-species insectivore flocks. This is supported in part by the reduced prevalence of flocks on predator-free islands (Beauchamp 2004) and the increased survival rate for obligate flock-followers in the Neotropics (Jullien and Clobert 2000). Improved vigilance, either by the actions of sentinel species or the presence of many individuals, has been cited as the most likely anti-predator mechanism operating in mixed-species forest flocks (Terborgh 1990, Greenberg 2000). Evidence for this hypothesis comes from numerous studies that document reduced scanning rates in individuals foraging in flocks compared to individuals foraging alone (Alves and Cavalcanti 1996, Dolby and Grubb 1998, Fernandez-Juricic et al. 2004, Sridhar et al. 2009). Furthermore, some species have been recorded foraging in more exposed situations in flocks than alone (Munn 1984, Dolby and Grubb 2000).

There is extensive variation in the proportion of time than a species or individual spends foraging with a flock (flocking propensity). A number of vulnerability attributes are correlated with the propensity of a species to join flocks (Buskirk 1976, Thiollay 1999, Sridhar et al. 2009); for instance, small- to medium-sized passerines that engage in active foraging maneuvers generally join flocks more frequently than ground-dwellers or species that engage in sit-and-wait tactics (Thiollay 1999, Sridhar et al. 2009).Habitat characteristics may influence the flocking propensity of species on a regional scale (Tubelis et al. 2006, Pomara et al. 2007), and species that inhabit areas of mature forest with an open understory also join flocks more frequently than species that occupy dense vine tangle or edge habitats (Thiollay and Jullien 1998).Another factor that may influence flocking propensity is the frequency at which a flock is present in a follower's home range, as a function of home range size and number of flocks present in the area (Pomara et al. 2007).

Mixed-species flocks of understory insectivores in the Amazon Basin generally consist of one or two antshrike (*Thamnomanes* spp.) species that appear to act as flock sentinels and leaders, and 10-12 obligate flocking species that share a common territory that is defended against other conspecifics (Munn and Terborgh 1979, Wiley 1980, English 1998, Jullien and Thiollay 1998). In addition, 30 or more species are facultative flock-followers, joining these flocks for varying lengths of time but also regularly foraging away from them (Munn and Terborgh 1979, Jullien and Thiollay 1998). It is often assumed that facultative species join flocks whenever there is opportunity, i.e. as the flock passes through an individual's territory (Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Marantz et al. 2003, Jullien and Thiollay 1998). Most of these obligate and regular flock-followers aggressively exclude other conspecifics from the flock, such that each species is represented in the flock by a single individual or family group.

The wedge-billed woodcreeper (*Glyphorynchus spirurus*) is a frequent member of mixed-species flocks throughout its range, but it also often forages alone and does not occupy a common territory with obligate flock members (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998).It is one of the most common understory birds of lowland rainforests throughout the Neotropics (Marantz et al. 2003, Blake and Loiselle 2012), and yet relatively little is known about its ecology or behavior. It appears to occupy relatively large, overlapping home ranges in Barro Colorado Island in Panama (Karr 1971, Gradwohl and Greenberg 1980), although this may not be the case across its range (Marantz et al. 2003), and in South America it appears to occupy much smaller home ranges (3-5 ha; Jullien and Thiollay 1998, Johnson et al.

2011) than many other small understory birds. The extent of home range overlap among individuals has implications for intraspecific interactions, includingthe possibility of conflict when a flock is present in an area of overlap among several individuals of one species, as may be the case for the wedge-billed woodcreeper.

Flocking propensity estimates for the wedge-billed woodcreeper range from 40-60% (Munn 1985, Marantz et al. 2003, Jullien and Thiollay 1998), although none of these studies have measured flocking propensity directly by following individuals for extended time periods; instead they have calculated flocking propensity as the proportion of the total number of observations of that species that were in a flock. Just as foraging behavior, body size, and microhabitat use are correlated with flocking propensity at the species level (Buskirk 1976, Thiollay 1999, Sridhar et al. 2009), many of these factors might be expected to influence flocking propensity at the individual level. Individuals might be expected to vary in flocking propensity as a function of individual variation in vulnerability attributes as a function of foraging behavior, body size, and microhabitat use are correlated with flocking propensity at the species level (Buskirk 1976, Thiollay 1999, Sridhar et al. 2009). If joining flocks is always beneficial, then wedge-billed woodcreepers would be expected to join a flock whenever one is present in the home range (Pomara et al. 2007), therefore flocking propensity should be correlated with home range size and/or flock space use patterns. Additionally, if flock-following provides anti-predator benefits, individuals that occupy home ranges with dense understory may spend less time in flocks because they are presumable less vulnerable to predation than those with an open understory. Finally, due to home range overlap among individuals, competitive interactions with neighbors may restrict some individuals from joining flocks as frequently as expected.

The purpose of this study was to investigate the influence physical and ecological factors on individual flocking propensity in the wedge-billed woodcreeper. Specific objectives were: 1) to determine if flocking propensity is proportional to flock-joining opportunities, 2) to examine the possibility that individuals compete for access to flocks, and 3) to determine if flocking propensity is influenced by habitat composition of the home range.

Methods

Study Area

This study was conducted at Tiputini Biodiversity Station (0°38’15”S, 76°08’59”W) in Orellana Province, Ecuador. The station encompasses 638 ha of rainforest within the 1,682,000-ha UNESCO Yasuni Biosphere Reserve. The forest is composed mainly of undisturbed *terra firme* rainforest, with a strip of *varzea* bordering the Tiputini River. The mean elevation at the station is ~220m above sea level, and the region receives roughly 3200mm of rainfall annually. The current project was conducted on two ~100-ha plots within the reserve, separated by ~1.5 km (Blake 2007). Each plot contained trails that form a grid, with ten 1000-m-long transects running east-west, spaced 100 m apart north-south, and six 800-m-long transects spaced 200 m apart running north-south. Both plots were dominated by *terra firme*forest, with one plot being overall flatter than the other but with a similar total range in elevation (~200-235 m).

Data Collection

Wedge-billed woodcreepers were captured in both study plots in 2011 and 2012 using 2.6-m mist nets as part of a long-term demographic study of understory birds (see Blake and Loiselle 2012 for additional details). Eighteen wedge-billed woodcreepers in Jan 2011 and 23 in Jan-Mar 2012 were captured and fitted with a radio transmitter (0.45g BD-2, Holohil Systems Ltd, Carp, Ontario, Canada) using a thigh harness (Rappole and Tipton 1991) made from either cotton or elastic thread. Body mass, tail length, tarsus length, bill length (nares to tip), and wing chord were measured. Individuals were released at the site of capture.

Wedge-billed woodcreepers (hereafter "woodcreepers") were tracked using Advanced Telemetry Systems Field Master receivers and hand-held three-element Yagi antennas for 2-3 h per day, beginning at least 24 h after capture, and continuing throughout the battery life of the transmitter (2-3 wks) or until the transmitter was dropped due to harness breakage (four cases in 2011, one case in 2012). Order of tracking was randomized each day such that individuals were tracked equally during all daily time periods. Location of the woodcreeper was determined by homing, in which the woodcreeper was approached until it was either seen, or until the lack of directionality in the signal indicated close proximity (~10m; two technicians in 2012 were trained with the transmitters prior to tracking to calibrate their abilities to judge distances using the equipment). A GPS unit was used to record the location to an accuracy of ~10 m. Location was recorded every 15 min during tracking sessions.

The flocking status of woodcreepers was continuously monitored during tracking sessions. A woodcreeper was determined to be a part of a flock (defined as two or more species traveling together, categorized as understory or canopy flock [Munn and Terborgh 1979]) if it was inside a flock or ≤10 m of a flock edge (maximum nearest-neighbor distance in Wiley [1980]). Time of any flock-joining or flock-leaving was recorded. Flocking propensity was calculated for each individual at the end of the season by dividing time spent in flocks by total observation time. Examination of plots of cumulative flocking propensity as a function of cumulative observation time suggested that 500 min of observation was sufficient to estimate flocking propensity of most individuals to an accuracy of ±0.05 (Fig. 1). Due to insufficient observation time per individual in 2011, only 2012 data were used in analyses involving individual flocking propensity.

Surveys for flocks and wedge-billed woodcreepers were conducted along the plot trails throughout the 2012 season (9 Jan – 13 Apr), primarily between 06:00-12:00. Observers walked slowly (15-20 m/min) along east-west trails, and recorded locations of all wedge-billed woodcreepers and understory flocks detected (understory flock defined as at least one *Thamnomanes* spp. individual with at least one individual of another regular flock attendant) using GPS or by plotting the location onto a gridded map. Due to the vocal activity of the *Thamnomanes* spp., flocks could be detected up to 50 m from the observer, allowing for complete coverage between transects (spaced 100 m apart).Detection probability at this distance may sometimes be < 1 during times of quieter flock activity (late morning/early afternoon), but the order of transect visitation was randomized each day to avoid bias. Flocks near the trail (< 25 m)were searched for wedge-billed woodcreepers for up to 20 min. The total survey area (96 ha divided equally between the two plots) was visited 15 times throughout the season. Surveys were halted during periods of wind or rain.

Habitat characteristics were measured at sampling points arranged in a 20 m x 25 m grid within each woodcreeper home range. At each sampling point, canopy cover was measured using a spherical densiometer, canopy height was measured to the nearest 5m using a laser range finder, and understory openness was estimated as the distance at which tree trunks were completely obscured by intervening foliage. Openness was estimated separately for the 4 cardinal directions and then averaged. The overall habitat type at each point was classified as mature forest, disturbed forest (characterized by presence of many saplings and/or vine tangles), swamp (with standing water and palms), or gap (those gaps that were large and dense enough to prevent entry by the observer).

Statistical Analysis

The utilization distribution (UD) for each individual in both years was estimated in Geospatial Modeling Environment (Beyer 2009) using fixed-kernel density estimation, with the smoothing parameter chosen using the least squares cross-validation method (Seaman and Powell 1996, Kernohan et al. 2001). The UD was used to generate a 95% volume contour to define the home range of each individual in 2012 (Worton 1989). Due to small sample sizes in 2011 (< 40 locations per individual), an 85% volume contour was used to estimate home range because of the tendency of kernel methods to overestimate home range size with few locations (Seaman et al. 1999).

Expected flocking propensity (EFP) based on home range size (h) and number of flocks (f) in the survey area (s) was calculated using the following formula from Pomara et al. (2007):

$$\mathrm{EFP} = 1 - [(\mathrm{s} - \mathrm{h})/\mathrm{s}]^{\mathrm{f}}$$

The number of flocks in the survey area was calculated as the mean number of flocks detected during each complete survey of the study area. EFP was calculated at the species and individual level using mean and individual home range sizes, respectively. Observed flocking probability (OFP) was compared to EFP using linear regression. In addition, a “naïve” estimate of flocking propensity was calculated as the number of wedge-billed woodcreepers detected in flocks during the surveys divided by the total number of wedge- billed woodcreeper detections.

The volume of intersection index (VI; Fieberg and Kochanny 2005) for pairs with overlapping home ranges was calculated using the kerneloverlap function in package adehabitat in Program R (R Development Core Team 2012). This measure improves upon a measure of areal overlap between two home ranges by accounting for the UD of both individuals, and thus considers the probability that each individual uses the shared space. The index is calculated using the following equation:

$$\mathrm{VI} = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \min\left[\widehat{\mathrm{UD}}_1(x,y), \widehat{\mathrm{UD}}_2(x,y)\right] dxdy$$

where $\widehat{\mathrm{UD}}_1$ and $\widehat{\mathrm{UD}}_2$ are the UD estimates for individuals 1 and 2, respectively. All pairs with a VI>0.10 were considered to have significant overlap (Walter et al. 2011) and were used in the following analysis. For each overlapping pair, the difference in flocking propensity and the difference in body mass were calculated. A linear regression was performed to test for a significant correlation between mass difference and difference in flocking propensity among potentially interacting woodcreeper pairs.

An investigation of the relationship between relative body mass and relative flocking propensity among non-interacting individuals was undertaken in attempt to differentiate between the influence of body mass relative to those of an individual's neighbors from the influence of body size only on individual flocking propensity. A bootstrap simulation was conducted in program R by generating 1000 random subsamples (n =21 per subsample) of the differences in body mass and flocking propensity for all possible pairwise combinations between individuals in the study. For each subsample, a linear regression was conducted to estimate the regression coefficient for effect of difference in body mass on difference in flocking propensity. A frequency distribution of regression coefficients from the simulation was generated, and the observed regression coefficient was compared to the simulation results by determining percent of simulated results that were greater than or less than the observed coefficient.

Body condition was estimated for each individual in 2012 by calculating the scaled mass index, $\widehat{\mathrm{M}}_{\mathrm{i}} = \mathrm{M}_{\mathrm{i}} \left[\frac{\mathrm{L}_0}{\mathrm{L}_{\mathrm{i}}}\right]^{\mathrm{b}_{\mathrm{SMA}}}$, where M_{i} is the body mass of individual i, L_{i} is a linear body measurement of individual i, L_0 is the mean linear body measurement of the sample population, and $\mathrm{b}_{\mathrm{SMA}}$ is the scaling exponent estimated by the SMA regression of mass and a linear body measurement (Peig and Green 2009). The relationship between body mass and all length measurements were examined using Pearson's correlation coefficients, and only wing chord hada significant correlation with body mass (r=0.43, n=47, p=0.003). Thus, wing chord was used as the linear body measurement in the above equation to calculate body condition.

Habitat sampling points and flock locations (from transect data) were imported into ArcMap 10 (ESRI, Redlands, CA). The Intersect tool was used to determine how many flock locations and which habitat sampling points occurred within each home range. A measure of flock density (no. points/ha) for each home range was calculated as the number of flock locations divided by the home range size. Average values of canopy height, canopy cover, and understory openness were calculated for each home range. Proportions of each habitat type within the home range were calculated by dividing the number of points characterized as a given habitat type by the total number of sampling points within the home range. There were significant correlations among all habitat characteristics except proportion swamp, and proportion gap was only correlated with canopy cover. Therefore, a principle components analysis (function prcomp in R) was conducted using all habitat variables except proportion gap and proportion swamp. The first principle component was used in subsequent analyses as a general measure of habitat type, with high values indicating mature forest with a taller canopy, greater canopy cover and greater understory openness (Fig. 2).

A set of *a priori* candidate models of flocking propensity as a function of habitat, body mass, body condition, and flock density within the home range was formed. Flock density was included as an index of flock-joining opportunities. The habitat principle component was used to model habitat effects. Regression coefficients were estimated using maximum likelihood (function glm in R) for each model in the candidate set and models were ranked using AIC_c values (Aikaike's Information Criterion corrected for small sample size; Burnham and Anderson 2002). Models with a $\Delta AIC_c < 2.00$ were considered to have the most support.

Results

Home Range Size and Overlap

Mean home range size using the 95% UD contour was 4.0 ha (0.6 SE) in 2011 and 4.1 ha (0.5 SE) in 2012, and did not differ between plots (t = 1.24, df = 36, p = 0.223; Harpia = 4.4 ha [0.4 SE], Puma = 3.7 ha [0.5 SE]). There were 10 cases of significant home range overlap (VI ≥ 0.10) in 2011 (mean 0.37 [0.1 SE], range 0.12-0.71) and 21 cases in 2012 (mean 0.30 [0.04 SE], range 0.10-0.63).

Correlates of Flocking Propensity

The EFP for 2012 was 0.46 based on a mean of 14.5 flocks in the survey area. The naïve flocking propensity, calculated as the proportion of all wedge-billed woodcreeper detections that were in a flock, was 0.51. The combined flocking propensity of 18 individuals in 2011(total 66.4 h of observation) was 0.32. The mean flocking propensity for23 wedge-billed woodcreepers in 2012 was 0.20 (range 0.02-0.35; 0.09 SE), with a mean of 24.6 (3.5 SE) observation hours per individual. OFP and EFP were not correlated (F = 0.16, p = 0.69). Flocking propensity did not vary by time of day (F = 2.7, df = 89, p = 0.368; Fig. 3) or by month (t = 0.03, df = 21, p = 0.976; Fig. 4).

Body mass was included in the top four models (Table 1). The two models with greatest support ($\Delta AIC_c \leq 2$) were the model with mass only and the model with habitat and mass (Table 1). The model-averaged coefficient estimate for body mass was 0.06 (0.03 SE, 0.01-0.11 CI), indicating a positive correlation between body mass and flocking propensity (Fig. 5). Flocking propensity was positively correlated (0.03, 0.03 SE, -0.03-0.08 CI) with the habitat principle component (higher flocking propensity with greater canopy height, canopy cover, and understory openness), although the effect was not significant because the confidence interval of the estimate overlapped zero.

Difference in flocking propensity between overlapping individuals in 2012 was significantly correlated with difference in mass between those individuals (F = 12.35, n = 21, p = 0.002; Fig. 6), with a regression coefficient estimate of 0.08 (0.024 SE). The bootstrap simulation comparing random pairs resulted in a mean coefficient estimate of 0.04 (0.0009 SE; Fig. 7). The regression coefficient using overlapping individuals was greater than 0.95% of the bootstrap estimates.

Discussion

Home Range Overlap

Home ranges overlapped extensively among individuals in both years, a pattern that has also been observed in Barro Colorado Island in Panama (Karr 1971, Gradwohl and Greenberg 1980). Such home range overlap may not be found across the species' range (Marantz et al. 2003); home range overlap was not mentioned for this species in French Guiana (Jullien and Thiollay

1998) or central Brazil (described as a “typical territorial species" [Johnson et al. 2011]) and is perhaps limited to areas of high density, such as the current study area (English 1998, Blake and Loiselle 2012).It is currently unknown if this overlap involves related or unrelated individuals, or if it occurs more extensively between individuals of the same or opposite sex.

Correlates of Flocking Propensity

The average flocking propensity for wedge-billed woodcreepers in this study was 32% in 2011 and 20% in 2012, which is considerably lower than the 40-60% reported for this species in other studies (Munn 1985, Marantz et al. 2003, Jullien and Thiollay 1998) and expected (47%) based on the assumption that flock-followers always join a flock in its home range. This discrepancy is most likely due to methodological differences. Previous studies have estimated flocking propensity as percentage of total number of sightings of a species that were within a flock, and when flocking propensity was estimated in the same way using observations in this study, the value was 51%, well within the range reported in the literature. This study is the first to present direct measures of flocking propensity fromindividuals that were followed over extended time periods. It is likely that individuals are more easily detected in a flock than alone, especially in studies that are focused on observing behavior of flocking species.

Body mass was the strongest predictor of individual flocking propensity, with larger birds spending more time in flocks than smaller birds. The causative nature of this relationship could lie in either direction. On one hand, it is possible that spending more time in flocks could result in a larger adult body size if individuals gain a significant foraging advantage from joining flocks. However, if this were the case, one would expect body condition to be at least as strongly correlated with flocking propensity as body mass, but it was unrelated to flocking propensity in this study. The alternative explanation, that larger birds are able to join flocks more frequently, is more plausible given the data. The extensive home range overlap among individuals in the study area sets up the possibility of intraspecific competition, and indeed when overlapping pairs were examined, difference in flocking propensity and difference in body size were significantly correlated. The strength of this effect was significantly greater than that obtained using random pairs of individuals, providing additional support that this resulted from interactions among individuals and not simple body mass per se. Competitive ability is positively correlated with body mass in many animals (Allen and Aspey 1986, French and Smith 2005, Calsbeek 2009), so it is likely that larger individuals are able to exclude smaller individuals from flocks in areas of home range overlap. Chasing and calling was frequently observed between individuals in flocks, but it was rarely possible to determine the identity of both participants in these encounters. The hypothesis that individuals compete for access to flocks in areas of overlapping home range, with larger individuals excluding smaller ones, must be tested further to ascertain if this pattern holds across seasons, years, and geographic range. A study involving simultaneous tracking of overlapping pairs and flocks would provide more direct evidence with which to test this hypothesis.

Neither home range nor flock location density within an individual's home range, both indices of flock-joining opportunities, were related to individual flocking propensity.This is contrary to Pomara et al.'s (2007) observations that home range size was a significant predictor of flocking propensity for four species in Panama, and it suggests that, unlike many other flock attendants in Amazonia (Munn and Terborgh 1979, Jullien and Thiollay 1998), wedge-billed woodcreepers do not always join a flock when one is present in its home range. It was common to observe individuals not to join flocks that were audible within their home range (generally 20-50 m from the observer). Intraspecific competition, as discussed above, could be one reason why an individual would fail to join a flock passing through that individual's home range. Other possibilities include costs associated with flock-following, such as interspecific competition, energy expenditure associated with keeping up with a moving flock, or the use of suboptimal movement patterns to conform to the flock (Hutto 1988, Terborgh 1990, Greenberg 2000). The relative size of these costs, and whether or not they are outweighed by benefits, may vary among individuals as a function of body size and condition, and may vary on a temporal or spatial scale as a function of local habitat characteristics, reproductive status, and weather conditions. An investigation of the effects of such factors is beyond the scope of this study.

There was a weak effect of habitat characteristics within the home range on individual flocking propensity, with a marginal tendency toward greater flocking propensity in individuals with home ranges encompassing more mature forest, greater canopy height and canopy cover, and a more open understory. However, due to the statistical insignificance of the effect, this observation does not provide strong support for the anti-predator benefit hypothesis. Little is known about the microhabitat preferences or hunting behavior of Neotropical raptors, but it might be reasonable to assume that a dense understory might confer reduced predation risk compared to an open understory, by providing additional concealment and nearby cover for the forager (Grubb and Greenwald 1982, Suhonen 1993). At a species level, it has been demonstrated that flocking propensity is positively correlated with habitat openness in Neotropical rainforests, with a greater proportion of mature forest understory species regularly joining flocks than species that occupy dense vine tangle or edge habitats, regardless of other ecological or behavioral factors (Thiollay and Jullien 1998). Examining flock-joining patterns of individual wedge-billed woodcreepers within their home ranges with respect to local habitat variation, rather than comparing overall flocking propensity of the individual to an average home range habitat value, may reveal a stronger relationship between flock-joining behavior and habitat.

Conclusions

The flocking propensity of wedge-billed woodcreepers at this site was considerably lower than estimates based on the proportion of total sightings in a flock, and was lower than the predicted value based on the assumption that a wedge-billed woodcreeper will always join a flock that is present in its home range. Intraspecific competition, as a result of significant home range overlap among individuals, may be an important factor limiting flocking propensity for some individuals, although a detailed study of simultaneous space use and flock movements would be necessary to test this hypothesis.

Acknowledgements

I would like to thank B. A. Loiselle and J. G. Blake for their invaluable comments and logistical assistance in the field, and for permitting us to use their plots for this study. Ithank the staff of Tiputini Biodiversity Station for their support and C. de Romo for arranging transportation to and from the field station. I thank N. Strycker and R. Rylander for volunteering their time to aid in data collection. Financial support was provided by the University of Arkansas Graduate School and the Arkansas Audubon Society Trust.

Literature Cited

Allen, D. S. and W. P. Aspey. 1986. Determination of social dominance in eastern grey squirrels (*Sciurus carolinensis*): a quantitative assessment. Animal Behaviour 34:81–89.

Alves, M. A. S. and R. B. Cavalcanti. 1996. Sentinel behavior, seasonality, and the structure of bird flocks in a Brazilian savanna. Ornitologia Neotropical 7:43–51.

Beauchamp, G. 2004. Reduced flocking by birds on islands with relaxed predation.Proceedings of the Royal Society of London B 271:1039–1042.

Beyer, H. L. 2009.Geospatial Modelling Environment. http://www.spatialecology.com/gme/.

Blake, J. G. 2007. Neotropical forest bird communities: a comparison of species richness and composition at local and regional scales. Condor 109:237–255.

Blake, J. G. and B. A. Loiselle. 2012. Temporal and spatial patterns in abundance of the wedge-billed woodcreeper (*Glyphorynchus spirurus*) in lowland Ecuador. The Wilson Journal of Ornithology 124:436–445.

Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Buskirk, W. H. 1976. Social systems in a tropical forest avifauna. The American Naturalist 110:293–310.

Calsbeek, R. 2009. Experimental evidence that competition and habitat use shape the individual fitness surface. Journal of Evolutionary Biology 22:97–108.

Dolby, A. S. and T. C. Grubb, Jr. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Animal Behaviour 56:501–509.

Dolby, A. S. and T. C. Grubb, Jr. 2000. Social context affects risk taking by a satellite species in a mixed-species foraging group. Behavioral Ecology 11:110–114.

English, P. H. 1998. Ecology of mixed-species understory flocks in Amazonian Ecuador. Ph.D. Dissertation, University of Texas, Austin.

Fernandez-Juricic, E., J. T. Erichsen, and A. Kacelnik. 2004. Flock density, social foraging, and scanning: an experiment with starlings. Behavioral Ecology 15:371–379.

Fieberg, J. and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346–1359.

French, A. R. and T. B. Smith. 2005. Importance of body size in determining dominance hierarchies among diverse tropical frugivores. Tropical Biology 37:96–101.

Gradwohl, J. and R. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. Auk 97:385–395.

Greenberg, R. 2000. Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. Pages 521–558 in On the Move: How and Why Animals Travel in Groups (S. Boinski and P. A. Garber, Eds.). The University of Chicago Press, Chicago.

Grubb, T. C., Jr. and L. Greenwald. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. Animal Behaviour 30:637–640.

Hutto, R. L. 1988. Foraging behavior patterns suggest a possible cost associated with participation in mixed-species bird flocks. Oikos 51:79–83.

Johnson, E. I., P. C. Stouffer, and C. F. Vargas. 2011. Diversity, biomass, and trophic structure of a central Amazonian rainforest community. Revista Brasileira de Ornitologia 19:1–16.

Jullien, M. and J. Clobert. 2000. The survival value of flocking in Neotropical birds: reality or fiction? Ecology 81:3416–3430.

Jullien, M. and J.-M.Thiollay. 1998. Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. Journal of Animal Ecology 67:227–252.

Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecological Monographs 41:207–233.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 in Radio Tracking and Animal Populations (J. J. Millspaugh and J. M. Marzluff, Eds.). Academic Press, San Diego.

Kotagama, S. W. and E. Goodale. 2004. The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. Forktail 20:63–70.

Marantz, C. A., A. Aleixo, L. R. Bevier, and M. A. Patten. 2003. Family Dendrocolaptidae (Woodcreepers). Pages 358–447 in Handbook of the Birds of the World, Vol. 8. Broadbills to Tapaculos (J. del Hoyo, A. Elliott, and D. Christie, Eds.). Lynx Edicions, Barcelona.

Munn, C. A. 1984. The behavioral ecology of mixed-species bird flocks in Amazonian Peru. Ph.D. Dissertation, Princeton University, Princeton.

Munn, C. A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. Ornithological Monographs 36:683–712.

Munn, C. A. and J. W. Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. Condor 81:338–347.

Partridge, L., and R. Ashcroft. 1976. Mixed-species flocks of birds in hill forest in Ceylon. Condor 78:449–453.

Peig, J. and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–1891.

Pomara, L. Y., R. J. Cooper, and L. J. Petit. 2007. Modeling the flocking propensity of passerine birds in two Neotropical habitats. Oecologia 153:121–133.

R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rappole, J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Seaman, D.E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimators. Journal of Wildlife Management 63:739–747.

Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Sridhar, H., G. Beauchamp, and K. Shanker. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Animal Behaviour 78:337–347.

Suhonen, J. 1993. Risk of predation and foraging sites of individuals in mixed-species tit flocks. Animal Behaviour 45:1193–1198.

Terborgh, J. 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups of birds and monkeys. American Journal of Primatology 21 87–100.

Thiollay, J.-M. 1999. Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: an intertropical comparison. Journal of Avian Biology 30:282–294.

Thiollay, J.-M and M. Jullien. 1998. Flocking behavior of foraging birds in a Neotropical rain forest and the antipredator defence hypothesis. Ibis 140:382–394.

Tubelis, D. P., A. Cowling, and C. Donnelly. 2006. Role of mixed-species flocks in the use of adjacent savannas by forest birds in the central Cerrado, Brazil. Austral Ecology 31:38–45.

Wiley, R. H. 1980. Multispecies antbird societies in lowland forests of Surinam and Ecuador: stable membership and foraging differences. Journal of Zoology, London 191:127–145.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Table 1.Model selection results[1] of logistic regression models incorporating various combinations of body mass, body condition, and home range characteristics as potential predictors of flocking propensity of individual wedge-billed woodcreepers (*Glyphorynchus spirurus*) at Tiputini Biodiversity Station, Orellana Province, Ecuador.

Model[2]	ΔAIC_c	AIC_c	LL	K	w_i
Mass+Hab	0.00	-42.70	26.46	4	0.29
Mass	0.65	-42.05	24.66	3	0.21
Mass+FD	2.13	-40.57	25.40	4	0.10
Mass+Hab+FD	2.19	-40.51	27.02	5	0.10
SMI	2.43	-40.27	23.77	3	0.09
FD	3.27	-39.43	23.34	3	0.06
Hab	3.68	-39.02	23.14	3	0.05
FD+SMI	4.26	-38.44	24.33	4	0.03
Hab+SMI	4.32	-38.38	24.30	4	0.03
Global	5.45	-37.25	27.25	6	0.02
Hab+FD	5.61	-37.08	23.65	4	0.02
SMI+Hab+FD	6.71	-35.99	24.76	5	0.01

[1] AIC_c = Aikaike's Information Criterion corrected for small sample sizes, LL = log likelihood, K = no. paramaters, w_i = model weights

[2] Mass = body mass (g); SMI = scaled mass index; Hab = first principle component incorporating canopy height, canopy cover, understory openness, proportion mature forest, and proportion disturbed forest within individual home ranges; FD = understory flock location density per home range.

Figure 1. Example graph of cumulative flocking propensity (proportion of observation time spent in mixed-species flock) as a function of cumulative observation time for a sample of five wedge-billed woodcreepers (*Glyphorynchus spirurus*) tracked using radio telemetry from 13 Jan – 11 Feb 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

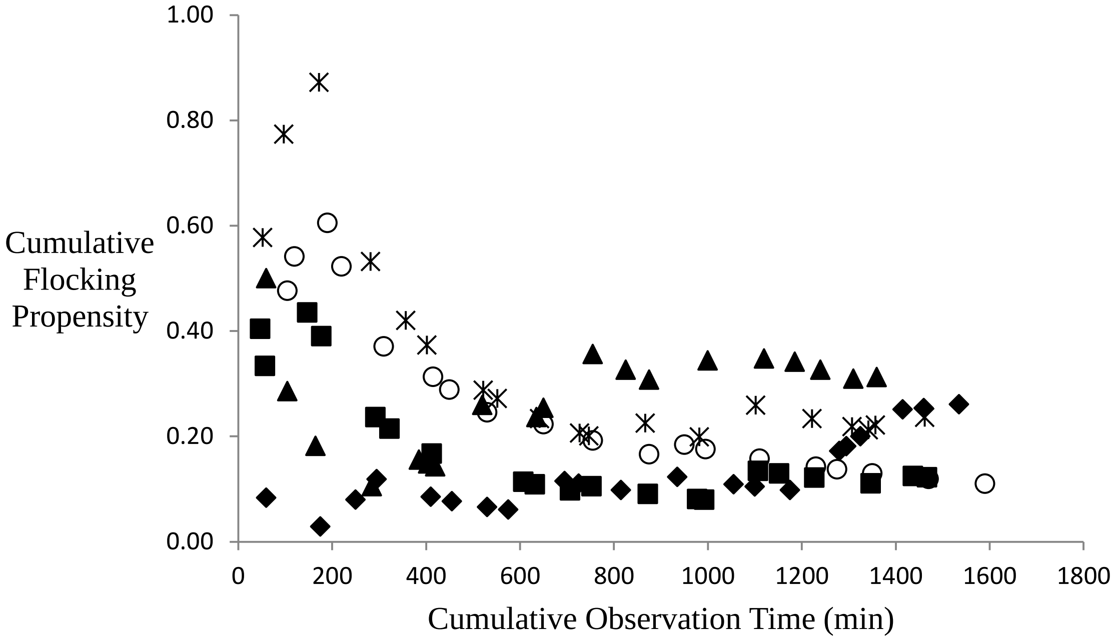


Figure 2. First two principle components of five habitat variables measured from 23 wedge-billed woodcreeper (*Glyphorynchus spirurus*) home ranges in 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador. Mature and disturbed forest indicate proportions of those habitat types within each home range.

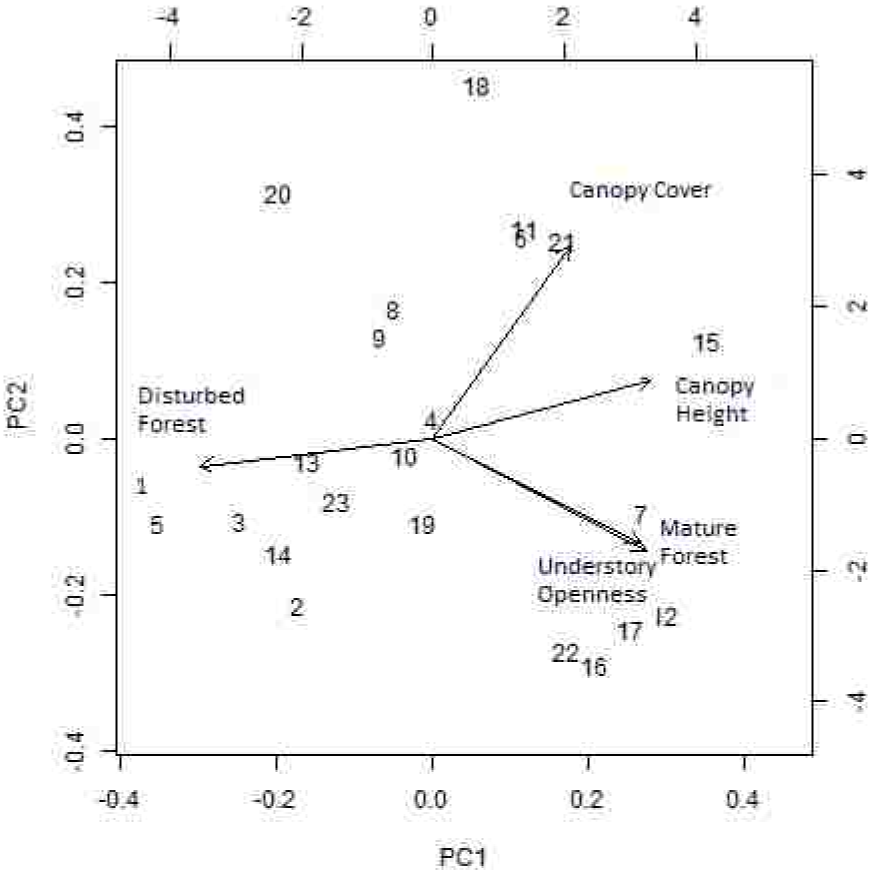


Figure 3. Average flocking propensities (proportion of observation time spent with a mixed-species flock) per daily time period of 23 wedge-billed woodcreepers (*Glyphorynchus spirurus*) tracked using radio telemetry from 13 Jan – 31 Mar 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

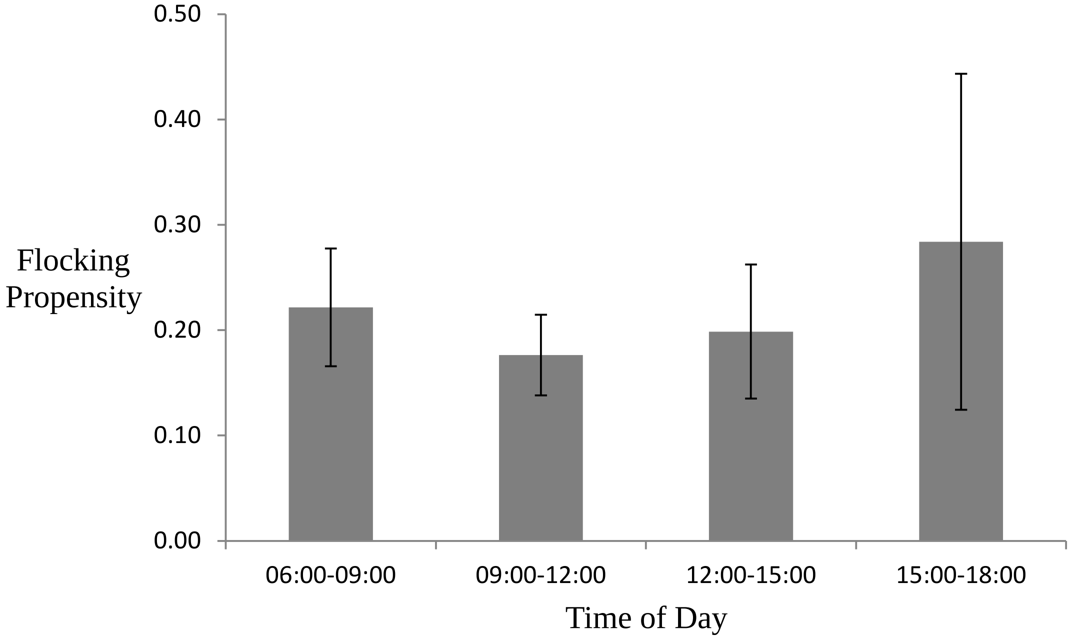


Figure 4. Average flocking propensities (proportion of observation time spent with a mixed-species flock) per month of 23 wedge-billed woodcreepers (*Glyphorynchus spirurus*) tracked using radio telemetry from 13 Jan- 11 Feb 2012 (n=14) and from 28 Feb – 31 Mar 2012 (n=9) at Tiputini Biodiversity Station, Orellana Province, Ecuador.

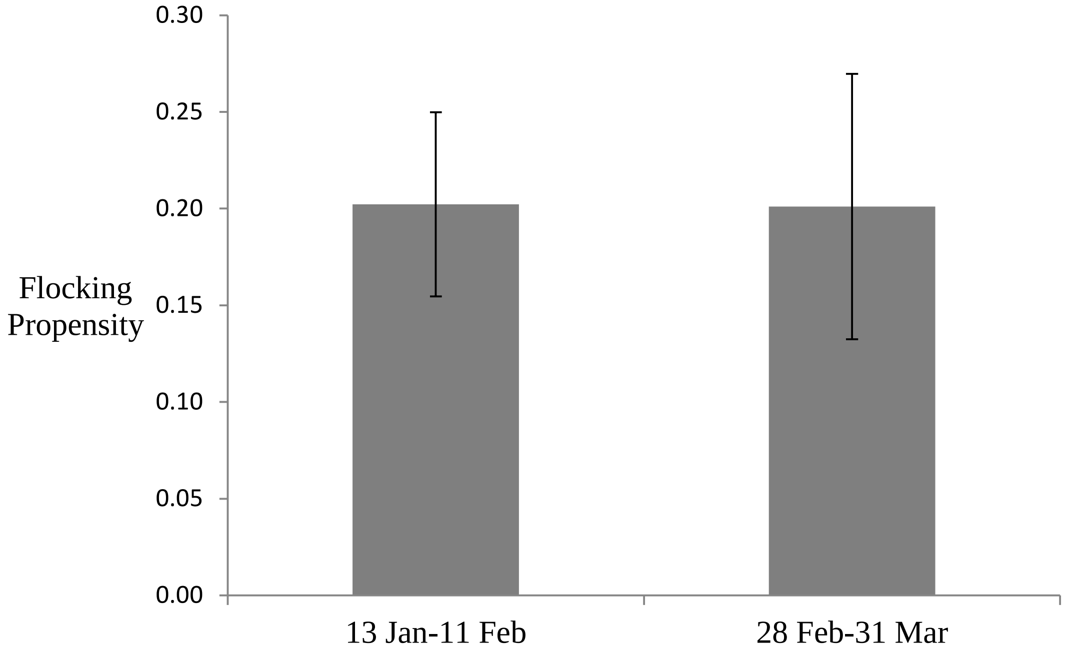


Figure 5. Relationship between body mass and flocking propensity in 23 wedge-billed woodcreepers (*Glyphorynchus spirurus*) tracked using radio telemetry from 13 Jan – 31 Mar 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador. Line represents predicted relationship using a model-averaged regression coefficient.

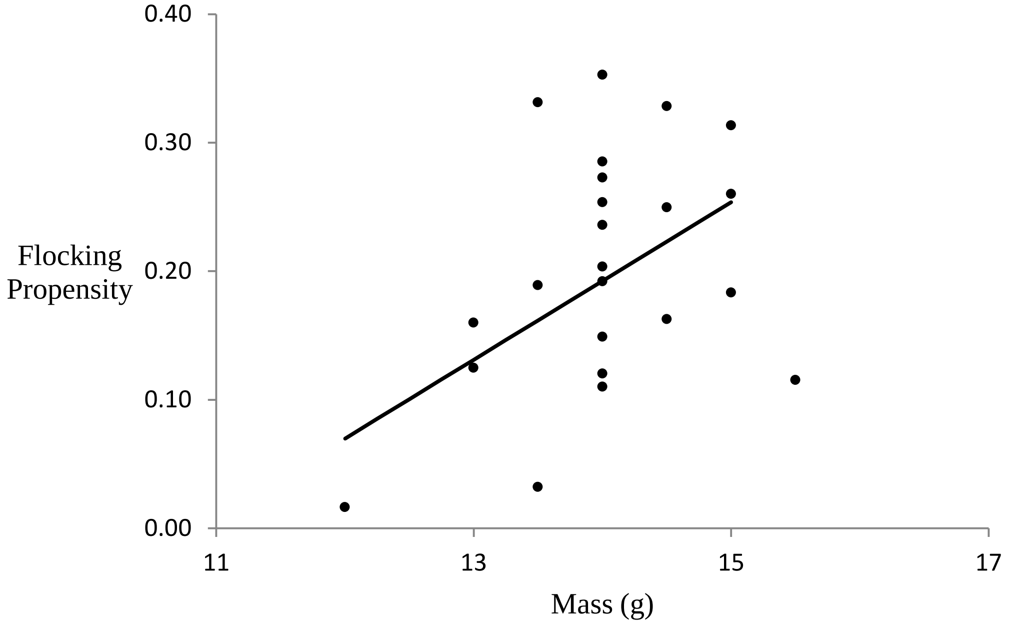


Figure 6. Relationship between difference in mass and difference in flocking propensity between individual wedge-billed woodcreepers (*Glyphorynchus spirurus*) with overlapping home ranges (defined as VI≥0.10). Woodcreepers were tracked using radio telemetry from 13 Jan – 31 Mar 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador. Line represents estimated regression (F = 12.35, n = 21, p = 0.002).

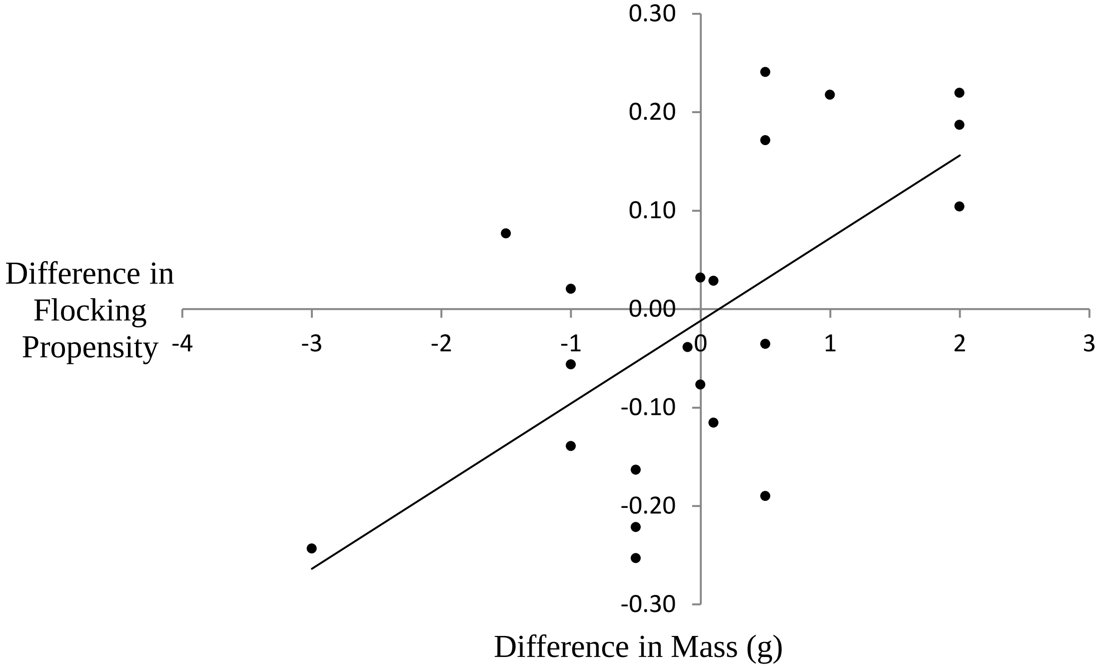
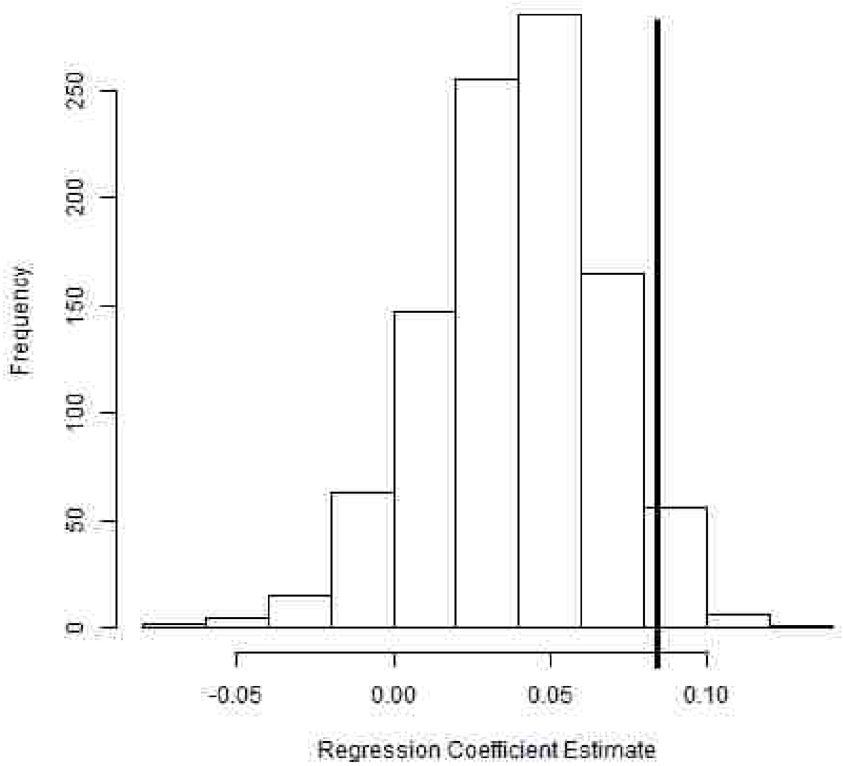


Figure 7. Frequency distribution of regression coefficients estimated using linear regression of mass differences and flocking propensity differences between individual (n =23) wedge-billed woodcreepers (*Glyphorynchus spirurus*) tracked using radio telemetry from Jan-Mar 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador. Bootstrap simulation was conducted with 1000 subsamples (n = 21 per subsample) of all possible pairwise combinations (n =252). Vertical line indicates regression coefficient estimate using data from pairs with significant home range overlap (VI≥0.10; n = 21).



CHAPTER 4: INTRASPECIFIC INTERACTIONS, HOME RANGE OVERLAP, AND SPACE USE PATTERNS OF THE WEDGE-BILLED WOODCREEPER (*GLYPHORYNCHUS SPIRURUS*) IN AMAZONIAN ECUADOR

Abstract

The wedge-billed woodcreeper (*Glyphorynchus spirurus*) is a frequent member of mixed-species understory flocks throughout the Neotropics. In some regions individuals appear to occupy overlapping home ranges, although the extent to which individuals use these shared areas, and the consequences for flock-following behavior in shared areas, are unknown. Wedge-billed woodcreepers were tracked using radio telemetry at Tiputini Biodiversity Station, Orellana Province, Ecuador. Home range size was estimated using a fixed kernel method with least-squares cross validation, and the 95% isopleth was used to define home range extent. Home range overlap was quantified by calculating the volume of intersection (VI) of the kernel distributions. There were ten cases in 2011 and 21 cases in 2012 of significant home range overlap ($VI>0.10$) between neighbors. For each overlapping pair, frequencies of use of shared and non-shared areas were compared to expected use probabilities based on the sizes of the respective areas. Of 14 directional interactions in 2011, one was a significant attraction and the remaining responses were non-significant; of 46 directional interactions in 2012, 23 were non-significant, 17 were significant attractions, and six were significant avoidances. Logistic regression was used to investigate the effect of the utilization distribution of overlapping neighbors and understory openness on the distribution of flock-following locations. There was no support for an effect of the space use of a larger neighbor ($p = 0.07$) or understory openness ($p = 0.55$) on the distribution of flock-following locations. This study reveals that the wedge-billed woodcreeper engages in considerably less territorial defense than is characteristic of most other rainforest insectivores. The distribution of flock-following locations does not support the hypothesis that individuals compete for access to flocks in overlapping areas, although I caution

that a study investigating simultaneous space use coupled with genetic analyses to reveal relationships between interacting neighbors is needed to resolve this issue.

Introduction

Vertebrates exhibit a range of territoriality and spacing patterns (Brown and Orians 1970, Maher and Lott 2000), ranging from aggressive defense of an area for exclusive use to a variety of non-defended space use patterns. In general, the term “home range” is used to indicate simply the area that an individual uses on a daily basis for foraging, roosting, and reproductive behaviors, whereas “territory” is used to indicate defense of an area by an individual to maintain exclusive use (Brown and Orians 1970). Defense of exclusive territories is characteristic of species that rely on resources that are predictable and uniformly distributed, because they are more economical to defend than patchily-distributed resources (Brown and Orians 1970, Maher and Lott 2000). For instance, most insectivores of the rainforest understory defend territories year-round (Munn and Terborgh 1979, Greenberg and Gradwohl 1986, Duca et al. 2006), whereas frugivores exhibit a wide range of spacing systems with little or no defense of exclusive areas (Stutchbury and Morton 2001).

Studies of movement patterns and space use within a territory or home range can reveal the importance of various features within the home range. While many studies focus on the importance of habitat or landscape features on space use patterns (e.g. Janke and Gates 2013, Montgomery et al. 2013), the movement patterns of other individuals or other species may also have a significant effect (e.g. Horne et al. 2008). This may include attraction to potential mates (Horne et al. 2008), or avoidance of competitors (Berger and Gese 2007, Kamler et al. 2012) or predators (Millspaugh et al. 2000, Proffitt et al. 2009).

The wedge-billed woodcreeper (*Glyphorynchus spirurus*) is a facultative flock-follower throughout its extensive range in Neotropical forests, often joining mixed-species understory flocks but also frequently foraging alone. Attendants of tropical mixed-species insectivore flocks are believed to benefit from joining flocks due to decreased predation risk as a result of the actions of sentinel species or the presence of many individuals (Munn and Terborgh 1979, Terborgh 1990a, Greenberg 2000, Jullien and Clobert 2000), as evidenced by observations of some species foraging in more exposed situations in flocks than alone (Munn 1984, Dolby and Grubb 2000). At the species level, it has been demonstrated that flocking propensity (proportion of time spent in flocks) is positively correlated with habitat openness in Neotropical rainforests, with a greater proportion of mature forest understory species regularly joining flocks than species that occupy dense vine tangles or edge habitats, regardless of other ecological or behavioral factors (Thiollay and Jullien 1998). The space use patterns of wedge-billed woodcreepers may therefore be influenced by the presence or absence of flocks within the home range, with the expectation that they would be more likely to join flocks in mature forest with an open understory than in more dense, disturbed areas.

In addition to habitat, another important factor that may influence the distribution of flock-following locations is the presence of another wedge-billed woodcreeper in that flock. In Neotropical understory flocks, most species aggressively exclude conspecifics from the flock territory, such that each species in the flock is represented by a single individual, pair, or family group (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998). Up to ten "core" species defend a common flock territory, while many other regular attendants join flocks only when one is present within its own territory (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998). However, Gradwohl and Greenberg (1980) offered evidence, based on several color-marked individuals, that the wedge-billed woodcreeper occupied extensively overlapping home ranges on Barro Colorado Island in Panama. If this is the case, this presents two possible scenarios: either 1) wedge-billed woodcreepers tolerate other conspecifics in flocks, unlike other flock members; or 2) wedge-billed woodcreepers actively exclude conspecifics in these overlapping areas, with one individual or pair exhibiting social dominance within this shared space, in a manner similar to that seen in obligate army-ant following antbirds (Willson 2004). Previous analyses revealed a positive correlation between body mass and flocking propensity (Darrah and Smith, in prep), with the suggestion that larger individuals may exclude smaller individuals from flocks in these shared spaces. However, further studies on individual space use are needed to test this hypothesis.

The objectives of this study were: 1) to quantify the extent of home range overlap among individual wedge-billed woodcreepers, 2) to determine if areas of intraspecific overlap are avoided, 3) to determine if understory openness or space use by conspecifics influence the locations at which individual woodcreepers join flocks.

Methods

Study Area

This study was conducted at Tiputini Biodiversity Station (0°38’15”S, 76°08’59”W) in Orellana Province, Ecuador. The station encompasses 638 ha of rainforest within the 1,682,000-ha UNESCO Yasuni Biosphere Reserve. The forest is composed mainly of undisturbed *terra firme* rainforest, with a strip of *varzea* bordering the Tiputini River. The mean elevation at the station is ~220 m above sea level, and the region receives roughly 3200 mm of rainfall annually. The current project was conducted on two ~100-ha plots ("Harpia" and "Puma") within the reserve, separated by ~1.5 km (Blake 2007). Each plot contained trails that form a grid, with ten 1000-m-long transects running east-west, spaced 100 m apart north-south, and six 800-m-long transects spaced 200 m apart running north-south. Both plots were dominated by *terra firme*forest, with Puma being overall flatter than the other but with a similar total range in elevation (~200-235 m).

Data Collection

Wedge-billed woodcreepers (hereafter "woodcreepers') were captured in both study plots in 2011 and 2012 using 2.6-m mist nets as part of a long-term demographic study of understory birds (see Blake and Loiselle 2012 for additional details). Eighteen woodcreepers in Jan 2011 and 23 in Jan-Mar 2012 were captured and fitted with a radio transmitter (0.45g BD-2, Holohil Systems Ltd, Carp, Ontario, Canada) using a thigh harness (Rappole and Tipton 1991) made from either cotton or elastic thread. Body mass, tail length, tarsus length, bill length (nares to tip), and wing chord were measured. Individuals were released at the site of capture.

Woodcreepers were tracked using Advanced Telemetry Systems Field Master receivers and hand-held three-element Yagi antennas for 2-3 h per day, beginning at least 24 h after capture, and continuing throughout the battery life of the transmitter (2-3 wk) or until the transmitter was dropped due to harness breakage (four cases in 2011, one case in 2012). Order of tracking was randomized each day such that individuals were tracked equally during all daily time periods. Location of the woodcreeper was determined by homing, in which the woodcreeper was approached until it was either seen, or until the lack of directionality in the signal indicated close proximity (~10m; two technicians were trained in 2012 with the transmitters prior to tracking in order to calibrate their abilities to judge distances using the equipment). A GPS unit was used to record the location to an accuracy of ~10 m. Location was recorded every 15 min during the tracking sessions. Identity (based on color bands or radio signal) of any woodcreepers observed near (< 15 m) the focal individual was recorded.

The flocking status of woodcreepers was continuously monitored during tracking sessions. A woodcreeper was determined to be a part of a flock (defined as two or more species traveling together, categorized as understory or canopy flock, Munn and Terborgh 1979) if it was inside a flock or ≤10 m of a flock edge (maximum nearest-neighbor distance in Wiley [1980]). Time of any flock-joining or flock-leaving was recorded.

Habitat characteristics were measured at sampling points arranged in a 20 m x 25 m grid within each woodcreeper home range. At each sampling point, understory openness was estimated as the distance at which tree trunks were completely obscured by intervening foliage. Openness was estimated separately for the four cardinal directions and then averaged. A raster dataset of understory openness was created in ArcMAP (ESRI, Redlands, CA) with a cell size of 5 m, and data extrapolated to cells up to 15 m from each sampling point by averaging the cell values within a 15-m radius.

Statistical Analyses

The utilization distribution (UD) for each individual in both years was estimated in Geospatial Modeling Environment (Beyer 2009) using fixed-kernel density estimation, with the smoothing parameter chosen using the least squares cross-validation (LSCV) method (Seaman and Powell 1996, Kernohan et al. 2001). The UD was used to generate a 95% volume contour to define the home range of each individual in 2012. Due to the small number of locations per individual in 2011(mean = 19, 2.1 SE, range 10-44) and resulting overestimation of the home range using kernel techniques (Kernohan et al. 2001), the 85% isopleth was used to delimit the home range for that year. Home range was also estimated using the minimum convex polygon

(MCP) method for comparison with previous studies (Kernohan et al. 2001). For each individual, the volume of the UD was measured at each cell of the kernel density raster by generating percent volume contours (1-99%; Kertson and Marzluff 2011) using the contour tool in Geospatial Modeling Environement. This was converted to a raster of UD volume measurements in ArcMAP using the Feature to Raster tool in ArcTool Box.

The volume of intersection index (VI; Fieberg and Kochanny 2005) for pairs with overlapping home ranges was calculated using the kerneloverlap function in package adehabitat in Program R (R Development Core Team 2012). This measure improves upon a simple measure of areal overlap between two home ranges by accounting for the UD of both individuals, and thus considers the probability that each individual uses the shared space. The index was calculated using the following equation (Fieberg and Kochanny 2005):

$$\mathrm{VI} = \iint\limits_{-\infty-\infty}^{\infty\infty} \min\left[\widehat{\mathrm{UD}}_1(\mathrm{x},\mathrm{y}), \widehat{\mathrm{UD}}_2(\mathrm{x},\mathrm{y})\right] \mathrm{dxdy}$$

where$\widehat{\mathrm{UD}}_1$and $\widehat{\mathrm{UD}}_2$ are the UD estimates for individuals 1 and 2, respectively. All pairs with a $\mathrm{VI} \geq 0.10$ were considered to have significant overlap (Walter et al. 2011).

Static Interaction Analysis

To test for significant attraction or avoidance of areas of home range overlap between potentially interacting pairs, the frequencies of observations of an individual in the shared and non-shared areas were compared to the expected probabilities using a χ^2test (Minta 1992). The expected probability of use of the shared area was calculated for each individual by dividing the size of the shared area by the total size of the individual's home range. Given two individuals α and β with a shared home range area AB, the divergence (main effect, L) between α's expected and observed use of the shared area (A) and its use of the non-shared area ($\overline{\mathrm{A}}$) is calculated as:

$$L_{A:\bar{A}} = \ln\frac{p_2 n_1}{p_1 n_2}$$

where p_i and n_i denote the expected probability and the recorded frequencies of occurrences, respectively, of α in the shared (p_1, n_1) and non-shared (p_2, n_2) areas. $L > 0$ indicates that α used the shared area more frequently than expected, while $L < 0$ indicates that alpha used the shared area less frequently than expected. To test for significance, the χ^2 statistic was calculated as:

$$\chi^2_{A:\bar{A}} = \frac{(n_1 - p_1 n)^2}{(p_2 p_1 n)}$$

with df = 1. Tests were conducted separately using total home range (95% or 85% isopleths) and core areas (50% isopleths). Space use in core areas was examined for 2012 only due to the small number of observations per individual in 2011.

Space use and flock status

To examine the influence of habitat and neighbor space use on the distribution of individual flock-following locations, separate files were created for locations where an individual was present in a flock and where it was found alone. The Sample tool in ArcMAP was used to extract understory openness and neighbor UD volume at each location. The effects of the following factors on probability of flock-following at a given location were examined: UD volume of the largest overlapping individual (body mass, or longer wing chord if body mass equal), the UD volume of the neighbor with greatest overlap regardless of size, and understory openness. Each factor was tested separately rather than as part of a set of candidate models because some factors could only be tested on a subset of the data (i.e. not all individuals had a larger neighbor). Maximum likelihood methods were used to fit logistic regression mixed models of the effect of each factor on flock-following probability, with flock status as a binary response variable and individual identity as a random effect.

Results

Home Range Size and Intraspecific Interactions

Mean home range size using the fixed kernel method was 4.0 ha (0.56 SE) in 2011 and 4.1 ha (0.47 SE) in 2012, and did not differ between plots (t = 1.24, df = 36, p = 0.22; Harpia = 4.4 ha [0.42 SE], Puma = 3.7 ha [0.47 SE]). In 2011, with fewer locations per individual (mean 19 [2.1 SE], range 10-44) the MCP method resulted in a much smaller estimate (mean 1.6 ha [0.37 SE]), while in 2012 with more points per individual (mean 96 [3.3 SE], range 60-114) the mean MCP was similar (3.8 ha [0.4 SE]) to the 95% volume kernel estimate for that year.

There were ten cases of significant home range overlap in 2011 between pairs of individuals and 21 cases in 2012 (Fig. 1). The VI in these cases ranged from 0.11-1.0 in both years with a mean of 0.45 (0.06 SE) in 2011 and 0.44 (0.04 SE) in 2012. There were five cases of core overlap in 2011 and eight cases in 2012, with VI ranging from 0.24-0.82 in 2011 and 0.17-1.0 in 2012, and a mean of 0.43 (0.5 SE) in 2011 and 0.45 (0.06 SE) in 2012. In two cases in 2011 and one case in 2012, high core area overlap was believed to involve mate pairings due to the frequency with which the individuals were observed in close proximity of each other.

In 2011, of 20 individual responses in ten pairwise interactions, one was a significant attraction,two were significant avoidances, while the remainder were non-significant. In 2012, of the 46 individual responses in 23 pairwise interactions, 23 were non-significant, 17 were significant attractions, and six were significant avoidances. For core areas, of 16 responses in 2012, two were significant attractions (one of which was believed to involve a mated pair) while the remainder were non-significant effects. In all cases of significant attraction where both members of a pair were tracked during the same time period (n=10), the individuals involved were documented using the shared space at the same time (within 15 m of each other) at least once, and of those with avoidance responses that were tracked during the same time period (n=5), only one pair was documented in close proximity, and that only a single instance.

Three individuals were tracked in both years, and investigation of the estimated home ranges suggested that they occupied areas of similar size and configuration in both years (Fig. 2). One individual tracked in 2011 occupied an area that closely matched that of another individual tracked in 2012 (Fig. 3); according to capture data, both individuals were present in this home range in 2011 but probably not in 2012. A similar situation existed for near-complete overlap involving three individuals (Fig. 3), one tracked in 2011 and two tracked in 2012; all three were present at least in 2010 and 2011 according to capture data (J. Blake, pers. comm.). Another individual tracked in 2011 was observed in 2012 and believed to be mated to a bird tracked in both years.

Individuals were observed associating with a mean of 2.6 (0.2 SE) other woodcreepers (range 1-5, not including fledglings [n=3]) in 2012. These other associations (color-banded birds plus one unbanded bird per plot) indicate the presence of at least 14 individuals with home ranges at least partially overlapping those of the 23 radio-tracked birds. This is necessarily an underestimate due to the likely presence of multiple unbanded birds in the area; eight of 15 radio-marked individuals in Harpia and seven of eight in Puma were seen at least once near an unbanded bird. If each of these associations is assumed to represent a separate unmarked individual, this gives a maximum estimate of 27 additional individuals with home ranges overlapping those of the radio-tracked birds.

Space Use and Flock Status

The locations where wedge-billed woodcreepers were found in flocks were not influenced by understory openness ($\hat{\beta}$= 0.02 [0.03 SE], z=0.58, p = 0.56, Fig. 4), space use by a larger neighbor ($\hat{\beta}$ = 0.005 [0.002 SE], z = 1.79, p = 0.07, Fig. 5), or space use by the neighbor with greatest overlap ($\hat{\beta}$ = 0.003 [0.002 SE], z = 1.45, p = 0.15).

Discussion

Home Range Size

Mean home range size in both years was ~4 ha, roughly similar to several published reports for this species (French Guiana: mean 2.94 ha, range 2.75-3.21 [Jullien and Thiollay 1998]; central Brazil: 5.2 ha[Johnson et al. 2011]), although considerably smaller than reported for central Panama (placed in a category of 9-16 ha [Robinson et al. 2000]). The MCP home range estimate was much smaller than the kernel estimate in 2011, but similar to the kernel estimate in 2012; this is likely due to the sensitivity of this method to sample size (Kernohan et al. 2001), which was much smaller in 2011.In both years, there was a wide variation in home range size, with a minimum of ~2 ha in both years and a maximum of almost 9 ha. Two individuals with home ranges > 7 ha made several movements > 300 m away from the home range boundary, one individual crossing the Tiputini River in the process. It is possible that one individual may have been in the process of dispersal, but the second individual was present in the same home range in consecutive years. Such presumed exploratory movements have been documented for this species in previous studies (English 1998, Blake and Loiselle 2012).There were two other individuals in 2012 with contiguous home ranges that exceeded 7 ha that were not observed to make such movements.

Intraspecific Interactions

The home ranges of wedge-billed woodcreepers in both years of this study overlapped considerably, which corroborates the observations of Gradwohl and Greenberg (1980) of color-banded wedge-billed woodcreepers on Barro Colorado Island. On the other hand, the home range maps for this species in Jullien and Thiollay (1998) do not show any overlap, and home range overlap was not mentioned by Johnson et al. 2011 in their study in central Brazil. A comparison of home ranges occupied by individuals in consecutive years, and by separate individuals in different years, suggests that despite this overlap, home range boundaries were stable over time, as suggested by long-term capture data (Blake and Loiselle 2012). Stable territoriality has been documented in many antbird species (Greenberg and Gradwohl 1997, Gorrell et al. 2005, Duca et al. 2006), with territory size remaining constant despite turnover in territory owners and temporal variation in resource abundance (Greenberg and Gradwohl 1997, Duca et al. 2006). It has been hypothesized that territory size in these species is determined by the size necessary to sustain the pair during times of food scarcity (Stutchbury and Morton 2001), and individuals may increase survivorship by switching to better territories when vacancies arise rather than by expanding territory borders (Morton et al. 2000, Fedy and Stutchbury 2004). It is unknown whether wedge-billed woodcreepers exhibit similar territory switching behavior, or whether they instead vary the extent of home range overlap in response to seasonal changes in resource abundance.

Wedge-billed woodcreepers generally did not avoid areas of home range overlap, and most individuals were documented within close proximity (<10m) of two or more separate individuals throughout observation. Therefore, much of the home range did not appear to be defended by a resident individual, although this does not exclude the possibility that some resources within the home range, such as the area surrounding a nest, might be defended. This contrasts with the pattern of territoriality documented for other rainforest insectivores, including antbirds (Munn and Terborgh 1979, Greenberg and Gradwohl 1986, English 1998, Duca et al. 2006) and other woodcreeper species (Pierpont 1986), which defend exclusive territories. Rivera et al. (2003) documented some overlap among home ranges of the ivory-billed woodcreeper (*Xiphorhynchusflavigaster*), although individuals were not observed using shared areas at the same time.

Territoriality theory predicts that for an insectivore in aseasonal environments of wet lowland tropics, where insect availability is relatively uniform over space in time compared to the seasonal patterns of abundance in flowers and fruits (Terborgh 1990b, Leigh and Wright 1990), individuals should defend exclusive territories (Brown and Orians 1970, Davis and Hartley 1996, Maher and Lott 2000). However, at extreme levels of resource abundance, territorial behavior may disappear, either because food is no longer limiting and therefore not worth defending, or because the resources support such a high density of intruders that defense becomes too costly (Gill and Wolf 1975, Carpenter and MacMillen 1976, Maher and Lott 2000, McLaughlin et al. 2000). Studies of a variety of vertebrates have documented that an increase in population density leads to a reduction in territoriality (Benson et al. 2006, Chaverri et al. 2006) or territory size (Mares et al. 1982, Kjellander et al. 2004). In the wedge-billed woodcreeper, arthropod abundance may be sufficiently great that defense of foraging areas for exclusive use does not outweigh the cost of defense, particularly given the large number of possible intruders present in areas of high population density (including the present study area; Blake and Loiselle 2012). Furthermore, because this species nests in cavities, it is possible that the availability of nest sites is a more important determinant of spacing behavior and population size than food resources (Sick 1993), thus only such localized resources may be defended. It would be informative to study patterns of territorial behavior and home range overlap in this species across a range of population densities and resource abundances.

Space Use and Flocking

It was hypothesized that woodcreepers might be more likely to join flocks in areas of mature forest with an open understory, where they might be more vulnerable to predation than in denser habitats that provide protective cover (Grubb and Greenwald 1982, Suhonen 1993). However, understory openness did not appear to influence the distribution of flock-following locations for individual wedge-billed woodcreepers in this study. Relatively little is known about the habitat use or hunting behaviors of Neotropical raptors, particularly for the genera *Micrastur* and *Accipiter* in primary forests of Amazonia (Bierregaard 1995), although observations indicate that most *Micrastur* species hunt for small vertebrates in the understory from concealed perches (Robinson 1994). It might be false to assume that a small passerine is significantly more vulnerable to attack in an open understory than in a denser, disturbed understory. Furthermore, while it is generally assumed that diurnal raptors are the primary predators of small understory passerines in Neotropical rainforests (e.g. Munn and Terborgh 1979), the extent to which other groups of vertebrates may prey on small passerines remains largely unexplored. Anecdotal evidence suggests that snakes may at least opportunistically capture wedge-billed woodcreepers (Greene 1997). It is possible that dense microhabitats harbor a separate suite of predators and are therefore not considerably safer than areas of open understory.

The space use of overlapping neighbors did not significantly affect flock-following locations of wedge-billed woodcreepers. It was expected, based on the observations of Darrah and Smith (in prep) that body mass was correlated with flocking propensity, that individuals would join flocks less frequently in areas of high use by a larger neighbor. On one hand, this suggests that wedge-billed woodcreepers might tolerate neighbors in the same flock, which is consistent with the apparently low degree of home range defense and associations with multiple conspecifics exhibited by this species at this site. However, the methods used in this study did allow for a detailed examination of simultaneous space use, and it is therefore possible that individuals joined flocks in the same locations, but not at the same time. In a concurrent study (Darrah and Smith, in prep) it was demonstrated that wedge-billed woodcreepers do not join flocks every time one is present in its home range; therefore in an area of intraspecific overlap, the subordinate individual could be present in a flock while the dominant individual is absent from that area.

One factor complicating this investigation is the unknown relationships between interacting pairs; it is unknown whether any of these pairs were siblings or parent and offspring, and although there were three pairs that appeared to be mates, such relationships could not be determined with certainty. Individuals are often less aggressive toward kin than non-kin in a wide range of organisms (Waldman 1988, Watson et al. 1994, Bilde and Lubin 2001, Griffiths and Armstrong 2002). It would be informative in future studies to determine what effect, if any, genetic relatedness has on home range overlap and intraspecific aggression in this species.

This study reveals significant overlap among individual wedge-billed woodcreeper home ranges, with no evidence that overlap areas were used less frequently than non-shared areas. Observations suggested that neighbors regularly used these overlap areas simultaneously, and may even tolerate one another in flocks, unlike all other regular members of understory mixed-species flocks. Understory openness did not influence the locations of flock-following, suggesting either than understory openness is a poor index of predation vulnerability, or that other factors are more important in determining where and when an individual joins flocks. A detailed study of simultaneous space use patterns of neighbors, combined with genetic analyses to reveal the sex and degree of relatedness of interacting individuals, is needed to understand the significance of the spacing pattern observed in this study and to what extent individuals may compete for access to flocks.

Acknowledgements

I would like to thank B. A. Loiselle and J. G. Blake for their invaluable comments and logistical assistance in the field, and for permitting me to use their plots for this study. I thank the staff of Tiputini Biodiversity Station for their support and C. de Romo for arranging transportation to and from the field station. I thank N. Strycker and R. Rylander for volunteering their time to aid in data collection. Financial support was provided by the University of Arkansas Graduate School and the Arkansas Audubon Society Trust.

Literature Cited

Benson, J. F., M. J. Chamberlain, and B. D. Leopold. 2006. Regulation of space use in a solitary felid: population density or prey availability? Animal Behaviour 71:685–693.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76:1075–1085.

Beyer, H. L. 2009.Geospatial Modelling Environment.http://www.spatialecology.com/gme/.

Bierregaard, R. O., Jr. 1995. The biology and conservation status of Central and South American Falconiformes: a survey of current knowledge. Bird Conservation International 5:325–340.

Bilde, T. and Y. Lubin. 2001. Kin recognition and cannibalism in a subsocial spider. Journal of Evolutionary Biology 14:959–966.

Blake, J. G. 2007. Neotropical forest bird communities: a comparison of species richness and composition at local and regional scales. Condor 109:237–255.

Blake, J. G. and B. A. Loiselle. 2012. Temporal and spatial patterns in abundance of the wedge-billed woodcreeper (*Glyphorynchusspirurus*) in lowland Ecuador. The Wilson Journal of Ornithology 124:436–445.

Brown, J. L. and G. H. Orians. 1970. Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1:239–262.

Carpenter, F. L. and R. E. MacMillen. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. Science 194:639–642.

Chaverri, G., M. Gamba-Rios, and T. H. Kunz. 2007. Range overlap and association patterns in the tent-making bat Artibeus watsoni. Animal Behaviour 73:157–164.

Davis, N. B. and I. R. Hartley. 1996. Food patchiness, territory overlap and social systems: an experiment with dunnocks *Prunella modularis*. Journal of Animal Ecology 65:837–86.

Dolby, A. S. and T. C. Grubb, Jr. 2000. Social context affects risk taking by a satellite species in a mixed-species foraging group. Behavioral Ecology 11:110–114.

Duca, C., T. J. Guerra, and M.Â.Marini. 2006. Territory size of three antbirds (Aves, Passeriformes) in an Atlantic Forest fragment in southeastern Brazil. RevistaBrasileira de Zoologia 23:692–698.

English, P. H. 1998. Ecology of mixed-species understory flocks in Amazonian Ecuador. Ph.D. Dissertation, University of Texas, Austin.

Fedy, B. C. and B. J. M. Stutchbury. 2004. Territory switching and floating in white-bellied antbird (*Myrmeciza longipes*), a resident tropical passerine in Panama. Auk 121:486–496.

Fieberg, J. and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346–1359.

Gill, F. B. and L. L. Wolf. 1975. Economics of feeding territoriality in the golden-winged sunbird. Ecology 56:333–345.

Gorrell, J. V., G. Ritchison, and E. S. Morton. 2005. Territory size and stability in a sedentary Neotropical passerine: is resource partitioning a necessary condition? Journal of Field Ornithology 76:395–401.

Gradwohl, J. and Greenberg, R. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. Auk 97:385–395.

Greenberg, R. 2000. Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. Pages 521–558 in On the Move: How and Why Animals Travel in Groups (S. Boinski and P. A. Garber, Eds.) The University of Chicago Press, Chicago.

Greenberg, R. and J. Gradwohl. 1986. Constant density and stable territoriality in some tropical insectivorous birds. Oecologia 69:618–625.

Greene, H. W. 1997. Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley.

Griffiths, S. W., and J. D. Armstrong. 2002. Kin-based territory overlap and food sharing among Atlantic salmon juveniles. Journal of Animal Ecology 71:480–486.

Grubb, T. C., Jr. and L. Greenwald. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. Animal Behaviour 30:637–640.

Horne, J. S., E. O Garton, and J. L. Rachlow. 2008. A synoptic model of animal space use: simultaneous estimation of home range, habitat selection, and inter/intra-specific relationships. Ecological Modelling 214:338–348.

Janke, A. K. and R. J. Gates. 2013. Home range and habitat selection of northern bobwhite coveys in an agricultural landscape. Journal of Wildlife Management 77:405–413.

Johnson, E. I., P. C. Stouffer, and C. F. Vargas. 2011. Diversity, biomass, and trophic structure of a central Amazonian rainforest community. RevistaBrasileira de Ornitologia 19:1–16.

Jullien, M. and J.-M. Thiollay. 1998. Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. Journal of Animal Ecology 67:227–252.

Jullien, M. and J. Clobert. 2000. The survival value of flocking in Neotropical birds: reality or fiction? Ecology 81:3416–3430.

Kamler, J. F., U. Stenkewitz, U. Klare, N. F. Jacobsen, and D. W. MacDonald. 2012. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. Journal of Wildlife Management 76:1241–1253.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 in Radio Tracking and Animal Populations (J. J. Millspaugh and J. M. Marzluff, Eds.). Academic Press, San Diego.

Kertson, B. N. and J. A. Marzluff. 2011. Improving studies of resource selection by understanding resource use. Environmental Conservation38:18–27.

Kjellander, P., A. J. M. Hewison, O. Liberg, J.-M.Bideau, and B. Cargnelutti. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. Oecologia 139:478–485.

Leigh, E. G., Jr. and S. J. Wright.1990. Barro Colorado Island and tropical biology.Pages 28–47 in Four Neotropical Rainforests (A. H. Gentry, Ed.). Yale University Press, New Haven.

Maher, C. R. and D. F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. American Midland Naturalist 143:1–29.

Marantz, C. A., A. Aleixo, L. R. Bevier, andM. A. Patten. 2003.Family Dendrocolaptidae (Woodcreepers). Pages 358–447 in Handbook of the Birds of the World, Vol. 8. Broadbills to Tapaculos (J. del Hoyo, A. Elliott, and D. Christie, Eds.). Lynx Edicions, Barcelona.

Mares, M. A., T. E. Lacher, Jr., M. R. Willig, N. A. Bitar, R. Adams, A. Klinger, and D. Tazik. 1982. An experimental analysis of social spacing in *Tamiasstriatus*. Ecology 63:267–273.

McLaughlin, P. D., S. H. Ferguson, and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology 14:39–60.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke.2000. Elk and hunter space-use sharing in South Dakota. Journal of Wildlife Management64:994–1003.

Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. Ecological Appliations 2:178–188.

Montgomery, R. A., G. J. Roloff, and J. J. Millspaugh. 2013. Variation in elk response to roads by season, sex, and road type. Journal of Wildlife Management 77:313–325.

Munn, C. A. 1984. The behavioral ecology of mixed-species bird flocks in Amazonian Peru. Ph.D. Dissertation, Princeton University, Princeton.

Munn, C. A. and J. W. Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. Condor 81:338–347.

Morton, E. S., K. C. Derrickson, and B. J. M. Stutchbury. 2000. Territory switching behavior in a sedentary tropical passerine, the dusky antbird (*Cercomacra tyrannina*). Behavioral Ecology 11:648–653.

Pierpont, N. 1986. Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae). Ph.D. Dissertation, Princeton University, Princeton, New Jersey.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. Journal of Wildlife Management 73:345–356.

R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rappole, J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Rivera, J. H. W., D. Ayala, and C. A. Haas. 2003. Home-range size, habitat use, and reproduction of the ivory-billed woodcreeper (*Xiphorhynchusflavigaster*) in dry forest of western Mexico. Journal of Field Ornithology 74:141–151.

Robinson, S. K. 1994. Habitat selection and foraging ecology of raptors in Amazonian Peru. Biotropica 26:443–458.

Robinson, W. D., J. D. Brawn, and S. K. Robinson. 2000. Forest bird community structure in central Panama: influence of spatial scale and biogeography. Ecological Monographs 70:209–235.

Seaman, D.E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Sick, H. 1993. Birds in Brazil: A Natural History. Princeton University Press, Princeton.

Stutchbury, B. J. M. and E. S. Morton. 2001. Behavioral Ecology of Tropical Birds. Academic Press, San Diego.

Suhonen, J. 1993. Predation risk influences the use of foraging sites by tits. Ecology 74:1197–1203.

Terborgh, J. 1990a. Mixed flocks and polyspecific associations: costs and benefits of mixed groups of birds and monkeys. American Journal of Primatology 21:87–100.

Terborgh, J. 1990b. An overview of research at Cocha Cashu Biological Station.Pages 48–59 in Four Neotropical Rainforests (A. H. Gentry, Ed.). Yale University Press, New Haven.

Thiollay, J.-M and M. Jullien. 1998. Flocking behavior of foraging birds in a Neotropical rain forest and the antipredator defence hypothesis. Ibis 140:382–394.

Waldman, B. 1988.The ecology of kin recognition. Annual Review of Ecology and Systematics 19:543–571.

Walter, W. D., J. Beringer, L. P. Hansen, J. W. Fischer, J. J. Millspaugh, and K. C. Vercauteren. 2011. Factors affecting space use overlap by white-tailed deer in an urban landscape. International Journal of Geographical Information Science 25:379–392.

Watson, A., R. Moss, R. Parr, M. D. Mountford, and P. Rothery. 1994. Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. Journal of Animal Ecology 63:39–50.

Wiley, R. H. 1980. Multispecies antbird societies in lowland forests of Surinam and Ecuador: stable membership and foraging differences. Journal of Zoology, London 191:127–145.

Willson, S. K. 2004. Obligate army-ant-following birds: a study of ecology, spatial movement patterns, and behavior in Amazonian Peru. Ornithological Monographs 55:1–67.

Figure 1. Home ranges of 14 wedge-billed woodcreepers (*Glyphorynchus spirurus*) tracked using radio telemetry during Jan-Mar 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

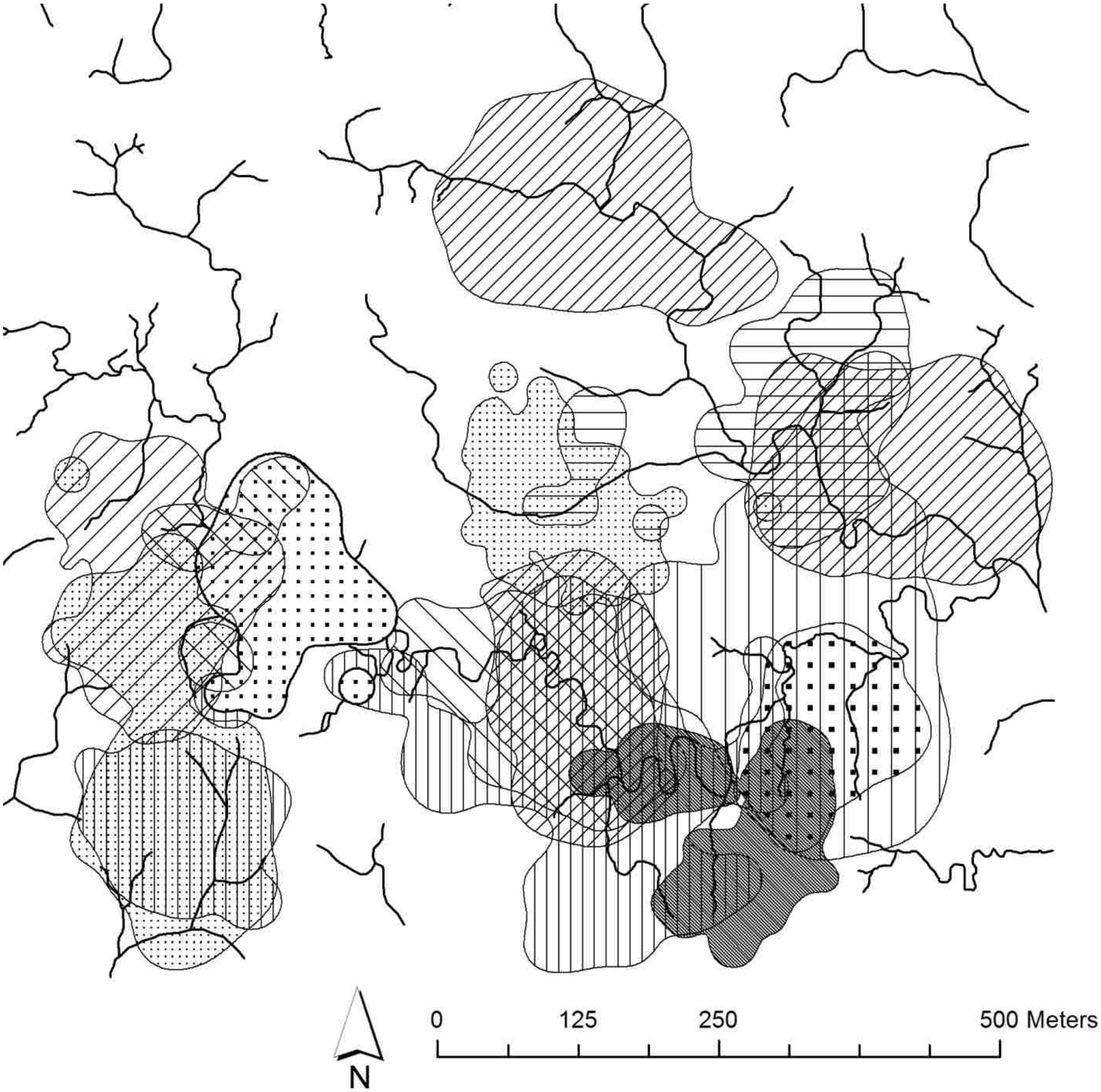


Figure 2. Home ranges of three wedge-billed woodcreepers (*Glyphorynchus spirurus*) tracked in consecutive years (Jan-Feb 2011 and Jan-Mar 2012) at Tiputini Biodiversity Station, Orellana Province, Ecuador.

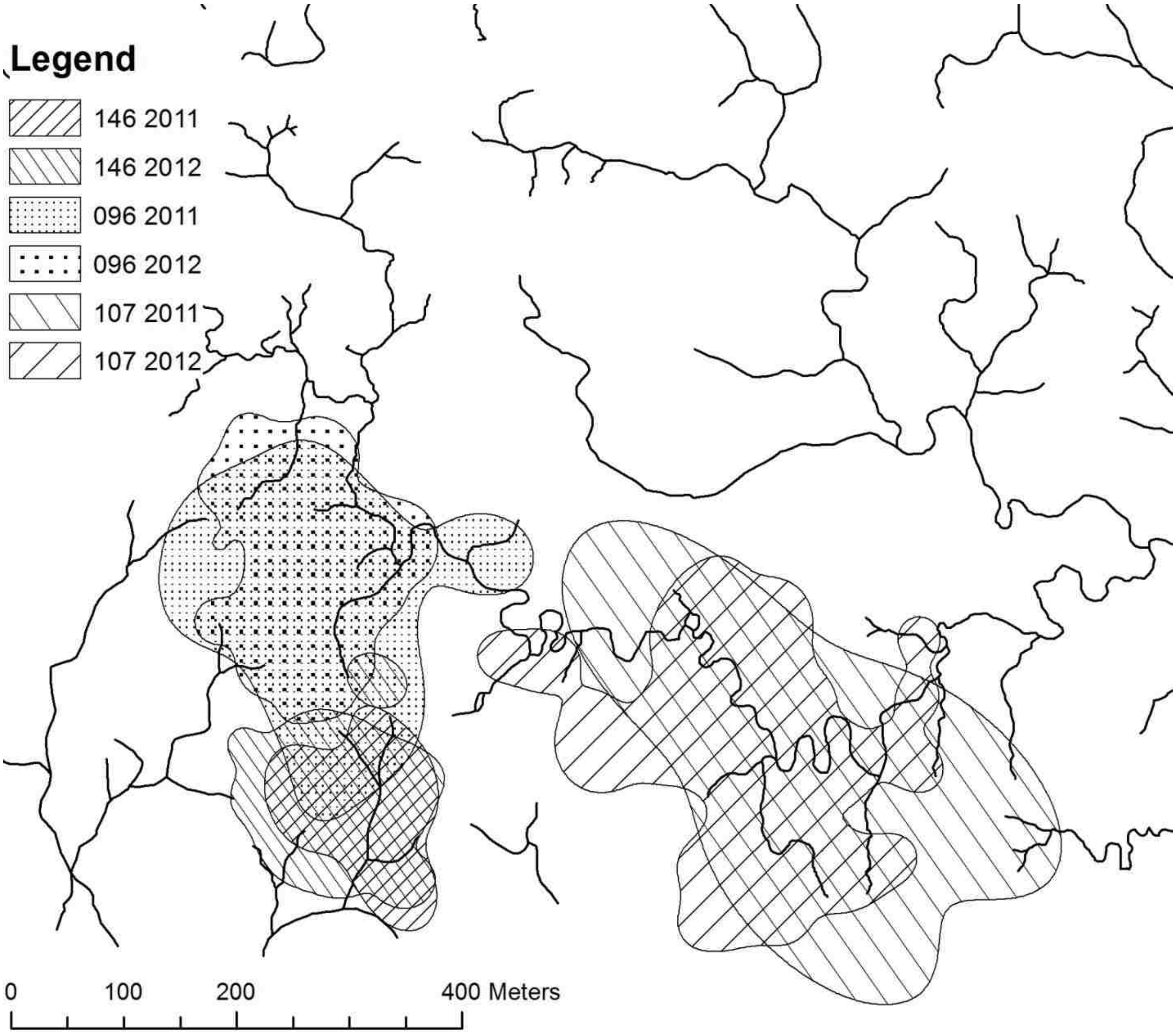


Figure 3. Home ranges of six wedge-billed woodcreepers (*Glyphorynchus spirurus*) tracked during Jan-Feb 2011 and Jan-Mar 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

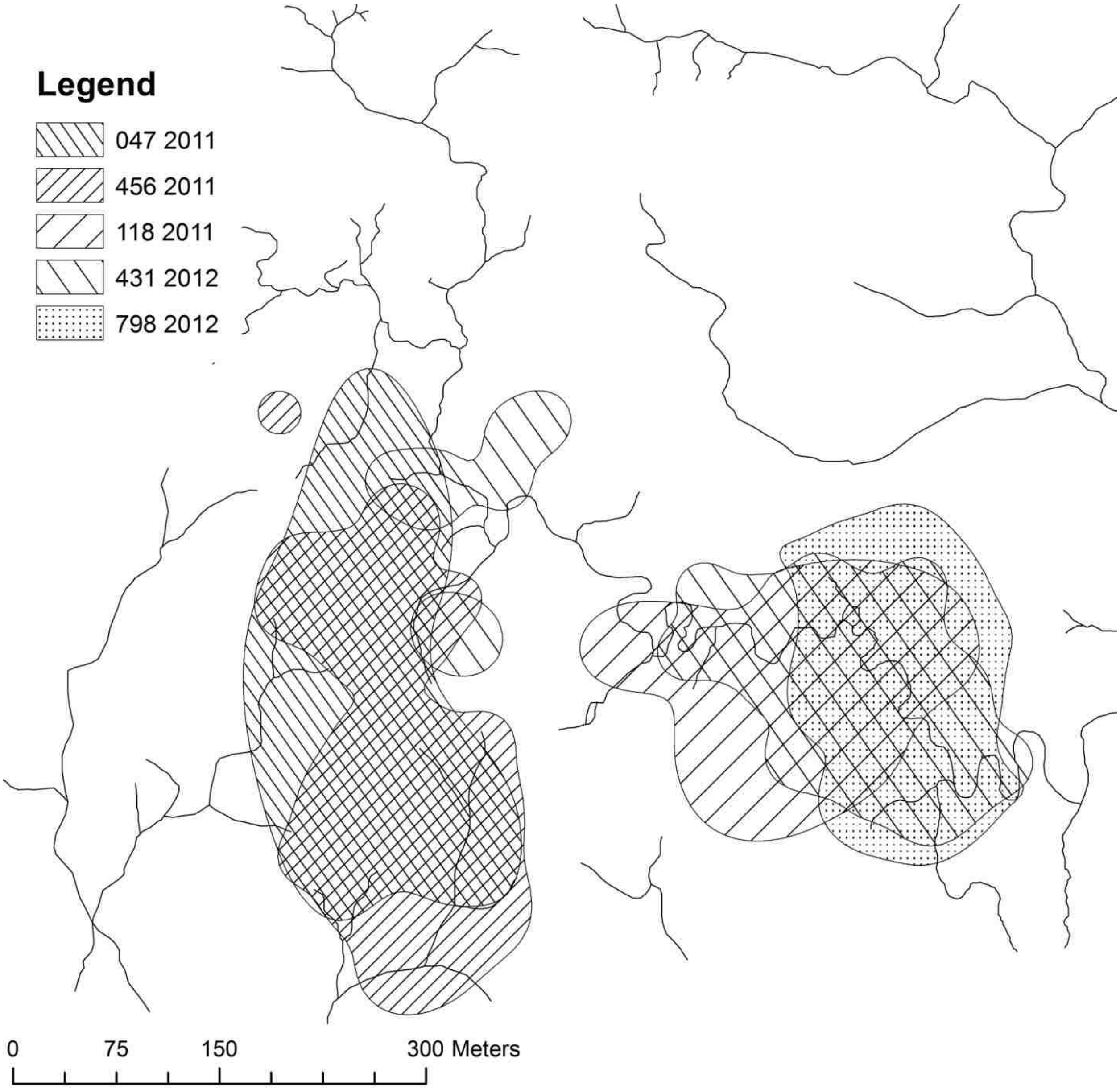


Figure 4. The relationship between understory visibility (m) and locations where 21 individual wedge-billed woodcreepers (*Glyphorynchus spirurus*) were observed in a mixed-species flock (Yes) or away from a flock (No) atTiputini Biodiversity Station, Orellana Province, Ecuador.

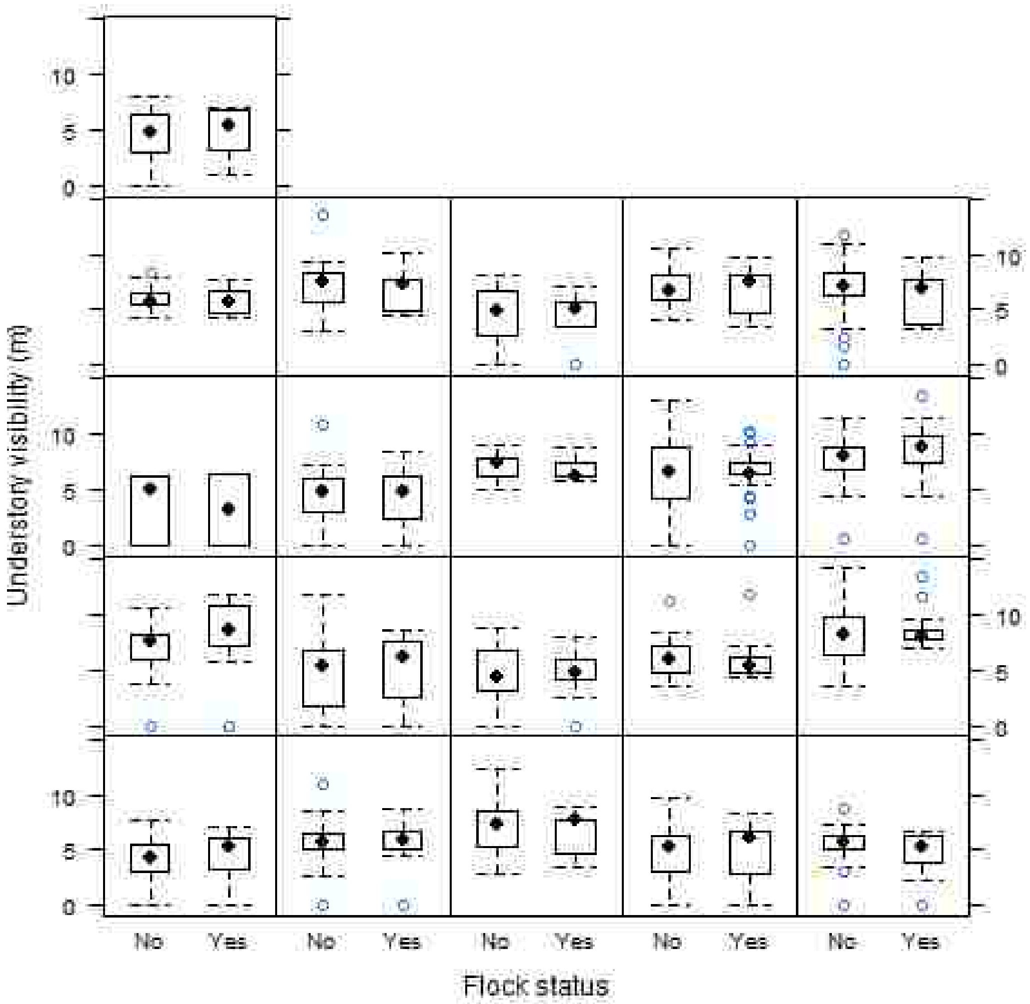
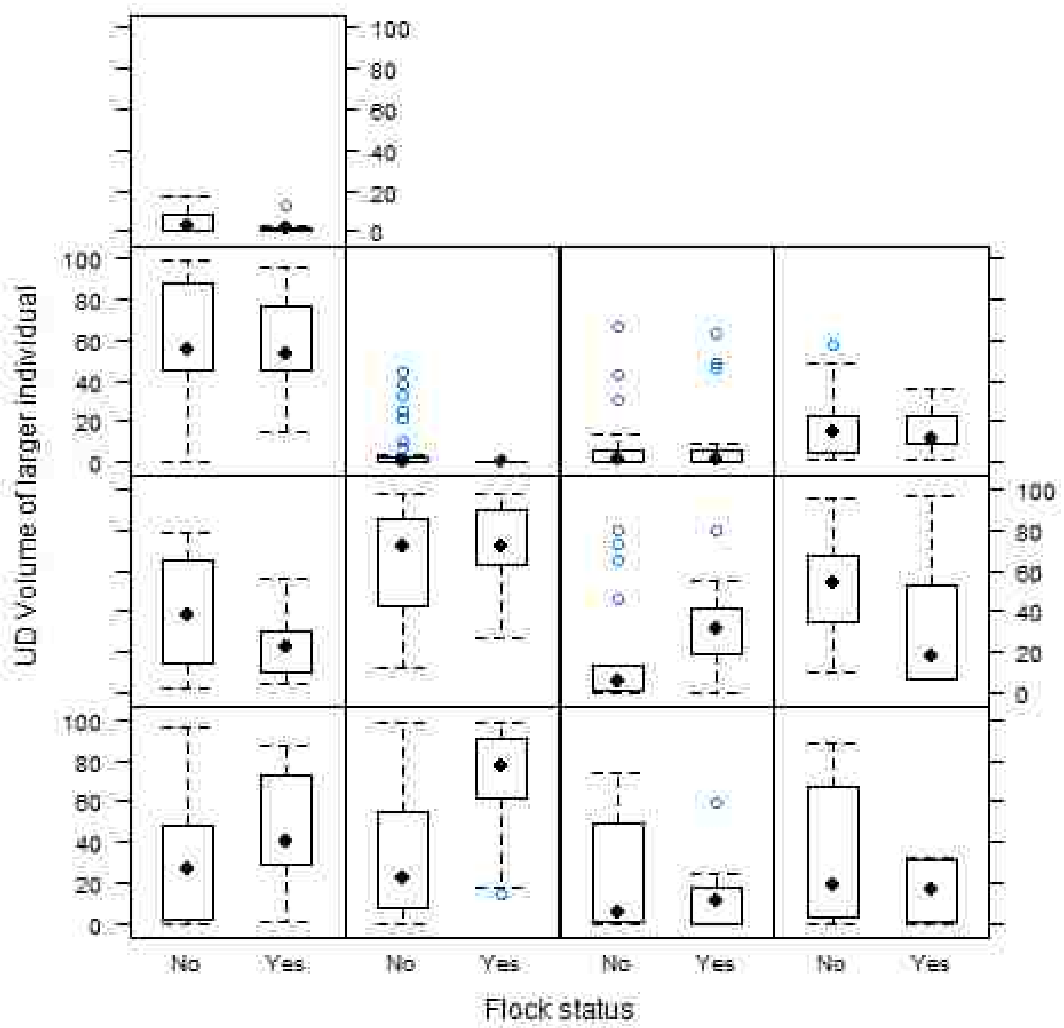


Figure 5.Relationship between the utilization distribution (UD) of a larger overlapping neighbor and locations where 13 individual wedge-billed woodcreepers (*Glyphorynchus spirurus*) were observed in a mixed-species flock (Yes) or away from a flock (No) atTiputini Biodiversity Station, Orellana Province, Ecuador.



CHAPTER 5: NOTES ON BREEDING AND COURTSHIP BEHAVIOR OF THE WEDGE-BILLED WOODCREEPER (*GLYPHORYNCHUS SPIRURUS*) IN EASTERN ECUADOR

Introduction

The wedge-billed woodcreeper (*Glyphorynchus spirurus*) is a common suboscine passerine of lowland forests of the Neotropics, ranging from southern Mexico to northern Bolivia and eastern Brazil (Marantz et al. 2003). Despite its abundance and extensive geographic range, few studies have investigated the behavior or ecology of this species. In this paper I provide dates of eggs and fledglings for a site in eastern Ecuador, describe a previously unknown display that is likely involved in courtship, and give notes on incubation and fledging care behavior.

Methods

This study was conducted at Tiputini Biodiversity Station (0°38’15”S, 76°08’59”W) in Orellana Province, Ecuador. The station encompasses 638 ha of rainforest within the 1,682,000-ha UNESCO Yasuni Biosphere Reserve. The forest is composed mainly of undisturbed terra firme rainforest, with a strip of varzea bordering the Tiputini River. The mean elevation at the station is ~220m above sea level, and the region receives roughly 3200mm of rainfall annually. The current project was conducted on two ~100-ha plots within the reserve, separated by ~1.5 km (Blake 2007).

Wedge-billed woodcreepers (hereafter "woodcreepers") were captured in both study plots in 2012 using 2.6-m mist nets as part of a long-term demographic study of understory birds (see Blake and Loiselle 2012 for additional details). Twenty-three woodcreepers were captured in Jan-Mar 2012 and fitted with a radio transmitter (0.45g BD-2, Holohil Systems Ltd, Carp, Ontario, Canada) using a thigh harness (Rappole and Tipton 1991) made from either cotton or elastic thread. Individuals were released at the site of capture.

Woodcreepers were tracked using Advanced Telemetry Systems Field Master receivers and hand-held three-element Yagi antennas for 2-3 h per day, beginning at least 24 h after capture, and continuing throughout the battery life of the transmitter (~2 wk) or until the transmitter was dropped due to premature harness breakage (one case). Order of tracking was randomized each day such that individuals were tracked equally during all daily time periods. Location of the woodcreeper was determined by homing, in which the woodcreeper was approached until it was either seen, or until the lack of directionality in the signal indicated close proximity (~10m; two technicians were trained with the transmitters prior to tracking in order to calibrate their abilities to judge distances using the equipment). While the primary aim of the radio-tracking was to investigate flock-following behavior and space use patterns of this species (Darrah and Smith, in prep), any behaviors related to breeding were noted during observation.

Display Behavior

One radio-marked individual (named “Brandt”) was observed engaging in the following display with an unmarked bird on 31 Jan, beginning at 10:40, while following a mixed-species flock. The unmarked bird was ~1m above the ground, and Brandt was ~ 30 cm above and slightly to the side on the same trunk. Both individuals were wing-flicking and calling while bowing their heads, the unmarked individual pointing its head up and toward Brandt, while Brandt was extending its head to the side and slightly down toward the other bird (Fig. 1). Each head extension lasted about one second, followed by a 1-2 s pause before performing another head extension. After performing this behavior for 10 min, Brandt flew to a different trunk ~1m away and continued calling. A third individual was heard calling, and the mixed-species flock began moving away from the area. At 11:05 Brandt and the second individual briefly rejoined the flock, but did not follow it as the flock continued to move. At 11:25 the two birds were again seen performing the display, with Brandt again above the other individual, <1m from the ground. Brandt hitched down the trunk between head extensions until the two birds were side-by-side on the trunk, pointing bills toward each other during each extension. The birds occasionally called, and frequently opened their bills during the extensions. It was difficult to determine which bird was initiating each extension; at times it appeared to be Brandt, at other times it appeared to be the unbanded individual. This display continued until 12:00, when the birds moved to a nearby trunk and continued the behavior, ~ 15 cm from the ground, with Brandt briefly switching to the bottom position. At 12:15 both birds tumbled to the ground, one on top of the other in what appeared to be copulation, and then flew back to the trunk. This behavior was repeated at 12:20, followed by a pause of several seconds with one bird on top of the other on the ground before returning to the trunk. Afterwards a third individual appeared nearby, followed by much calling and moving around by all three individuals.

Brandt was again observed performing this display on 8 Feb, this time in an area ~300 m from its core home range,toward one individual of a pair of unmarked birds. The unmarked bird responded with display, but also repeatedly flew away from Brandt. Brandt performed this display for 20 min, following the unmarked pair for a distance of at least 50 m.

A brief version of this display was observed twice in what appeared to be different contexts from that described above. At 9:10 on 2 Feb, one individual ("Juliet") approached to within 30 cmunder a banded individual on the same trunk. Both birds were calling, and Juliet performed a head extension, with head flat against the trunk and bill open and pointing up toward the other bird, after which the other bird flew away. Juliet was discovered with a fledgling 30 min later (details below), and the banded bird was never subsequently observed near the fledgling. On 6 Mar, an unmarked individual was seen performing this display toward a fledgling associated with another radio-marked bird. The fledgling responded by repeatedly sidling away from the displaying bird and after ~30 s flying from the trunk. Fifteen minutes later in the same area, the unmarked bird (assumed to be the same) once again approached the fledging, which again flew away in response.

Breeding Notes

Of the 23 individuals radio-tracked from 12 Jan - 31 Mar, five were discovered to be breeding, as evidenced by eggs or fledglings. One individual was flushed from a nest on 27 Jan. The nest was located in a cavity ~1 m high in a stump, with two eggs located on the floor of the cavity at the level of the entrance, and hence easily visible. During the first tracking session of this bird (29 Jan, 6:45-8:30), it incubated for at least one hour, starting at 7:30. It was not observed at the nest on 30 Jan from 10:30-12:30, and on 31 Jan the eggs had disappeared, with half an eggshell at the base of the stump.

A nest of another individual was discovered on 20 Mar within the home range of one of the birds being tracked ("Spongy"), although the bird that flushed from the nest was unbanded. The nest was in a hollow between trunks, with an opening ~1.5 m high, although the contents could not be seen. On 23 Mar at 11:30, Spongy was flushed from this nest. It did not approach the nest during a tracking session later that same day from 13:50-14:50. During 2-h tracking sessions from 24-28 Mar, incubation by Spongy ranged from 0-45 minutes (Table 1). At the end of one session during which Spongy did not approach the nest (28 Mar), the unbanded bird was flushed from the next. Nestlings were first heard on 29 Mar. On 31 Mar Spongy's transmitter battery died, and when the nest was checked that day and again several times that week, no bird was flushed nor nestlings heard, and the nest was presumed to have failed.

Three radio-tracked birds were observed caring for a fledgling from 2-10 Feb, 1-14 Mar, and 4-14 Mar. A fourth fledgling was observed briefly on 28 Mar near a radio-tracked bird, but it was not observed again during the remaining three tracking days and was believed to belong to a different pair. In the other three cases, the fledgling was observed until transmitter failure. All three individuals were observed feeding the fledgling during one or more observation periods (Table 2), and in one case an additional individual (presumably the other parent) was observed feeding a fledgling.Juliet followed a mixed-species flock with its fledgling on 7 Feb for 20 minutes, with two other adults present in the flock. During three observation periods, another radio-tracked individual gave soft versions of its song while near its fledgling, and the fledgling responded by calling and flying toward the parent. This behavior was also observed twice during observation of the third radio-tracked individual, and during a later observation period of that same individual, an unmarked bird gave a quiet song to which the fledgling called in response.

Discussion

Wedge-billed woodcreepers were observed breeding throughout the study period (Jan-Apr), coinciding with breeding times given for northern Amazonia and southeastern Colombia in Marantz et al. (2003). Given the low proportion of individuals observed breeding (5/23) during this period, it is likely that breeding in this area extends beyond the observation period. It is possible that some proportion of the population might be found breeding at any time of the year, as has been documented in antbirds in the area (Tallman and Tallman 1997). Two of the five breeding individuals in this study were simultaneously undergoing molt; this coincidence of molt and breeding was also observed for antbirds by Tallman and Tallman (1997).

Both members of a pair were observed incubating one of the two nests discovered, corroborating previous observations (Marantz et al. 2003). Despite an average clutch size of 2 eggs, only one fledgling was ever observed in this study. Both parents apparently take part in feeding fledglings, although the rate of feedings appeared to be low and fledglings were observed foraging for themselves occasionally. A soft version of the adult song appears to play an important role in parent-offspring communication.

The head-extension behavior described in this paper is an inconspicuous part of the behavioral repertoire of this species, which perhaps accounts for its lack of formal description in the literature until now. I know of no other similar behavior described for other species of woodcreepers. It appears to play an important role in courtship, with one instance of this behavior leading up to copulation, but the other contexts in which this display was observed suggested an additional function in aggressive encounters.

Acknowledgements

I would like to thank B. A. Loiselle and J. G. Blake for their invaluable comments and logistical assistance in the field, and for permitting us to use their plots for this study. I thank the staff of Tiputini Biodiversity Station for their support and C. de Romo for arranging transportation to and from the field station. I thank N. Strycker and R. Rylander for volunteering their time to aid in data collection. Financial support was provided by the University of Arkansas Graduate School and the Arkansas Audubon Society Trust.

Literature Cited

Blake, J. G. 2007. Neotropical forest bird communities: a comparison of species richness and composition at local and regional scales. Condor 109:237–255.

Blake, J. G. and B. A. Loiselle. 2012. Temporal and spatial patterns in abundance of the wedge-billed woodcreeper (*Glyphorynchus spirurus*) in lowland Ecuador. The Wilson Journal of Ornithology 124:436-445.

Marantz, C. A., Aleixo, A., Bevier, L.R. & Patten, M.A. 2003.Family Dendrocolaptidae (Woodcreepers).Pages 358–447 in Handbook of the Birds of the World, Vol. 8. Broadbills to Tapaculos (J. del Hoyo, A. Elliott, and D. Christie, Eds.). Lynx Edicions, Barcelona.

Rappole, J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Tallman, D. A. and E. J. Tallman. 1997. Timing of breeding by antbirds (Formicariidae) in an aseasonal environment in Amazonian Ecuador. Ornithological Monographs 48:789–789.

Table 1.Duration and times of egg incubation by a radio-tracked wedge-billed woodcreeper (*Glyphroynchus spirurus*) at Tiputini Biodiversity Station, Orellana Province, Ecuador, in 2012.

Date	Observation Period	Time of Incubation	Duration (min)
21-Mar	6:40-8:40	none	0
23-Mar	13:50-14:50	none	0
24-Mar	8:25-10:10	8:25	30
25-Mar	6:55-8:55	7:47	18
26-Mar	8:45-10:45	none	0
27-Mar	12:05-14:05	13:00	45
28-Mar	6:15-8:15	none	0
29-Mar	9:25-11:25	none	0

Table 2.Frequency of fledgling feedings by three radio-tracked adult wedge-billed woodcreepers (*Glyphorynchus spirurus*), with additional behavioral notes, observed at Tiputini Biodiversity Station, Orellana Province, Ecuador, in 2012.

Individual	Date	Observation	Feeding Frequency	Other Notes
1	2-Feb	9:10-11:10	0	
1	4-Feb	8:30-10:30	0	
1	5-Feb	12:20-13:35	0	
1	6-Feb	13:25-14:30	0	
1	7-Feb	10:10-13:10	2	joined flock with fledgling
1	8-Feb	6:20-8:20	0	
1	9-Feb	13:40-16:45	1	
1	10-Feb	6:20-9:00	1	
2	1-Mar	6:15-8:00	1	fledgling foraging, song and approach[1]
2	2-Mar	10:20-12:05	0	
2	3-Mar	11:25-12:25	0	
2	4-Mar	9:55-12:55	1	fledgling foraging
2	5-Mar	8:35-10:35	0	
2	6-Mar	14:45-16:45	0	song and approach
2	7-Mar	11:15-13:15	0	
2	8-Mar	9:50-11:50	0	
3	4-Mar	13:20-16:20	0	song and approach
3	5-Mar	6:25-8:25	0	
3	6-Mar	9:40-11:40	0	
3	6-Mar	16:45-17:30	1	song and approach
3	7-Mar	8:40-11:15	0	
3	8-Mar	12:35-13:35	0	
3	9-Mar	6:45-7:45	0	
3	10-Mar	6:40-9:40	0	
3	11-Mar	7:45-10:45	0	fledgling foraging
3	12-Mar	9:10-10:40	1	song and approach
3	13-Mar	6:35-9:35	0	
3	14-Mar	10:55-11:55	0	

[1] "Song and approach" refers to the adult giving one or more songs, followed immediately by the fledgling approaching the adult.

Figure 1. Photos of two wedge-billed woodcreepers (*Glyphorynchus spirurus*) in a) neutral position and b) performing head extensions.

CHAPTER 6: CONCLUSIONS

Foraging observations of wedge-billed woodcreepers in and out of flocks supported the anti-predator hypothesis for the benefits of joining flocks, although some predictions based on this hypothesis were not upheld. As expected, wedge-billed woodcreepers foraged in more exposed microhabitats while in flocks than while alone, a behavior that has been documented for other flock-following species (Munn 1984, Dolby and Grubb 2000, Tubelis et al. 2006). However, scanning rates were not significantly lower in flocks as was expected. Given the few scanning behaviors observed in this study in either situation, wedge-billed woodcreepers can likely maintain some level of vigilance while feeding without cocking the head in scanning behavior (Lima and Bednekoff 1999, Dukas and Kamil 2000, Cresswell et al. 2003), although with the likely result of reduced awareness of threats perceived in the peripheral vision (Dukas and Kamil 2000). Also unexpectedly, the extent of understory openness did not influence the distribution of flock-following locations, suggesting that wedge-billed woodcreepers are no more likely to join a flock in open areas than in dense areas. It is possible that understory openness is not a good index of vulnerability to predation in this species, due to the paucity of information of the importance of non-avian predators. Furthermore, as will be discussed below, other factors such as intraspecific competition and costs of following may be more important in determining where and when an individual will join a flock.

The most likely cost incurred to a wedge-billed woodcreeper joining a flock appears to be energetic, in the form of reduced foraging efficiency, increased energy expenditure, or both. Wedge-billed woodcreepers spent less time per trunk in flocks than when alone, which resulted from an increase in search movement (hitch) rate without a concurrent increase in prey attack (peck) rate, suggesting a reduction in foraging efficiency (Giraldeau and Caraco 2000). However, the difficulty in observing and quantifying prey capture rate for this species, and hence energy intake, precluded a robust interpretation of this observation, and it remains possible that wedge-billed woodcreepers are able to compensate for the increased search rate by selecting only larger, more profitable prey (Giraldeau and Caraco 2000). Despite this limitation, the observation that the time wedge-billed woodcreepers spent following a flock decreased with flock movement rate provides additional support for an energetic cost associated with conforming to flock movements.

Flocking propensity at the species level (20-30% per year) was considerably lower than the 40-60% generally reported in the literature (Munn 1985, Marantz et al. 2003, Jullien and Thiollay 1998), and predicted based on flock-joining opportunities using respective territory sizes of wedge-billed woodcreepers and mixed-species understory flocks (Pomara et al. 2007). The discrepancy between the values in this study and those in the literature appear to be methodological; this is the first study to measure flocking propensity directly via radio telemetry, rather than estimating flocking propensity as the proportion of total sightings that were within a flock (e.g. Jullien and Thiollay 1998). Individual flocking propensity was not correlated with the frequency of flock presence within the home range, and individuals were regularly observed foraging alone when a flock was audible neaby. Additionally, the distribution of flock-joining and flock-leaving locations indicated that individuals do not simply join a flock as it enters its home range and leave the flock when it crosses back out of the home range, unlike most other regular flocking species (Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Jullien and Thiollay 1998).

Individual flocking propensity was positively correlated with body mass, and the correlation between the differences in body mass and flocking propensity of interacting neighbors suggests the existence of intraspecific competition for access to mixed-species flocks.

Contrary to this hypothesis, the distribution of flock-following locations of individuals was not influenced by the space use of larger neighbors. However, the methods used in this study did not allow for a detailed examination of simultaneous space use, and it is therefore possible that individuals joined flocks in the same locations, but not at the same time. Furthermore, it is unknown whether any of these pairs were siblings or parent and offspring, and although there were three pairs that appeared to be mates, such relationships could not be determined with certainty. Individuals are often less aggressive toward kin than non-kin in a wide range of organisms (Waldman 1988, Watson et al. 1994, Bilde and Lubin 2001, Griffiths and Armstrong 2002). Therefore, a robust test of the hypothesis of intraspecific competition for access to flocks would necessitate collecting simultaneous space use and interaction data along with a study of genetic relatedness among interacting individuals.

Home ranges of individual wedge-billed woodcreepers overlapped extensively, and individuals regularly used these overlap areas simultaneously, contrasting with the defense of exclusive territories seen in many antbirds (Thamnophilidae; Munn and Terborgh 1979, Greenberg and Gradwohl 1986, English 1998, Duca et al. 2006) and other woodcreeper species (Pierpont 1986). It is unknown why the wedge-billed woodcreeper does not defend exclusive territories in the manner of other insectivores, which is the spacing pattern predicted by theory due to the defensibility of arthropod resources distributed relatively uniformly over space and time (Brown and Orians 1970, Maher and Lott 2000). However, at extreme levels of resource abundance, territorial behavior may disappear, either because food is no longer limiting and therefore not worth defending, or because the resources support such a high density of intruders that defense becomes too costly (Maher and Lott 2000, McLaughlin et al. 2000). In the wedge-billed woodcreeper, arthropod abundance may be sufficiently great that defense of foraging areas for exclusive use does not outweigh the cost of defense, particularly given the large number of possible intruders present in areas of high population density (including the present study area; Blake and Loiselle 2012). It would be informative to study patterns of territorial behavior and home range overlap in this species across a range of population densities and resource abundances.

Literature Cited

Bilde, T. and Y. Lubin. 2001. Kin recognition and cannibalism in a subsocial spider. Journal of Evolutionary Biology 14:959–966.

Blake, J. G. and B. A. Loiselle. 2012. Temporal and spatial patterns in abundance of the wedge-billed woodcreeper (*Glyphorynchusspirurus*) in lowland Ecuador. The Wilson Journal of Ornithology 124:436–445.

Brown, J. L. and G. H. Orians. 1970. Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1:239–262.

Cresswell, W., J. L. Quinn, M. J. Whittingham, and S. Butler. 2003. Good foragers can also be good at detecting predators. Proceedings of the Royal Society of London, Series B 270:1069–1076.

Dolby, A. S., and T. C. Grubb, Jr. 2000. Social context affects risk taking by a satellite species in a mixed-species foraging group. Behavioral Ecology 11:110–114.

Duca, C., T. J. Guerra, and M.Â. Marini. 2006. Territory size of three antbirds (Aves, Passeriformes) in an Atlantic Forest fragment in southeastern Brazil. RevistaBrasileira de Zoologia 23:692–698.

Dukas, R., and A. C. Kamil. 2000. The cost of limited attention in Blue Jays. Behavioral Ecology 11:502–506.

English, P. H. 1998. Ecology of mixed-species understory flocks in Amazonian Ecuador. Ph.D. Dissertation, University of Texas, Austin.

Giraldeau, L.-A., and T. Caraco. 2000. Social Foraging Theory. Princeton University Press, Princeton, New Jersey.

Gradwohl, J. and R. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. Auk 97:385–395.

Greenberg, R. and J. Gradwohl. 1986. Constant density and stable territoriality in some tropical insectivorous birds. Oecologia 69:618–625.

Griffiths, S. W., and J. D. Armstrong. 2002. Kin-based territory overlap and food sharing among Atlantic salmon juveniles. Journal of Animal Ecology 71:480–486.

Jullien, M. and J.-M.Thiollay. 1998. Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. Journal of Animal Ecology 67:227–252.

Lima, S. L., and P. A. Bednekoff. 1999. Back to the basics of antipredatory vigilance: Can nonvigilant animals detect attack? Animal Behaviour 58:537–543.

Maher, C. R. and D. F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. American Midland Naturalist 143:1–29.

Marantz, C. A., A. Aleixo, L. R. Bevier, and M. A. Patten. 2003. Family Dendrocolaptidae (Woodcreepers). Pages 358–447 in Handbook of the Birds of the World, Vol. 8. Broadbills to Tapaculos (J. del Hoyo, A. Elliott, and D. Christie, Eds.). Lynx Edicions, Barcelona.

McLaughlin, P. D., S. H. Ferguson, and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. Evolutionary Ecology 14:39–60.

Munn, C. A. 1984. The behavioral ecology of mixed-species bird flocks in Amazonian Peru. Ph.D. Dissertation, Princeton University, Princeton.

Munn, C. A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. Ornithological Monographs 36:683–712.

Munn, C. A. and J. W. Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. Condor 81:338–347.

Pierpont, N. 1986. Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae). Ph.D. Dissertation, Princeton University, Princeton.

Pomara, L. Y., R. J. Cooper, and L. J. Petit. 2007. Modeling the flocking propensity of passerine birds in two Neotropical habitats. Oecologia 153:121–133.

Tubelis, D. P., A. Cowling, and C. Donnelly. 2006. Role of mixed-species flocks in the use of adjacent savannas by forest birds in the central Cerrado, Brazil. Austral Ecology 31:38–45.

Waldman, B. 1988.The ecology of kin recognition. Annual Review of Ecology and Systematics 19:543–571.

Watson, A., R. Moss, R. Parr, M. D. Mountford, and P. Rothery. 1994. Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. Journal of Animal Ecology 63:39–50.