

PROXIMATE MECHANISMS UNDERLYING PARTIAL BIRD MIGRATION IN SOUTH  
AMERICA

By

ALEX EDWARD JAHN

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To Arthur Jahn, who believed that the best gift that one person can give another is an education,  
and to my family for all their support

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Alex Edward Jahn

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In the New World, most research on bird migration has been carried out in North America, which has led to the unfortunate situation that in most cases, evolutionary hypotheses have been both formulated and tested in the same migratory system, which is arguably not a true test of hypotheses. A much more logical approach would include tests of hypotheses in an evolutionarily related set of species that migrate within a different migratory system. Neotropical austral migration, in which birds migrate wholly within South America, provides such a system. I tested hypotheses on the regulation of partial migration by studying a population of Tropical Kingbirds (*Tyrannus melancholicus*) at a study site in eastern Bolivia. I found that the non-breeding season at the site is characterized by much lower food abundance for kingbirds than the breeding season, suggesting that environmental constraints are in place to create partial migration in the population. I employed maximum-likelihood theory to model the probability of migration by Tropical Kingbirds at my Bolivian study site. I show that partial migration does exist in the population, and by including demographic, life-history and morphological covariates in the model, I show that the hypotheses tested (the Dominance and Body size hypotheses) are not supported in the Tropical Kingbird partial migration model, possibly because these hypotheses have been developed for bird species that inhabit a colder

continent (North America), and on granivorous species (e.g., sparrows, finches). I present a new hypothesis that accounts for these differences and that could be typical of many if not most Neotropical austral migrant passerines. This research provides some of the first quantitative measures of the mechanisms driving bird migration in South America. The results indicate that models on the regulation of bird migration primarily developed in the Northern Hemisphere are likely to be inadequate for many species migrating within South America, especially at tropical latitudes.

CHAPTER 1  
REFLECTIONS ACROSS HEMISPHERES: A SYSTEM-WIDE APPROACH TO NEW  
WORLD AVIAN BIRD MIGRATION RESEARCH

In 1938 John Zimmer wrote, “It is not uncommon . . . to hear the statement made that South American birds do not migrate . . . A few writers have noted the disappearance or reappearance of certain species at certain places and seasons, but there has been little evidence to show where the period of absence has been spent” (Zimmer 1938). Surprisingly, almost 60 years later, a similar statement was echoed by Stotz et al. (1996:77): “Research is urgently needed on the winter distributions and habitat use of austral migrants . . .”

South America’s austral migration system, comprised of species that breed in the south-temperate portion of the continent and move north towards tropical latitudes to over-winter, has received little attention relative to the other major New World migratory system, the Nearctic-Neotropical system (comprised of species that breed at north-temperate latitudes and move south to over-winter in Latin America). An obvious explanation for this disparity is the relative lack of financial resources for basic field research in South America, compared to North America. In many ways, however, the challenge is far more than financial. Access to sites across South America varies considerably from lack of infrastructure, as well as a history of locally unstable political climates.

I argue the importance of understanding austral migration, both on its own merits and as a sister system to Nearctic-Neotropical migration. The two migratory systems are related because they share a common evolutionary origin in the Neotropical avifauna. Most species of long-distance migrants in the New World are thought to have their evolutionary origins in the Neotropics (e.g. Cooke 1915, Levey and Stiles 1992, Rappole 1995, Joseph 1997, Chesser and Levey 1998). Thus, study of one system will inform the other. More generally, a broad view of New World migration – one that encompasses all directions and scales of seasonal movements –

promises to reveal ecological and evolutionary mechanisms that may not be otherwise apparent (Levey 1994, Joseph 1997). Analogous to looking for a lost object under a streetlight because that is where the light is best, trying to disentangle the complexities of migration based on the most convenient or obvious migration system is restrictive at best, and misguided at worst.

Our goal is to review current knowledge on South American austral migration and place it in the context of New World migration. I start with a brief history of research on austral migration, then describe the similarities and differences between austral and Nearctic-Neotropical migration. I place New World migration in an evolutionary context and explain why such a perspective is necessary to understand the causes and consequences of the processes underlying seasonal movements. Intraspecific patterns of migration such as partial migration, a condition in which a portion of the breeding population migrates away at the end of the breeding season (Lack 1943, Berthold 2001), will be highlighted. Although “austral” generally refers to Southern Hemisphere patterns, for the sake of brevity I here use the term “austral migration” in referring exclusively to birds that breed in southern South America and winter closer to or within tropical latitudes.

### **A Brief History of Austral Migration Research**

Aside from regional publications that are largely unavailable, most literature on austral migration can be relatively easily summarized. According to Chesser (1994), the first report was by de Azara (1802-1805), who reported changes in the abundance and composition of the avifauna of Paraguay and northeastern Argentina. Dabbene (1910) and Wetmore (1926) followed with descriptions of the seasonality of species occurrences. Zimmer (1938) provided the first overview of movements of several species throughout the year over the entire continent. The literature was then silent for almost 50 years. In the 1980’s came the first report of winter site fidelity of an austral migration (McNeil 1982). Belton (1984, 1985) and Willis (1988)

described austral migration patterns in southern Brazil and Robinson et al. (1988) studied winter habitat occupancy of austral migrants in southeastern Peru.

The 1990's witnessed an awakening of interest in austral migration, as museum records were mined for data and species lists were systematically compiled and analyzed. Marantz and Remsen (1991) described the breeding and wintering range distributions of the Slaty Elaenia (*Elaenia strepera*). Hayes et al. (1994) described austral migrant occurrence and timing in Paraguay. Stotz et al. (1996) reviewed austral migrant habitat use, distribution and conservation status and Parker et al. (1996) provided a hypothetical list of complete and partial austral migrants. The most in-depth work to date is Chesser's (1994, 1995, 1997, 1998) study of the biogeography of austral migrant flycatchers (Tyrannidae), including the first comprehensive list of austral migrant species (1994). Joseph (1996) studied winter distributions of migrants, later calling attention to the spectrum of New World migratory patterns (Joseph 1997). Chesser and Levey (1998) hypothesized evolutionary origins of austral migrants and Joseph et al. (2003) investigated the phylogeography and evolution of migration in Swainson's Flycatcher (*Myiarchus swainsoni*).

Although such theory-based research and geographically-broad descriptions of austral migration have recently emerged, descriptive work at the local scale, upon which conclusions at broader geographic scales are based, continues. In Argentina, for example, habitat selection (Marone et al. 1997) and seasonality (Marone 1992, Cueto and Lopez de Casenave 2000, Fraga 2001, Malizia 2001) of austral migrants has been described. In Paraguay, Brooks (1997) and in eastern Bolivia, Davis (1991) and Jahn et al. (2002a, b) have described seasonality and other basic patterns of austral migration. The take-home message is that almost the entire literature on

austral migration can be summarized in three paragraphs. Imagine trying to accomplish that for Nearctic-Neotropical migration!

### **An Imperfect Mirror Image**

The basic pattern of migration in North and South America is the same: species generally move towards the equator in fall and away from it in spring. An interesting way to visualize this is to imagine migratory birds breeding in southern and northern hemispheres moving in the same direction at the same time: north when the Northern Hemisphere is tilted toward the sun and south when the Southern Hemisphere is tilted toward the sun (Fig. 1). Despite this reciprocity between hemispheres in direction and timing of migration, differences in the relative size, position, and shape of land masses differ significantly. These differences “distort” the mirror image that the two migratory systems might otherwise display.

First, because southern South America is smaller than northern North America, area effects help explain why there are fewer migrant species in South than North America (Chesser 1994, Chan 2001). Estimates of the number of austral migrants range from 220 to 237 species (Chesser 1994, Stotz et al. 1996), compared to 338 species of Nearctic-Neotropical migrants (Rappole 1995). Although this 1.5 fold difference may seem large, it is somewhat surprising that it is not larger, given that the land mass north of the Tropic of Cancer is approximately 5-fold that to the south of the Tropic of Capricorn. For such a relatively small area, temperate South America has a rich diversity of migratory species. I will return to this point.

Second, temperate South America has a larger portion of its land mass situated near the equator than does North America. This means that South American birds need not migrate as far in fall as North American breeders, whose breeding grounds generally experience more severe winter temperatures (Chan 2001). It also means that the ratio of breeding area to wintering area is low ( $<1$ ), in contrast to the situation in the Northern Hemisphere, where there is far more

breeding than wintering area. Both of these factors likely explain the relatively close proximity of breeding and wintering ranges that typify many austral migrants (Chesser 1994, Hayes et al. 1994, Stotz et al. 1996). This, combined with the lack of topographic barriers to north-south migration in South America (Chesser 1994), provides another explanation for the relatively high species diversity of austral migrants. Likewise, one could argue that the species diversity of migrants in temperate North America is comparatively low because the source pool (Central and equatorial South America) is generally farther away and hindered in northward expansion by the Gulf of Mexico.

Continental position and shape could also be important factors promoting the high incidence of partial migration in the Southern vs. Northern Hemispheres in the Americas. The general pattern of shorter distances between the breeding and wintering grounds in South America, compared to those in the Nearctic-Neotropical and Palearctic-African systems (Chesser 1994) and the lack of geographic barriers at the center of the continent (a situation associated with high levels of partial migration; Chan 2001), likely promote such a condition.

In terms of taxonomic affinities, South America's austral system is unique in the predominance of one family. Tyrannidae comprise 33% of all species, reflecting the overall predominance the family across the continent (Chesser 1994). In contrast, the most speciose families of Nearctic-Neotropical migrants comprise only 15% (Parulidae) and 9 % (Tyrannidae) of all species in the system (Rappole 1995, American Ornithologists' Union 2003). In ecological terms, the majority of austral migrants are open-country breeders, north-temperate migrants tend to nest in more forested habitats (Chesser 1994). Nevertheless, migrant ecology between these systems is overall remarkably similar, given that both groups appear to be habitat generalists

during the non-breeding season in the tropics and that they are both composed primarily of species which depend on open water or which feed on active insects (Stotz et al. 1996).

Finally, I draw attention to a curious lack of reflection in migratory patterns between north-temperate and south-temperate breeders. Many north-temperate breeding species over-winter in the south-temperate zone (e.g. Scolopacidae) but none do the opposite; there are no south-temperate breeding migrant populations that over-winter in North America (Chesser 1994). As far as I know, nobody has explored why this might be so. Cracking the mystery will require an evolutionary approach.

### **An Evolutionary Framework**

Although migration has arisen multiple times via different evolutionary pathways (Berthold 2001), the consensus is that many species that breed in the temperate zone and over-winter in the tropics evolved from tropical ancestors (Sinclair 1983, Levey and Stiles 1992, Safriel 1995, Rappole 1995). Joseph (1997) and Chesser and Levey (1998) applied this hypothesis to the southern hemisphere, proposing a Neotropical origin for austral migrants. From this point of view, breeding at south temperate latitudes may have been constrained by a relatively small breeding area, while fall migration back to the tropical ancestral home may have been limited by competition with non-migratory conspecifics. Indeed, South America's austral migrants generally do not winter as far north as the tropics: only 32 species migrate in fall as far as Amazonia and 14 north of the Amazon basin, while two-thirds have non-breeding ranges that overlap the ranges of conspecific residents (Stotz et al. 1996). In contrast, almost one quarter of Nearctic-Neotropical migrants winter south of Amazonia and less than one half of these have ranges that are non-disjunct (Stotz et al. 1996).

Utilizing an evolutionary framework in the study of migration, as proposed already by Gauthreaux (1982), can reveal why some species are migratory and others are not. For example,

if small scale seasonal movements by Neotropical species are viewed as an evolutionary precursor to austral migration (Levey and Stiles 1992, Chesser and Levey 1998), one can predict the extent of migration in various taxa. In particular, families containing many species that show small scale seasonal movements within the tropics are more likely to also contain austral migrants than families whose species show no seasonal movements within the tropics. An untested application of this prediction lies within the Tyrannidae. Because so many species of flycatchers are austral migrants, I predict that closely related species and genera that are not austral migrants will display a high degree of seasonal movement within the tropics.

Unfortunately, we are a long way from being able to test such predictions because so little is known about the extent of migration *on any scale* within South America. Figuring out which austral species migrate and where they go is greatly complicated by the fact that most have overlapping populations of migratory and resident individuals. Although these species of “partial migrants” are an obstacle, they also present an opportunity to unravel the evolutionary pathway of austral migration. In particular, because partial migration is considered an evolutionary step towards migration (e.g. Cox 1985, Alerstam and Hedenström 1998, Berthold 1999), documenting the ecological, taxonomic, and geographic correlates of partial migration will reveal at least some of the processes driving the evolution of migration. South America is the best place for such a study, as partial migration typifies it more than any other system.

### **Intraspecific Patterns of South American Avian Migration**

Partial migration is common worldwide (Lack 1943). In South America, almost 70% of austral migrants have populations which migrate to south-temperate breeding grounds away from tropical resident breeding populations (Stotz et al. 1996). I distinguish between two types, one in which some individuals post-breeding migrate away from an otherwise non-migratory (breeding) population in the temperate zone to over-winter nearer the equator (e.g., Vermilion Flycatcher,

*Pyrocephalus rubinus*) and one in which some individuals pre-breeding migrate away from an otherwise non-migratory population in the tropics to breed in the temperate zone (e.g., Tropical Kingbird, *Tyrannus melancholicus*). The first type, referred to as partial migration, is well known. For example, Berthold (2001) reports that over 60% of approximately 400 of Europe's breeding bird species are partial migrants. In South Africa the proportion is 10% (Dowsett 1988) and in Australia it is 36% (Chan 2001). The second type, which I term *population partial migration*, is less well appreciated. Forty-eight percent of Nearctic-Neotropical migratory species have conspecifics which breed in the Neotropics, while 23% of Palearctic-Paleotropical migratory species (breeding in the temperate Old-World and migrating to tropical Africa) have populations which breed in the Tropics (Rappole 1995). The fundamental difference between partial migration and population partial migration is that population partial migrants leave a breeding population to breed elsewhere (i.e. the temperate zone), whereas partial migrants leave a breeding population to overwinter elsewhere (i.e. the tropics). Nevertheless, the two are not mutually exclusive in a species and the door is open to the possibility that both operate in some austral migrant species.

The evolutionary significance of differentiating between these two types of migration rests on where the migratory behavior first appeared. If we assume a species originated in the tropics, migration can result in a reproductively isolated population in the temperate zone, possibly leading to migration away from the tropics by all populations (e.g., *via* interspecific competition during the non-breeding season, Cox 1985). This seems most plausible for population partial migrants. If, on the other hand, we assume a species originated in the temperate zone and migration evolved towards tropical over-wintering grounds, migratory and resident populations are likely not reproductively isolated. Partial migration in such cases can be driven by condition-

dependent mechanisms (e.g. sex and dominance hierarchies; Ketterson and Nolan 1976, 1979). This seems most plausible for partial migrants. Recognizing the difference between the two patterns leads to a distinction between population-level (i.e. population partial migration) vs. individual-level (i.e. partial migration) processes. For example, a study on phenotypic plasticity in migratory birds would do better to focus on a partial migrant (in which individuals may migrate in an individual-level, condition-dependent manner) than on a population partial migrant species, in which migration is population-specific.

Unfortunately, such differences in the evolutionary histories of these intraspecific migratory patterns have been overlooked at times, at least partly as a result, I believe, of a north-temperate bias when considering migratory behavior. The matter is not trivial, since designing tests for the reasons generating virtually any migratory pattern rests on clear assumptions on the evolutionary origin of such mechanisms. If the assumption is made that a species first evolved within tropical latitudes, research on the ultimate causes of migration would focus on a species in which the migratory population migrates towards the temperate breeding zone, while research on the proximate causes of partial migration would focus on a population in which some individuals breed in the temperate zone, while others migrate to tropical wintering grounds. If the assumption is made that a species first evolved as a temperate resident, the study location would be reversed.

To track the ecological and evolutionary pathways *via* partial migration to complete migration, the austral system is perhaps the best in the world. In many austral migrant species, the migratory individuals are those migrating out of the tropics (the putative ancestral home), whereas in systems with temperate partial migration, migratory individuals are migrating towards the tropics, while sedentary conspecifics remain at temperate latitudes (where they

presumably did not evolve). Furthermore, such a population-level pattern of migration in South America would presumably lead to a situation which optimizes conditions for population isolation and therefore speciation (see Joseph et al. 2003 for further discussion).

### **Classifying Types of Austral Migration**

There exist many types of austral migrants. Distinguishing among them is an important first step in understanding their evolutionary ecology, as demonstrated in the previous section with partial migrants. This theme of embracing the full range of migratory movements has been championed by many ornithologists, both temperate and tropical (e.g. Levey 1994, Rappole 1995, Berthold 2001). In the context of austral migration, Joseph (1997) called attention to the danger of using one broad nomenclature for a general migratory pattern, when in fact various species-specific patterns exist.

The challenge of distinguishing amongst different types of austral migrants is unusually daunting in large part because of South America's shape, latitudinal position, and topography: as mentioned earlier, the relatively large tropical/subtropical area, small temperate area and lack of east-west barriers result in a situation where most birds on the continent have many migratory options. Although practically nothing is known about which options are taken by which species, it's likely that the entire spectrum is represented. While interspecific patterns (e.g. migratory route use, habitat use) will probably be the first to emerge with further research, distinguishing between the various intraspecific, population-level migratory strategies employed will require research capable of gathering detailed information locally (e.g. age, sex of individuals exhibiting different migratory behaviors) across a range of sites across the landscape. To draw attention to the various possibilities and help focus research on teasing them apart at the population level, I define the following intraspecific patterns potential patterns of austral migration, divided into

population- and intra-population level phenomena, with examples where the phenomenon is known or could potentially occur.

Population-level:

- Complete migration: all individuals of a population migrate in both the fall and spring (e.g., Cinnamon-bellied Ground-Tyrant, *Muscisaxicola capistrata*).
- Leapfrog migration: some non-migratory populations of permanent residents are located between breeding and non-breeding ranges of migratory populations, with migratory populations flying over or around them (e.g., White-banded Mockingbird, *Mimus triurus*).
- Post-breeding displacement migration: after breeding, southern populations migrate towards the equator and displace conspecifics, which then migrate closer to the equator to overwinter (e.g., Southern Martin, *Progne modesta*).
- Breeding displacement migration: one population migrates to breed at the wintering location of other conspecifics which are then displaced to breed at higher latitudes (e.g., Creamy-bellied Thrush, *Turdus amaurochalinus*).
- Population partial migration: migration of some individuals towards south-temperate latitudes to breed, with some individuals residing year-round within tropical latitudes (e.g., Lesser Elaenia, *Elaenia chiriquensis*).
- Temperate population partial migration: migration of some breeding populations towards tropical latitudes to over-winter, with other populations overwintering in south temperate latitudes (e.g., Black-crowned Monjita, *Xolmis coronata*).

Intrapopulation-level:

- *Partial migration*: migration of some individuals towards tropical latitudes to over-winter, with some individuals residing year-round in the south-temperate zone (e.g., White-winged Black-Tyrant, *Knipolegus aterrimus*).
- *Dual partial migration*: migration of some individuals northwards and some southwards, away from a permanent resident population in the tropics (e.g., White-throated Kingbird, *Tyrannus albogularis*).
- *Leapfrog partial migration*: migration of some individuals between a seasonal breeding range and a seasonal wintering range, overflying populations in which some individuals are migratory and others permanent residents (e.g., Crowned Slaty Flycatcher, *Empidonomus aurantioatrocristatus*).

## Suggestions for Future Research

In light of the pervasive and acute habitat alterations occurring on the South American continent (e.g. Stotz et al. 1996), knowledge of basic ecology such as resource use and migratory timing of austral migrants, as well as population trends and relative abundances at various spatial scales will be imperative to the success of long-term conservation efforts. Such information has been collected for decades in North America (reviewed in Gauthreaux 1996) and has proven useful for understanding migratory bird requirements. Standardized equivalents beyond the local scale do not exist in South America, where it is not only unclear whether most populations of migratory species are declining, it is impossible with current data to even explore such a possibility. Although what knowledge on the ecology of austral migrants exists points to most having low habitat specificity (Stotz et al. 1996), the rapidly growing environmental alteration of various habitats on the continent by humans (e.g. dry forests; Gentry 1977, 1995), as well as the more general threat of global climate change (e.g. Berthold 2001) may pose significant threats to South America's migrants. An example of such a group is the *Sporophila* seedeaters, which face the threat of habitat alteration (Stotz et al. 1996) and, in some cases, capture for the pet trade, many of whose ranges are, "still surprisingly imperfectly known" (Ridgely and Tudor 1989).

I believe that the most fundamental challenge towards correcting this situation is one of critical mass - the few South American ornithologists interested in migration are widely scattered and faced with an enormous and complex migration system about which even the most basic information is lacking. Thus, a top priority should be to establish a dialogue to prioritize needs, set research goals, and establish collaborative ties across countries and continents. If a collective vision is clearly articulated, the next significant challenge — securing financial resources — will be less difficult.

As a first step in this direction, a symposium on austral migration was held at the VII Neotropical Ornithological Congress at Termas de Puyehue, Chile, in October 2003. To the best of our knowledge, this was the first such symposium. Even within the context of major symposia on migrant birds, contributions about austral migration appear almost totally absent (e.g., most recently at the “Birds of Two Worlds” symposium). (It is important to note that this absence is not due to neglect by the organizers but rather by the almost total absence of researchers publishing on austral migration in international journals.) The major goal of the austral migration symposium in Chile was to bring together researchers from South and North America to share ideas and techniques, and to help plot foster collaborative projects (see Acknowledgments).

Perhaps the most effective way to promote migratory bird research and conservation in South America would be to establish an international, multi-agency consortium that focuses on and promotes research, conservation, and management of austral migrants. An obvious and successful model is Partners in Flight, comprised of disparate government agencies (e.g., Bureau of Land Management, Department of Defense, Fish and Wildlife Service, Forest Service), academic, and nongovernmental organizations (e.g., American Bird Conservancy, National Audubon Society, The Nature Conservancy). It is international and emphasizes representation from organizations in Canada, United States, and several Central American countries.

In this context, I note that a diverse array of avian ecology projects are already underway across South America. These projects have untapped potential for providing basic data on austral migrants across a broad geographic range. A strong collaborative effort could unite such projects and provide standardized methodologies for monitoring migrant populations. In some cases, valuable information on austral migration has already been collected, albeit

unintentionally. Museum records are an especially promising but relatively unexplored example. What is lacking is a means of compiling such information for analysis and dissemination. Just as the synthesis of data from museums yielded much information on seasonality and ranges of austral migrant species (e.g. Chesser 1995), collating information from already-existing field studies could elucidate important details of migration from across the continent. Collecting, compiling and synthesizing such data would best be carried out under the auspices of a network of scientists, who could champion the need to collect specific data on migration in a highly standardized manner.

Utilization of novel technologies such as on-line interactive databases would greatly facilitate the maintenance of a migration research monitoring and research network in South America (see Vuilleumier [2003] for similar and further suggestions for future research in Neotropical ornithology). For example, during the 2004 fall migration in South America, a group of ornithologists led by Jennifer Johnson (Swarthmore College), conducted nocturnal migratory bird censuses by moon-watching. Ornithologists from each country entered data into an on-line database, thus compiling continent-wide information. Because New World migratory birds generally move in the same direction in the same season, this effort simultaneously monitored the migration of north-temperate as well as south-temperate breeders. Such collaborative efforts could open doors for the use of a variety of new technologies for migration research in South America. Stable isotope analysis, satellite telemetry, and weather radar, which have been recently and widely applied in studies on Nearctic-Neotropical migrants, are known and largely available in South America (e.g. hydrogen stable isotope, K. Hobson et al., unpublished data), although their potential remains virtually untapped.

Finally, opening a new avenue to the study of avian migration I believe will not only lead to improved understanding of the how's and why's birds migrate, it is a chance to make great strides in our understanding within the immediate future. Zimmer's (1938) statement which opened this article on the poor state of knowledge of bird migration in South America at the first half of the 20th century continues to ring true, but so also does the fact that this very situation presently provides an opportunity within this century to produce a much clearer picture — and possibly a new paradigm — of the *how's* and *why's* New World birds migrate.

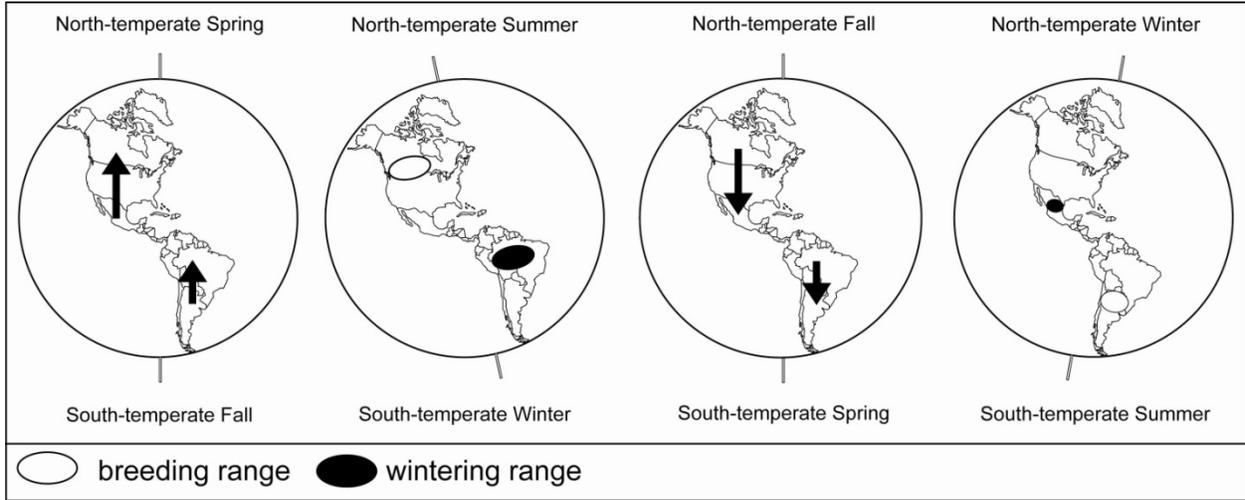


Figure 1-1. Generalized seasonal movement and ranges of a hypothetical population of a Nearctic-Neotropical and South American austral migrant species. The position of the sun is to the left of the diagram.

## CHAPTER 2 TOWARDS A MECHANISTIC INTERPRETATION OF BIRD MIGRATION IN SOUTH AMERICA

### **Introduction**

Research on various aspects of bird migration – from biogeography to ecology and physiology - has demonstrated that migratory behavior is an extraordinarily diverse and complex phenomenon. For example, migratory behavior can evolve relatively rapidly (e.g., Able and Belthoff 1998, Berthold 1999, Piersma et al. 2005), is phylogenetically flexible (Böhning-Gaese and Oberrath 1999), and can appear and disappear through time within a lineage (e.g., Zink 2002, Joseph et al. 2003, Outlaw et al. 2003) or even within an individual's lifetime (e.g. Schwabl and Silverin 1990). In the New World, a continuum of migratory strategies exists, from long-distance migrations undertaken by all populations of a species to short-distance migrations undertaken by only some populations (Levey and Stiles 1992) or individuals (e.g., Ketterson and Nolan 1976). Migration can even play a central role in speciation (Winker 2000, Winker and Pruett 2006).

To solve persistent riddles about the evolution and regulation of migration requires teasing apart factors confounded in space and time. This is difficult to accomplish without a broad geographic scope. In the New World, almost all work on migration has been restricted to the north-temperate latitudes (Levey 1994, Jahn et al. 2004), with relatively little attention paid to migration within South America (austral migration, *sensu* Chesser 1994).

Some species of austral migrants move annually between the temperate zone and tropics and some species migrate within the temperate regions of the continent (Joseph 1997). There are more than 220 species of austral migrants, comprising the largest migratory system in the Southern Hemisphere (Chesser 1994). Recent literature on migration in South America principally explores biogeographic patterns (e.g., Chesser 1994, da Silva 1999, Capllonch and

Lobo 2005), evolution (Joseph et al. 2003), habitat associations (e.g., Chesser 1995, Stotz et al. 1996, Jahn et al. 2002) and the timing of migratory movements (e.g., Hayes et al. 1994).

The geographical patterns in austral migration are complex (Morton 1977, Winker 1997, Bildstein 2004). In some species all populations migrate, but in others different populations migrate in the same or in different directions. Furthermore, all of these strategies can occur within one genus. (e.g., *Tyrannus*, Fig. 1; Ridgely and Tudor 1994, Chesser 1995). This stands in sharp contrast to the situation in North America, where all the populations of migratory species generally move in the same direction during each season.

Given the diversity of migration strategies evident within South America, it is clear that the phrase "bird migration in South America" encompasses a multitude of inter- and intra-specific patterns at smaller scales than the overall pattern at the continental level would suggest. Thus, to better understand how migratory birds respond to competing ecological and physiological demands, it will be essential to form links between patterns observed at different spatial and temporal scales and among taxonomic (e.g. families and species) and biological levels of organization (e.g. genotypes, individuals, ecosystems) (Levin 1992).

Our objective is to demonstrate that research on the mechanisms generating specific patterns of bird migration in South America is a prerequisite to gaining a better theoretical foothold, as well as for the ability to formulate sound, proactive conservation and management strategies. I use as an example the high incidence of seasonal range overlap in the distributions of South American migratory bird populations to highlight the power of existing theory on population-level variation in migratory behavior to explain such patterns as range overlap.

### **A Focus on Mechanisms**

Studying mechanisms — the proximate relationships between what an individual experiences and how it responds — is the key to being able to explain the causes for observed

patterns, advancing both basic science (i.e., explanations, predictions, the formulation of original questions) as well as practical applications (i.e., conservation and environmental planning and management). Such rewards will only result from studies that are focused on specific questions and employ testable hypotheses (Vuilleumier 2004).

Tests of mechanistic hypotheses (i.e., how component parts of the phenomenon interrelate) - rather than phenomenological explanations (i.e., models that extrapolate future trends based on past trends) - are useful for interpreting the reasons for changes observed in a pattern (e.g., migratory timing or direction)(Koehl 1989), especially in light of the magnitude and speed of contemporary anthropogenic changes in global biogeochemical cycles (Lubchenco 1998). From an applied perspective, knowing where species are located during the entire annual cycle is necessary to formulate a basic conservation plan. However, an understanding of the factors influencing survival and reproduction at smaller spatial scales enables a more effective conservation strategy. For example, Marra et al (1998) demonstrated that the quality of habitats occupied by *Setophaga ruticilla* individuals during the non-breeding season can affect their physical condition and thus their arrival date on the North American breeding ranges, which has consequences for their reproductive success. In this case, knowledge of the life-history consequences of habitat use opens the door to the formulation of more detailed conservation priorities.

Studying the mechanisms that regulate the components of a system also allows patterns to be placed within an evolutionary context. As pointed out by Moore and Aborn (2000), research about habitat selection during migration has historically focused on describing habitat use rather than examining the mechanisms through which selection acts. To elucidate the processes responsible for observed patterns, it is important to consider the evolutionary history of a species

as well as contemporary constraints. Taking just such an approach, Böhning-Gaese and Oberrath (2003) concluded that contemporary habitat preferences of migrants have been strongly influenced by the historical occupation of relatively open habitats in Africa (by ancestors of Holarctic migrants) and of Neotropical forests (by ancestors of Nearctic migrants), as well as by contemporary processes.

Nevertheless, an ability to understand the causes of patterns evident at the population level demands research on processes occurring at the individual level (Koehl 1989). This is because the evolutionary mechanisms that generate population-level migratory patterns originate from variation among individuals. Thus, a focus on the individual is essential for formulating and testing hypotheses about the evolution of migration (Bell 2000).

Research focused at the level of the individual requires consideration of the ecological constraints encountered by individuals on different scales throughout their annual cycle. For example, a bird that forages on a scale of hundreds of meters may migrate hundreds of kilometers to search for similar resources at another site. Thus, migratory species are affected by processes occurring on vastly different temporal and spatial scales (e.g., Alerstam et al. 2003). Forming links between these disparate scales is one of the central challenges not only of migrant bird ecology, but of science in general (Levin 1992).

Finally, since migratory behavior is an attribute regulated by a suite of characters (e.g. physiological, social; Piersma et al. 2005), it is important to formulate hypotheses about these characters within an explicitly phylogenetic context (Zink 2002). In South America, the diversity of movement patterns, even within a single species (e.g., *Myiarchus swainsoni*, Joseph et al. 2003), may be a complex and long-term response to changing environmental conditions on the continent. However, diverse migratory behaviors can also appear on much shorter time

scales. One notable example is the appearance of populations of *Hirundo rustica* that are beginning to reproduce within their historical non-breeding range, particularly in the coastal zone of the province of Buenos Aires, Argentina (Martínez 1983).

We now have the opportunity to design studies within South America to test theories formulated in other migration systems. With such an approach, we can both enrich our understanding of migration within South America and test the explanatory power of extant theories across migratory systems. We can begin to answer such questions as: Do similar ecological, physiological, and genetic mechanisms underlie all migratory systems? Does migration within South America operate under different "rules" than other systems?

For example, the capacity for nocturnal compass orientation is highly conserved phylogenetically in migratory birds around the world (Piersma et al. 2005). In mid- and high-latitudes, migratory birds can use a magnetic inclination compass for orientation - but this orientation system cannot function at equatorial latitudes (Wiltschko and Wiltschko 1995). Thus, what alternative cues can migrants use to orient and navigate in equatorial South America? Clearly, research in this area will allow us to test extant mechanistic theories as well as formulate new hypotheses about the migrations of birds.

In the next section, I use the seasonal overlap of ranges to launch a discussion of how to distinguish between populations of migratory species, as well as how to study the mechanisms operating within these populations.

### **Range Overlap**

What patterns characterize bird migration within South America? Stotz et al. (1996) and Chesser (1994) identified several key features: 1) Taxonomic composition. In South America, the family Tyrannidae makes up nearly a third of all migratory species on the continent, 2) Distance of migration. Within South America, most migrants move over shorter distances than

do Nearctic-Neotropical migrants, 3) The proportion of migratory species along a latitudinal gradient. In South America, the gradient of increasing number of migratory species with latitude is less dramatic than in North America, 4) Range overlap. Approximately two-thirds of austral migrants (159 species) exhibit overlap in population ranges across seasons. Migrants of one population migrate to areas already occupied by conspecifics that do not migrate.

Although these four patterns are coarse-grained and described at a continental scale, they offer a point of departure from which to look for more specific patterns (Stotz et al. 1996). I focus on the pattern of range overlap among populations as an interesting pattern to explore potential mechanisms that may underlie it.

Several biogeographical explanations have been offered to explain the causes of range overlap. Chesser (1994) offered two hypotheses. First, given that the South American continent is wider towards the equator, birds moving northwards towards the equator after the breeding season could experience a reduction in interspecific competition as a consequence of lower population densities due to the increasing land area, reducing their need to continue migrating northward. Second, there are no geophysical barriers to the east of the Andean Cordillera to segregate breeding and non-breeding ranges. In a similar vein, Hayes et al. (1994) proposed that the diminished land area at high latitudes corresponded to a reduced capacity to sustain populations of migratory species, thus producing relatively short migrations between tropical and temperate latitudes.

To test mechanistic hypotheses on the pattern of range overlap, however, we must know something about the variation in migratory distance among individuals, since different strategies among individuals may be present across the species' range. In essence, seasonally overlapping ranges obscure any pattern of exactly where migratory individuals pass the non-breeding season

(Stotz et al. 1996). Some populations may even be migrating within the area of overlapping ranges. For example, within any one species, there may be populations that are completely resident, as well as some that are partially migratory (Fig. 2). Thus, the area of overlap may "mask" substantial variation in migratory movements among populations. Furthermore, migrant and resident individuals may be partitioning the area of overlap in different ways. For example, Tellería and Pérez-Tris (2004) studied habitat associations in *Erithacus rubecola*, a European migrant species comprised of migratory populations whose non-breeding distribution overlaps with the distribution of resident populations in the south of the continent. They found that residents and migrants were physiologically different and occupied distinct habitats.

Consequently, in order to study the mechanisms underlying range overlap, it will be important to differentiate between populations and to define their "connectivity"—the origin and destination of migratory populations (for a review, see Webster et al. 2002). Once the migratory patterns of populations have been characterized as migratory, resident, or partially migratory, research can turn to the question of which processes underlie their migratory pattern.

Information on connectivity of populations and, at a local level, on habitat use by different individuals (i.e., migrants vs. residents) has obvious relevance for conservation policy. For example, if one population is in decline in the breeding area, knowledge of where it spends the non-breeding season within the area of overlap can greatly help to pinpoint the part of the life cycle in which the greatest threats to survival occur.

I now focus on some ideas about how to study mechanisms that operate on an intra-population level and produce population-level patterns. I use partial migration as an example (Fig. 2). For a recent review of other population level migration patterns, see Boulet and Norris (2006).

## Partial Migration

Partial migration is perhaps the most common type of bird migration in the world (Berthold 2001). From an evolutionary standpoint, partial migration is thought to be an intermediate step in the evolution of complete migratory behavior in birds (Berthold 1999). Consequently, studying the processes that produce partial migration could be key to understanding more about the proximate and ultimate processes that govern migratory movements in species with overlapping ranges.

Before discussing the processes producing partial migration, it is important to distinguish between population-level partial migration and intra-population partial migration. In population-level partial migration, some populations of a species migrate and other populations do not. For example, in *Tyrannus savana*, the nominate subspecies is an austral migrant, while another subspecies (*sanctaemartae*) remains as permanent resident in the northern part of the continent (Chesser 1995, Stiles 2004). This population-level variation in migration characterizes at least 70% of the migratory species in South America (Parker et al. 1996). In the case of intra-population partial migration, some individuals *of the same population* migrate after the breeding season and others do not (sensu Lack 1943; for a review, see Berthold 2001, Jahn et al. 2004). Differences in migratory behavior between individuals in the same population have been widely documented in other migratory systems but have not yet been documented in South America. Hereafter, when I refer to "partial migration," I refer specifically to intra-population partial migration.

The first studies on partial migration tended to be descriptive or to focus on evolutionary, population-level processes (e.g., Lack 1943, 1954, Kalela 1954, Cohen 1967, von Hartman 1968, Biebach 1983). More recently, emphasis has moved towards identifying and weighing the differences between individuals. Within this context, "migrant" and "resident" are considered to

be alternative strategies with differential benefits for different individuals in a population (e.g., Swingland 1983). Individual asymmetries are postulated to determine migratory status because of differences in competitive advantage between individuals. Lundberg (1987) contributed to this framework by adding the parameter of frequency-dependent choice, in which individuals of different social rank (e.g., juveniles low in the social hierarchy) decide whether to migrate, depending upon the relative frequencies of the dominant and subdominant individuals in the population with which they have to compete.

Indeed, factors such as age, sex and social status in a population can determine migratory behavior (Gauthreaux 1982, Schwabl 1983, Adriaensen and Dhondt 1990). For example, Able and Beltoft (1998) demonstrated that among *Carpodacus mexicanus* migrating within North America, younger individuals were characterized by a higher tendency to migrate. These demographic and social conditions are often tightly linked to such parameters as competitive ability, physiological tolerance and habitat associations, which in turn are postulated to affect migratory status (Ketterson and Nolan 1983, Cristol et al. 1999, Tellería and Pérez-Tris 2004). Thus, a test of the relationship between these parameters (e.g., physiological tolerance, social dominance) and migratory strategy (e.g., migratory timing, migratory distance) produces mechanistic models on the causes of such patterns as range overlap. It follows that identifying demographic (e.g. age, sex), social (e.g. dominance), and morphological (e.g. body size) differences between individuals is a prerequisite to studying the processes responsible for variation in the migratory behavior among individuals of a partially migratory population (i.e., whether or not an individual migrates).

What, then, are some specific, testable mechanistic hypotheses which can begin to tease apart potential causes for range overlap? Partial migration is one class of the broader category of

differential migration, in which individuals within a population undertake migrations of varying distances (e.g. Ketterson and Nolan 1976). In partial migrants, the distance traveled by some members of the population falls at an extreme of a gradient: zero migration (i.e., residence). Thus, since partial migration is a class of differential migration (Alerstam and Hedenström 1998), much of the theory about differential migration is applicable to partial migration and vice versa. A great variety of theories attempt to explain partial and differential migration, but the majority are variations on three general hypotheses (Bell 2005): 1) Dominance hypothesis. Subdominants are poor competitors for available food; when there are not sufficient resources for all the individuals in a population, subdominants are therefore more likely to migrate in order to avoid competition with dominant individuals. Supporting data are principally indirect, based upon the observation that in different species younger individuals or females are subdominant and migrate longer distances (e.g., *Junco hyemalis*, Ketterson and Nolan 1976). 2) Arrival time hypothesis. In contrast to individuals that do not establish territories, individuals that establish territories at the beginning of the breeding season are less likely to migrate as far because a short migration distance ensures a rapid return to the breeding range and access to the best territories. For example, in a study of *Anser caerulescens*, Bêty et al. (2004) found a significant relationship between the arrival date on the breeding grounds and the probability of reproducing (although excessively early arrivals suffered from negative climactic effects). 3) Body size hypothesis. In accordance with the relationship between body surface area and volume, larger individuals can better withstand lower temperatures and endure food limitations, giving them a lower probability of migrating. For example, in *Carpodacus mexicanus*, females are socially dominant, but also smaller in size and tend to migrate further than males (Belthoff and Gauthreaux 1991).

Studies evaluating these hypotheses have generally failed to produce data that predict migratory distance (e.g., *Junco hyemalis*, Ketterson and Nolan 1985). Future research in South America could test the explanatory power of these hypotheses in a context independent of the North-temperate system within which the hypotheses were originally formulated.

### **Future Directions**

Given the challenge of understanding the mechanisms underlying such a complex system, it is timely to note several themes that may put this type of research in perspective.

### **Comparisons Among Common Taxa in the New World**

Current theory postulates a Neotropical origin for migratory species in the New World, both Nearctic-Neotropical and austral migrants (Levey and Stiles 1992, Rappole 1995, Joseph 1997, Chesser and Levey 1998, Joseph et al. 1999, Böhning-Gaese and Oberrath 2003). A review of the data from Parker et al. (1996) reveals that at least 34 families, 56 genera and 23 species have populations of both Nearctic-Neotropical and austral migrants. For example, both *Accipiter striatus* and *Pyrocephalus rubinus* have populations which are Nearctic-Neotropical migrants and other populations which are austral migrants (Parker et al. 1996).

Intraspecific comparisons of populations employing different strategies (austral vs. Nearctic-Neotropical migration) are therefore possible and have the advantage of avoiding the confounding effects of phylogeny that commonly haunt interspecific comparative studies. Specifically, intraspecific research among populations of one species rather than comparisons between species decreases the effects of a shared phylogenetic history, which is problematic because it leads to a lack of independence in the parameters being compared (e.g., Gittleman and Luh 1992, Garland and Adolph 1994).

Conducting comparative studies among migratory systems offers the additional benefit of avoiding the circular logic of attempting to test a hypothesis explaining the causes of a pattern in

the same system within which the hypothesis was originally developed. For example, within South America, at least two distinct migratory sub-systems have evolved (Joseph 1997). Extant hypotheses can be evaluated in each sub-system independently.

### **Available Techniques and Technologies**

What tools can be applied to migration research in South America? New technologies exist that can supply data on diverse temporal scales (between years, months, or days), spatial scales (meters or kilometers), and between levels of biological organization (cellular, organismal, population-level). One particularly exciting new tool is stable isotope analysis, which can be used to determine the origins of migratory individuals (see Hobson 2005 for a review). Base isotope maps do not currently exist for many isotopes throughout the whole of South America, but may be available in the near future. Another exciting, novel technology that could be employed in South America is that of geolocators, which permit tracking long distance Passerine migrants throughout the year (Stutchbury et al. 2009).

Because migratory species confront varying constraints throughout the annual cycle (Sillett and Holmes 2002), and since events in one season can exert substantial influence over processes in subsequent seasons (Marra et al. 1998), research should be conducted throughout all phases of the annual cycle. This may most easily be accomplished by establishing collaborative international networks of researchers and conservation practitioners (e.g. Barlein 2003). Such associations could standardize methods and share data about the same species. These activities will be essential for advancing the study of patterns and mechanisms (see Stiles 2004 for suggestions and questions), as well as advancing the conservation of populations of migratory species that cross political boundaries. The complexity of migration within South America demands an interdisciplinary research approach, incorporating a variety of techniques and technologies (Alerstam et al. 2003, Barlein 2003).

### **Research at the Individual Level:**

I emphasize the value of collecting individual-specific data (e.g., through color-banding and genetics). Mechanisms apparent at the population level originate at the individual level, such that descriptive studies conducted at the individual level, such as McNeil's (1982) work documenting winter site fidelity in *Elaenia parvirostris*, are particularly useful to guide development and testing of mechanistic hypotheses.

### **Conclusion**

Numerous questions are wide-open lines of research, both descriptive and hypothesis-based, in South America. Much progress has been made on other continents about problems that remain unsolved in South America, such that existing bodies of theory, technologies and methods could be readily applied to research on South American migration. Interesting questions concerning the evolution of migration, for which we know little in South America include: 1) Biogeography: What is the relationship between speciation rates and migratory behavior across clades?, How does this relationship compare in South America to other migratory systems?; 2) Ecology: What is the winter ecology of austral migrants? What is the relationship between migratory timing and biotic vs. abiotic factors?; 3) Physiology: Do austral migrants employ a similar navigation system as migrants in other systems? What are the energetic constraints to migration in South America relative to other systems?; 4) Life-history: Which part of the life cycle is most limiting in terms of reproductive success and survival? Are there carry-over effects for reproductive success between seasons?

The answers to such questions will provide a basis upon which to ask other questions and further develop more detailed, mechanistic hypotheses. Given the complexity that characterizes austral migration, our understanding of New World bird migration will be greatly enriched when

we undertake a multidisciplinary approach that incorporates both descriptive and theoretical research to elucidate the origins and maintenance of migratory patterns in South America.

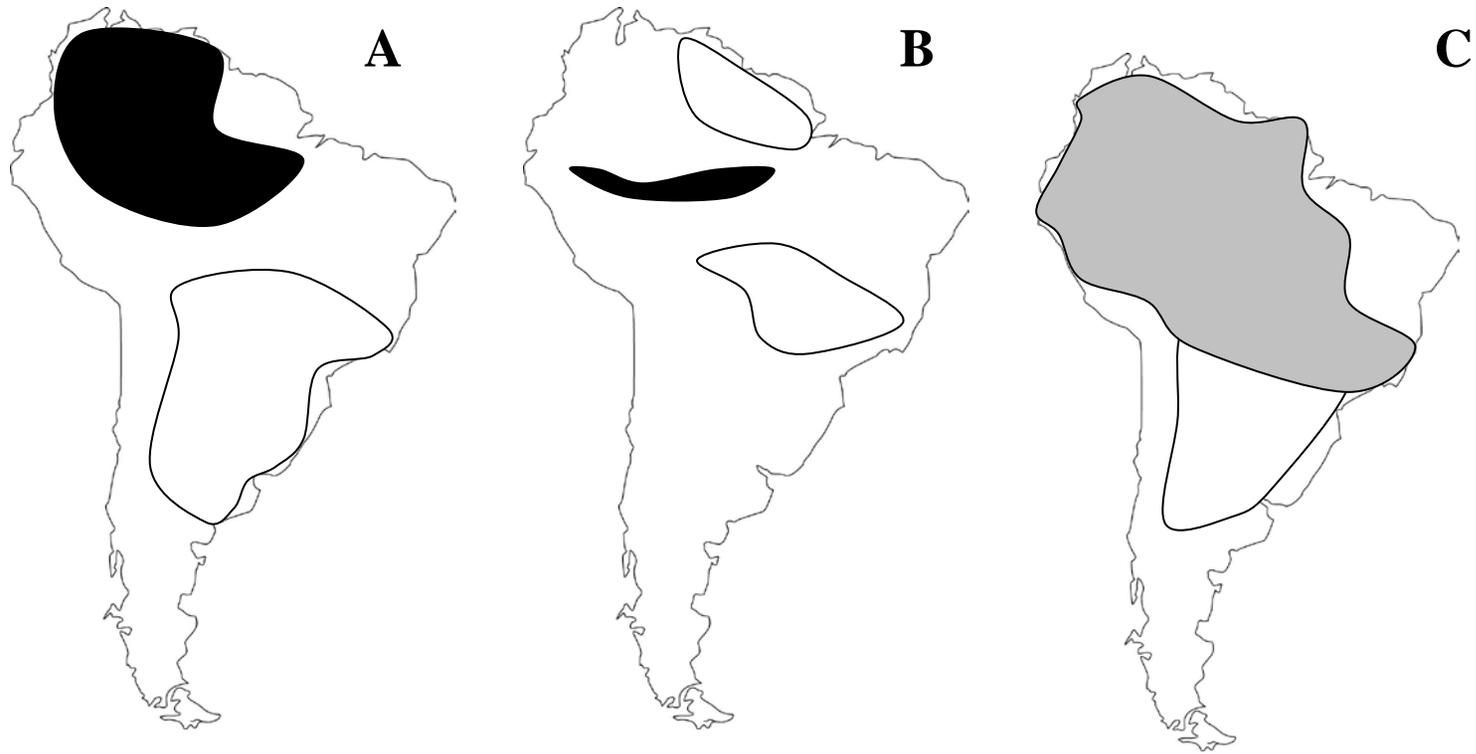


Figure 2-1. Generalized seasonal distributions of A) *Tyrannus s. savana*, B) *T. albogularis* and C) *T. m. melancholicus* in South America. Black polygons represent seasonal non-breeding ranges, white polygons represent seasonal breeding ranges and gray polygon represents area of overlap in which permanent residents as well as non-breeding (i.e., overwintering) migratory individuals from the south occur together. Adapted from Chesser (1995).

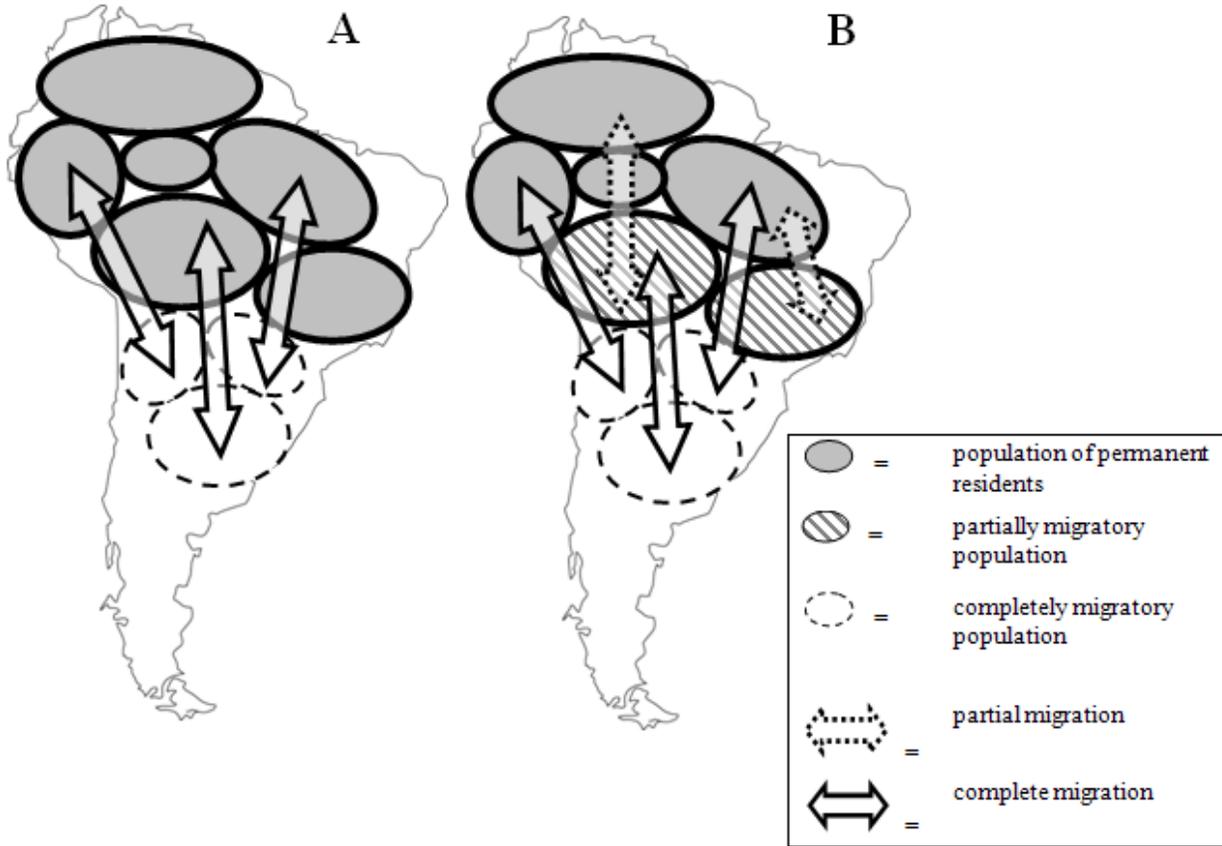


Figure 2-2. Two hypothetical patterns of population-level migration of *Tyrannus m. melancholicus*. a) migration exclusively of populations between a seasonal breeding area and an area of range overlap, b) migration of populations between a seasonal breeding area and an area of overlap, as well as partial migration of some populations within the area of overlap.

CHAPTER 3  
A MORPHOLOGICAL AND GENETIC COMPARISON OF MIGRATORY AND NON-  
MIGRATORY TROPICAL KINGBIRDS (*TYRANNUS M. MELANCHOLICUS*) DURING  
SPRING MIGRATION IN CENTRAL SOUTH AMERICA

**Introduction**

Almost 70% of bird species that migrate within South America are characterized by both migratory and non-migratory (permanent resident) populations (Stotz et al. 1996). In most cases, populations of permanent residents occur within or close to tropical latitudes, whereas populations of migratory individuals occur in temperate latitudes during the breeding season and in tropical latitudes during the non-breeding season. Thus, ranges of migratory and resident populations typically overlap during the non-breeding season. This pattern is especially common in tyrant flycatchers (Chesser 1995, 1997). To date patterns of migration within the range of overlap have not been documented because distinguishing between migratory and resident individuals is difficult. Therefore, we know little about such topics as migratory routes, non-breeding season migratory bird biology, population connectivity and intraspecific interactions between residents and migrants.

In other migratory systems, significant morphological differences exist between migrant and resident individuals of the some species; such differences can be used to classify co-occurring migrants and residents. For example, migratory Blackcaps (*Sylvia atricapilla*) have longer, more pointed wings and smaller bodies than resident conspecifics in Iberia (Telleria and Carbonell 1999), allowing accurate classification of migrants and residents in winter (Pérez-Tris et al. 1999). Likewise, a migratory subspecies of Reed Bunting (*Emberiza schoeniclus*) in Spain has larger and more convex wings than a sedentary subspecies (Copete et al. 1999). In addition to morphological differences, molt schedules may differ between co-occurring resident and migrant individuals (Lundberg and Eriksson 1984).

Range overlap of resident and migrant populations in the non-breeding season occurs in Tropical Kingbirds (*Tyrannus melancholicus*), which are permanent residents in most of tropical South America. Two subspecies (*satrapa* and *despotes*) are presumably permanent residents in northern Amazonia (Traylor 1979a, Chesser 1995), whereas the *melancholicus* subspecies is a resident from most of Amazonia southwards to approximately 18° S. South of this latitude, it occurs only in summer, migrating northwards after breeding into the range of permanent resident populations (Chesser 1995)(Fig. 1).

While studying a resident population of Tropical Kingbirds (*T. m. melancholicus*; hereafter “kingbirds”) at a site in eastern Bolivia, I noticed that many kingbirds captured during spring migration (i.e., September and October) were much fatter than others and that many of these fatter individuals were never seen again at the site. I hypothesized that those individuals were passage migrants, on their way to breeding grounds further south. I was interested in determining if morphological, molt or genetic differences exist between these putative migratory individuals and resident kingbirds at the site. I hypothesized that if kingbirds that had large amounts of subcutaneous fat and that were never seen again after color-banded were passage migrants, they would also differ in molt schedule, morphology and genetic structure, as has been documented in migrants breeding at North temperate latitudes. I tested this hypothesis by measuring fat content, flight feather, body and tail molt, wing chord, and primary feather wear of kingbirds captured during spring migration. I also hypothesized that at least some of the putative passage migrants were en route to latitudes south of 18° S, well south of my study site at 15° S. I tested this hypothesis by comparing the wing chord of the putative migrants at my site with those from study skins of kingbirds collected south of 18° S.

## Study sites and methods

My study site was Caparú Biological Station (CBS), Department of Santa Cruz, eastern Bolivia (14° 49' S, 61° 11' W; 170 m elev.). It is located at the center of the continent, at a latitude just north of the boundary of migratory kingbirds' breeding range and a just south of a large expanse of potential wintering area (i.e., Amazonia; Fig. 1). Habitat is primarily cerrado grassland, humid forest edge and cattle pasture. Kingbirds were captured using nylon and polyester mist nets (12 m and 18 m x 2.6 m, 36 mm and 38 mm mesh size) at locations where they were most abundant (e.g., ponds where they would bathe most afternoons, or at the edge of humid forest and cattle pasture). Kingbirds were also banded as nestlings and parents were captured at their nest by placing a stuffed Purplish Jay (*Cyanocorax cyanomelas*), a common nest predator, nearby.

Kingbirds were banded with uniquely-numbered aluminum bands provided by the Museo de Historia Natural Noel Kempff Mercado (MHNNKM), Santa Cruz, Bolivia as well as with up to three celluloid color bands. Banding was conducted during most months from October, 2004 to July, 2007. Data recorded on captured kingbirds included reproductive condition (presence/absence of cloacal protuberance or brood patch), fat score (measured on an 8-point scale), and body molt (measured on a 4-point scale), primary feather wear (measured on a 4-point scale), length of unflattened wing chord, tail, bill and tarsus length, and mass (Ralph et al. 1993, Pyle 1997). I classified flight feather and tail molt as present or absent (i.e., if at least one secondary or primary feather was molting, then molt was classified as present). These measurements were taken by myself and Ana Maria Mamani, with whom I worked on a regular basis to minimize observer error. To classify age, I define birds in their first year of life as first-year individuals (FY) or after first-year individuals (AFY) for individuals that are of unknown

age but at least one year old. Each year begins on September 1 because the kingbird breeding season lasts from mid-September to February.

Blood was taken from all color-banded individuals by piercing the brachial vein with a sterile needle. Blood was collected in a 0.5 mL heparinized capillary tube and stored in DNA lysis buffer (Seutin et al. 1991). I sexed live birds based upon primary notch length (Pyle 1997) and when necessary, through molecular methods using primers 2550F and 2718R (Fridolfsson and Ellegren 1999). Optimal cycle conditions were 95° for 5 min, 95° for 30 sec, an annealing temperature of 50° for 1 min, and 72° for 45 sec, repeated 39X, then held at 72° for 10 min, using 15 µl Mg. Blood samples were deposited at the MHNNKM.

To determine which individuals are residents, I documented the presence/absence of color-banded kingbirds after banding. I divided the ~ 700 ha study site into 23 sampling plots and methodically searched for banded individuals in each block at least once/month throughout most of the year. Visits to sample plots were done from February 2005 - August 2007. I did not visit plots during most of the non-breeding season of 2005 because I was absent June-September. I also visited plots on 28 January-12 February, 2-19 March and 15-27 June, 2008. When a color-banded individual was observed, I geo-referenced its location using a GPS receiver (Garmin GPS 76), noting the date, time and color band combination.

### **Morphological Measurements from Study Skins**

To determine whether morphological variation among populations could be useful in determining the breeding locations of passage migrants at CBS, I measured 120 kingbird skins from Argentina and Paraguay housed at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) and 79 skins at the Louisiana State Museum of Natural Science (LSUMZ). Ben Freeman measured 60 study skins from Paraguay and Argentina at the American Museum of Natural History (AMNH). Unflattened wing chord was measured in the same way that it was

measured on live kingbirds at CBS, according to methods in Ralph et al. (1993). Wing chord was not measured skins with excessively worn feather tips. I had previously standardized our measurements to minimize inter-observer measurement error.

### **Molecular Analysis**

I isolated DNA from blood samples using the PUREGENE DNA Purification Kit (Gentra Systems) and reviewed the literature to identify potentially polymorphic primers developed from related species in the Tyrannidae. Six microsatellite primers were successfully optimized from the genera *Empidonax* (GATA5; Pearson et al. 2006) and *Sayornis* (SAP22, SAP32, SAP47, SAP50, SAP156; Watson et al. 2002, Beheler et al. 2007). Optimal PCR cycling conditions for all primers except SAP39 were: 95° for 4 min followed by 94° for 1 min, then 55° for 1 min and 72° for 1 min, repeating the last three steps 35X, with a final cycle of 72 for 10 min. The only difference for SAP39 was that the annealing temperature was 59° instead of 55°. For all primers I used 12.5 µL of master mix, 800 µM dNTP's, 2.5 µM MgCl<sub>2</sub>, 0.26 µM of each primer, and a concentration of 10-20 ng of sample DNA.

Due to low sample sizes of kingbirds of known sex and for which I had DNA available for analysis, I combine males and females for genotyping purposes. I analyzed DNA from 15 migrants and 15 residents. DNA was run on an ABI 3730XL, 96 capillary automated sequencer (Biosystems, Foster City, CA). The program GeneMapper (Softgenetics, State College, PA) was used to score the alleles. Population structure was tested in the program STRUCTURE 2.2 (Pritchard et al. 2000) assuming a model of admixture, correlated allele frequencies and K=1-2 (where K is the number of populations), with 10 independent replicates for each K (length of the run 1000000 MCMC re-samples), and 100000 burn-in. I used the program Arlequin 3.01 (Excoffier et al. 2005) to test for Hardy-Weinberg equilibrium, and calculation of linkage disequilibrium between pairs of loci. For both tests Bonferroni correction was assumed for

multiple comparisons. Population differentiation was tested by performing a hierarchical analysis of molecular variance (AMOVA) to calculate global and pair-wise  $R_{st}$  (i.e., an analog of Slatkin's  $R_{st}$  (Slatkin 1995) using the sum of squared differences performed in Arlequin 3.01.

To avoid potential confounding effects of age with wing chord (Low 2006), fat content (e.g., Lundberg 1985) and molt (e.g., Debruyne et al. 2006), I hereafter only consider adult kingbirds (i.e., those with only trace juvenile plumage or 95% or more of the skull ossified).

After-fledgling-year (AFY) kingbirds captured in September and October that had higher subcutaneous lipid scores (i.e., a 6 or higher on an 8-point scale, *sensu* Ralph et al. 1993) were re-observed significantly less often than those with lower lipid scores (i.e., less than a 6 on the same scale; Fig. 2). This was true of both males ( $\chi^2 = 11.842$ ,  $P = 0.001$ ) and females ( $\chi^2 = 7.143$ ,  $P = 0.008$ ). I therefore classified as passage migrants all AFY kingbirds captured in September or October with lipid scores of 6 or higher and that were never re-observed after being color-banded, and that had no incubation patch or cloacal protuberance (to exclude the possibility that they were breeding at the study site). I classified residents as individuals that were captured in September or October, had subcutaneous lipid scores of 1-5 and were re-observed at least once later on the study site. Because there were not sufficient residents for which DNA was available for analyses, I include as residents for purposes of DNA analyses individuals with the same characteristics captured in November, which is well into the breeding season (A. Jahn, unpub. data).

## Results

Resident kingbirds at CBS tended to molt during and just after the breeding season (Fig. 3). When data from sexes are combined, spring passage migrants had significantly less flight feather molt (Kruskal-Wallis  $\chi^2 = 5.96$ ,  $P = 0.015$ ,  $N = 81$ ) and significantly less tail molt (Kruskal-Wallis  $\chi^2 = 7.66$ ,  $P = 0.006$ ,  $N = 79$ ) than residents, but there was no significant

difference between migrants and residents in body molt (Kruskal-Wallis  $\chi^2 = 1.07$ ,  $P = 0.302$ ,  $N = 81$ ). Migrants also had less primary feather wear (Kruskal-Wallis  $\chi^2 = 10.36$ ,  $P = 0.001$ ,  $N = 80$ ) and longer wings ( $t = 4.17$ ,  $P < 0.0001$ ,  $N = 79$ ) than residents.

Female passage migrants had significantly less flight feather molt, less primary feather wear and longer wings than resident females (Table 1). Male residents had significantly more tail molt than male migrants, but there was no significant difference in flight feather molt or primary feather wear between male migrants and male residents. Male migrants were also characterized by a significantly longer wing chord than male residents (Table 1).

I used discriminant function analysis (DFA) to determine the level at which I could correctly classify migrants and residents at the site during spring migration. Due to the relatively low sample size per sex, I combined data across sexes. I first determined which of the five morphological measurements (flight feather molt, tail molt, primary feather wear, body feather molt and wing chord) provided the most explanatory power within the discriminant function. A test of the equality of group means revealed that body molt contributed the least amount of explanatory power to the discriminant function ( $F_{1,72} = 1.09$ ,  $P = 0.30$ ), so it was excluded from further analysis. All four remaining variables significantly contributed to the discriminant function and were retained in the full model. The parameter with the least explanatory power was flight feather molt ( $F_{1,72} = 4.48$ ,  $P = 0.04$ ) and the parameter with the highest explanatory power was wing chord ( $F_{1,72} = 16.84$ ,  $P < 0.0001$ ). The resulting DFA correctly classified 86.0% of migrants and 71.0% of residents, with an overall success rate of 79.7%.

Among males, wing chord from study skins at  $>18^\circ$  S ( $N = 146$ ) is significantly longer than that of both resident ( $t = -6.93$ ,  $P < 0.0001$ ,  $N = 15$ ) and passage migrant kingbirds at the study site ( $t = -2.71$ ,  $P = 0.007$ ,  $N = 21$ ) (Fig. 4). Among females, wing chord from study skins

at  $>18^{\circ}$  S ( $N = 83$ ) is significantly longer than that of residents ( $t = 6.787$ ,  $P < 0.0001$ ,  $N = 11$ ) but not of passage migrants at the study site ( $t = 1.055$ ,  $P = 0.29$ ,  $N = 16$ )(Fig. 4).

Based on Bayesian population structure genetics analyses implemented in the program STRUCTURE 2.2 (Excoffier et al. 2005), I found better support for the presence of one population (log likelihood = -515.2) than for the presence of two populations (log likelihood = -516.6). This result suggests there is no significant genetic structure between migrant and resident kingbirds. AMOVA also showed no indication of genetic differentiation between migrants and residents ( $-0.02467$ ,  $P = 0.838$ ). There was no indication of departures from Hardy-Weinberg equilibrium or of linkage disequilibrium in the data set (Table 2).

I also conducted DFA on migrants and residents classified in the same way as above, but without taking re-sighting data into account (i.e., using only fat scores). Body molt had the least amount of explanatory power ( $F_{1,153} = 0.01$ ,  $P = 0.94$ ), so it was excluded. The resulting test of equality of group means revealed that flight feather molt had the highest explanatory power ( $F_{1,159} = 4.10$ ,  $P = 0.04$ ) and that wing chord had the least ( $F_{1,159} = 0.28$ ,  $P = 0.60$ ). The DFA correctly classified 75% of migrants and 26.5% of residents, with an overall success of 41.0%.

## Discussion

Kingbirds with high lipid scores and those that were never re-observed after banding (i.e., putative migrants) were characterized by traits typical of long-distance spring migrants in the Northern Hemisphere: advanced molt schedules (Lundberg and Ericksson 1984) and longer wings (Haberman et al. 1991, Tellería and Carbonell 1992, Milá et al. 2008) than those with less fat and which were re-observed at the site (i.e., residents). The differences between the two groups in molt, feather wear, wing chord and tail length from my site at the middle of the continent, where passage migrants would be expected to pass through if migrating between low latitudes to the north and the south temperate breeding grounds, strongly suggest that the

Tropical Kingbird is a long-distance migrant that overwinters in central or northern Amazonia. Additionally, migrant females at CBS had similar wing chords compared to breeders from the seasonal breeding range at  $>18^{\circ}$  S (Fig. 4), whereas male migrants had significantly longer wings than residents at CBS (Table 1) but had significantly shorter wings than kingbirds from the seasonal breeding range (Fig. 4).

Female spring passage migrants were likely returning to the seasonal breeding range, south of  $18^{\circ}$  S. Male migrants may therefore have been heading to the seasonal breeding range, as well as to latitudes closer to the study site. Future research on the geographical variation in wing chord and genetic structure south of the study site may reveal geographical variation in traits that could be useful in determining breeding location of these migrant birds.

Molt of resident kingbirds at CBS tends to occur primarily just before, during and immediately after the breeding season (Oct-Dec)(Fig. 3). Therefore, many resident kingbirds at CBS likely have not molted prior to the passage of spring migrants. Passage migrant male kingbirds had a more advanced pre-alternate tail molt compared to local resident males, and female migrants had a significantly more advanced flight feather molt than residents at CBS (Table 1), indicating that migratory kingbirds have more advanced pre-alternate molt schedules than non-migratory conspecifics at CBS. Similarly, Lundberg and Eriksson (1984) found that the post-juvenile molting period of migratory Starlings (*Sturnus vulgaris*) was shortened relative to that of non-migratory conspecifics, with migrants finishing the molt of primary and secondary feathers significantly earlier than residents. They postulated that the shortened molting period of migrants was constrained by the need to migrate after breeding. Although my study focuses on spring migration, the more advanced flight feather and tail molt of migrant kingbirds relative to resident kingbirds suggests that migration can be a constraint on molt timing, such that migrants

in this species finish the pre-alternate molt earlier than residents. To the best of my knowledge, whether migration constrains the scheduling of molt at tropical latitudes has not been studied.

That residents were more likely to exhibit primary feather wear than migrants makes intuitive sense, given that worn primaries would likely be less efficient in flight and therefore be a detriment to long-distance migration. In contrast, body molt was the trait with least difference between migrants and residents in the DFA, which is not surprising given that the flight feather and tail molt more directly affect a migrant's ability to fly than do other feathers.

The genetic analysis revealed no significant population subdivision between the migrant and resident kingbirds (Table 2), which could be due to a small sample size of birds or from too few loci sampled. Distinguishing passage migrants from residents at the molecular level may be possible with other types of genetic markers or with species-specific microsatellite primers. Using analysis of mitochondrial DNA, Joseph et al. (2003) found that migratory populations of Swainson's Flycatcher (*Myiarchus swainsoni*) breeding in the south-temperate latitudes of South America are not closely related to populations of conspecific residents at tropical latitudes or shorter-distance migrants on the continent. They concluded that evolution of migration and distribution of breeding ranges of the different populations is likely a consequence of several climatically-related southward range expansions. If kingbird populations are only recently isolated, the lack of microsatellite structure may be due to a recent colonization of southern latitudes. The observed phenotypic differences may have no genetic basis (e.g., James 1970), or may be controlled by a relatively small number of genes, none of which are in linkage disequilibrium with the analyzed microsatellite markers. Conversely, kingbird populations in South America may not be very isolated, with relatively high gene flow occurring between populations.

Notably, these results corroborate previous evidence that populations of this species breeding at high southern latitudes in South America (i.e., *T. m. melancholicus*) have a longer wing chord than populations breeding closer to the equator (i.e., *T. m. satrapa* and *T. m. despotes*; Cory and Hellmayr 1927). A similar pattern is found in eastern Mexico, where kingbird populations characterized by longer wings occur at higher latitudes (Traylor 1979b). Likewise, Joseph et al. (2003) found evidence that southern breeding populations of Swainson's Flycatcher in South America have longer wing chords than populations breeding at tropical latitudes on the continent. Because I did not have enough other morphological data on the kingbirds I measured, I am not able to evaluate whether wings of passage migrant kingbirds were proportionally longer than those of residents.

In spite of the apparent conformity of this pattern to Bergmann's Rule, which predicts geographical variation in body size within many bird species (Ashton 2002), the ultimate reason why migrants have longer wings than residents in this species will likely not be straightforward, as Bergmann's Rule is of questionable relevance to migratory bird species (Zink and Remsen 1986, Meiri and Dayan 2003). Within the genus *Tyrannus*, Van Wynsenberghe et al. (1992) found no evidence for Bergmann's Rule in Eastern Kingbirds (*Tyrannus tyrannus*) and Haberman et al. (1991) found evidence suggesting that wing length of migratory Gray Kingbirds (*Tyrannus dominicensis*) was proportionately longer than that of sedentary conspecifics.

I was primarily interested in distinguishing migrants from residents in order to understand the movement patterns of kingbirds at my study site, as well as to study the ecology of migrants vs. residents within a partially migratory population of kingbirds (Chapter 5). An ability to distinguish passage migrants from residents may benefit numerous future studies that focus on the biology of residents or migrants. Although color-banding and subsequent searching for

color-banded individuals is more labor intensive than banding alone, my results show that a combination of subcutaneous fat scoring combined with color-banding to determine migratory status is a much better way to distinguish migrants from residents than fat scoring alone (i.e., a success rate of almost 80% vs. 41%).

Because the tropics are the postulated origin of migratory species (Sinclair 1983, Levey and Stiles 1992, Chesser and Levey 1998), distinguishing between migrant and resident conspecifics when they occur together at tropical latitudes is important in advancing our knowledge on the evolution of migratory behavior. Using data on wing chord length and molt of flight and tail feathers, I was able to classify more than 85% of kingbirds as migrants. However, because austral migrants that overwinter in South America's tropics only migrate an average of  $9.2^{\circ}$  ( $\pm 8.5$ ) latitude (Chesser 1994), migrants may not be obviously morphologically different from permanent resident individuals in most species. Although kingbirds breed from northern Venezuela to central Argentina (Chesser 1995), how far south breeders from the seasonal breeding range migrate into the tropics remains unknown and will remain so until a complete population connectivity analysis is conducted utilizing techniques as stable isotope analysis (Webster et al. 2002) or miniaturized electronic devices for tracking migrants (e.g., Stutchbury et al. 2009).

Table 3-1. Morphological and molt comparisons of resident and passage migrant Tropical Kingbirds at Caparú Biological Station (Bolivia). Values for flight feather and tail molt are percent of migrants and residents with molt present. Values for body feather molt and primary feather wear represent mean score on 4-point scale, with 4 representing the highest amount of molt. Value for wing chord is the mean.

<b>Males</b>				
	Residents (N)	Migrants (n)	Test statistic	P =
Flight feather molt	12% (17)	0% (21)	2.54 <sup>a</sup>	0.111
Tail molt	20% (15)	0% (21)	4.46 <sup>a</sup>	0.035
Body feather molt	2.44±1.09 (16)	2.24±1.18 (21)	0.28 <sup>a</sup>	0.595
Primary feather wear	2.06±0.25 (16)	1.86±0.48 (21)	2.42 <sup>a</sup>	0.120
Wing chord (mm)	111.27 ±2.87 (15)	113.9 ±2.84 (21)	2.735 <sup>b</sup>	0.010
<b>Females</b>				
	Residents (N)	Migrants (n)	Test statistic	P =
Flight feather molt	25% (12)	0% (16)	4.06 <sup>a</sup>	0.044
Tail molt	8% (12)	0% (16)	1.25 <sup>a</sup>	0.264
Body feather molt	2.82±0.98 (11)	2.47±1.19 (15)	0.50 <sup>a</sup>	0.481
Primary feather wear	2.58±0.79 (12)	1.80±0.56 (15)	6.92 <sup>a</sup>	0.009
Wing chord (mm)	106.09 ±1.97 (11)	110.63 ± 2.63 (16)	4.846 <sup>b</sup>	< 0.0001

<sup>a</sup> Kruskal-Wallis test

<sup>b</sup> Independent samples *t*-test

Table 3-2. Summary of genetic diversity for resident and migrant Tropical Kingbirds. The genetic diversity parameters include average number of alleles per locus (*A*), observed heterozygosity (*H<sub>O</sub>*), expected heterozygosity (*H<sub>E</sub>*), and the inbreeding coefficient (*F<sub>IS</sub>*), based on the average of six loci.

	<i>H<sub>O</sub></i> - <i>H<sub>E</sub></i> (Mean)	<i>F<sub>IS</sub></i>	Average gene diversity across loci	<i>A</i>	<i>N</i>
Residents	0.423-0.478 (>0.05)	- 0.46118 (>0.05)	0.422 ± 0.259	6.67	15
Passage migrants	0.438-0.611 (>0.05)	- 0.01246 (>0.05)	0.582 ± 0.339	8.00	15

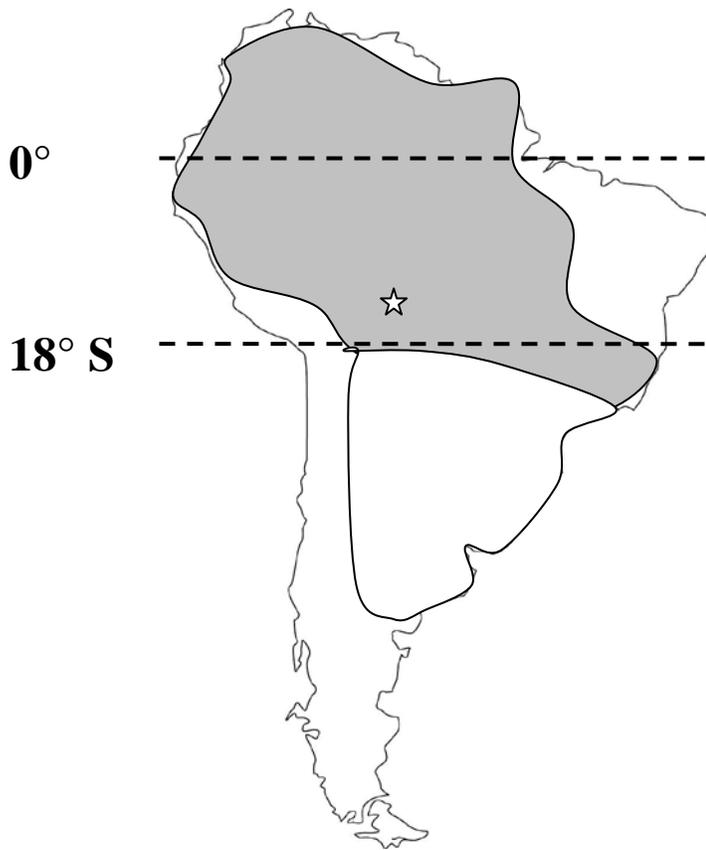


Figure 3-1. Distribution of Tropical Kingbird in South America. Gray polygon represents the permanent distribution of the species. The white polygon south of 18° S represents the seasonal breeding range. Star represents location of Caparú Biological Station. Adapted from Chesser (1995).

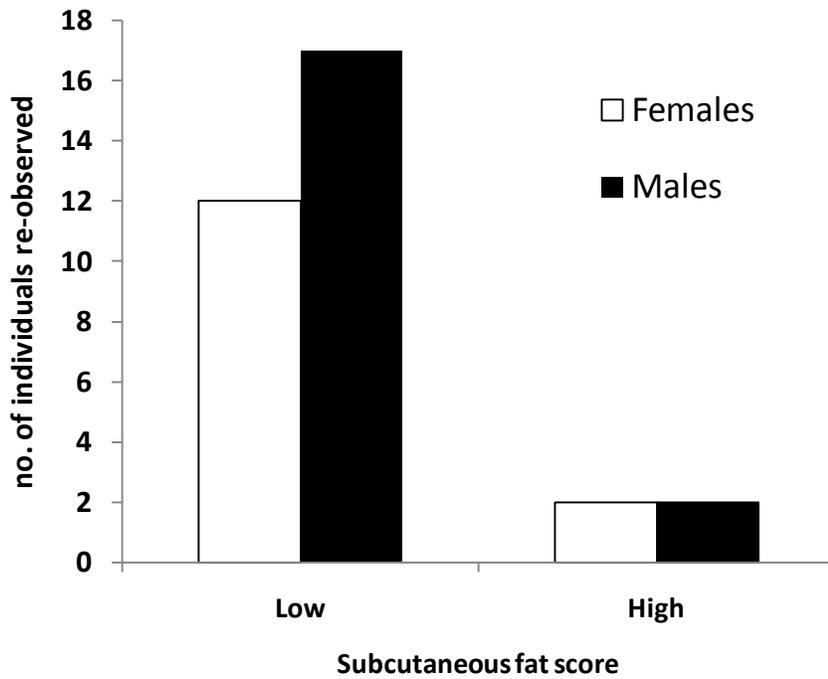


Figure 3-2. Relationship between amount of subcutaneous fat and frequency of being re-observed in AFY Tropical Kingbirds color banded during spring migration at Caparú Biological Station.

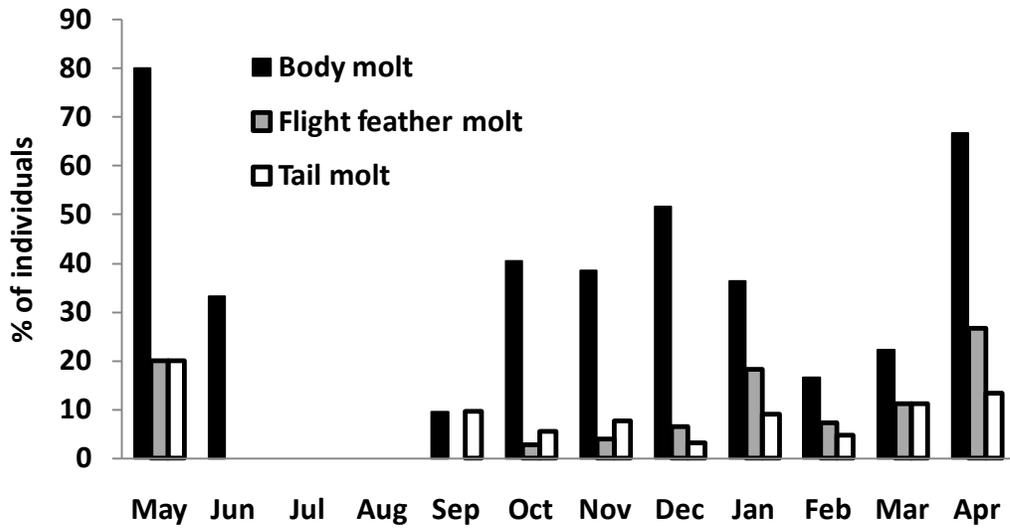


Figure 3-3. Molt schedule of AFY resident Tropical Kingbirds at Caparú Biological Station. Data represent the percent number of kingbirds per month with each molt type (does not necessarily add to 100% because individuals can have more than one molt type). Includes only individuals that were color-banded and re-observed at least once.

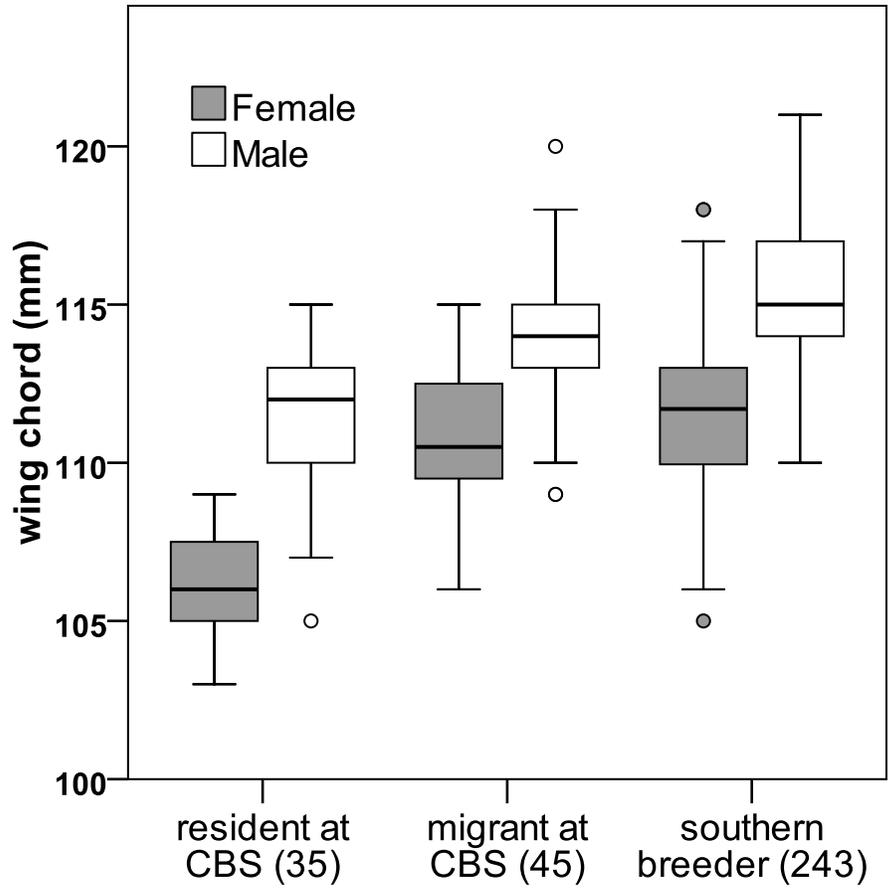


Figure 3-4. Box-and-whisker diagram depicting wing chord of Tropical Kingbird residents, passage migrants and breeders from seasonal breeding range south of 18° S in South America. Numbers in parentheses on x-axis labels represent sample size.

CHAPTER 4  
VARIATION IN FORAGING AND SOCIAL BEHAVIOR OF TROPICAL KINGBIRDS  
(*TYRANNUS M. MELANCHOLICUS*) IN RELATION TO RAINFALL AND FOOD  
RESOURCE ABUNDANCE IN SOUTHERN AMAZONIA

**Introduction**

In seasonal environments, declines in temperature and rainfall often generate effects that ripple throughout the local food web, triggering changes in behavior, ecology and life history of local species. Food is commonly regarded as a limiting resource for birds, particularly in winter (e.g., Alerstam and Hogstedt 1982, Lovette and Holmes 1995, Brown and Sherry 2006). Yet most of what is known about winter food limitation comes from work in the temperate zone, where the scarcity of resources in the non-breeding season is relatively obvious, and in the Neotropics, where attention on food limitation has focused on overwintering migrants, not residents (e.g., Strong and Sherry 2000, Studds and Marra 2007, Smith and Robertson 2008, Brown and Sherry 2006).

In the tropics, abundance of arthropods, a major food resource for many species, is often positively linked to rainfall, although variation exists among arthropod taxa in their response to rainfall (e.g., Wolda 1978, 1988, Frith and Frith 1985, Poulin et al. 1992, Diniz and Kitayama 1998, Strong and Sherry 2000). It is therefore not surprising that the breeding cycle (e.g., Gibbs 2007), survival (Dugger et al. 2004), abundance (e.g., Faaborg et al. 1984, Tarroux et al. 2003, Herremans 2004, Williams and Middleton 2008) and community diversity (e.g., Rompré et al. 2007) of many birds in the tropics are positively associated with rainfall (but see Schaefer et al. 2006). In general, tropical bird abundance appears positively correlated to arthropod resource availability (e.g., Tarroux et al. 2003, Herremans 2004).

In the tropics of South America, some of the most seasonal environments are grasslands and dry forests. Cerrado is a biome in central South America characterized by highly seasonal

dry and wet seasons, resulting in strong seasonality of flowering and fruiting (Batalha and Martins 2004), and in the abundance of insects (Pinheiro et al. 2002, Amorim et al. 2009). As part of a broader study on processes driving bird migration in South America, I studied effects of seasonal conditions on the behavioral ecology of the Tropical Kingbird (*Tyrannus m. melancholicus*) (hereafter “kingbird”) at a site primarily comprised of cerrado grassland.

The kingbird population at the site is partially migratory – some individuals leave at the end of the breeding season, while others remain throughout the non-breeding/dry season (Chapter 5). My overall goal is to understand the proximate mechanisms driving partial migration in this population. Because the rainy season and the kingbird breeding season are partially coincident, it is quite likely that seasonal rainfall patterns will strongly affect the timing of breeding and migration, especially if the dry period, the presumed period of food scarcity, does not fully overlap the non-breeding season. Indeed, it is possible that migration at these altitudes will be more strongly affected by rainfall seasonality than by changes in temperatures, which are relatively minor at this latitude. I censused kingbirds, assessed arthropod prey abundance, and collected data on kingbird foraging and intraspecific social behavior over an annual cycle. Because tropical insect abundance is generally low in the dry season (Janzen 1973, Frith and Frith 1985, Poulin et al. 1992), I expected the dry season to be a period of food scarcity for kingbirds. I predicted there would be fewer kingbirds at the site in the dry season than in the wet season (i.e., that some individuals would migrate away) and that kingbirds would sally after insects less often in the dry season than in the wet season. To determine if the dry season is food-limited, I also explored the relationship between food resource availability, Kingbird behavior, and kingbird abundance during the dry season. If food is limiting during the dry season, I expect that food abundance and search time for food should be negatively correlated, that food

abundance and the incidence of intraspecific aggression should be negatively correlated, and that kingbird abundance and the incidence of intraspecific aggression should be positively correlated.

### **Study Site and Methods**

My study site was Caparú Biological Station (CBS), Department of Santa Cruz, eastern Bolivia (14° 49' S, 61° 11' W; 170 m elev.). I worked in an area of approximately 700 ha. It was mostly comprised of cerrado grassland with a low tree layer of 4-6 m in height, dominated by *Curatella americana* and bordered to the north, east and west by humid forest. On the west side there was a 50 ha patch of cattle pasture, which was created by logging humid forest (Fig. 1). Kingbirds treated the pasture much like cerrado, foraging from and nesting in isolated trees. Some cattle from the pasture occasionally entered the cerrado, although at low densities.

Because I was not at the study site every day, I could not collect continuous data on rainfall. Thus, rainfall data reported here are from El Refugio Biological Station, approximately 9 km north of CBS. Those data match closely the rainfall data I collected at CBS.

### **Arthropod Sampling**

Kingbirds typically forage by aerial sallies (*sensu* Remsen and Robinson 1990), flying outwards from an exposed perch to catch a flying insect in mid-air (Fitzpatrick 1980, Cintra 1997, Gabriel and Pizo 2005). Although kingbirds at CBS also gleaned insects from leaves and consumed fruit, >95% of observed attempts at foraging were aerial sallies (A. Jahn unpub. data). I therefore assessed prey availability by sampling flying insects using aerial malaise traps. Malaise traps were made of fine green mesh and were open on four sides (108 X 106 cm per side). At the top and bottom were collection bottles with 70% alcohol. Ten traps were placed at 100 m intervals along a census transect in cerrado grassland and five traps were similarly placed in the cattle pasture. Traps were suspended 2-4m above the ground and positioned as much as

possible away from vegetation, thereby sampling arthropods in the open airspace where kingbirds typically forage.

All traps were opened at dawn and closed at dusk on five consecutive days per month from February 2006 to January 2007. However, in March traps were opened for only two days, in May they were opened for four days and in April and June they were not opened at all. All insects were collected from traps each day at closing and stored in 70% alcohol. Insects were later identified by Mirtha Saldias to the lowest taxonomic category possible and counted using a dissecting microscope. All insects were deposited in the entomological collection of the Museo de Historia Natural Noel Kempff Mercado, Santa Cruz de la Sierra, Bolivia.

### **Fecal Sample Analysis**

I collected fecal samples from kingbirds by holding recently captured individuals in a clean cotton bag for approximately 30 min before banding them. Each fecal sample was placed in a plastic centrifuge tube in 70% alcohol and later examined under a dissecting microscope (again, by M. Saldias) to identify arthropod remains to the lowest possible taxonomic category. Because insects in the samples were in small pieces, it was impossible to determine the number of individual arthropods per taxonomic group in each fecal sample. Thus I used presence or absence of each arthropod taxonomic category to calculate the proportion of samples containing each prey taxon.

The use of fecal samples to document bird diets has important limitations, which have been thoroughly reviewed (e.g., Jenni et al. 1990, Rosenberg and Cooper 1990, Kleintjes and Dahlsten 1992). Nevertheless, fecal sample analysis is useful for estimating basic diet when detailed knowledge of the hard parts can be used to identify insect taxa (Davies 1976, Ralph et al. 1985, Poulin and Lefebvre 1997). I rejected an alternative technique, stomach flushing, because it

entailed a greater risk of mortality than collecting fecal samples (Moody 1970, Durães and Marini 2003, Carlisle and Holberton 2006).

### **Behavioral Data**

To ensure an even representation of individual kingbirds across the study site, I divided the study site into 23 sampling plots (5–20 ha each) and methodically searched for kingbirds on each plot during most months from October 2005 to July 2007. I attempted to visit each plot at least once per month. Behavioral data were collected by following individual kingbirds for as long as possible during visits to sampling plots and recording their behavior using digital voice recorders (Sony ICD-B16) until the target individual disappeared from sight. All behavioral data were collected by five individuals (A. Jahn, A. Mamani, B. Flores, Q. Vidoz, and B. Freeman). To maintain standardized techniques and minimize observer error, observers regularly worked together.

I define search time as the period (to the nearest second) between consecutive aerial sallies by an individual kingbird. Time was measured using the digital clock on the voice recorder. Although binoculars were used, the speed of aerial sallies and the distance between observer and the bird usually prevented determination of whether a particular sally was successful. To avoid pseudoreplication, I used only the interval between the first two aerial sallies in each observation of a given kingbird to calculate search time. I calculated mean monthly search time as the mean of all search times documented in a given month. I also documented the manipulation time of prey items from all aerial sallies observed. I define manipulation time as the time between capture of prey and when it was swallowed by the kingbird. I also quantified the number of perch changes by kingbirds, defining a perch change as movement to a perch at least one meter distant from the previous perch. These occurred either after an aerial sally or were not associated

with foraging. Based upon encounters of banded to non-banded kingbirds in the population, I estimate that I was sampling from a population of approximately 50 individuals.

I defined an agonistic encounter as occurring when an individual emitted a characteristically sharp and repetitive call and exhibited a crouched posture (*sensu* Smith 1966) to a conspecific, or when it did not crouch but emitted the call with a conspecific nearby ( $\leq 20$  m). I quantified monthly agonistic intraspecific interactions by calculating the number of censuses on sample plots during which at least one intraspecific agonistic encounter was observed, divided by the total number of censuses for a given month.

### **Breeding Data**

To document the breeding cycle of the local population, I searched for kingbird nests in the same way that I searched for color-banded individuals. After finding a nest, it was monitored every three days until nestlings fledged or the nest failed, using methods described in Ralph et al. (1993).

### **Kingbird Abundance**

I conducted transect censuses using methods similar to those in Bibby et al. (2000). I censused kingbirds along two transects, one in cerrado grassland and one in the cattle pasture. Transects were 1 km long and 100 m wide. Censusing was conducted between dawn and 09:00, with each census lasting 25-35 min. A total of 57 censuses were conducted from 14 April 2005-26 June 2008, with 38 censuses in the dry season and 19 in the wet season, with a least two censuses during each month of the year. All censuses were conducted by myself or Ana Maria Mamani. We periodically conducted censuses together to minimize observer error. Monthly kingbird abundance was calculated as the mean number of kingbirds seen on census transects per month. Although I collected data on distance to kingbirds, I use total number of kingbirds detected on transects to calculate abundance because I am primarily interested in the relative

abundance of kingbirds between seasons. Additionally, color-banded individuals tended to avoid observers (pers. obs.), such that using a measure of distance to calculate kingbird would likely bias results.

## **Results**

### **Rainfall Patterns**

There are well-defined and pronounced wet and dry seasons at the site, with precipitation dramatically increasing in November, reaching a peak in December and steadily decreasing thereafter (Fig. 2). I therefore define the wet season as Oct-Feb and the dry season as all other months. Temperature variation between dry and wet seasons is not as high as variation in rainfall, although the average daily temperature from mid-September to mid-February ( $27.5^{\circ}\text{C}$ ,  $\text{SD} \pm 13.8$ ) is slightly warmer than during the rest of the year ( $26.4^{\circ}\text{C}$ ,  $\text{SD} \pm 9.2$ ).

### **Fecal Sample Analysis**

I collected a total of 68 fecal samples from 67 individuals. Coleoptera were found in 100% of samples, Hymenoptera in 29.4%, and Odonata in 13.2%. Hemiptera, Homoptera, Orthoptera, Lepidoptera and Diptera were each found in less than 5% of the samples. There was no consistent pattern in the occurrence of any of these taxa in fecal samples throughout the year. Because coleopterans and hymenopterans disproportionately accounted for the majority of insect remains in kingbird fecal samples throughout the year, and because Dipterans were very common in the traps, I focus discussion of the abundance of food resources for kingbirds to these three groups. I collected very few odonates in the traps, precluding an analysis of seasonal abundance for this group.

### **Arthropod Abundance**

Coleopteran, Diptera and Hymenoptera were the most common orders caught in malaise traps; all were more abundant in the wet season than in the dry season (Fig. 3). The number of

Coleoptera more than doubled ( $P < 0.0001$ ) and the number of Diptera tripled ( $P < 0.0001$ ) from dry to wet season (Table 1). Hymenoptera captures increased by 36% over the same period ( $P = 0.179$ ). The same seasonal pattern was generally followed by the other arthropod taxa captured in the traps: Arachnida, Dictyoptera, Hemiptera, Homoptera, Isoptera, Orthoptera (A. Jahn, unpub. data).

### **Kingbird Breeding and Abundance**

Kingbirds bred at the site from September through February (earliest date of nesting activity among three seasons, 2004-2006: 14 September, latest date: 26 February), although most nests (>80%) were active in Oct-Dec, with very few in either September or February. Most nesting activity therefore occurred during the first months of the wet season. Kingbird abundance at the study site was more than twice as high in the wet season (Oct – Feb) than in the dry season ( $9.1 \pm 6.7$  vs.  $4.1 \pm 3.4$  kingbirds/census; repeated measures ANOVA  $F_{1,18} = 7.053$ ,  $P = 0.016$ ).

### **Kingbird Behavior**

Because I collected data on arthropod abundance from Feb 2006 - Jan 2007, I limit kingbird behavioral analyses to that time period. The only exception is for data on search time collected in July 2007, which I included because I lacked sufficient search time data for July 2006. I am confident that the 2007 data would be similar to that of 2006, because July is predictably one of the driest months of the year in the region and rainfall data from July 2006 and 2007 were typical of other years (unpubl. data from El Refugio).

I observed 311 aerial sallies by kingbirds during the dry season and 147 during the wet season. Search time was significantly longer in the wet season, when prey was more abundant than in the dry season (Wilcoxon  $Z = -10.482$ ,  $P < 0.0001$ ; Fig. 4). This difference was not an artifact of rare events with unusually high values, as it reflects an increase in skew of search

times (Kolmogorov-Smirnov  $Z = 1.812$ ,  $P = 0.003$ ; Fig. 5). Mean manipulation time after prey capture was 13.0 min ( $\pm 9.6$ ) during the dry season ( $N = 376$ ) and 35.9 min ( $\pm 17.0$ ) during the wet season ( $N = 225$ ).

Within the dry season, search time and Coleopteran abundance were negatively correlated ( $r^2 = 0.749$ ,  $F_{1,4} = 11.954$ ,  $P = 0.026$ ; Fig. 6). Search time and Hymenopteran abundance were also negatively correlated, although the relationship was not significant ( $r^2 = 0.290$ ,  $F_{1,4} = 1.637$ ,  $P = 0.270$ ; Fig. 7).

Frequency of agonistic encounters in the dry season was significantly and positively related to kingbird abundance ( $r^2 = 0.697$ ,  $F_{1,4} = 9.216$ ,  $P = 0.039$ ; Fig. 8). Frequency of agonistic encounters in the dry season was not related to abundance of coleopterans or hymenopterans ( $r^2 = 0.192$ ,  $F_{1,4} = 0.953$ ,  $P = 0.384$  and  $r^2 = 0.116$ ,  $F_{1,4} = 0.524$ ,  $P = 0.509$ , respectively).

## Discussion

Results point to a dramatic decline in insect prey availability for kingbirds in Bolivian cerrado in the dry season. During the dry season, the availability of Coleopterans and Hymenopterans, the kingbird's two main prey items, is negatively correlated with search time for food by kingbirds. This, plus the positive relationship between kingbirds abundance and intraspecific aggression points to the dry season as being a time of limited food and higher stress for kingbirds at the study site. . These patterns also provide an explanation for why some kingbirds disappear from the study site after the breeding season – they either die or migrate to an area with higher prey availability. The latter possibility agrees with the conclusion from Chapter 5 that kingbirds at my study site are partially migratory (i.e., some individuals migrate away at the end of the breeding season).

More generally, kingbird abundance is greatest when arthropod abundance is greatest. Other studies have documented a similar correspondence between tropical bird abundance and food availability (e.g., Blake and Loiselle 1991, Tarrow et al. 2003, Herremans 2004), although the pattern does not hold for all tropical bird species (Karr and Brawn 1990). In Australia, migratory Silvereyes (*Zosterops lateralis*) are primarily insectivorous, and their movements are likely determined in large measure by insect availability at different latitudes (Chan 2005).

The large seasonal fluctuation in arthropod abundance in the cerrado at CBS is almost certainly driven by parallel fluctuations in rainfall, exacerbated by the open nature of the habitat. The cerrado is relatively unbuffered climatically compared to more closed habitats such as humid forest. Arthropods are therefore likely to be more susceptible to rainfall and/or temperature changes between or within seasons in cerrado relative to forest habitats. Janzen and Schoener (1968) found river-bottom forest in Costa Rica to exhibit less variation in arthropod abundance than adjacent dry forest. In humid tropical forests, arthropod abundance can even increase during the dry season (Karr and Brawn 1990; Lefebvre et al. 1994; Smith and Robertson 2008).

Seasonal variation in arthropod abundance at a site of similar climate, habitat, and latitude was documented by Pinheiro et al. (2002). Using window, Malaise and pitfall traps, they found the greatest decrease in overall arthropod abundance in February, similar to what I found. However, they documented a wet season as well as a dry season peak in Hymenopteran abundance, which I did not detect. Because Pinheiro et al. (2002) pooled results among trap types, it is difficult to assess the cause of this discrepancy. Additionally, Amorim et al. (2009) found higher richness and abundance of hawkmoths in the rainy season than in the dry season at a site in the Brazilian cerrado.

The pattern of higher insect prey abundance and longer search time between kingbird sallies at the site in the wet season relative to the dry season (Figs. 2, 3) is unexpected because searching intervals should decrease with higher food abundance (e.g., Hutto 1990, Lovette and Holmes 1995, Johnson 2000), especially because kingbirds are likely to have a higher energetic demand due to reproductive activities (e.g., the need to provide food to nestlings) in the wet season. I expected a pattern between seasons similar to the within-season negative relationship I documented between search time and Coleopteran abundance (Fig. 6). Note, however, that I was unable to document foraging success. It is possible that kingbirds sallied less often in the wet season because there was a greater selection of types of prey (e.g., different sizes) than in the dry season, and as a consequence they were more selective (i.e., waited longer between sallies) in the wet season, as predicted by optimal foraging theory (Stephens and Krebs 1986). In particular, kingbirds in the wet/breeding season may have been selecting larger and more nutritious prey. Indeed, food manipulation time in the wet season was well over double that in the dry season, suggesting that larger food prey was being taken in the wet season. This supports the idea that high nest predation should select for a decrease in the number of visits to nests by parents (thereby reducing the risk of predation), which compensate for the lower nest visitation rates taking larger prey items to nestlings (Martin 1996). During the dry season kingbirds may be forced to consume smaller prey, resulting in more frequent sallies and shorter search times.

Choteau and Fenosa (2008) documented a higher foraging rate of Red-capped Coua (*Coua ruficeps*) in the dry season than in the wet season in Madagascar, even though the abundance of arthropods, their main source of food, was higher at the study site in the wet season. They proposed that couas may switch prey consumed to track seasonal variation in the availability of different arthropod taxa. Yet, kingbirds in our study did not noticeably switch

foraging strategies between seasons, since aerial sallying was the predominant foraging mode in all months and Coleoptera were always present in their fecal samples (A. Jahn, unpubl. data).

The increase in kingbird abundance toward the end of dry season (Fig. 4) may reflect an attempt by adults to arrive as early as possible from wintering grounds to get claim high quality territories. Indeed, if rainfall drives the life history cycle of kingbirds as occurs in other tropical bird species (e.g., Dugger et al. 2004, Gibbs 2007), it may be beneficial for an adult kingbird to be present on its territory if rains begin unusually earlier in a given year, therefore increasing food supply and providing a chance to nest early. Alternatively, the increase in kingbird abundance in the late dry season could simply reflect arrival of kingbirds from other populations, which could be escaping harsh winter conditions further south until early spring.

Intraspecific aggression in wintering birds has been well-documented in north-temperate latitudes. For example, Lundberg's (1985) work on European blackbirds (*Turdus merula*) demonstrates a strong positive relationship between intraspecific agonistic interactions and harsh environmental conditions (i.e., snow cover) in winter. In my study, the significantly positive relationship between kingbird abundance and intraspecific aggressive encounters during the dry season (Fig. 5) may be due to competition for mates or breeding territories, as an early preparation for the breeding season, not because of competition for food. Several lines of evidence support this argument. First, there is no significant relationship during the dry season between arthropod abundance and kingbird agonistic interactions. Second, flying insects (the kingbird's main prey) are not a patchily distributed resource, and kingbirds do not forage in flocks at the site. Finally, there was a dramatic drop in insect abundance before the dry season began (Fig. 2), such that there was little temporal variation in insect abundance throughout the

rest of the dry season; rather, there was simply very little food available throughout the dry season.

A potentially fruitful line of research could be on the social hierarchy in the population in the dry season. Among passerines, responses to stressful environmental conditions are often proximally regulated within a social hierarchy (e.g., Cristol 1995, Lendvai et al. 2007), with dominant individuals often attaining greater access to food resources. For example, larger, dominant Great Tits (*Parus major*) increase feeding and feather growth rate during colder, more food-limited conditions whereas subdominants do not (Carrascal 1998). In Willow Tits (*Parus montanus*), dominance is positively correlated with mass gains in winter, but the relationship disappears with food supplementation, when subordinates also gain weight (Koivula et al. 1995). Such stressful conditions, in which higher competition exists for more limited food resources, may be more energetically costly for subdominants in a population because of their higher metabolic rates relative to dominant individuals (Senar et al. 2000, but see Vézina and Thomas 2000) and can ultimately result in lower survival rates of subdominants (e.g., Piper and Wiley 1990, Koivula et al. 1996). Yet, dry season conditions do not always translate to lower survival rates. In Kenya, Schaefer et al. (2006) found that non-breeding season survival of resident *Sylvia* warblers was not lower in the dry season than in the wet season, though they did not measure food resource availability.

Another interesting line of research would be the effects of micro-habitat use during the dry season. There are artificial ponds at the study site to provide water for cattle, which are likely the only sources of water during the middle of the dry season. These may areas where more insects are available during the dry season. I am currently not able to evaluate the potential effect of these sources of water on feeding rates because I did not quantify the distance of

kingbird aerial sallies from these bodies of water. Further research may demonstrate that, during this time of year, these may represent the best foraging sites. During the breeding season, however, the extreme territoriality of kingbirds might force them to spread out over territories of very uneven quality. In any case, the most dominant individuals should be able to hold onto dry season territories with the most water and would be expected to do better.

Understanding the constraints operating on organisms throughout the entire annual cycle offers insight into the implications of global climate change on population dynamics (Ådahl et al. 2006) as well as whether processes in one season affect those at other times of year (i.e, seasonal carry-over effects). For example, Robb et al. (2008) found an effect of supplementation of winter food supply on breeding success the following season. Until such experimental, hypothesis-driven research on tropical bird ecology is employed in the tropics, our understanding of the pathways linking climate, food resource abundance, behavioral ecology, and population trends in tropical birds will be hampered (Stutchbury and Morton 2001, Vuilleumier 2004). Indeed, how the biology of birds and other organisms at tropical latitudes is linked to rainfall and food resources is likely to become a topic of much interest, as increasingly dry conditions are predicted for at least some parts of the Neotropics (Neelin et al. 2006).

Table 4-1. Abundance of the three most common Orders of insects in traps at Caparú Biological Station. Numbers represent mean number of captures/net-hr/month; numbers in parentheses are standard deviation.

<b>Aerial Malaise trap</b>				
	<b>Wet season mean (SD)</b>	<b>Dry season mean (SD)</b>	<b>F<sub>1,67</sub> = <sup>a</sup></b>	<b>P =</b>
Coleoptera	4.7 (3.98)	2.3 (2.28)	19.292,	< 0.0001
Diptera	9.2 (7.02)	3.0 (3.53)	39.039	< 0.0001
Hymenoptera	1.9 (2.55)	1.4 (2.90)	1.843	0.179

a. Based upon a repeated-measures ANOVA

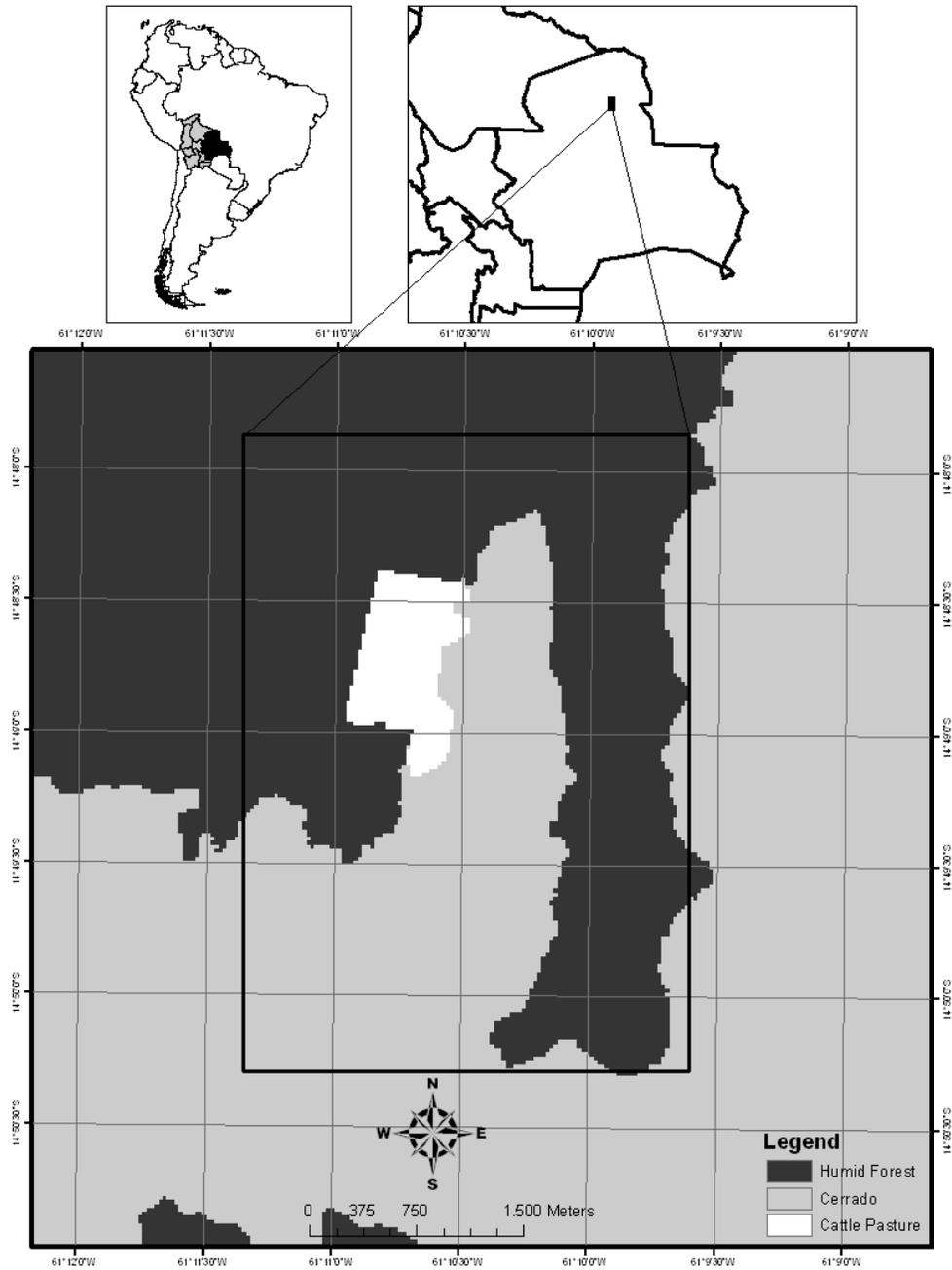


Figure 4-1. Map of Caparú Biological Station habitat types.

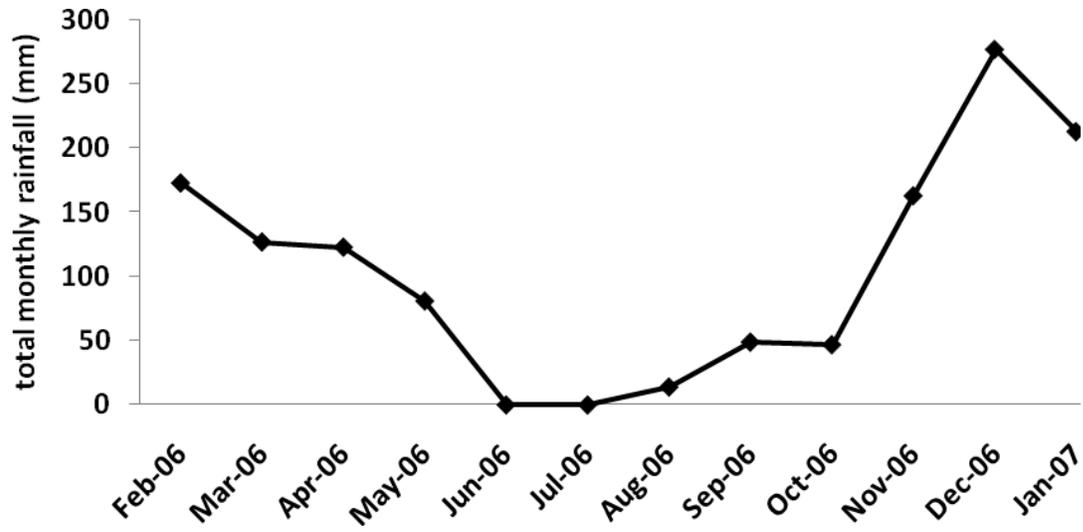


Figure 4-2. Total monthly rainfall in the study area. From L. Emmons (unpub. data).

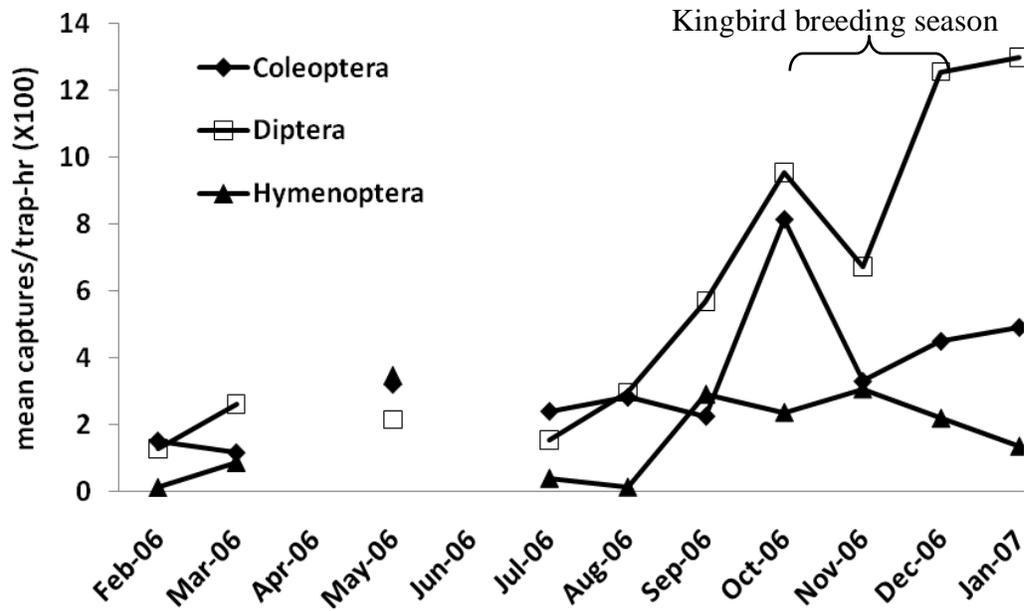


Figure 4-3. Abundance of the three most abundant Orders of arthropods at Caparú Biological Station. April and June were not sampled.

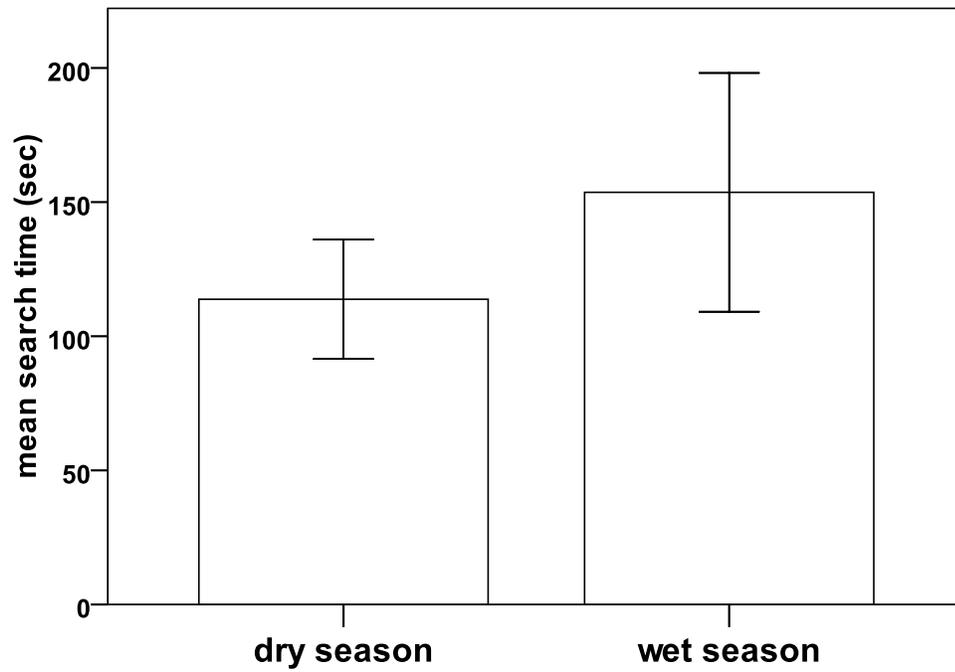


Figure 4-4. Time between sallies of Tropical Kingbirds at CBS, between seasons. The interval between the first two aerial sallies in each observation is used in the analysis. Error bars represent 95% confidence intervals. Data represent monthly mean from Oct 2005- Jul 2007.

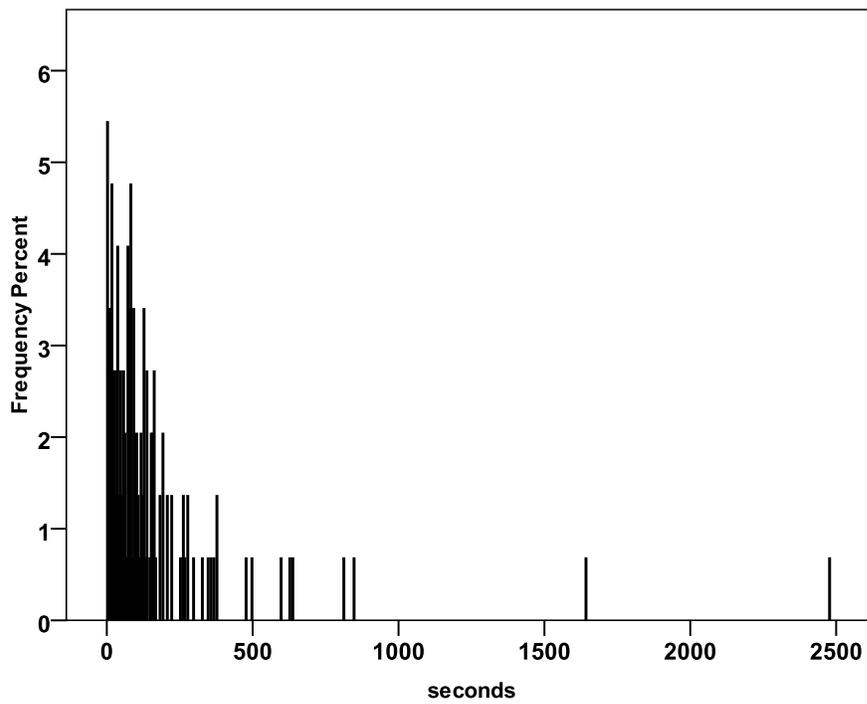
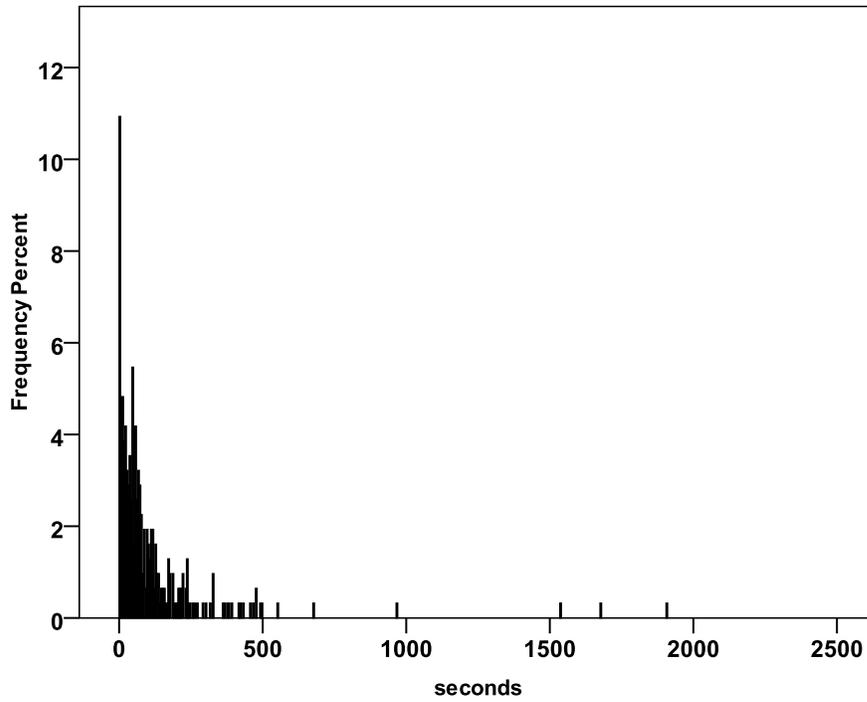


Figure 4-5. Frequency percent histogram of search time by kingbirds in dry (top) and wet seasons (bottom). Bins on the x-axis are of 5-second intervals.

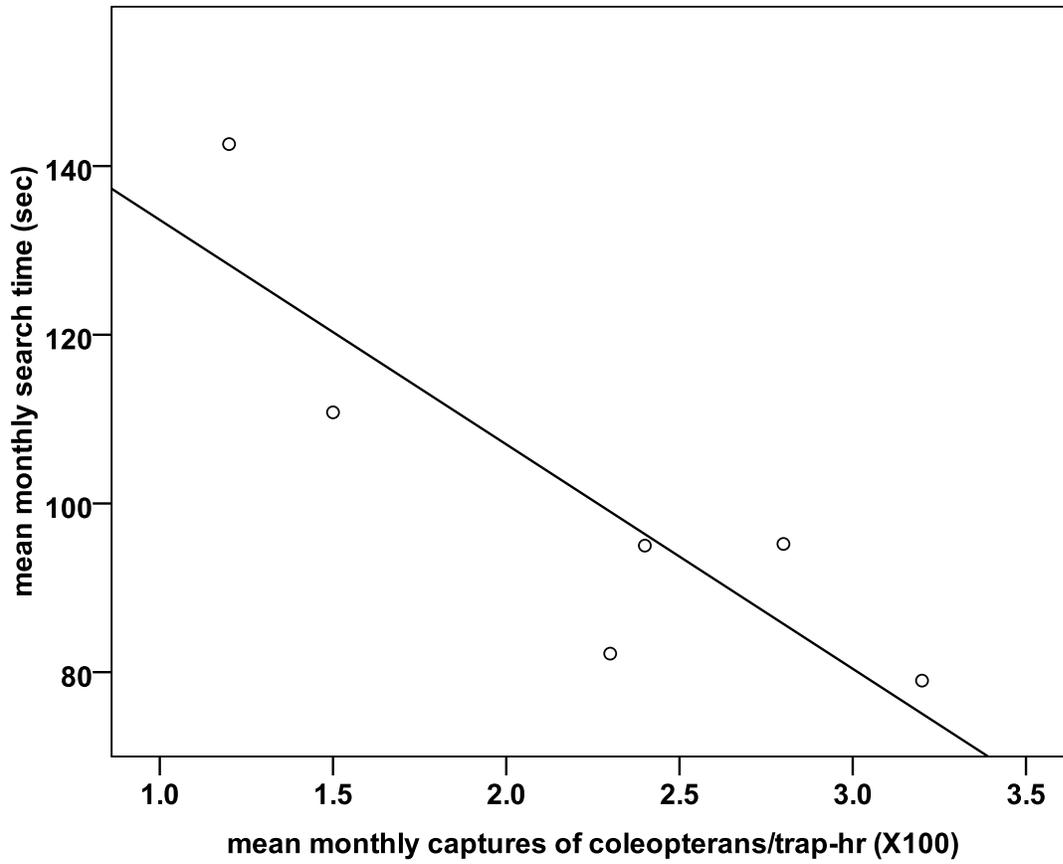


Figure 4-6. Mean monthly search time between sallies by Tropical Kingbirds as a function of mean monthly Coleopteran abundance.

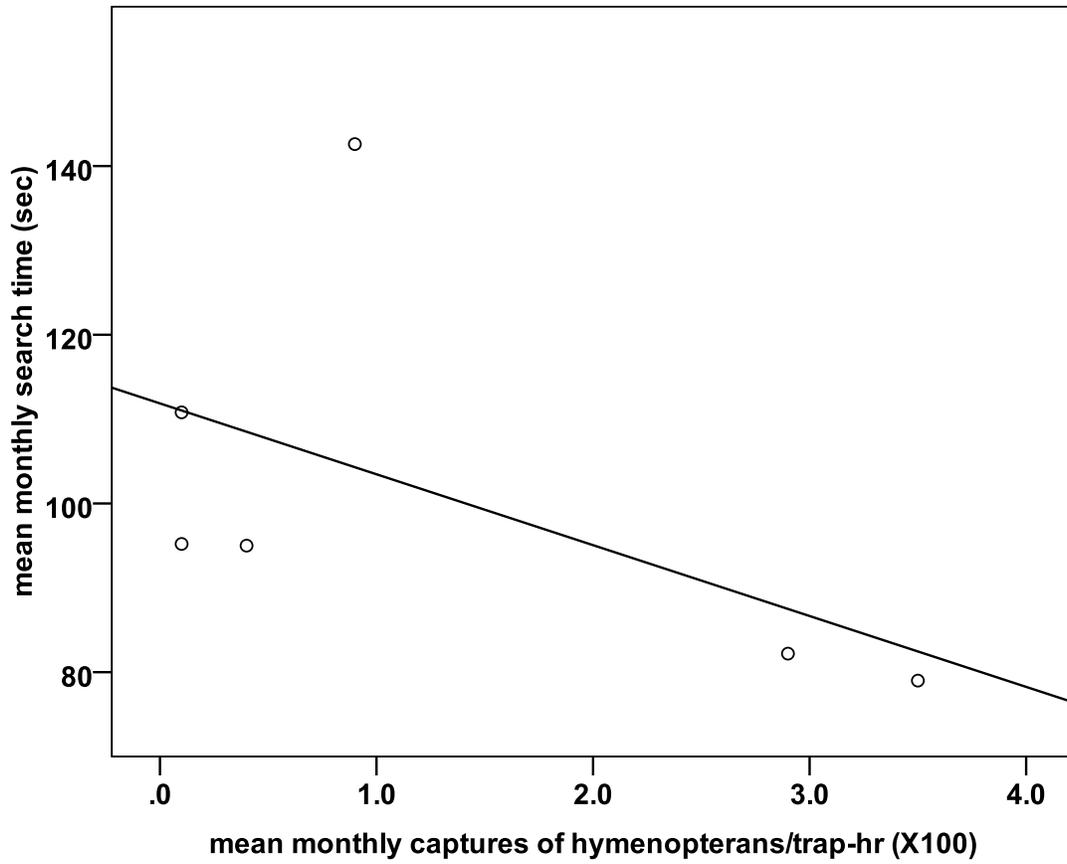


Figure 4-7. Mean monthly search time between sallies by Tropical Kingbirds as a function of mean monthly Hymenopteran abundance.

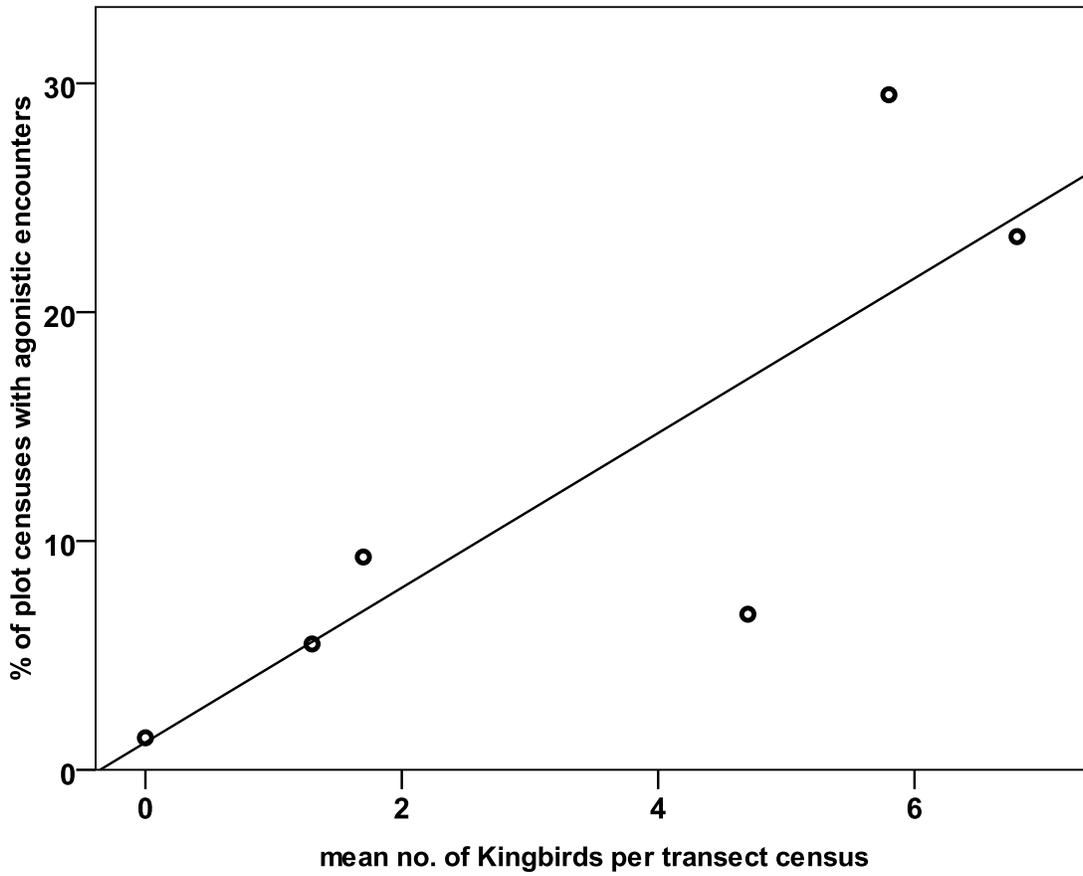


Figure 4-8. Intraspecific agonistic interactions observed on sample blocks as a function of Tropical Kingbird abundance during the dry season (February 2006 - Sep 2006). Data points represent monthly values.

CHAPTER 5  
PROXIMATE MECHANISMS UNDERLYING PARTIAL BIRD MIGRATION IN SOUTH  
AMERICA

**Introduction**

Because birds must track resources across time and space to maintain their high rates of food intake, it is not surprising that migration is a signature characteristic of bird behavior. It is a seasonal world and birds can move around relatively easily; therefore, it is no surprise that birds migrate. Yet, as with many behaviors, there is no specific “rule” to migration that applies to all populations of a migratory species or to all individuals of a population. Instead, a continuum of responses to environmental and social cues exists within and among species. The location of an individual along this continuum depends on such factors as age, sex and physical condition such that individuals of different ages and sexes may migrate different distances (e.g., Ketterson and Nolan 1976). In species with partial migration, some individuals in a population remain sedentary throughout the year, while others migrate at the completion of the breeding season (Lack 1943). Partial migration may be facultative, depending on the condition and previous history of each individual (e.g., Nice 1937, Brackbill 1956) or obligate, in which an individual is born a migrant or resident for life (e.g., Terrill and Able 1988, Berthold 1991). For the rest of this chapter, I focus only on facultative partial migration.

What determines which individuals in a partially migratory bird population migrate? Some workers have focused on ultimate processes, such as balancing selection between years (von Haartman 1968, Kalela 1954), but most research, especially recently, has sought a mechanistic understanding of how and why the costs and benefits of migration differ among individuals (e.g., Nice 1937, Gauthreaux 1982, Adriaensen and Dhondt 1990, Boyle 2008, Gillis et al. 2008). In this framework, “migrant” and “resident” are viewed as alternative strategies, available but not equally beneficial to all individuals due to individual asymmetries such as body

size (i.e., condition dependence, Swingland 1983) or because of frequency-dependence, in which an individual's likelihood of migrating depends upon the relative frequencies of dominant and subdominant individuals in the population (Lundberg 1987, 1988).

Partial migration could be especially common in South America, where more than two-thirds of Neotropical austral migrants, which migrate wholly within the continent, are characterized by having a part of their distribution where individuals always occur, usually closer to or within the tropics of the continent (Stotz et al. 1996; Fig. 1). Thus, seasonal migration within this area by some individuals could exist (i.e., partial migration). Given that there are no physical barriers to migration east of the Andes (again, opposite to the pattern in North America, where the Gulf of Mexico is an important barrier), the fact that there are so many species characterized by a lack of disjunct breeding and wintering populations is not surprising (Chesser 1994).

Three hypotheses encapsulate the mechanistic underpinnings of partial migration (reviewed by Cristol et al. 1999, Bell 2005). The Dominance hypothesis (Ketterson and Nolan 1979, Gauthreaux 1982, Lundberg 1985) states that because subordinate individuals are poor competitors, they are most likely to accept the costs associated with migration to avoid competition with dominant individuals when food becomes scarce. Dominant individuals migrate less far or not at all. The Arrival Time Hypothesis (Ketterson and Nolan 1976) states that individuals that establish territories in the spring (typically adult males) are less likely to migrate as far as individuals who do not establish territories because a shorter migration distance ensures a more rapid return to the breeding grounds and thereby provides first access to the best territories. The Body Size hypothesis (e.g., Belthoff and Gauthreaux 1991) holds that individuals with larger body sizes (typically males) are able withstand colder temperatures and

better endure food shortages than smaller individuals. Thus, larger individuals are less likely to migrate to areas of warmer temperature and higher food abundance.

I studied partial migration in Tropical Kingbirds (*Tyrannus m. melancholicus*; hereafter “kingbirds”). They are present year-round north of approximately 18° S latitude in South America and are migrant at higher latitudes to the south (Chesser 1995)(Fig. 1). I tested the Dominance and Body Size hypotheses. For the Dominance hypothesis, I predicted that (1) dominant individuals are less likely to migrate than subordinate individuals, and (2) dominant individuals have higher reproductive success than subordinate individuals. The second prediction provides a fitness advantage to non-migratory behavior. For the Body Size hypothesis, I predicted that (1) individuals of the smaller sex are more likely to be migratory than individuals of the larger sex, and (2) within a given sex, smaller individuals are more likely to be migratory than larger individuals. These predictions assume that the rationale about endurance of cold temperatures and low food availability should apply both within and between sexes.

### **Study site and Methods**

My study site was Caparú Biological Station (CBS), Department of Santa Cruz, eastern Bolivia (14° 49' S, 61° 11' W; 170 m elev.). I chose this site because I assumed partial migration would be most likely to occur just north of the southern limit of the kingbird’s permanent distribution, which is 18° S (Fig. 1). This region is characterized by pronounced wet (October-February) and dry (March-September) seasons (Chapter 4), resulting in strong seasonality of flowering and fruiting (Batalha and Martins 2004, Chapter 4) and in insect abundance (Pinheiro et al. 2002). Habitat at CBS site is primarily cerrado – grassland with scattered trees (primarily *Curatella americana*, 4-6 m height). Humid forest surrounds the site from the north, east and west. Kingbirds are present throughout the year, although they are less abundant in the dry/non-breeding season than in the wet/breeding season (Chapter 4).

Kingbirds were captured using nylon and polyester mist-nets (12 m and 18 m x 2.6 m, 36 mm and 38 mm mesh size) at locations where they were easiest to catch (e.g., near ponds). In the breeding season, most kingbirds in the population were captured at the nest when they mobbed a stuffed Purplish Jay (*Cyanocorax cyanomelas*, a common nest predator at the site), placed 10 m from the nest. All kingbirds were banded with uniquely-numbered aluminum bands provided by the Landbird Monitoring Program of the Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia as well as with up to three celluloid color bands in unique color combinations. Banding was conducted during most months of the year, intermittently from October 2004 to July 2007. Data recorded on captured birds included skull pneumatization, reproductive condition, age, fat class, molt, primary feather wear, unflattened wing chord, tail, culmen and tarsus lengths, and weight (Ralph et al. 1993, Pyle 1997). Kingbirds were sexed based upon primary notch length (Pyle 1997), although this was not useful for juveniles because their primaries do not have a notch. Kingbirds were also sexed using molecular methods described in Chapter 3, although I was not able to determine the sex of all individuals. I define kingbirds in their first year of life (prior to their first breeding season) as first-year individuals (FY), second-year individuals (SY), third-year individuals (TY), or after first-year individuals (AFY) for those of unknown age but not in their first year of life. Because the Kingbird breeding season lasts from mid-September to February, each year for the purpose of ageing begins on September 1. See Table 1 for definitions and abbreviations of individual measurements.

I use body mass and wing chord as measures of body size. Although wing chord has been criticized as a measure of body size (e.g., Freeman and Jackson 1990, Wiedenfeld 1991), I include it to determine how well it competes with body mass as a predictor of migration because

wing length is known to be a correlate of migratory tendency in other species (Haberman et al. 1991, Tellería and Carbonell 1999, Milá et al. 2008).

To detect the presence/absence of color-banded kingbirds, I divided the ~700 ha study site into 23 sample plots. I methodically searched for banded individuals on each plot, visiting most plots approximately every two weeks from February 2005 - August 2007, throughout the year. I did not visit plots from June-September of 2005. I also searched for banded birds at the site on 28 January-12 February, 2-19 March and 15-27 June, 2008. When a color-banded individual was observed, I geo-referenced its location using a GPS receiver (Garmin GPS 76), noting the date, time and color band combination. I also searched for kingbird nests in the same way as I searched for color-banded kingbirds, by thoroughly searching every sample plot. After finding nests, I attempted to band the parents and nestlings, and monitored the nests every three days until nestlings fledged or the nest failed (i.e., eggs were missing or destroyed, or nestlings that were not ready to fledge were missing), using methods described in Ralph et al. (1993). Nest monitoring was conducted during three breeding seasons (2004-2006) and I am confident I found almost all kingbird nests at the site.

I documented intraspecific agonistic encounters of kingbirds via focal observations on individuals, taking continuous data by following kingbirds and recording observations using digital voice recorders (Sony ICD-B16). I define an agonistic signaler (i.e., the individual transmitting agonistic behavior to a receiver) as an individual that signals using the crouch posture (*sensu* Smith 1966) while emitting a characteristic, sharp, repetitive call, or an individual not crouching, but emitting the agonistic call with the receiver present, usually within 20 m of the signaler. A winner in such an encounter is defined as an individual that displaces the receiver from the perch it was on and a loser is defined as the individual that was displaced. When color-

banded kingbirds were observed in such encounters, the color-band combination, location, time and date were noted.

Migration is difficult to document when based upon mark-recapture data because probability of migration is confounded with probability of survival, the probability of detection, and the probability of dispersal (Fig. 2a). Failure to observe a particular kingbird during the dry season, for example, does allow one to conclude that it migrated; it could have died, dispersed, or become less conspicuous (Kendall et al. 1997, Kendall and Nichols 2000). To tease apart probabilities of survival, dispersal, detection and migration, I used a maximum-likelihood modeling approach. Specifically, I employed the robust design with Huggins closed captures (Pollock 1982, Kendall and Nichols 1995, Kendall et al. 1995) in R (R Development Core Team 2008) package RMark (Laake and Rexstad 2008) as an interface for program MARK (White and Burnham 1999). To estimate detectability vs. temporary emigration (i.e., migration), the robust design relies on data collected when the population is assumed to be closed to immigration or emigration (i.e., “secondary sampling occasions”) within each primary sampling occasion. Between each primary occasion, the population is allowed to be open. For the purposes of this study, I built an encounter history for each color-banded kingbird in the population based upon a half-month sampling interval as the secondary sampling occasion and a one month interval as the primary sampling occasion (Table 2). Because there were an odd number of secondary sampling occasions, one primary sampling occasion (number 20) had three secondary occasions.

To model migration, the robust design estimates two independent movement parameters:  $\gamma'$ , the probability of being unavailable for both initial capture and subsequent capture (staying off the study site), and  $\gamma''$ , the probability of temporarily emigrating off the study site after capture (Fig. 2b)(Kendall and Nichols 1995, Cooch and White 2007). Because my primary

interest is to model post-breeding partial migration (i.e., emigration from the breeding grounds to elsewhere in fall), I define  $\gamma_t$  as the probability of an individual migrating from the site in month  $t$  in fall, given that it was on the site during the breeding season and  $1-\gamma_t$  as the probability of returning to the site in month  $t$  in the spring, given that it was away from the site during the winter. I defined the fall migration season as late January – early May ( $\gamma_t$  fixed at 0 for all other months) and the spring migration season as October – November ( $\gamma_t$  fixed at 1 for all other months; Table 2). Because of the small sample size relative to the number of parameters, I conducted model selection using second-order Akaike's Information Criterion ( $AIC_c$ ) (Anderson et al. 1994, Burnham and Anderson 2002).

Because the number of possible combinations of model covariates was larger than the *a priori* models I wanted to test, I first modeled the following “nuisance” parameters: 1) survival (fixed, by age and by season), 2) detectability (fixed, by season and by sampling effort), and 3) spring migration (fixed, by year and by age). I used a general model for the covariates of interest ( $\gamma_{age + sex + mass}$ ) to model nuisance parameters. I defined competing models as those within two  $AIC_c$  values of the best model, and discarded any models that did not estimate all parameters. The best survival model, which was used in all subsequent models, had an additive effect of capture, age at capture and season. The best detectability model, which was also used in all subsequent models, had a seasonal effect of sampling effort (person-hours spent searching for color-banded individuals). The two best spring migration models which were included in subsequent modeling represented an effect of returns by banded nestlings (higher than that of other kingbirds), and an effect of nestling returns with an additive year effect.

Because the study period spanned four migration seasons (Table 2), I also tested for a year effect on the probability of partial migration in the population, and found high support for an

additive effect of year (Fig. 3). I therefore include an additive effect of year in all subsequent models. I modeled fall migration ( $\gamma''$ ) using these effects of nuisance parameters on the migration model. In order to include all potentially useful models during subsequent model selection, I define competing models as those within four  $\Delta AIC_c$  values.

## Results

To confirm that partial migration itself is a highly supported model, I first tested for the existence of partial migration in the population. There was very strong support for partial migration in this population, as the  $\Delta AIC_c$  of the model with no migration was about 147 (Table 3). The probability of migration demonstrates notable variation between years, with the highest probability of migration in the population in 2005 and the lowest in 2006 (Fig. 3).

Model selection produced nine competing models with  $\Delta AIC_c$  values  $< 4$ . Of these, the two best models include an interactive effect of age and sex, with variations of effects of year and spring migration (Table 4). Females and individuals of unknown sex are both more likely to migrate in their first year of life than as adults, while adult males are more likely to migrate than FY males (Fig. 4). I attempted to model an interactive year effect in the best model, but MARK could not estimate all parameters. Most of the remaining models include effects of producing fledglings or successful nests, with the probability of migrating diminishing as the number of fledglings or nests produced increases (Fig. 5). When an interactive effect of year was included for this model, MARK was not able to estimate all parameters. The last competing model includes the interactive effect of sex and body mass, in which smaller females and larger males are more likely to migrate (Table 4 and Fig. 6). I also tried to model an interactive effect of year in this model, but it was not among the competing models.

## Dominance Hypothesis

I was not able to assign a dominance score (number of wins divided by the total number of interactions; Poisbleau et al. 2006) to individual kingbirds because most banded kingbirds that were observed in intraspecific encounters were only seen in one encounter. However, I found evidence that dominance in the population is age- and sex-dependent. AFY individuals (including SY individuals) were more likely to be winners than losers in intraspecific encounters ( $\chi^2 = 5.143$ ,  $P = 0.023$ ) and FY individuals were rarely observed in any agonistic encounters (Fig. 7). Adult females were winners as often as they were losers, but males were more likely to win than lose in intraspecific agonistic encounters ( $\chi^2 = 5.444$ ,  $P = 0.020$ ; Fig. 8). I never observed an encounter in which a female signaled to a male, but I did observe on five occasions a male signaling to a female. I therefore use age and sex as proxies for dominance in the model set for testing the dominance hypothesis, with older kingbirds dominant over younger kingbirds and males over females. The three best models indicate that younger females are more likely to migrate than older females but that older males are more likely to migrate than younger males (Table 4), such that the effects of dominance on probability of migration may only apply to females. In short, dominance does not provide a full explanation of partial migration.

Results of nest monitoring demonstrated a nest failure rate of 83% over three seasons. Although a limited number of Kingbirds were successful, reproductive success was a covariate among the most competitive models (Table 4), demonstrating a negative relationship between reproductive success and the probability of migration (Fig. 5). Results of nest monitoring suggest that reproductive success of kingbirds increases with age, since the average number of nests built per individual was similar across age groups, but the mean number of nestlings increased from SY to TY parents and no known SY or TY parents produced any fledglings (Fig. 9). That reproductive success is positively correlated with age, and age is positively correlated

with dominance (i.e., most adults were winners in intraspecific aggressive encounters) supports the prediction that dominant individuals have higher reproductive success. I attempted to model the additive and interactive relationship between sex and reproductive success (i.e., number of successful nests or number of nestlings fledged), but MARK was not able to estimate all the parameters.

### **Body Size Hypothesis**

Adult males (SY or older) have a significantly larger body mass ( $P = 0.037$ ), wing chord ( $P < 0.0001$ ), and bill length ( $P = 0.030$ ) than adult females (Table 5). Likewise, adults (SY or older) are significantly larger ( $P < 0.0001$ ) in these three measures than FY individuals (Table 6). Overall, adult males are the group with the largest body mass in the population (Fig. 10). Given that the best model in my study is an interactive effect between age and sex, with the probability of migration by adult males higher than that of adult females or FY males (Fig. 4), I find no general support for the prediction that individuals of the smaller sex are more likely to migrate than individuals of the larger sex.

Only one model with body mass or wing chord was among the competing models and it was the lowest of the competing models (Table 4). This model demonstrates a negative relationship between mass and migration probability for females and individuals of unknown sex, and a strong positive relationship between body mass and migration for males (Fig. 6). Although it is not as strong as models with the effects of age, sex and reproductive success, it was 12  $\Delta AIC_c$  above the model with year effect only. Because larger males are more likely to migrate than smaller males, these results do not support the prediction that within a sex, smaller individuals are more likely to migrate than larger individuals.

## Discussion

Overall, model selection points to the existence of partial migration in the population, and that it does not conform to predictions of either the Dominance or the Body size hypotheses. Rather, the probability of migration in this population appears to be related in a complex way to age, sex and previous reproductive success.

Among the competing models predicting which individuals migrate at my site, the best model is that of juvenile females being the most likely to migrate relative to individuals in other sex and age classes (Table 4 and Fig. 4). Because males are heavier than females (Fig. 10), I found no general support for the prediction that the smaller sex is more likely to migrate. The best model also indicates that adult males, which are also the heaviest individuals in the population (Fig. 10), are more likely to migrate than FY males. Additionally, another top model indicates that body mass is positively related to probability of migration in males (Fig. 6). I therefore did not find general support the prediction that within a sex, smaller individuals are more likely to migrate.

Similar to previous studies on other passerine species (Arcese and Smith 1985, Zink and Watt 1987, Piper and Wiley 1989, Rogers et al. 1989, Keys and Rothstein 1991), I found evidence that older kingbirds are dominant to younger individuals and that as adults, males are dominant over females (Figs. 7 and 8). Indeed, given the fact that FY individuals rarely interact with adults (Fig. 7), dominance status of a kingbird may be determined relatively quickly early in life. Age and sex are thought to influence migratory status in other species because they affect competitive ability and/or physiological tolerance (Ketterson and Nolan 1983; Cristol et al. 1999) and several studies on North-temperate breeding birds have found support for age, sex, and social rank as predictors of partial migration (e.g., Nice 1937, Gauthreaux 1982, Adriaensen and Dhondt 1990). I found that a class of dominant individuals (adult males) was more likely to

migrate than subordinate individuals of the same sex (FY males), whereas the Dominance hypothesis predicts that subdominant individuals are most likely to migrate. I found evidence only for females that dominant individuals are less likely to migrate than subordinates.

I found support for dominant kingbirds to have higher reproductive success than subordinates (Fig. 9), in spite of an overall high rate of nest failure in the population (i.e., 83%). I also found good support for a negative relationship between the probability of migration and reproductive success (Table 4 and Fig. 5). The negative relationship between the probability of migration and age of females (Fig. 4), and the increase in reproductive success with age (Fig. 9) suggests that as females age and become more reproductively successful, their probability of migrating decreases. In contrast, the increased probability of migration with age in males (Fig. 4) suggests that an increase in reproductive success with age for males plays less of a role in determining whether they migrate. Thus, the idea that there is a difference in fitness between migrants and residents, with migrants making the best of a bad situation (reviewed by Lundberg 1988) likely does not apply to male kingbirds. It may be that, for an adult male kingbird, there is relatively little risk of failing to acquire a female and breeding territory upon returning from the wintering grounds.

The strong relationship between nest predation and tendency to migrate may have also played a role in the evolution of migration. Nest predation rates in tropical latitudes are relatively high (in many but not all cases) compared to those at temperate latitudes (reviewed by Martin 1996). For many birds, an urge to escape areas with chronically high nest predation rates may have been one of the selective forces that first promoted migration.

Thus, similar to some previous research on other species (Rogers et al. 1989, Boyle 2008), I found no conclusive evidence for the Dominance hypotheses for the Tropical Kingbird.

Dominance has been shown to be positively correlated with survival (Arcese and Smith 1985, Koivula et al. 1996, Piper 1997, Schubert et al. 2008) but in kingbirds, such benefits may only apply to adult females. The only other study I know of that found a higher probability of migration by older males than younger males in a partially migratory population is that of Boyle (2008), who found that older male White-ruffed Manakins (*Corapipo altera*) were more likely to migrate than younger males, possibly because by not migrating, younger males may have a chance to establish themselves in a lek during the non-breeding season.

Taken together, model selection results suggest that partial migration in kingbirds at my study site is regulated in a sex-specific manner that likely involves dominance, reproductive success and body size. FY females and adult males, the two groups of kingbirds most likely to migrate, likely do so as a result of different selective pressures on each of them. The high probability of migration by FY females is clearly predicted by the Dominance and Body Size hypotheses but the higher migration probability by adult males than FY males or adult females does not follow predictions.

An implicit assumption of all theory on partial migration is that the non-breeding season represents a period of limited resources and/or harsh climatic conditions, such that some individuals of a population are forced to temporarily emigrate. At issue is why adverse conditions affect individuals differently. I found a dramatic decline in arthropod prey for kingbirds in the dry/non-breeding season relative to the wet/breeding season (Chapter 4). This is noteworthy because food is often a limiting resource for birds (Lack 1954, Wiens 1989), especially in winter (e.g., Alerstam and Hogstedt 1982, Lovette and Holmes 1995, Brown and Sherry 2006). Kingbirds are primarily insectivores, with > 95% of their foraging for arthropods consisting of aerial sallies (Fitzpatrick 1980, Cintra 1997, Gabriel and Pizo 2005). At my site,

they used this foraging maneuver throughout the year, usually to capture coleopterans (Chapter 4 and unpub. data). Coleopterans were not only significantly more abundant at the study site in the wet season than in the dry season (i.e., the non-breeding season), but they significantly decreased in abundance at the end of the breeding season (i.e., when Kingbirds began to leave the site). Furthermore, I found that the search time between aerial sallies by kingbirds decreased whenever more flying coleopterans were available during the dry season (Chapter 4), suggesting that the kingbirds are food limited. Within this context, it is not surprising that partial migration exists in this population.

I propose that because the dry season at the site is characterized by such drastically low levels of insect food abundance (Chapter 4), adult males, because of their body size, are at more risk of starvation due to food limitation than are FY males or adult females, which are generally smaller. Smaller individuals have higher energetic demands than adults on a per-gram basis because of their larger surface-to-volume ratio and because their mass-specific metabolic rate is higher (Calder 1974). However, because of their smaller size, their *total* energy demands are lower than those of larger conspecifics. Larger individuals do not benefit from a low surface to volume ratio because non-breeding season temperatures at this latitude are not severely cold. In effect, a threshold may be reached in which individuals with larger bodies and therefore higher total energetic demands may have to migrate away to find sufficient food.

Adult males may not risk losing a breeding opportunity by migrating if upon their return in the spring, they can quickly re-assert their dominance status. For example, previous research on dominance in the well-studied White-throated Sparrow (*Zonotrichia albicollis*), a migrant in North America, has shown that dominance is established during a brief period early in life and may permanently determine that individual's dominance status throughout its lifetime (e.g., Piper

and Wiley 1989, Piper 1995). Subordinate members of the dominance hierarchy recognize dominant individuals, such that dominant individuals remain dominant (Wiley 1999).

Additionally, site familiarity in this species is positively correlated with dominance (e.g., Snell-Rood and Cristol 2005). Adult male kingbirds, which have for the most part spent their first non-breeding season at the site and have likely become familiar with it, may therefore be free to choose to stay or migrate, independent of the constraints of a dominance hierarchy. In contrast, young birds may need to stay to acquire this same site familiarity. Additionally, migrating north into Amazonia may not be very risky because there are no obvious barriers to migration at these latitudes. Indeed, intracontinental migration may not pose a higher risk to survival than residency, as has been shown in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) in North America (Morton 2002). FY males, on the other hand, may be less likely to migrate, since prior residency can increase one's chances of being dominant (e.g., Cristol et al. 1990, Holberton et al. 1990) when the next breeding season begins. In contrast, FY females may be more likely to migrate than FY males because they do not need to compete for a breeding territory in the following breeding season.

I suggest two reasons why previous research has not found that larger males are more likely to migrate from a partially migratory population. First, most partial migration research has been conducted in the northern hemisphere, mostly at latitudes  $> 35^{\circ}$  N, where study species have been primarily granivores (e.g., Song Sparrow, *Melospiza melodia*; Nice 1937; Dark-eyed Junco, Ketterson and Nolan 1979; House Finch, *Carpodacus mexicanus*; Belthoff and Gauthreaux 1991) or generalists (e.g., European Robin, *Erithacus rubecola*; Biebach 1983; European Blackbird, *Turdus merula*; Lundberg 1985). Their food resources are generally found in patches, where they forage in flocks in winter, and access to these patches of food is

determined by competitive ability within the flock. Thus, large, dominant individuals acquire more food than subdominants in these situations (Piper 1997, Leary et al. 1999). As a result, poor competitors must migrate away because they cannot compete for food with larger or older individuals (e.g., Lundberg 1985).

In contrast, kingbirds specialize on flying insects, which are not concentrated in patches but rather are dispersed throughout the airspace. As a result, Kingbirds do not forage in flocks at any time of year (pers. obs.), and they likely do not deplete food resources around the perches from which they forage (Fitzpatrick 1981). Thus, for a kingbird, an ability to compete directly with conspecifics for available food during the non-breeding season may not matter. If the overall availability of flying insects is too low, adult males may simply not be able to sustain the energetic requirements of their larger bodies. In contrast, seeds are available in the winter in the mid-latitudes of North America and Europe except under extreme conditions such as heavy snow cover, such that granivores and generalists can get at them if they can successfully compete with flock members.

Second, winter temperatures at North temperate latitudes where most partial migration has been studied (i.e., northern North America and Europe) are generally much lower than at the latitude where my study took place ( $15^{\circ}$  S). It has been suggested that bird migration in the Northern Hemisphere may be primarily driven by temperature variation, but that in the milder and drier Southern Hemisphere it may be more tightly linked to seasonal variation in precipitation (Chesser 1994, Dingle 2008). Indeed, my study site is characterized by high variation in precipitation, with an average daily rainfall of 6.3 mm (SD  $\pm$ 13.6) from mid-September to mid-February and a daily average of 2.9 mm ( $\pm$ 9.3) during the rest of the year (data from October 2004 to August 2007). Variation in temperature at my site, on the other hand, is

extremely low. The average daily temperature from mid-September – mid-February (the wet season) is 27.5° C ( $\pm 13.8$ ), whereas the average daily temperature during the rest of the year is 26.4° C ( $\pm 9.2$ ). Minimum daily temperatures in the non-breeding season at my site are 10-15° C (unpub. data), while at latitudes where most previous research on partial migration has been conducted (i.e.,  $> 35^\circ$  N latitude), minimum daily non-breeding season temperatures are regularly well below freezing. The ability of a bird to remain near its North temperate breeding grounds may depend more on its ability to withstand cold temperatures, in which case a large body size may be desirable (due to the lower surface area to volume ratio), given sufficient food to maintain a high intake rate. As stated above, the fact that most partial migrants studied to date are feeding on food resources such as grains that are available in winter may permit the dominant individuals in a flock to acquire enough food (e.g., Leary et al. 1999). For a kingbird at my study site, however, where minimum non-breeding season temperatures are much warmer than at North temperate latitudes, large body size may not be advantageous but rather a liability, if food (i.e., flying insects) is limited. Notably, the year with the lowest population-wide probability of migration (i.e., Feb-May 2006; Fig. 3), was also the one in which the preceding wet season (i.e., Oct 2005-Feb 2006) had the most rainfall of all years of the study (unpub. data).

Kingbirds steadily increase in size to the south (Chapter 3), where all individuals are migratory south of 18° S. Thus, a gradient may exist in migration tendency: at  $> 18^\circ$  S, there are so few flying insects in winter that all kingbirds must migrate away for winter, irrespective of body size. At slightly lower latitudes such as those at my study site, only large kingbirds must migrate away because enough food resources are available smaller individuals to stay throughout the non-breeding season. Likewise, in Australia, migratory Silvereyes (*Zosterops lateralis*) are

primarily insectivorous, and their movements are likely determined in large measure by insect availability at different latitudes (Chan 2005).

Taken together, the kingbird's specialization on flying insects, the strong seasonality in insect availability, and the higher probability of males - especially large ones - to migrate suggest that partial migration of the Tropical Kingbird at the southern edge of Amazonia is mediated through food availability in an age- and sex-specific manner. In most of the Southern Hemisphere, a milder climate predominates due the smaller ratio of land area to ocean area relative to that of the Northern Hemisphere. Here, the decision to migrate (or how far to migrate; Chesser 1994) may be determined more by dry rather than cold non-breeding seasons, although at higher latitudes, temperature may nevertheless be a strong influence (e.g., Chesser 2005).

As found by recent studies of other partial migrants (Boyle 2008, Gillis et al. 2008), the decision by kingbirds to migrate is likely condition-dependent. However, although some studies have found support for the Body Size hypothesis (e.g., Belthoff and Gauthreaux 1991, Boyle 2008) and others for the Dominance hypothesis (e.g., Smith and Nilsson 1987), I found no conclusive evidence for either in Tropical Kingbirds. Similarly, Ketterson and Nolan (1982, 1983, 1985) and Cristol et al. (1999) concluded that dominance, arrival time, and body size were all inadequate predictors of where Dark-eyed Juncos (*Junco hyemalis*) overwinter.

Given the dozens of publications to date devoted to testing partial migration theory, it is becoming evident that existing theory is not likely to be very generalizable across species. One reason for this is that bird migration research has principally been conducted at North-temperate latitudes and less so in the tropics or South Temperate latitudes (Jahn et al. 2004). Notable exceptions are Boyle's (2008) work in Costa Rica, and extensive research on the Silvereye (*Zosterops l. lateralis*) in Australia (reviewed by Chan 2001, 2005). We still know very little

about the underpinnings of partial bird migration outside of North America and Europe, or even how widespread partial migration is in the Southern Hemisphere or the tropics. Partial migration may be an even more common strategy in the tropics than at temperate latitudes, and according to Berthold (2001, pg. 8) it is, “highly likely that partial migration is a widespread phenomenon there . . .” Further, interdisciplinary research at different latitudes and across species is necessary to unveil the mechanisms underlying the decision to migrate because that decision is likely affected by such variables as habitat, latitude, feeding guild, interspecific competition and climatic variation between years.

Table 5-1. Definitions of model variables. Morphological, reproductive and demographic parameters correspond to each individual kingbird.

Model notation	Description
age	Three categories: nestling, FY (i.e., First-year individual, an individual in its first year of life; year begins on 1 Sep of every year), SY (second-year individual), TY (third-year individual), and AFY (i.e., individual whose exact age is not known but is not a FY)
fledged	Number of nestlings a parent fledged during study period. In no case did a kingbird produce a successful nest in more than one breeding season.
fledgedbin	Binary variable: individual fledged at least one nestling or not during the study period
mass	Body mass, measured in grams
nests	Number of successful nests (i.e., those which produced at least one fledgling) produced by the individual during the study period
p	Probability of re-sighting or recapturing a color-banded individual after initial capture (i.e., detectability)
sex	Three categories: male, female, unknown
year	A 12 month period, used as a categorical variable for modeling purposes

Table 5-2. Definitions of gaps between primary intervals for purposes of modeling migration using the robust design.

Primary interval gap	Year	Spring migration		Fall migration		
		Immigration permitted?	Year label in MARK	Emigration permitted?	Month label in MARK	Year label in MARK
late Oct-early Nov	2004	-		No		
late Nov-early Dec	2004	No		No		
late Jan-early Feb	2005	No		Yes	1	1
late Feb-early Mar	2005	No		Yes	2	1
late Mar-early Apr	2005	No		Yes	3	1
late Apr-early May	2005	No		Yes	4	1
late May-late Sep	2005	No		No		
early Oct-late Oct	2005	Yes	1	No		
early Nov-late Nov	2005	Yes	1	No		
early Dec-early Jan	2005/2006	No		No		
late Jan-early Feb	2006	No		Yes	1	2
late Feb-early Mar	2006	No		Yes	2	2
late Mar-early Apr	2006	No		Yes	3	2
late Apr-early May	2006	No		Yes	4	2
late May-early Jul	2006	No		No		
late Jul-early Aug	2006	No		No		
late Aug-early Sep	2006	No		No		
late Sep-early Oct	2006	Yes	2	No		
late Oct-early Nov	2006	Yes	2	No		
early Dec-late Dec	2006	No		No		
late Jan-early Feb	2007	No		Yes	1	3
late Feb-early Mar	2007	No		Yes	2	3
late Mar-early Apr	2007	No		Yes	3	3
late Apr-early May	2007	No		Yes	4	3
early Jun-late Jun	2007	No		No		
early Jul-late Jul	2007	No		No		
early Aug-late Jan	2007/2008	Yes	3	No		
early Feb-early Mar	2008	No		Yes	2	4
late Mar-early Jun	2008	No		Yes	4	4

Table 5-3. Model selection results for probability of partial migration in the population. A total of five models were run. Model effects are:  $\gamma''$  = fall migration,  $\gamma'$  = spring migration,  $\gamma''_{\text{zero}}$  = fall migration fixed at zero,  $\gamma'_{\text{zero}}$  = spring migration fixed at zero.

Model	Deviance	K	$\Delta\text{AIC}_c$	$\Delta\text{AIC}_c$ weight
$\gamma''_{\text{year}}, \gamma'_{\text{nestling}}$	7533.73	13	0.00	0.666
$\gamma''_{\text{year}}, \gamma'_{\text{nestling} + \text{year}}$	7531.02	15	1.38	0.334
$\gamma''_{\text{zero}}, \gamma'_{\text{zero}}$	7693.30	7	147.38	0.000

Table 5-4. Model selection results for the best models (i.e.,  $\Delta\text{AIC}_c < 4$ ) of fall migration. The lowest  $\text{AIC}_c$  value was 6632.98.

Model	Deviance	K	$\Delta\text{AIC}_c$	$\Delta\text{AIC}_c$ weight
$\gamma''_{\text{age} \times \text{sex} + \text{year}}, \gamma'_{\text{nestling}}$	7507.498	18	0	0.248921
$\gamma''_{\text{age} \times \text{sex} + \text{year}}, \gamma'_{\text{nestling} + \text{year}}$	7504.068	20	0.691	0.176203
$\gamma''_{\text{fledged} + \text{year}}, \gamma'_{\text{nestling}}$	6442.229	14	0.9387	0.155678
$\gamma''_{\text{fledgedbin} + \text{year}}, \gamma'_{\text{nestling}}$	6443.336	14	2.0453	0.089522
$\gamma''_{\text{nests} + \text{year}}, \gamma'_{\text{nestling}}$	6443.447	14	2.1564	0.084685
$\gamma''_{\text{fledged} + \text{year}}, \gamma'_{\text{nestling} + \text{year}}$	6439.633	16	2.4379	0.073566
$\gamma''_{\text{fledgedbin} + \text{year}}, \gamma'_{\text{nestling} + \text{year}}$	6440.779	16	3.5832	0.041494
$\gamma''_{\text{nests} + \text{year}}, \gamma'_{\text{nestling} + \text{year}}$	6440.922	16	3.7262	0.03863
$\gamma''_{\text{sex} \times \text{mass} + \text{year}}, \gamma'_{\text{nestling}}$	6437.002	18	3.9152	0.035147

Table 5-5. Mean morphological measurements of adult Tropical Kingbirds from the study population (i.e., those observed at least once after color-banding), by sex. Numbers in parentheses represent standard deviation.

Trait	Adult males	N =	Adult females	N =	t =	P =
Body mass	41.31 (3.158)	45	39.91 (3.189)	48	2.117	0.037
Wing chord	112.83, (2.572)	35	107.81 (2.202)	36	8.848	< 0.0001
Bill length	17.50 (0.760)	37	17.16 (0.6211)	43	2.215	0.030

Table 5-6. Mean morphological measurements of first-year and first-year adult (i.e., second-year or older) Tropical Kingbirds from the study population (i.e., those observed at least once after color-banding). Numbers in parentheses represent standard deviation.

Trait	First-year	N =	Adults	N =	t =	P =
Body mass	32.72 (4.209)	64	40.47 (3.092)	120	-12.980	< 0.0001
Wing chord	105.05 (2.539)	21	110.05 (3.373)	93	-7.640	< 0.0001
Bill length	14.15 (3.782)	42	17.35 (0.712)	95	-5.435	< 0.0001

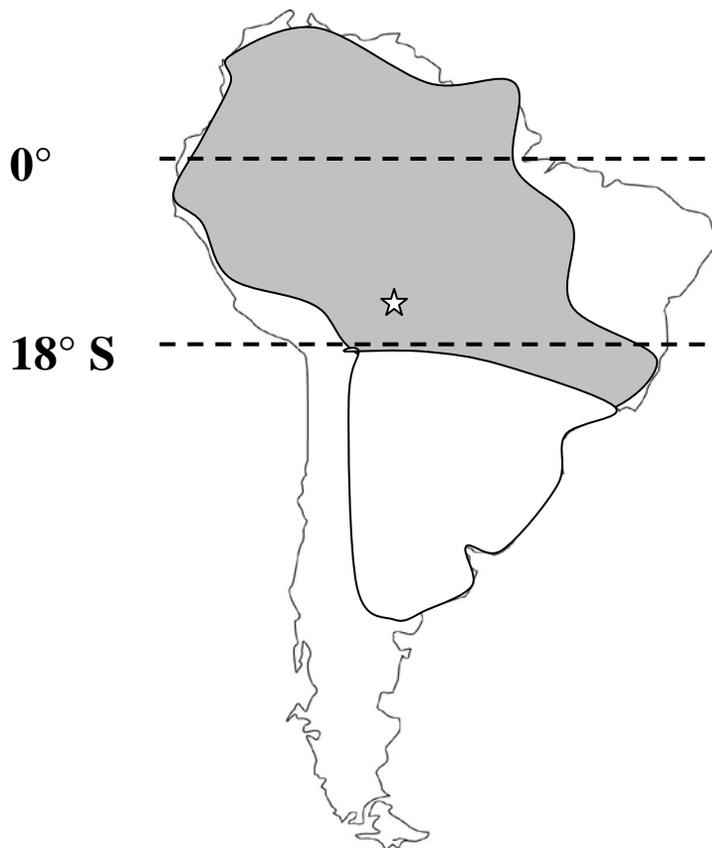
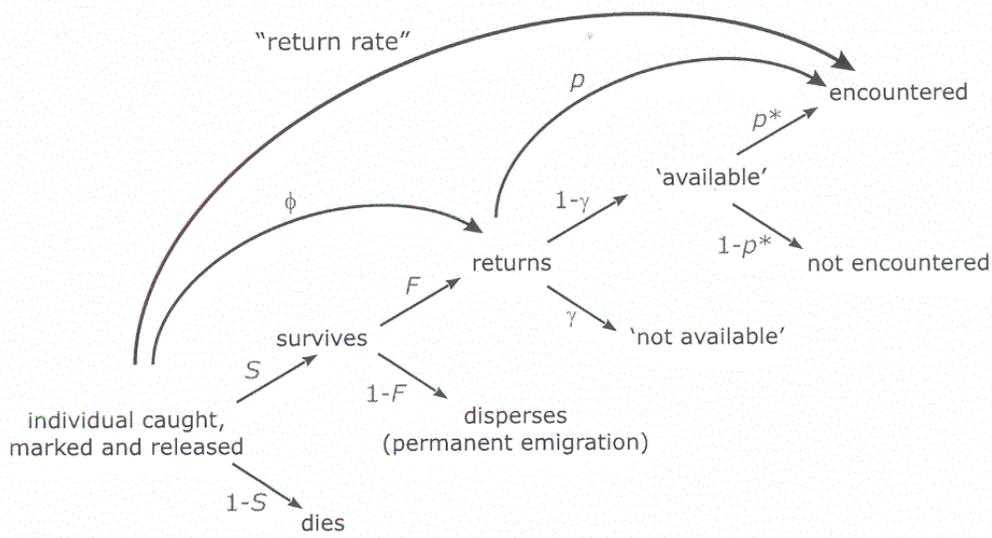
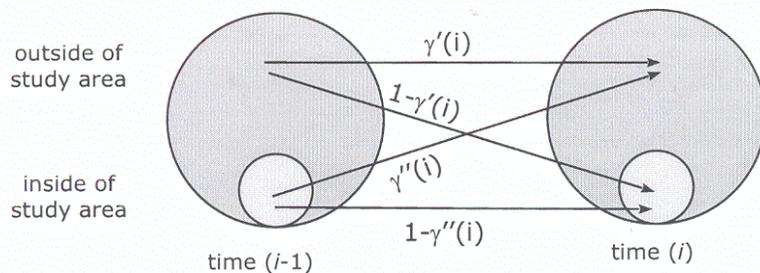


Figure 5-1. Distribution of Tropical Kingbird in South America. Gray polygon represents the approximate year-long distribution of the species. The white polygon south of 18° S represents the summer-only distribution. Star represents location of Caparú Biological Station. Adapted from Chesser (1995).

a.



b.



parameter	definition
$\gamma'_i$	the probability of being <i>off</i> the study area, unavailable for capture during primary trapping session ( $i$ ) given that the animal <i>was not</i> present on the study area during primary trapping session ( $i - 1$ ), and survives to trapping session ( $i$ ).
$\gamma''_i$	the probability of being <i>off</i> the study area, unavailable for capture during the primary trapping session ( $i$ ) given that the animal <i>was</i> present during primary trapping session ( $i - 1$ ), and survives to trapping session ( $i$ ).

Figure 5-2. a) Visual representation of the parameters in the robust design;  $\theta$  = apparent survival;  $S$  = true survival,  $\gamma$  = probability of temporarily emigrating,  $p$  = probability of observer encountering marked individual, and b) Transition probability parameters within the robust design. From Cooch and White (2007).

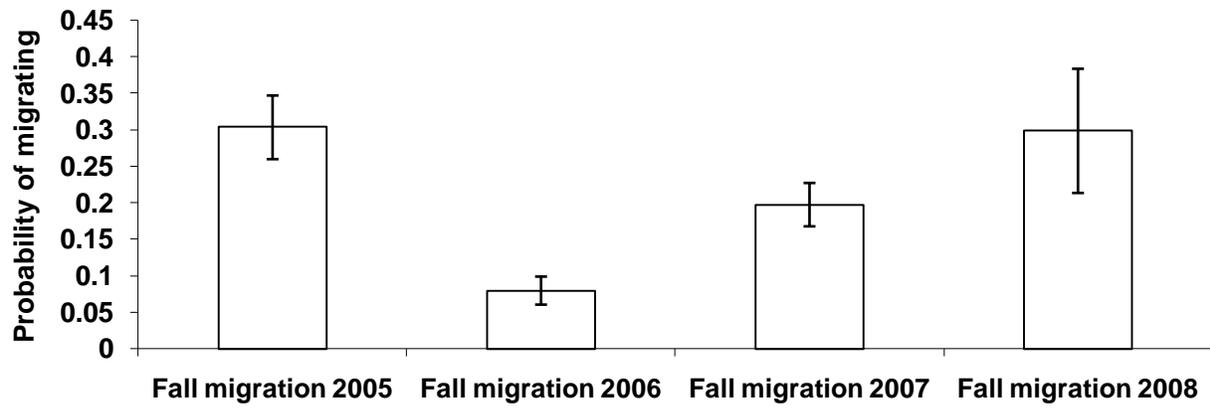


Figure 5-3. Monthly probability of fall migration in a partially migratory Tropical Kingbird population, by year. Error bars represent standard error.

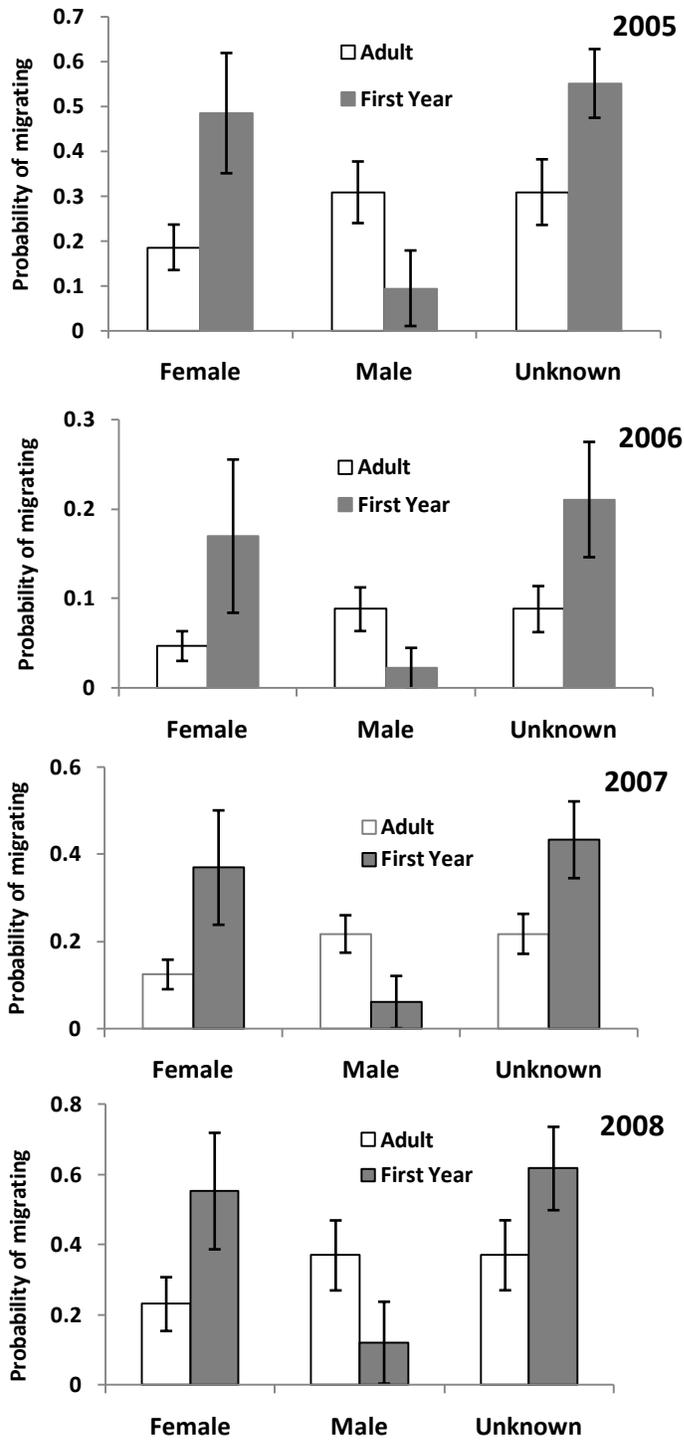


Figure 5-4. Monthly probability of fall migration as a function of age and sex in a Tropical Kingbird population, by year. Error bars represent standard error.

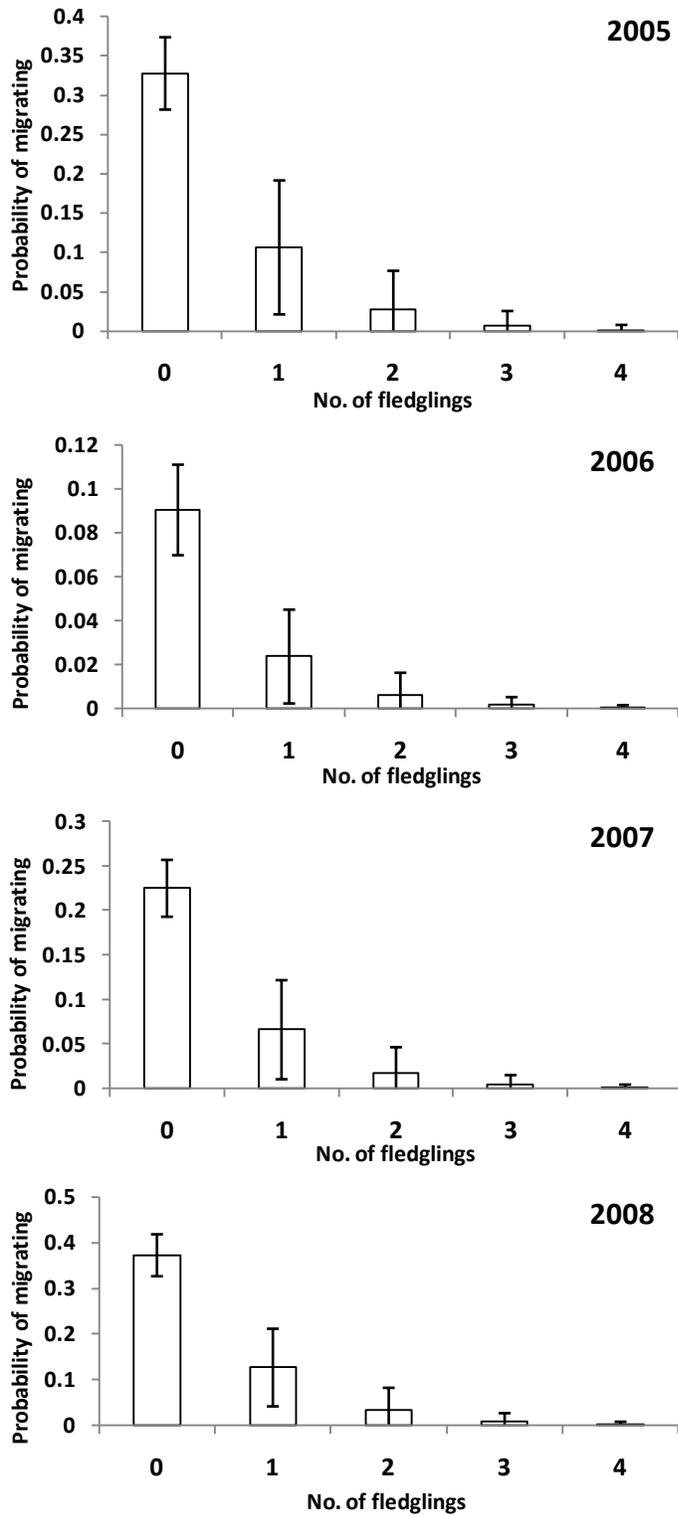


Figure 5-5. Monthly probability of fall migration of Tropical Kingbirds as a function of number of fledglings produced, by year. Error bars represent standard error.

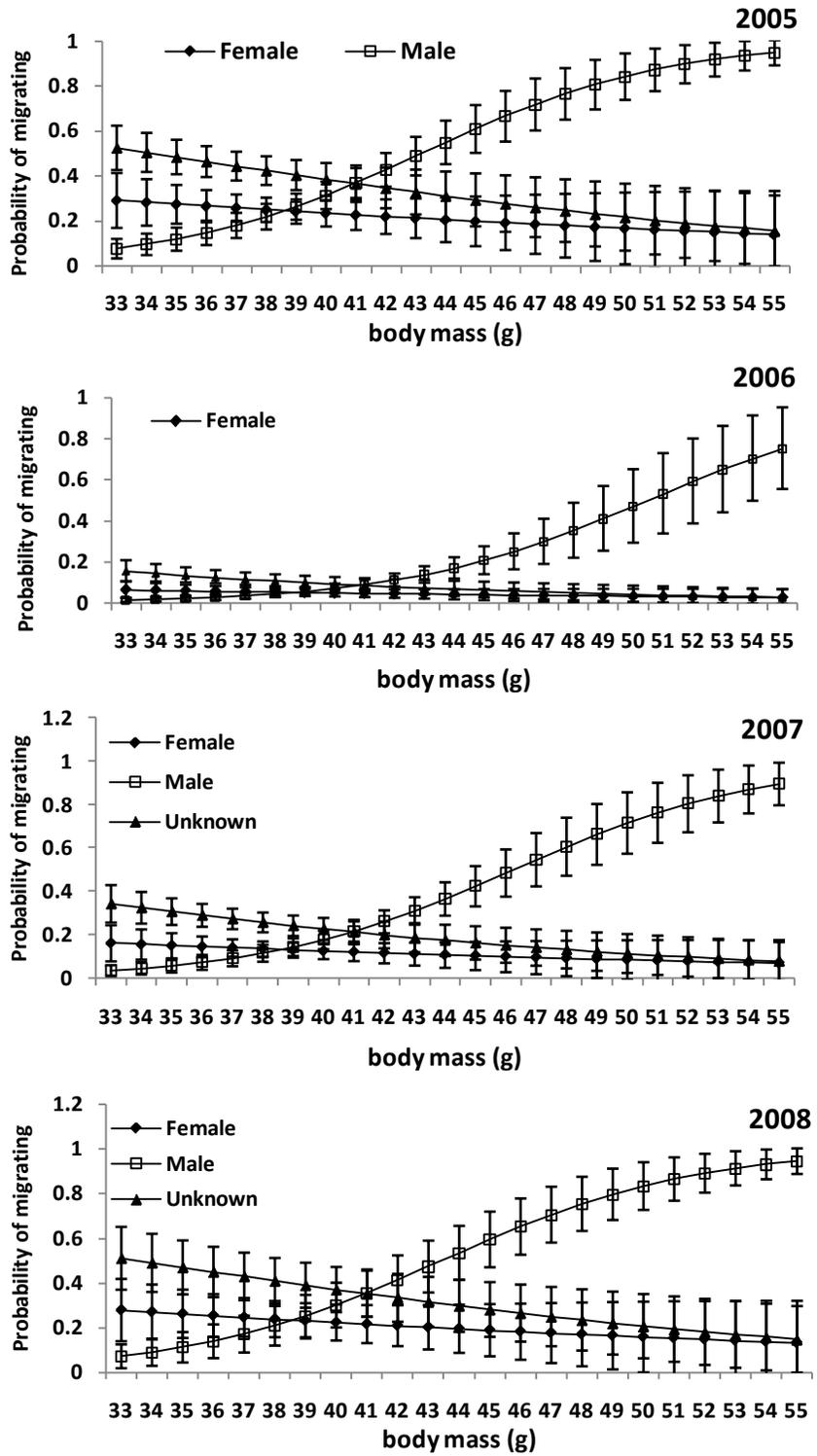


Figure 5-6. Monthly probability of fall migration as a function of body mass and sex of Tropical Kingbirds. Error bars represent standard error.

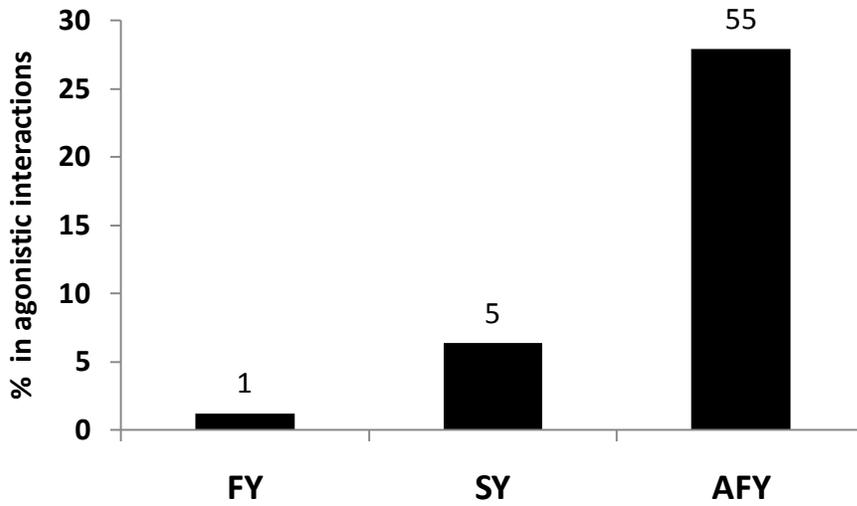


Figure 5-7. Percent of each age group of Tropical Kingbirds originally banded that were observed in agonistic interactions. SY = Second-year individual, TY = Third-year individual, AFY = After first-year individual.

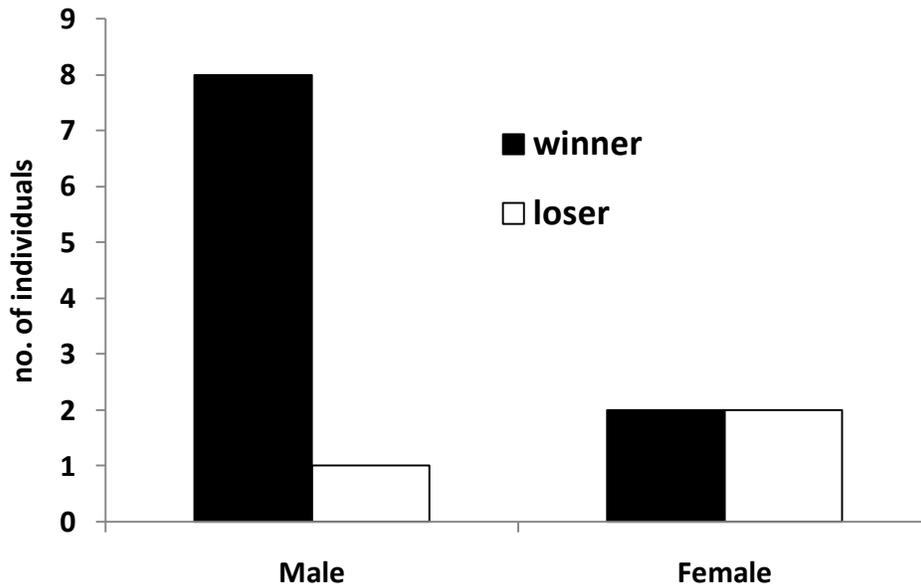


Figure 5-8. Number of individuals that were winner or losers in intraspecific agonistic encounters of Tropical Kingbirds, by sex.

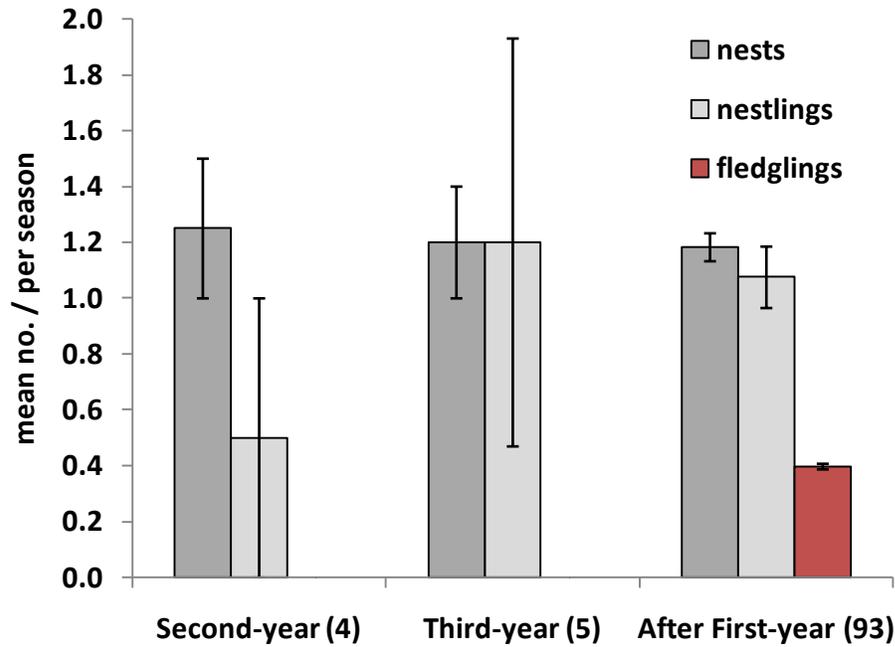


Figure 5-9. Mean number of nests constructed, number of nestlings, and number of fledglings per season as a function of age in the Tropical Kingbird study population. SY = Second-year individual, TY = Third-year individual, AFY = After first-year individual. Numbers in parentheses represent number of individuals. Data represent three breeding seasons.

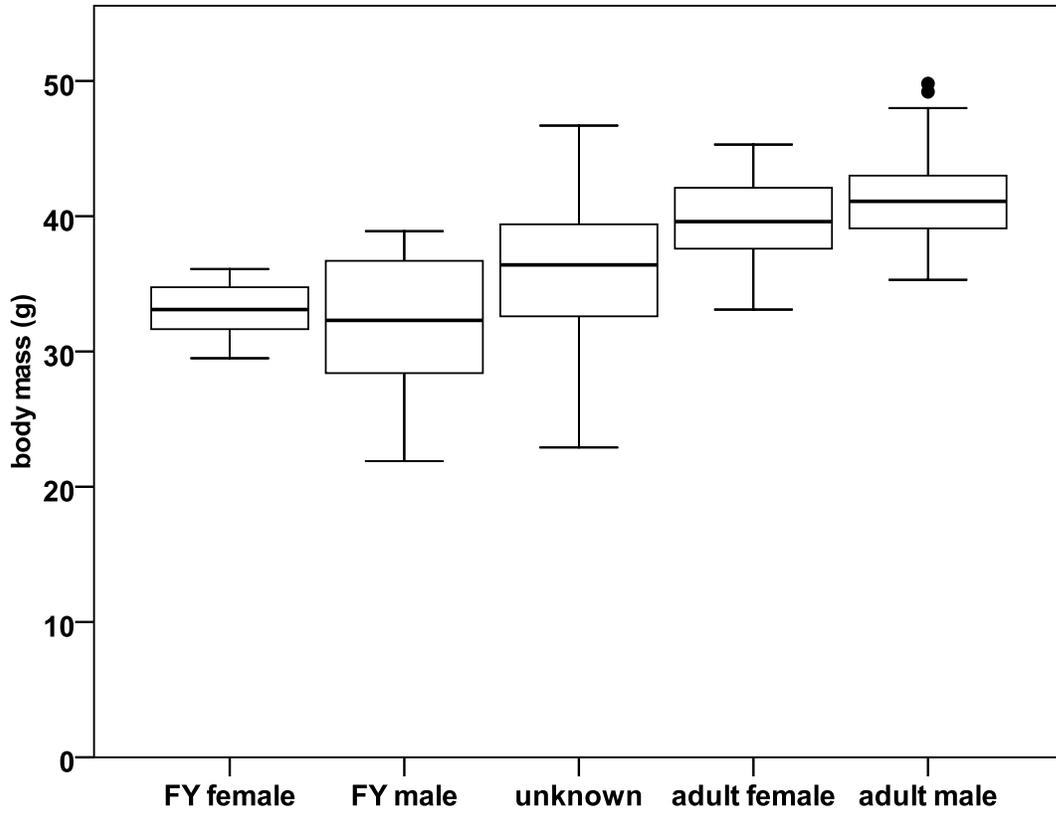


Figure 5-10. Boxplot of body mass of Tropical Kingbirds from the study population (i.e., those observed at least once after color-banding), by age and sex.

CHAPTER 6  
OPPORTUNITIES THROUGH PARTNERSHIPS FOR CONSERVATION AND RESEARCH  
OF NEOTOPICAL AUSTRAL MIGRANTS

**Introduction**

South America is home to two major bird migration systems: the Nearctic-Neotropical and the Neotropical austral, the latter being the most extensive bird migration system in the Southern Hemisphere (in terms of distance travelled; Chesser 1994). Nearctic-Neotropical migrants overwinter in the tropics, whereas Neotropical austral migrants (hereafter “austral migrants”) breed in the south temperate latitudes of South America, then migrate north towards, and sometimes into, tropical latitudes, staying wholly within South America (see reviews for the latter by Chesser 1994, Joseph 1997, Jahn et al. 2004). Although other types of migration, such as altitudinal and intra-tropical also occur on the continent, most well-defined, long-distance bird movements in South America occur as part of these two systems.

Very little information exists on the ecology and distribution of many species in these systems during the non-breeding season (Stotz et al. 1996). What is the non-breeding season micro-habitat use? What are the principal sources of mortality during this period? What is the population connectivity between breeding and non-breeding seasons? What seasonal carryover effects exist between seasons? Such questions basically remain unanswered for species overwintering in the South American tropics.

Nearctic-Neotropical migrants that over-winter within the tropics of South America (i.e., north of the Tropic of Capricorn) have generally broad habitat tolerances (Stotz et al. 1996). Similarly, austral migrants largely use scrubby and open habitats on both the breeding and non-breeding grounds (Chesser 1994). Due to this predominant use of secondary habitats, as well as the relatively large ranges of most species, migrants in both systems are thought not to be highly threatened by anthropogenic changes in their wintering habitat (Stotz et al. 1996), although

recent research on some Nearctic-Neotropical migrants suggests that winter habitat is limiting and may affect reproductive success (e.g., Marra et al. 1998, Studds and Marra 2005).

Nevertheless, migratory birds may be especially vulnerable to habitat loss throughout the annual cycle because they rely on widely separated breeding and overwintering habitats as well as those along the migratory route. Indeed, numerous studies have documented steep and widespread declines in North American migratory species (Sauer et al. 2005, Valiela and Martinetto 2007), yet the situation for migratory birds in South America is largely unknown. There is a strong consensus that what are lacking are studies that connect populations at breeding sites to those same populations at particular wintering sites (Webster et al. 2002). These studies are rare for Nearctic-Neotropical migrants and essentially nonexistent for austral migrants.

A case in point is that of migrant ecology in the cerrado grassland of central Brazil, of which approximately 2.2% is legally protected (Klink and Machado 2005). According to Mantovani and Pereira (1998), by 1993 only approximately 35% of the cerrado was left undisturbed. Extensive mechanized agriculture is the main threat (Stotz et al. 1996). According to Alho and Martins (1995) nearly one-quarter of all grain produced in Brazil comes from the cerrado region. Yet, most research on bird migration in cerrado is recent – we are still in the stage of identifying which species are migratory and determining their migratory routes (Cavalcanti 1990).

Given the current state of knowledge of migrant bird ecology in South America, the study of austral bird migration is timely for several reasons: First, austral migration provides an independent test of theory developed mainly in north temperate latitudes (Jahn et al. 2004). By testing hypotheses in South America, researchers can test the generality of theory, thereby

developing a greater appreciation of how birds migrate in South America and gain a better theoretical foothold on the *how's* and *why's* of bird migration from a global perspective.

Second, migratory birds are internationally important disease vectors. For example, various strains of avian influenza are found in wild birds on all continents and are transported between continents by migration (Gilchrist 2005, Spackman et al. 2006). Migratory birds are also hosts to Equine Encephalitis, Newcastle, and West Nile viruses; the latter has caused human deaths and alarming population declines in North American birds (LaDeau et al. 2007) and has recently been discovered in Argentina (Morales et al. 2006). To predict the spread of avian transmitted diseases, it is imperative for epidemiologists to understand the very basic ecology of migratory birds. Which species migrate? When do they migrate? And, what habitats do they use? Because this information is already known in North America, public health officials in 2006 were able to focus their monitoring efforts for the H5N1 strain of avian influenza in North America on a small set of species predicted to transport the virus. The scientific community is unprepared to make such predictions with species that migrate within South America or between North and South America.

Third, migratory birds are a proven barometer of global climate change. Numerous studies from the Northern Hemisphere have reported that migratory birds have advanced the timing of spring migration in response to recent climate change (e.g., Root et al. 2003, Jonzén et al. 2006, Zalakevicius et al. 2006). These shifts have resulted in population declines of some migrants (Both et al. 2006). Similar data simply do not exist in South America. A long-term database on the phenology of austral migration across most of southern South America could provide an independent (Southern Hemisphere) barometer of global warming already observed in the Northern Hemisphere.

I have two objectives: 1) to review the biogeography, habitat use, and conservation and research status of migratory bird species in South America, with a focus on austral migrants and 2) to illustrate the value of developing international partnerships among researchers in South America, as well as between researchers and private landholders for the study and conservation of migratory birds.

### **Methods and Results**

I use data from Parker et al. (1996) to quantify the proportion of migrants in South America as a whole, as well as per country. I also use these data to describe habitat occupancy of austral migrants and to evaluate current conservation and research priorities for austral migrants.

Chesser (1998) showed that the proportion of migratory flycatcher species (Tyrannidae) increases dramatically with increasing latitude within the temperate latitudes of South America, with 20% of flycatcher species migratory at the northern end and 100% migratory at the southernmost extreme.

I divided the number of Nearctic-Neotropical migrant species found in each South American country by the total number of migratory species found in that system (416 Nearctic-Neotropical migrant species); I performed the same analysis for the austral system (a total of 232 austral migrant species). All data were taken from Parker et al. (1996).

The results generally corroborate the pattern in the Tyrannidae from Chesser (1998) in that the percent of austral migrants increases towards the south, with French Guiana holding the lowest percent at 29.3% and Argentina holding the highest at 97.0%. Conversely, the percent of Nearctic-Neotropical migrant species per country does not change dramatically from country to country, although the highest proportions are in the north, in Colombia (41.8%) and Venezuela (35.8%) (Fig. 1).

## **Habitat Occupancy**

I evaluated habitat occupancy of austral migrants by summing the number of species listed by Parker et al. (1996) occupying each habitat. Habitat occupancy of austral migrants is concentrated in generally open and edge-dominated habitats, with secondary forest, freshwater marshes and second growth scrub being the most common habitats occupied in each category (Fig. 2).

Our analysis combines breeding and non-breeding habitat occupancy, as there is no distinction between these in the Parker et al. (1996) database. However, the winter habitat occupancy from this database is summarized by Stotz et al. (1996) who found that the most commonly used winter habitats occupied by austral migrants are grasslands, lowland evergreen forests and freshwater marshes. According to Chesser (1994), the breeding habitats of most austral migrant passerine species are generally open or scrubby while the least used is forest.

## **Conservation Priorities**

For each species, Parker et al. (1996) listed a “conservation priority” on a scale of 1 to 4 (1 = urgent, 2 = high, 3 = medium, 4 = low), subjectively based on population status and vulnerability, habitat, range size, and other variables. They also list a “research priority” for each species on a scale of 1 to 3 (1 = high, 2 = medium, 3 = low), based on the life history, distribution and taxonomy of species. The average conservation priority of austral migrants is 3.8 (median = 4.0) and the average research priority is 2.6 (median = 3.0).

Stotz et al. (1996), in the same book in which the databases of Parker et al. (1996) are presented, state that migrants are generally of a lower conservation concern than many residents because of the former’s generally large wintering ranges and low habitat specificity. However, they single out one group of conservation concern: species occupying native grasslands and marshes at the center of the continent, mainly Emberizids of the genus *Sporophila*. In a review

of the movements made by this genus, Silva (1999) found that the cerrado grasslands of Brazil are likely the most important wintering habitat for long-distance migrants in this genus. As mentioned previously, this ecosystem is critically threatened (Myers et al. 2000) by conversion to agriculture (Stotz et al. 1996).

Although research priority for austral migrants is relatively low according to Parker et al. (1996), Stotz et al. (1996) emphasize that research is “urgently needed” on winter distributions and habitat use of austral migrants. It is noteworthy that we know very little about the population status or distribution of most austral migrant species, such that the level to which they are threatened is not well known. As new distributional information becomes available, the conservation concern for a species could quickly change if it is found to inhabit ecosystems under threat of anthropogenic change (Stotz et al. 1996).

Likewise, although austral migrants readily occupy secondary and disturbed habitats, information on whether these could represent an ecological trap (i.e., when an animal settles in a habitat where it does worse than in other habitats, Robertson and Hutto 2006) is lacking. Another direct threat to both Nearctic-Neotropical and austral migrants in South America is the use of pesticides and herbicides now banned in many developed countries but used in Latin America (e.g., Lacher and Goldstein 1997).

### **Discussion**

Given that most austral migrants in South America are found in the south of the continent, the most “bang for the buck” increases southward, in terms of research and conservation of the highest number of austral migrant species. Likewise, prioritizing the conservation of open habitats such as native grasslands would help protect a larger number of austral migrants than a focus on more closed habitats such as humid forest. Nevertheless, as information such as population trends and habitat needs of individual austral migrant species or groups of species

becomes available, research and conservation schemes will do best to tailor their priorities accordingly in terms of where to work and in what habitats to concentrate on.

Parker et al. (1996) classified the research and conservation priorities as low for austral migrants, and I generally agree that, based upon current information, the outlook for many bird species in the Neotropics, especially local endemics and habitat specialists, is dire in comparison to that for most austral migrant species. Nevertheless, I propose that both applied and theoretical research on austral migration should be high priorities due to the lack of information on the population trends and ecology of these species, and because of recent findings from other migration systems that migrants can be habitat-limited while overwintering (e.g., Studds and Marra 2005), that migratory birds may be negatively affected by climate change (Both et al. 2006) and that there may exist population-specific patterns between population decline and connectivity (Jones et al. 2008). Additionally, migratory birds in the tropics may be limited in the breeding season by high nest predation rates (Chapter 5) and in the non-breeding season by food limitation (Chapter 4).

As mentioned earlier, we know little of how diseases are transported by migratory birds in South America, or of the usefulness of austral migrants as monitors of climate change, such that knowledge of migration routes, population connectivity and timing of migration should be priorities for research in South America. In order for researchers and conservationists to be successful in this endeavor, strong partnerships with local government agencies and private organizations to promote the study and protection of at least target species is fundamental. This has already begun for a few Nearctic-Neotropical migratory species, such as the Cerulean Warbler (*Dendroica cerulea*), through the Cerulean Warbler Technical Group, which includes government and private organizations from the U.S. and in several South American countries.

Surprisingly, no such international collaborative networks exist for research on austral migrant species. Given that on average each South American country holds approximately half of all austral migrant species (52.5%), research across various countries will greatly increase the number of migrant species which could be studied.

Ornithologists are studying Neotropical austral migrants in South America but are mostly doing it without standardized, coordinated data collection among countries. Thus, elucidating continental patterns, such as migratory timing and population trends, remains out of reach. As is often the case in South America, strong research skills and commitments are present, but are limited by funding and logistical constraints. I believe one way to address this situation is through the creation of strong partnerships at different levels. I focus on two types of partnerships for promoting a better understanding of austral migration: 1) International partnerships among researchers and 2) partnerships among researchers, conservationists and private landholders at the local level.

### **Creating International Research Partnerships**

There are obstacles to partnership creation at large scales. South America is comprised of 13 countries that speak 6 official languages (i.e., Dutch in Suriname, French in French Guiana, English in Guyana, Portuguese in Brazil, Guaraní and Spanish in Paraguay, and Spanish in all remaining countries). There is a general lack of funding in most South American countries for ornithological research relative to most North American and European countries. Combined with the large distances and access problems, the logistic challenges to the establishment of an international network of researchers in South America are formidable.

According to Karlsson et al. (2007), the “knowledge divide” that generally exists between north temperate countries and those in the more southerly sub-tropics and tropics can be at least partially ameliorated through such actions as increasing the transfer of financial resources for

research, increasing collaboration among researchers in southern countries as well as between northern and southern countries, and making research originating in southern countries more accessible to the scientific community by strengthening southern scientists' publication records. Thus, creating a research initiative among South American migratory bird researchers will likely be most successful through a strategy that incorporates lobbying across various agencies for lower restrictions on research funding, interdisciplinary research that incorporates both north temperate and South American researchers on an equal footing, and promoting first-authorship among South American researchers.

Given the challenges and opportunities, I offer the following list of recommendations for an international network of collaborators for the study of bird migration within South America.

- 1) Set specific and prioritized research objectives. These will define the structure of the research design and will help keep partners focused on common objectives throughout the research process. Prioritizing research needs is an important step in defining these objectives. Given that little natural history information is available for most austral migrants, compiling a natural history database on austral migrants would logically be one of the first steps. Another priority is understanding the when and where austral migrants migrate, as well as the mechanistic underpinnings driving their migratory behavior (Jahn et al. 2006).
- 2) A network should incorporate a variety of institutions (e.g., government, private, academic). Partners in Flight or Alliance for the Grasslands (which operates in southern South America) may be good models to follow initially, with possible later modifications. Students, who are the future of science on the continent, as well as established professionals, should be involved.
- 3) Good communication is essential. In the case of research partnerships among countries in South America, overcoming language barriers (e.g., Portuguese vs. Spanish) and cultural differences will be a challenge. Regular meetings, regular communications, and jointly managed websites are essential tools to ensuring fluid contact among participants.
- 4) Training is imperative, as collection of meaningful, accurate data depends on well-trained observers. Furthermore, since comparisons across study sites cannot be made unless the same protocols are used, training network partners in the use of common methods should be a high priority. This will be a challenge for any international initiative on bird migration across South America, as data collection protocols (e.g., census and banding methods) vary among workers both within and among countries. The training can be delivered in the form of training workshops organized by the network itself, or by sponsoring the

attendance of partners to already existing training venues such as courses held by the Organization for Tropical Studies. Once protocols are agreed upon and followed, ensuring that methods remain standardized across observers through time (e.g., by holding regular workshops), will be equally important. Although training in data collection techniques is the focus here, a successful collaborative network could also act as a sponsor for partners at institutions of higher education (e.g., graduate school) through grants and academic advising.

- 5) Data sharing is obviously essential for such an initiative to produce meaningful results. However, a researcher's proprietary rights to data should be respected. Fortunately, web-based tools are now in place (e.g., Landbird Monitoring Network of the Americas, Avian Knowledge Network, Movebank) to permit data sharing along with filters each participant can use to establish how much of their database is viewable by others.
- 6) Because science cannot be accomplished without money, fundraising may be the biggest initial challenge to establishing such a network. Government funding within South America has been historically low for ecological studies. Government funding from overseas is at times possible but often has restrictions (e.g., Neotropical Migratory Bird Conservation Act). Possible funding sources include private foreign institutions, conservation groups, and international foundations (e.g., British Petroleum Conservation Leadership Programme, World Health Organization).

### **Partnerships with Landholders**

Working on the ground in South America also presents logistical challenges not easily overcome in many areas. For this reason, strong partnerships with local government agencies and private or public institutions are imperative. Public protected areas, such as national parks, exist across much of South America. Research documenting biodiversity and basic natural history is necessary to implement sound management within their boundaries, as well as to demonstrate to the public the value of such areas. Another partnership often pursued by researchers and conservationists in South America's tropics is with private landholders. Costs and benefits to work on private lands vs. public lands vary by situation, and may be influenced by availability of proper infrastructure (e.g., lodging), permits required to work on different types of land (e.g., there is often more paperwork involved when working in protected areas), and accessibility (e.g., roads open in all seasons to study sites).

Additionally, partnering with private landholders can educate them about the importance of properly managing their land for plants and wildlife and in the long-run potentially encourage development of a conservation ethic in them and others in the community.

I use two privately-owned facilities in South America's tropics as examples:

Estación Biológica Caparú. This is a 15 000-ha property in northeastern Bolivia, primarily comprised of seasonally inundated savannas and *terra firme* humid forest. The primary economic activity is low-intensity cattle ranching. However, the owners expressed interest in developing a biological research station on the property, such that dependence on cattle could be reduced through fees charged to visiting scientists.

I have been working with the owners of Caparú Ranch since 2004 to create better infrastructure for visiting researchers. As a result, Bolivian students, foreign students and professional biologists have begun research projects or attended bird banding workshops. A primary benefit of working on the property is accessibility, as much of the nearby Noel Kempff Mercado National Park is difficult to access during the rainy season.

By working on a private property in the region, colleagues and I have been able to contact other property holders and now have the option to work on a series of ranches in the region. Additionally, through avian influenza sampling of the local chicken population, we have expanded research into a nearby village, thereby exposing local people to scientific activities.

Hato El Frio. This second site is an extensive cattle ranch located in the flooded savannahs (Llanos) of the Orinoco river basin of Venezuela. Spanning 63 000 ha, conservation on the property has been a cornerstone since 1929, when hunting or trading with wildlife was completely banned. It also forms part of the Caño Guaritico Wildlife Refuge, Fishing Reserve and Protective Zone, created in 1989 with the main purpose of preserving 9 300 ha of habitat for

conservation and reintroduction programs for the globally endangered Orinoco Crocodile (*Crocodylus intermedius*).

The savannahs, dry forests and riverine habitats of the ranch are home to 80 mammal species, 50 reptiles, 20 amphibians and over 225 fish. El Frio is considered an Important Bird Area (IBA) by Birdlife International, hosting a total of 319 species, including the globally threatened Orinoco Goose (*Neochen jubata*) and Yellow-knobbed Curassow (*Crax daubentoni*) and 10 species restricted to the Orinocan Llanos.

In 1974, the El Frio Biological Station was established to promote conservation and research in this important ecosystem. To date, over 120 research projects from national and international institutions have been conducted at the ranch, providing invaluable knowledge of this dynamic ecosystem and its sustainable use.

These are only two cases of partnerships with landowners that can greatly expand both research and education about migratory birds on their tropical wintering grounds. I believe such models not only make a lot of sense in terms of overcoming logistical obstacles to research, they also offer an opportunity for landholders to become active stakeholders in the conservation of wintering migratory birds locally.

Migratory species hold great potential for promoting research and conservation of other species in the ecosystems they inhabit. From a layperson's perspective, they are visitors from distant lands, such that even short distance, intracontinental migrants, can serve as a rallying point for promoting conservation and research on other species of fauna and flora on private lands in tropical South America. Interest in migrants can carry over into initiatives for resident species, with conservation funding for migratory species helping to conserve the same habitats used by residents.

Because migratory birds have different requirements and face different challenges in different seasons, more multi-faceted questions about migratory birds can be answered through research across the entire annual cycle. Given that migrants do not recognize international borders, international networks of researchers are essential for conducting research and indeed, they are becoming a more common model for migratory bird research. An international network of researchers across South America, along with local partnerships, both public and private, will be fundamental to pursuing questions about austral migratory species and gaining a better understanding of the complex lives of migratory birds at those latitudes.

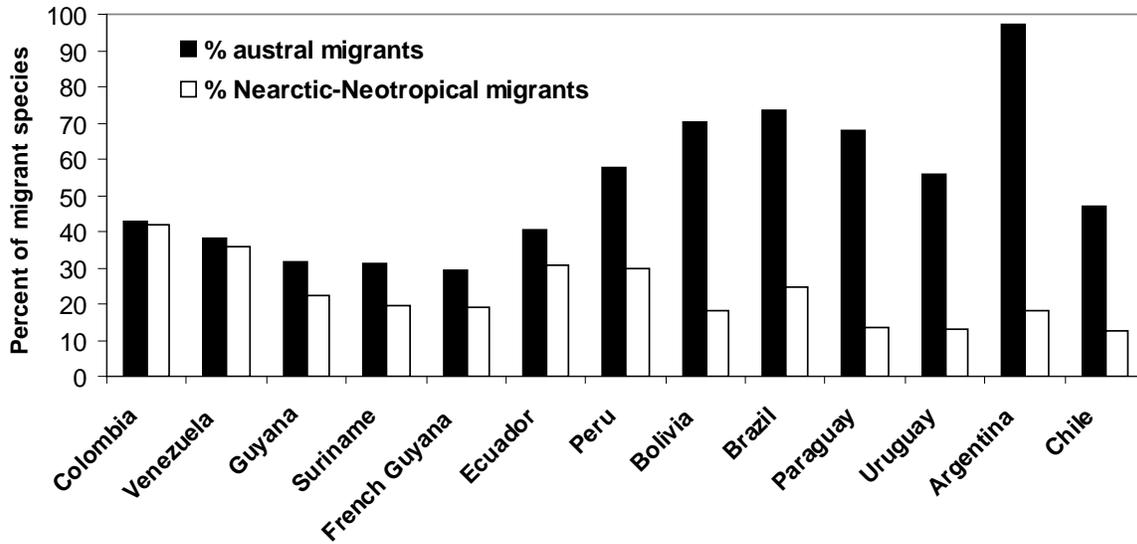


Figure 6-1. Percent of Nearctic-Neotropical and Neotropical austral migrants in each South American country, organized north to south, from left to right. Data from Parker et al. (1996).

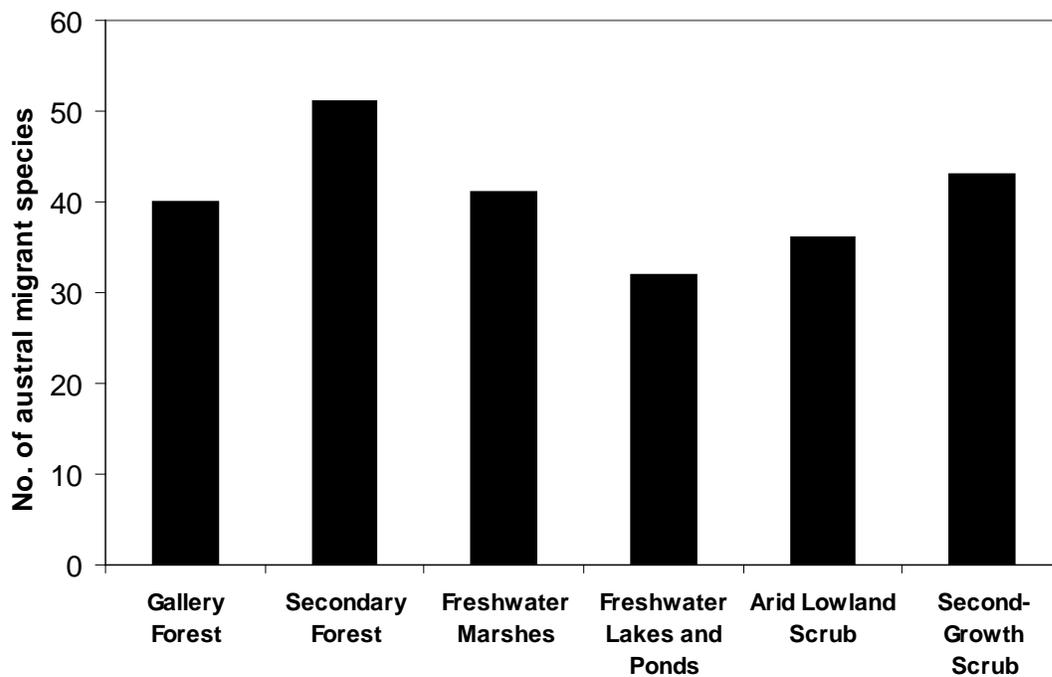


Figure 6-2. Habitats most occupied by austral migrants, according to Parker et al. (1996). Parker et al. (1996) listed habitats as part of three general types: forested, aquatic and non-forested habitats. The three most common habitats used by austral migrants within each of these categories are presented in the graph.

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## BIOGRAPHICAL SKETCH

Alex Jahn received a B.S. from Lake Superior State University, and an M.S. from the University of Arkansas. His Ph.D. is in Interdisciplinary Studies from the School of Natural Resources and Environment, University of Florida.