

**ARRIVAL ECOLOGY AND BEHAVIOR OF  
WINTERING OVENBIRDS (*SEIURUS AUROCAPILLA*):  
UNDERSTANDING TERRITORY ACQUISITION AND  
SPACE USE STRATEGIES**

**Ross Jonathan Kresnik**

A thesis submitted to the faculty of graduate studies in partial fulfillment of the  
requirements for the degree of

**Master of Science**

Graduate Program in Biology

York University

Toronto, Ontario, Canada

June 2012

© Ross Jonathan Kresnik, 2012



Library and Archives  
Canada

Published Heritage  
Branch

395 Wellington Street  
Ottawa ON K1A 0N4  
Canada

Bibliothèque et  
Archives Canada

Direction du  
Patrimoine de l'édition

395, rue Wellington  
Ottawa ON K1A 0N4  
Canada

*Your file Votre référence*

*ISBN: 978-0-494-90072-7*

*Our file Notre référence*

*ISBN: 978-0-494-90072-7*

#### NOTICE:

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

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

#### AVIS:

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

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

---

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

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

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

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

# Canada

## Abstract

Wintering territoriality among migratory songbirds is critical for overwinter survival, yet our understanding of the factors that impact the early arrival period are limited. I radio-tracked Ovenbirds (*Seiurus aurocapilla*) during early wintering (October-November) in Southern Belize, to determine the causes and consequences of non-breeding territoriality. Most (77.5%) ovenbirds possessed small, fixed home ranges with the remaining individuals exhibiting a wandering strategy. The foraging rate of wanderers was significantly lower than that of sedentary birds. Wanderers' reduced rate was likely caused by unfamiliarity of foraging habitat rather than territory defence from conspecifics because wanderer's had access to sedentary bird's territories. Fall territory acquisition was dependent on age, as most (90%) wanderers were first-year birds, and on breeding origin. First-year birds from Northern breeding origins were less likely to acquire territories. A body condition index revealed that older birds (second year or older) and territory owners were in better condition than first year birds and wanderers. Longer migration distances due to more northern breeding origin in conjunction with social dominance and inexperience of birds in their first fall could have reduced energetic condition. Since insect resources typically decline during the dry season and territory defence intensifies, it is likely that wanderers would experience even greater energetic constraints which could reduce survival on the wintering grounds or during spring migration.

## **Acknowledgements**

I would like to express my gratitude to the Stutchbury laboratory for logistical support and funding throughout the course of my study. Specifically, I must thank Dr. Bridget Stutchbury for her excellent advice and guidance during my field seasons and throughout the analyses stage of this project. Over the five years that I have known Bridget I have been given several opportunities in avian research that have helped me hone my skills while pursuing a career in biology and education. To think that the banding of Black-capped Chickadees in a York University woodlot would lead to field work in Pennsylvania, Ontario, Maui and quite recently Belize is phenomenal. I would also like to thank Dr. Gail Fraser and the Stutchbury Lab team, both past and present, including Dr. Eugene Morton, Patrick Kramer, Cassandra Silverio, Dr. Ioanna Chiver, Dr. Kevin Fraser, Emily McKinnon, and Pam Bezic for the insight they provided throughout this project as well as their friendship. I must also thank my family and friends for supporting my research endeavours and nurturing my love of the outdoors.

Much of the research presented in this thesis would not have been possible without the support of the Belize Foundation for Research and Environmental Education. I must give a large thank you to Jacob Marlin for his continued logistical support at his field site in Belize, as well as the Belize Forestry Department for allowing me to conduct this research in the unspoiled rainforest of the Maya Mountains. Special thanks go to Dr. Jamie Rotenberg and the local team of avian technicians including, William Garcia, Liberato Pop, Alejandro Cholom, Thomas Pop, and Roni Florian-Navas. Both their sense of humour and dedication to avian conservation made my research and time spent in the jungle even more enjoyable. This research was made possible through an NSERC Alexander Graham Bell Canadian Graduate Scholarship, Ontario Graduate Scholarship, the York University Faculty of Graduate Studies field work cost fund, as well as funding from Dr. Bridget Stutchbury's grants.

**Table of Contents**

Abstract.....ii

Acknowledgements .....iii

Table of Contents.....iv

List of Figures.....v

List of Tables.....vi

Introduction.....1

Methods.....9

Results.....18

Discussion.....22

References.....32

Figures.....39

Tables.....49

## List of Figures

Figure 1. Multiple factors proposed to influence autumn territory acquisition.....	39
Figure 2. A) The study location and wintering range of Ovenbird ( <i>Seiurus aurocapillus</i> ). B) Map of the two study sites.....	40
Figure 3. Fixed home ranges of Ovenbird in both years.....	41
Figure 4. Movement pattern of a long distance wanderer.....	42
Figure 5. Short distance wanderer's movement patterns before and after territory acquisition.....	43
Figure 6. Foraging rate and average distance moved for sedentary versus wandering birds.....	44
Figure 7. Residual body mass of Ovenbirds versus age and territory status.....	45
Figure 8. Baseline and elevated corticosterone titres versus territorial strategy.....	46
Figure 9. Ovenbird breeding region assignments.....	47
Figure 10. $\delta D$ of Ovenbird P1 feather compared with territorial status of HY birds.....	48

## List of Tables

Table 1. Summary data of home range, core use, and % neighbour overlap of wintering Ovenbird.....	49
Table 2. Ovenbird age and sex compared among the entire sample population and spatial use strategy.....	50
Table 3. <i>Plasmodium</i> and <i>Haemoproteus</i> infection rate (%) with respect to the entire sample population and spatial use strategy.....	51

## Introduction

For many migratory birds the ability to acquire and hold a territory is of fundamental importance throughout the annual cycle. During the breeding season territoriality ensures access to the highest quality resources, mates, and can serve to increase annual fecundity (Lozano et al. 1996; Kokko, 1999; Norris et al. 2004). During the non-breeding season territory acquisition can be critical for over-winter survival (Stutchbury, 1994) especially for insectivorous species that defend arthropod based food resources (Greenberg and Salewski, 2005). The autumn arrival period in the tropics represents an important stage of the annual cycle since it is at this time that dominance patterns are established as migrants arrive and seek high quality “wintering” territories. Possessing high quality territory over a wintering period can have a positive impact on body condition and survival (Latta and Faaborg, 2002; Smith et al. 2011a), which may influence spring migration and future breeding (Marra et al. 1998).

While vying for a winter territory, migrants must cope with carry-over effects from the breeding season and fall migration including; parasitic infection, breeding/natal origin, and body fitness (Morton, 1976; Bearhop et al. 2004; Moller et al. 2004; Angelier et al. 2009). These various factors in addition to sex and age constraints have the potential to influence social competition for territory, but the degree to which they do remains unknown. The individuals that are unable to acquire a winter territory may adopt a nomadic wandering strategy, also known as floating. Currently there is limited information on the consequences of possessing a fixed territory (i.e. sedentary) versus wandering (Brown and Long, 2007). Previous work on the Ovenbird has documented both sedentary and floating behaviour (Brown and Sherry, 2008), with territorial birds occupying small overlapping home ranges throughout the wintering period (Strong and Sherry, 2000; Brown and Sherry, 2008). Here, I test how foraging



activity, social behaviour, resource access, and subsequent survival in the Ovenbird differs between sedentary territory owners versus wanderers, and explore what factors influence non-breeding territory acquisition (Figure 1).

### *Space Use Strategy*

Although many studies have examined the spatial use strategy associated with fixed territory ownership, there exists limited information on the alternative floating strategy due to the nomadic behaviour and wide scale movement of these individuals (Winker et al. 1990). By definition a winter floater is a bird which possesses a substantially larger home range as compared with sedentary individuals in the population (Smith, 1984; Winker, 1998). While several studies have noted the presence of floaters within a wintering population (e.g. Rappole et al. 1989; Stutchbury, 1994; Brown et al. 2000; Townsend et al. 2010; Smith et al. 2011a), few have examined the underlying consequences of this strategy. Winker et al. (1990) suggested that Wood Thrush (*Hylocichla mustelina*) engaged in a floating strategy would have reduced access to available food resources and be less familiar with foraging sites, both of which could cause poor survival.

Several removal experiments have shown that when given the opportunity to hold territory, wandering is quickly abandoned for a territorial strategy (Morton et al. 1987; Marra et al. 1993; Stutchbury, 1994). While some studies have attempted to use radio-telemetry as a means of examining floater behaviour (Winker et al. 1990; Brown et al. 2000; Townsend et al. 2010; Smith et al. 2011a) most have only been able to document movements over a short period of time (e.g. 2-3 weeks) due to the limited range and short battery life of radio-transmitters.

Although floating is considered a behaviour undertaken by subordinates, there remains a

great deal of plasticity in this strategy. Brown and Long (2007) suggested three habitat/space use choices that could be used by floaters: 1) establishing a territory in a poor quality edge habitat; 2) becoming a wanderer in a low quality habitat; 3) becoming a wanderer in a high quality habitat. Each of the above strategies has different risks and gains associated with it. For example, becoming a wanderer in a high quality habitat may allow for greater food access but would carry a higher risk of attack from territorial conspecifics.

### *Foraging and Habitat Quality*

On the wintering grounds, site persistence and territoriality are thought to be influenced by habitat quality and its associated factors. For insectivorous warblers that feed primarily on arthropod based food resources the importance of establishing a territory in high quality habitat is critical, given that insect forage is much more constrained than widespread fruit resources (Marra et al. 1993; Marra, 2000; Greenberg and Salewski, 2005). Floating occurs when high quality habitats are saturated preventing surplus individuals from establishing territories (Brown, 1969). Therefore, it may be expected that measurable differences exist in the habitat quality used by wandering birds since sedentary birds are expected to defend their high quality habitat from intruders. Both the abundance of available food resources and vegetation structure represent two main factors affecting the habitat quality of migratory birds.

Food availability has been implicated as a primary factor controlling movement patterns and site fidelity throughout the non-breeding period (Lefebvre and Poulin, 1996; Sherry and Holmes, 1996; Smith et al. 2011b). Territoriality is used to ensure food access and it has also been shown to have a positive effect on body condition while on the wintering grounds (Strong and Sherry, 2000; Strong and Sherry, 2001, Latta and Faaborg, 2002; Smith et al. 2011a).

Although it has been suggested that non-territorial birds would have reduced food access resulting in poorer body condition and lower survival (Winker et al. 1990), this has not yet been shown for wintering migratory songbirds. Moreover, there may even be benefits to a wandering strategy (Brown and Long, 2007). Brown and Sherry (2008) found that floaters were better able to exploit experimental feeding stations as compared with sedentary individuals restricted within their home range. This suggests that floaters may have an advantage over birds with fixed home ranges during times of unpredictable food availability. Experimental food manipulation on wintering Hermit Thrush (*Catharus guttatus*) and Ovenbird (*Seiurus aurocapilla*) found that sedentary individuals remained rigid in their territories despite reductions in available food resources (Brown and Long, 2006; Brown and Sherry, 2008). This suggests that when birds are arriving to the wintering grounds in the fall, the territories established may carry throughout the entire non-breeding period (Brown and Long, 2007). Although floaters may be able to better exploit resources during food shortages, I predict that during the rainy season territory owners will have greater food security and higher insect resources.

An important aspect of food availability is the foraging pattern used to exploit potential resources as well as the vegetation structure of the habitat utilized. While the foraging pattern of the Ovenbird has been documented (Strong, 2000) there exists limited information on how it may differ among territory owners and wanderers. Specifically, the hypothesis that wanderers are unfamiliar with their environment and less likely to acquire food resources (Winker et al. 1990), suggests that differences in their diurnal and foraging activity should be evident (i.e. foraging rate, foraging time, average distance moved etc.). I expect that the mean distance moved within a tracking session will be greater for wanderers and that foraging rate will be

reduced for these birds due to unfamiliarity with their surroundings.

The vegetation structure used while foraging should also dictate foraging success. Studies have shown that insect abundance is often linked to measures of vegetation structure and productivity (Buskirk and Buskirk, 1986, Wolda, 1988) which often influence the distribution and abundance of birds (Parrish and Sherry, 1994; Lopez and Moro, 1997). Since floaters often wander in poorer quality edge habitats (Rappole et al. 1989) and sedentary birds are thought to forage in high quality habitat, it is predicted that vegetation analysis will reveal significant difference in vegetative structure among wandering and territorial birds.

#### *Factors Influencing Territory Acquisition*

A variety of factors may influence the ability to acquire a high quality territory including age/sex, malarial infection, body condition, and breeding/natal origin. The term social dominance is used when a particular age or sex class is dominant, therefore having access to the highest quality resources. In the case of wintering American Redstarts (*Setophaga ruticilla*), older males dominate high quality territories while females and juvenile birds are forced to take territory in poorer quality scrub habitat (Studds and Marra, 2005; Marra, 2000). In species where there exists sex-specific habitat specialization, the effects of social dominance on age are often more pronounced (Lynch et al. 1985; Holmes et al. 1989; Ornat and Greenberg, 1990; Stutchbury, 1994). In the Hooded Warbler (*Wilsonia citrina*) males and females prefer different habitat types while on the wintering grounds (Morton, 1990), and non-territorial Hooded Warblers are primarily juveniles (Stutchbury, 1994). This suggests that age is the factor driving social dominance in many species. For example, although male American Redstarts typically acquire better quality habitat, they often arrive earlier and in superior condition when compared

with female and juvenile birds (Marra, 2000) so it is difficult to determine if arrival date, versus age, is the mechanism that confers competitive advantage.

### *Parasite Infection*

Parasitism often imparts negative effects on their avian hosts, which can be measured through changes in survival, reproductive success, and migration timing. Davidar and Morton (2006), for instance, discovered that cross-infections in Purple Martin (*Progne subis*) of a filarial nematode and a haematozoan were lethal to their host. When parasitism does not directly cause death, it can affect other key stages of the annual cycle. For example, Barn Swallows (*Hirundo rustica*) with high blood parasite infections typically arrive later on the breeding grounds which can compromise their ability to acquire a suitable mate or territory (Møller et al. 2004).

Malarial infections (*Plasmodium* and *Haemoproteus*) in migratory songbirds are common and transmitted by blood feeding insects primarily during the breeding season and autumn migration. At this time birds are usually under more stress causing infections to re-emerge after lying dormant in the liver (Garvin et al. 2006; Valkiunas, 2005). During the wintering period these parasites retreat from the blood to the spleen and liver tissue therefore preventing transmission via tropical vectors (Valkiunas, 2005). Although parasites become dormant during non-breeding they remain detectable by PCR approximately four months after initial infection (K. Durrant pers. comm. 2010). The presence of infection during migration and at arrival could reduce competitive ability, in which cases wanderers are predicted to have a high infection rate.

### *Energetic Condition and Survival*

The mechanisms that impact overall fitness, such as parasitic infection and carry over effects from the breeding season, should be reflected in individual body condition. In the past, body condition measures were based on coarse indices that corrected body mass for structural size (Strong and Sherry, 2001). Recently, however, the use of adrenocortical indicators of stress (i.e. corticosterone) has proved to be a useful tool in assessing the physiological condition of birds. Corticosterone is the primary glucocorticoid released into the avian bloodstream in response to physiological stressors such as food shortages, attacks from predators, territory defence, storms etc. (Wingfield, 1984; Marra and Holberton, 1998; Silverin, 1998, Brown and Long, 2006).

Angelier et al. (2009) found that wintering American Redstarts that were able to produce a strong adrenocortical response (elevated corticosterone after a stressful event) were more likely to return to the non-breeding grounds the following year. The ability to mount a strong elevated response prior to migration is thought to be beneficial to survival given that it increases feeding activity and promotes fattening (Astheimer et al. 1992; Angelier et al. 2009). At the territorial level, high elevated stress responses following social competition have been associated with reductions in territoriality through decreased aggression, territory defence, and increased motility (Woodley and Moore, 1999; Brown and Long, 2006).

On the wintering grounds birds in poorer quality habitats may exhibit a higher baseline and a reduced elevated CORT response (Marra and Holberton, 1998). This higher baseline response is thought to alter physiological and behavioural processes (e.g. increases foraging activity) which help a bird to meet energetic demands in a potentially food limited environment

(Marra and Holberton, 1998). A reduction in elevated CORT is used to avoid the deleterious effects of higher stress levels on the immune system, cognitive function, physical condition, and muscle catabolism (Kitaysky et al. 2003). Therefore, measures of physiological condition can be used to assess individual quality and may be related directly to territory acquisition. In the Gray Catbird (*Dumetella carolinensis*) different autumn strategies for fat deposition among hatch year and after hatch year individuals could explain the age bias in non-breeding territoriality (Heise and Moore, 2003). In Ovenbirds, I predict that wanderers will have higher baseline CORT and a lower CORT response to acute stress.

### *Migratory Origin*

Arrival dates may have an important impact on competitive ability, and may depend in part on the geographic origin of birds that arrive on the wintering grounds (i.e. more distant birds arrive later). Although knowledge surrounding the effects of breeding origin on subsequent winter territoriality remains limited, observations have indicated that Northern populations may be at a disadvantage either due to late breeding or greater migratory distance (Morton, 1976; Kelly, 2006). The result of late breeding or longer migration distances could impact arrival date which has been shown to be an important factor affecting territory acquisition on the breeding and wintering grounds (Kokko, 1999; Marra, 2000; Bearhop et al. 2004).

The migratory connectivity between breeding and wintering sites of most avian populations still remains unknown despite some recent advances (Stutchbury et al. 2009). In the past decade, biogeochemical markers known as stable isotopes have been widely used to determine the migratory origin of breeding birds (Hobson and Wassenaar, 1997). Stable

isotopes in nature are incorporated into organisms' tissues and will often hold the geographic signature of a migratory animal's previous location. For migratory birds that moult prior to leaving the breeding area, feathers can be used to determine breeding origin since they are metabolically dead following formation (Chamberlain et al. 1997; Hobson and Wassenaar, 1997; Hobson, 2005). Thus, feathers sampled on the wintering grounds can reveal the latitude at which they were originally grown. Particularly measures of isotopic deuterium in feathers ( $\delta D_f$ ), which varies with latitudinal patterns of deuterium in precipitation ( $\delta D_p$ ), have been important in examining migratory origin.

### *Summary of Predictions*

- 1) Wandering birds will have fewer available insect resources, lower foraging rate, and vegetative structure indicative of edge quality habitat, when compared with sedentary birds.
- 2) Hatch year birds will be less likely to hold wintering territory and, since Ovenbirds are sexually monomorphic, there will be no effect of sex on territoriality.
- 3) Parasite prevalence will be higher for wanderers than sedentary birds, and negatively influence territory status. Hatch year birds (who are immunologically naïve) will have higher parasite prevalence.
- 4) Individuals in poorer body condition, or with elevated levels of baseline corticosterone and a reduced acute corticosterone response, will be less likely to hold a wintering territory.
- 5) Individuals with fixed home ranges will have higher survival probability.
- 6) Individuals originating from more northern breeding populations are less likely to acquire a territory due to later arrival and/or longer migration distances.



## Methods

### *Study Site*

I studied Ovenbirds during the fall of 2010 and 2011 at the Belize Foundation for Research and Environmental Education (BFREE) in Southern Belize (Figure 2a). The station consists of 1,153 acres of private reserve land which is home to an incredible number of tropical and migratory birds. The topography of BFREE is unique in that the reserve consists of virgin tropical rainforest that has experienced significant natural disturbance within the past decade. In 2001, Hurricane Iris (category 4) passed through Southern Belize destroying much of the pristine rainforest of BFREE. This has left much of the area consisting of a mosaic of early and late successional vegetation with very few undisturbed locations. Although two different study sites were used each year (Figure 2b), both were located within a large river island that was surrounded by the Bladen River during the rainy season but connected to the mainland from September onward. Sandy soil with loosely dense vegetation characterized the site, making behavioural observations of Ovenbird possible.

### *Study Species*

The study species of choice was the Ovenbird (*Seiurus aurocapillus*) a small, ground-foraging, migratory warbler that prefers large tracts of contiguous forest for breeding (Horn and Donovan, 1994). This species was ideal for a study of arrival ecology since much of its wintering behaviour during the dry season has been described (see Strong, 2000; Brown and Sherry, 2008a; Brown and Sherry, 2008b). This allowed for a comparative analysis between early arrival and mid-winter behaviour as well as a comparison among different wintering habitats (island versus mainland dynamic).

### *Capture and Sampling Methods*

Capture and sampling methods were approved by York University's animal care committee prior to the beginning of each sampling season. Ovenbirds at this site are thought to arrive in September, based on observations of resident staff. Beginning in early October, I used mist nets and a combination of playback vocalizations and passive netting to capture adult and hatch year Ovenbirds ( $n=118$ ). During the first year of the study, radio-transmitters were placed on birds captured passively (i.e. no playback was used) to remove the bias of sampling territorial birds only. I found later, however, that Ovenbirds responded to the breeding playback regardless of space use strategy and modified the radio-tracking protocol to include birds captured using playback. In hand, birds were measured for the physical attributes of age, fat score (ranging from 0= no fat to 5=thick fat layer), pectoral muscle (concave, flat, concave), body moult, flight feather moult, wing chord length, rectrix length, tarsus length, lesions and several bill measurements (length, width, and depth) (Pyle, 1997). Both the primary feather (P1) and the secondary feather (S1) were sampled for hydrogen isotope analysis because they are thought to grow early in the moult cycle when birds are still on the breeding grounds (Pyle, 1997). Age was determined as either hatch year (HY) or after hatch year (AHY) using several morphological indicators (Pyle, 1997, Brown and Sherry, 2008) and skull ossification. Each bird was then given a Canadian Wildlife Service aluminium band and a unique colour combination for identification during radio-tracking sessions. Fecal samples were collected from paper bags that were used to transport birds from mist nets to the nearby banding station. Samples were placed in 1.5 mL Eppendorf tubes, stored in a freezer, and a dissecting microscope was used to identify the digested content approximately 2 months later. I attempted to identify insects and plant content to its nearest order.

Blood samples were collected from the brachial vein using heparinized micro-hematocrit capillary tubes and 26.5 gauge sterile needles. For each captured bird approximately 30-50  $\mu$ L of blood was stored in 1.5 mL Eppendorf tubes containing 1 mL of Queen's Lysis Buffer which was then stored in a refrigerator. Molecular sexing using a polymerase chain reaction technique adapted for several avian species was used (Kahn et al. 1998) and 100% of Ovenbirds were effectively sexed. Detection of avian malarial infection was determined using a polymerase chain reaction assay that identifies parasite lineages of *Haemoproteus* and *Plasmodium* (Fallon et al. 2003).

#### *Foraging and Spatial Analysis*

In order to accurately assess differences in the activities of floaters and territory owners, radio-transmitters (PicoPip Ag376, Lotek Wireless, Ontario, Canada) were placed on wintering Ovenbirds (n=51) using a leg-loop harness (Rappole and Tipton 1991). These radio-transmitters weighed approximately 0.61 grams, had a battery life of 88 days, and could be detected at a range of 400-600 meters. The location of radio-tagged Ovenbirds was acquired using Communication Specialists, INC. Model R1000 receivers and model F170-3FB AF Antronics, INC. antennas. I radio-tracked Ovenbirds during early morning (6:00-9:00), midday (10:00-14:00), and late afternoon (15:00-18:00) for a total of ten 1 hour sessions per bird (n=28) over the course of the study period (~60 days). Tracking sessions began with the observer locating the bird and recording temperature and initial location (Universal Transverse Mercator; datum WGS84) using a handheld Global Positioning System (Garmin 60Cx) at an accuracy of  $\pm 5$  meters. Birds were found using the radio-tracking technique of stealth homing (White and Garrot, 1990). While radio-tracking, several observations were recorded including: aggressive or submissive behaviour, time spent defending or fleeing territory, time spent foraging, feeding

events per hour, and the foraging substrate utilized. Average distance moved per hour was determined at the end of each session by measuring the distance to the initial location bearing using the GPS. Additional radio-tracking sessions were performed on separate days to acquire more location data for a minimum of 15 waypoints per sedentary bird.

I analyzed home ranges using ArcView version 3.3 and the Animal Movement Extension (Hooge and Eichenlaub, 2000) to create fixed-kernel utilization distributions (UD). Kernel analysis estimates an individual's spatial boundaries by calculating the densities (i.e. the distance of each point to subsequent points) of observed locations (Worton, 1989). Previous work on Ovenbirds used 95% and 30% isopleths to assess home range and core area sizes (Brown and Sherry, 2008). Recent analysis has revealed that 95% isopleths typically overestimate territorial boundaries (Borger et al. 2006), and that a 30% isopleth typically underestimates core use area (Howell and Chapman, 1997). I calculated the 90% and 50% isopleths of each individual and used the least squared cross validation method to determine the ideal smoothing parameter (Seaman et al. 1999). To test for saturation among the home ranges of sedentary birds, bootstrap analysis (using 100 replicates for each fix and a starting sample of five) was conducted on sedentary birds using the Animal Movement Extension in Arcview 3.3. This analysis revealed that at 25-30 location points home range size began to level off. Minimum convex polygons (MCP) were calculated for comparison with previous studies and also used to determine territorial strategy in situations where fewer than 25 location points were obtained (n=11). I then determined the intensity of core territory use by calculating both the percentage of total core area and the percentage of locations found in the core (Samuel et al. 1985). To test for site fidelity a module from the Animal Movement Extension was used which compared observed movement with 100 randomly created paths. Finally, overlap in Ovenbird

territories was calculated, but because of the high density of un-banded birds at the study site this measure may have been underestimated.

### *Habitat Quality*

Habitat quality was assessed by measuring the vegetation structure and insect abundance available to wandering and sedentary birds. Measurements of vegetation structure were recorded during the last week of November in the first year of the study. Vegetation was measured using a method similar to James and Shugart (1970) and Strobel and Boal (2010) but was adapted based on space use strategy. Therefore, when measuring the vegetation available to sedentary birds, the centre of each territory was determined using GPS waypoints. For each territory, four 10x10 meter quadrants were used and consisted of a single central quadrant with the remaining three quadrants radiating outward at random distances (0-25 meters) and bearings (0-360°). Since wandering birds' movement patterns were largely random and varied widely in distance, I selected at random four location waypoints from telemetry sessions, to determine the vegetation structure available to wandering birds. Within each quadrant measurements of % canopy cover (recorded using a forestry concave densiometer), % leaf cover, under-story vegetation <50 cm, under-story vegetation >50 cm, and diameter at breast height for trees between 7.5-15 cm, 15-30 cm, 30-45 cm, and >45cm were recorded. Percent ground cover was determined by using a 4.5cm diameter tube held at waist level and used to spot the presence of vegetation for twenty points along the North/South and East/West axis lines. Finally, vegetation density was measured using a 2cm x 2 m pole containing 10 cm alternating bands of black and pink, held at each of the cardinal points within a quadrant. An observer standing 15 meters away from the pole counted the number of bands which were >75% visible and these values from each of the cardinal points were averaged to produce a single estimate (Barlow et al.

2002).

Since wintering Ovenbirds typically glean insects from the forest floor, and their diet during winter has been found to consist largely of ground surface arthropods such as ants (Strong, 2000); I sampled insect abundance using methods that would best quantify available Ovenbird forage. Pitfall traps have recently been found to outperform other sampling methods when examining the species richness and abundance of ground surface arthropods (Parr and Chown, 2001). Therefore, I utilized a pitfall trap sampling method similar to McGlynn et al. (2007) in order to quantify the insect abundance available to sedentary and wandering birds. For both spatial use strategies location points where birds had been observed feeding were used as potential trap deployment sites. In total four pitfall traps were deployed per home range during mid-November of the first sampling season. The traps were half-filled with soapy water and left in the field for approximately 48 hours after which all specimens were collected and placed in 70% ethanol for storage. In the lab, insects were identified to their order using a dissecting microscope before being placed in a drying oven at 50 degrees Celsius for 24 hours. The dry weight of insects was then recorded to the nearest 0.0001 grams.

### *Energetic Condition and Survival*

To test if body condition influenced territory status I used two body condition indices, fat score and body condition corrected for structural size. The regression of body mass and tarsus length (Linear Regression:  $r^2=0.28$ ,  $p<0.001$ ,  $n=98$ ) was used to create the following equation: expected body mass = (tarsus length x 0.9335) – 1.7057. Residual body mass was calculated as the deviation of actual body mass from expected.

From each Ovenbird selected to carry a radio-transmitter, an additional two blood

samples were taken early in October for analysis of corticosterone concentrations. For these birds, all individuals were captured using target netting since this method does not affect the HPA-axis prior to sampling (Angelier et al. 2010). The first of these samples was extracted in less than 3 minutes to examine baseline corticosterone and the second after 30 minutes to analyze the elevated corticosterone response (Wingfield et al. 1992). Blood samples were kept on ice until centrifugation (at 10,000 RPM for 11 minutes) at the field station, and plasma from each sample (separated into >6 $\mu$ L aliquots) was frozen in 1.5 mL Eppendorf tubes. An ImmuChem Double Antibody Corticosterone <sup>125</sup>I RIA kit, adapted for avian plasma (MP Biomedicals No. 07-120103) was used to perform corticosterone assays (Washburn et al. 2002) in Dr. Elizabeth Hampson's lab, University of Western Ontario. Samples were assayed in duplicate and any concentration that fell outside of the standard curve was excluded. Assay sensitivity over two years was between 0.65-1.99 ng/mL. Duplicate samples were typically averaged to yield the most accurate corticosterone measure. Since the sample size for plasma corticosterone was small, when one duplicate sample was below the sensitivity or registered as a negative, it was removed from analysis and the other duplicate was used.

Survival was determined at the end of the rainy season for all radio-tagged Ovenbirds. If a bird went missing during the study it would only be treated as dead if supporting evidence was found. Therefore, in the event that a radio signal was lost I did not conclude that death had occurred, but rather, that that bird's fate remained unknown.

### *Isotope Analysis*

Stable hydrogen isotope analysis was performed at the Colorado Plateau Stable Isotope Laboratory in Northern Arizona University. Stable hydrogen isotopic ratios ( $\delta$ D) were

expressed in delta notation in units of ‰ and standardized to Vienna Standard Mean Ocean Water according to the following equation:  $\delta D = [(H_{\text{sample}}/H_{\text{standard}}) - 1] \times 1000$ . Surface debris from feathers was removed using a 2:1 chloroform:methanol mixture and allowed to air dry under a fume hood for 72hrs. Samples were then equilibrated with the local atmosphere for approximately 72hrs. In order to control for seasonal changes in atmospheric moisture and ultimately  $\delta D$  values in the laboratory, analysis occurred within the same 3 month period over the two years. Feather samples were cut (0.10-0.15 mg), loaded into a silver capsule, and heated in an oven at 100°C for 24hrs to remove any remaining surface water. Each silver capsule was crushed with metal tweezers and loaded into a reduction furnace (Finnigan TC/AC) at 1450°C and introduced online to an isotope ratio mass spectrometer (Finnigan MAT Delta Plus XL). A single duplicate sample was run for every ten samples along with a single in house standard.  $\delta D$  data were normalized using three keratin standards (CFS, BWB, and CHS) and the repeatability of each sample was found to be within  $\pm 3\text{‰}$ .

To determine the breeding origin of Ovenbirds sampled at BFREE I conducted likelihood assignment tests (Royle and Rubenstein, 2004). I divided the breeding region into five distinct bins (northwest, midwest, northeast, central-east, southeastern) based on data available from the Breeding Bird Survey and prior knowledge of North American patterns of  $\delta D$  in precipitation (Norris et al. 2006, Wassenaar and Hobson 2001). For each breeding region I determined the expected mean and standard deviation  $\delta D$  values from an equal area grid of long-term average growing season  $\delta D$  values of precipitation (Bowen et al. 2005) using ArcGIS 9. These values were then adjusted based on the  $-13\text{‰}$  isotopic discrimination factor between hydrogen in feathers and precipitation (Norris et al. 2006). Therefore, the breeding region values obtained were: northwest ( $-117.5\text{‰} \pm -12.12\text{‰}$ ); midwest ( $-88.68\text{‰} \pm -11.82\text{‰}$ );



northeast (-75.84‰ ± -5.25‰); central east (-64.67‰ ± -4.92‰); southeastern (-43.55‰ ± -9.24‰). Since migration distance was the variable of interest it was assumed that individuals were equally likely to come from anywhere within a region (Jones et al. 2008). Using the below equation (Royle and Rubenstein, 2004) I was able to determine the likelihood of each bird originating in the defined breeding areas.

$$f(y^*|\mu_w, \sigma_w) = \frac{1}{\sqrt{2\pi\sigma_w}} \left[ -\frac{1}{2\sigma_w^2} (y^* - \mu_w)^2 \right]$$

### *Statistical Analysis*

I used SPSS 19.0 (SPSS. Chicago, U.S.A., 2010) to perform all statistical analyses. Shapiro-Wilk tests were used to test the normality of the data and the appropriate non-parametric tests were adopted in the event that normality could not be assumed. All statistical tests were two-tailed and carried out at the  $p < 0.05$  significance level. All other values were presented as the mean ± SE. Statistical analysis revealed that there were no significant differences between study years, and therefore I combined the data across both years of the study.

## **Results**

### *Space Use Strategy*

Kernel analysis was performed for 40 individuals for which, at least 25 location points had been obtained. Based on territorial analysis, 77.5% of Ovenbirds were found to possess fixed home ranges (ca. 1 ha; Figure 3) with the remaining 22.5% exhibiting a wandering (non-territorial) space use strategy. Site fidelity tests revealed that observed movement paths were significantly more constrained than randomly generated paths for both sedentary ( $p < 0.001$ ) and

wandering birds ( $p < 0.05$ ) indicating high site fidelity in both space use strategies.

Wanderers were defined by their larger home ranges (ca. 7 ha) compared with sedentary individuals (Table 1; Student t-test:  $t = 6.23$ ,  $df = 38$ ,  $p < 0.001$ ). Although all wanderers had high site fidelity, two movement patterns of long (Figure 4) and short (Figure 3, 5) distance wandering were evident. Long distance wandering ( $n=6$ ) appeared random, and movement varied widely during tracking, while short distance wanderers ( $n=3$ ) remained in the vicinity of nearby sedentary territories. In the case of one individual, short distance wandering resulted in territory acquisition 11 d after tracking began (Figure 5). Among sedentary birds, home range area was not significantly different with respect to age (ANOVA:  $F_{1,27} = 0.48$ ,  $p = 0.49$ ) or sex class (ANOVA:  $F_{1,27} = 1.84$ ,  $p = 0.18$ ), however, the interaction between age and sex was nearly significant (ANOVA:  $F_{1,27} = 3.08$ ,  $p = 0.09$ ) with male HY birds having larger territories than female HY birds (Table 1).

To examine whether wanderers intrude onto territories of sedentary birds versus move through un-defended areas, movement patterns were analyzed. Radio-tagged Ovenbirds responded to playback of breeding song and despite some displays of defence among territory owners (observed primarily within core areas), analysis of wanderers' location points revealed that they could be found in the territories of known sedentary birds 49.5% of the time (Range: 5.6-96.7). If territory boundaries allow individuals exclusive use of the territory, then the 90% core usage areas should not overlap between adjacent territories. On average, territories of sedentary birds overlapped by  $47.41 \pm 6.67\%$ . The degree of overlap at 90% utilization distribution did not differ with respect to age (ANOVA:  $F_{1,27} = 2.18$ ,  $p = 0.15$ ) or sex (ANOVA:  $F_{1,27} = 0.081$ ,  $p = 0.78$ ). The interaction between sex and age on territorial overlap was almost significant (ANOVA:  $F_{1,27} = 3.92$ ,  $p = 0.06$ ) and suggested that HY females possessed less

territorial overlap with neighbours than AHY females (Table 1).

To classify an individual as wanderer vs sedentary, without mapping the home range in detail, at least 15 location points must have been collected ( $n = 51$  birds). In this study, age strongly influenced territorial status (Chi Square:  $\chi(2) = 10.28$ ,  $p = 0.01$ ) with 90% of wanderers in their hatch year (Table 2). Sex did not predict territory status (Chi Square:  $\chi(4) = 3.52$ ,  $p = 0.47$ ), however, the entire sample population (all birds banded) revealed a slightly skewed sex ratio with males in greater abundance than females (Table 2).

### *Foraging Rate and Habitat Quality*

Foraging rate (feeding events/per hour) was found to be significantly different among wandering and sedentary birds (Figure 6a, ANOVA:  $F_{1,6} = 38.45$ ,  $p = 0.001$ ) and declined significantly with time of day (Figure 6a; ANOVA:  $F_{9,54} = 2.32$ ,  $p = 0.03$ ). Bonferroni pairwise comparisons revealed that sedentary birds' foraging rate was greater than that of wandering birds (Figure 6a;  $p = 0.001$ ). Mean distanced moved per tracking session changed with time of day (Figure 6b; ANOVA:  $F_{9,54} = 2.02$ ,  $p = 0.05$ ), but did not differ with space use strategy (Figure 6b; ANOVA:  $F_{1,6} = 2.43$ ,  $p = 0.17$ ).

In order to assess the habitat quality used by wandering and sedentary birds both the vegetation structure and insect abundance in each home range were measured. Ants were previously described as a primary component of Ovenbird diet (Strong, 2000). This was confirmed in this study as 92% of fecal samples ( $n=25$ ) contained ants, with 26.9% of content consisting of ants, 6.3% beetles, 1.7% seeds, 3.3% spiders, with a remaining 61.7% of unknown digested content. Thus I used three categories (dry insect biomass, dry ant biomass, and number of ants) when examining insect abundance available to wandering and sedentary birds. Analysis

revealed no difference among the territories of sedentary and wandering birds in terms of dry insect biomass (Student t-test:  $t = -1.13$ ,  $df = 18$ ,  $p = 0.27$ ), dry ant biomass (Student t-test:  $t = -0.13$ ,  $df = 18$ ,  $p = 0.89$ ) and the number of ants (Student t-test:  $t = 1.26$ ,  $df = 18$ ,  $p = 0.22$ ). Principal components analysis of vegetative structure revealed high loading in component 1 for the factors of shrubs above and below 50 metres, vegetation density, and trees above 45 meters. Given that these factors accounted for 27.9% of variance, the factor scores for component 1 were compared among sedentary and wandering birds and revealed no significant difference in habitat quality (Student t-test:  $t = -2.09$ ,  $df = 18$ ,  $p = 0.55$ ).

### *Parasite Infection and Territorial Status*

*Plasmodium* and *Haemoproteus* infection in Ovenbirds was common (45.8%) during the early stages of the wintering period (Table 3). If malarial prevalence reduces the condition of infected birds during autumn arrival, this should be reflected in subsequent space use strategy. However, malarial infection did not predict territorial status (Chi Square:  $\chi^2(2) = 0.58$ ,  $p = 0.75$ ; Table 3). Furthermore, malarial prevalence did not differ significantly with age (Chi Square:  $\chi^2(1) = 2.31$ ,  $p = 0.13$ ; Table 3) or sex class (Chi Square:  $\chi^2(1) = 2.50$ ,  $p = 0.11$ ; Table 3).

### *Energetic Condition and Survival*

Territory owners had higher body condition index values than non-territorial birds (Student t-test:  $t = -2.16$ ,  $df = 49$ ,  $p = 0.04$ ; Figure 7). When analyzing the body condition of the entire sample population, AHY birds possessed higher index values than HY birds (Student t-test:  $t = 2.11$ ,  $df = 115$ ,  $p = 0.04$ ; Figure 7).

In this study, I predicted that those individuals in poorer body condition with elevated levels of baseline corticosterone and a reduced acute corticosterone response would be less

likely to hold a wintering territory. General linear models were used to determine if the factors of age, sex, malarial infection, and territorial status could account for variation in baseline and elevated CORT titres. The GLM explained 49.9% of the variation in baseline CORT titres ( $F_{10,16} = 1.59$  ,  $p = 0.19$ ). Although territory status was not related to baseline CORT titres ( $F_{1,16} = 1.53$  ,  $p = 0.23$ ) mean baseline CORT of wanderers was more than double that of sedentary birds (Figure 8). The GLM for elevated CORT accounted for only 9.8% of the variation ( $F_{10,22} = 0.24$  ,  $p = 0.99$ ; Figure 8). As expected, CORT titres increased from baseline to elevated (Paired t-test:  $t = -6.70$ ,  $df = 25$ ,  $p < 0.001$ ; Figure 8), validating the in-field stress protocol.

Survival of radio-tracked Ovenbirds was 100% from Oct-Dec. Although three wandering birds went missing during the study, their fates remain unknown (i.e. battery failure or long distance dispersal cannot be ruled out) and they were not treated as dead.

### *Migratory Origin*

Likelihood assignment tests performed on hydrogen isotope values in feathers revealed that more than 90% of the sample population originated from north-western and mid-western breeding origins (Figure 9). A general linear model that included age, sex, winter territorial status and interactions, explained only 15.6% of the variation in  $\delta D_{\text{feather}}$  (ANOVA:  $F_{6,43} = 1.33$ ,  $p = 0.27$ ; Figure 9). The interaction among age and territorial status with  $\delta D_f$  was almost significant (ANOVA:  $F_{1,43} = 3.05$ ,  $p = 0.08$ ) and suggested that among hatch year birds, non-territorial individuals had slightly lighter  $\delta D_f$  values (i.e. originated from farther north) than territory owners (Figure 10).

## Discussion

### *Space Use Strategy*

The “winter” floating strategy has been described as nomadic large scale movements in the peripheries of habitat where birds are subjected to a reduced food supply, unfamiliarity of habitat, and increased predation (Winker et al. 1990). Brown and Sherry (2008) reported floating in 7-18% of wintering Ovenbirds in Jamaica all of which were thought to exhibit low site fidelity. As expected, I found a comparable rate of floating (22.5%), however high site fidelity among floaters and sub-strategies within this space use pattern were evident. High site fidelity suggests that floaters benefitted from restricting their movements to some extent. The size of wandering home range varied among individuals and consisted of two strategies; short versus long distance wandering. Smith (1978) found that Rufous-collared Sparrows, (*Zonotrichia capensis*) engaged in a floating strategy which encompassed the size of one to four sedentary territories, and proposed that this was an “underworld” strategy which allowed floaters to obtain a competitive advantage in acquiring a territory should an owner die. This could also be the case for Ovenbirds, since one wanderer acquired a territory. It is unclear whether long or short distance wandering is more effective in gaining a winter territory or whether there are other benefits of long distance wandering, such as opportunistic use of widely scattered food resources (Brown and Sherry, 2008).

In this study, as well as in previous work on wintering Ovenbirds (Brown and Sherry, 2008), the presence of floaters suggests that habitat was saturated. At the territorial (sedentary) level an average home range size of  $1.0 \pm 0.1$  hectares was consistent with other songbird species. For example, Winker et al. 1990 discovered wintering Wood Thrush (*Hylocichla*

*mustelina*) home range in Mexico averaged 0.44 hectares, Brown et al. 2000 reported Louisiana Hermit Thrush (*Catharus guttatus*) home range averaged 0.55 hectares, and Townsend et al. 2010 suggested Bicknell's Thrush (*Catharus bicknelli*) in the Dominican Republic had territories averaging  $1.41 \pm 0.93$  hectares. Previous estimates of sedentary Ovenbird have ranged between 0.39 - 0.93 hectares depending on habitat type (Brown and Sherry, 2008). In this study sedentary HY females had less territorial overlap with neighbours than AHY females which may suggest they were occupying poorer quality territories, or were less tolerated by neighbours. Typically high neighbour overlap is observed when territory quality is high and individuals are competing for the best quality territories (Reitsma et al. 2002; Smith 2011a).

#### *Foraging Rate and Habitat Quality*

My study was the first to investigate whether or not foraging activity patterns differ with space use strategy. As predicted, the foraging rate of floaters was lower than sedentary birds however, the underlying factors affecting this pattern were not clear. Floaters could have a reduced foraging rate if they move greater distances during a foraging period (radio-tracking session) due to occupying suboptimal habitat with limited food resources, or if in high quality habitat they are subjected to attack from territorial conspecifics. Floaters were found in sedentary bird's territories nearly 50% of the time and subjected to limited aggression, yet they nevertheless had lower foraging rates. Ovenbirds are thought to move away from conspecifics after chance encounters (Strong, 1999). Brown and Sherry (2008) suggested that Ovenbirds maintain a weak form of territorial behaviour by defending core areas rather than the entire home range. In this study floaters may have taken advantage of this reduced territorial defence behaviour as they were subjected to aggression only when found in territorial cores. Whether

this behaviour changes throughout the wintering period in response to changing food resources should be investigated further.

Another explanation for the lower rate of foraging success among floaters is a lack of familiarity with foraging habitat. Although floaters movements did not differ from sedentary birds during hour long tracking sessions they varied greatly over the duration of the study as indicated by the differences in home range size. Winker et al. (1990) suggested that Wood Thrushes engaged in a floating strategy would be less familiar with their foraging environment and therefore be less likely to capitalize on potential food caches thus reducing foraging success. Familiarity of foraging environment may be one of the greatest advantages for an insectivorous bird and a reason why some individuals who were unable to acquire territory developed a short distance wandering strategy.

Although this study was not able to compare foraging success among long and short distances wanderers the relative advantages and disadvantages of these strategies should be explored. It is predicted that short distance wanderers would be more familiar with foraging sites since their movements were less random and more constrained. Long distance wanderers, however, may be more likely to acquire a wintering territory since they travel through a larger matrix of habitat and would therefore be more likely to discover unoccupied space. In this study, a short distance wanderer was able to acquire a territory however it is unknown if this occurred after territorial loss or death of sedentary birds in the immediate area (Smith, 1978). Brown and Sherry (2008) found floaters wandered long distances and could not be tracked over extended periods of time. If the short distance wanderer is more successful at acquiring territory it is possible that this strategy would not be evident in a mid-late season study.



Contrary to what was predicted, insect abundance was not greater for territorial birds nor were there substantial differences in vegetative structure among space use strategies. Although it has been suggested that territory defence is high among migrants in the tropics (Stutchbury, 1994; Marra, 2000; Koronkiewicz et al. 2006; Sogge et al. 2007; Townsend et al. 2010), the minimal defence among sedentary Ovenbirds allowed floaters access to their territories and food resources. Ants constituted a large proportion of Ovenbird diet and this specialized food resource has been shown to vary based on ecological factors such as moisture availability, food, nest sites, predation etc. (Levings, 1983; Levings and Windsor, 1984; Basu, 2006) making the availability of this resource unpredictable. This may partially explain the limited territorial aggression of Ovenbirds in this study since it could be beneficial to keep territorial boundaries fluid when food resources become patchy in both time and space. The high degree of overlap observed among the home ranges of sedentary birds further supports this prediction.

#### *Factors Influencing Territory Acquisition*

Age and migratory origin appeared to have the greatest influence on autumn territory acquisition. Although these factors were not directly related, it was found that 90% of non-territorial birds were in their hatch year and, although not significant, possessed lighter  $\delta D$  values than HY territorial birds. A previous mid-winter study of Ovenbirds in Jamaica found no relationship among age and territorial status (Brown and Sherry, 2008) however this could have been the result of breeding origin and seasonality. Norris et al. (2006) found that wintering populations of American Redstarts in the Greater Antilles were from more southern breeding origins as compared with birds wintering through Mexico and Belize. Since our population of Ovenbird had breeding origins in the Northwest, Midwest and Northeast it is expected that

migratory distance to the wintering grounds would be greater, more variable, and more likely to impact territory acquisition when compared with the short migration of a southern breeding population.

Although not directly tested, the effect of age on wintering territorial strategy may have been due to social dominance. Stutchbury (1994) found that HY hooded warblers were excluded from winter territory by adult birds. If age biased social dominance occurred in this study and HY birds of Northern origin arrived later to the wintering grounds (Kelly, 2006) both social structure and unavailable habitat could lead to the adoption of a wandering strategy. While the effect of sex was not found to contribute to territory acquisition as predicted, the skewed sex ratio found in this study points to latitudinal sexual segregation. Komar et al. (2005) compared sex ratios of wintering Ovenbird among sites in Mexico and Southern Central America and found that males were in greater abundance in the north and that females were in greater abundance in the south. In this study HY males possessed larger territories than HY females which could explain the skewed sex ratio, if more females migrated to southern wintering locations to avoid male competition.

#### *Parasite Infection and Territory Status*

Of the factors explored in this study, malarial infection appeared to have little effect on territory acquisition and was not associated with the other factors. On arrival, the prevalence of malaria was among one of the highest rates (45.8%) recorded in a study examining wintering migrants in the Caribbean. Garvin et al. (2004) used blood smears and found that early in the wintering period only 5% of American Redstarts had a malarial infection which disappeared when resampling in the spring. The use of blood smears, however, has been shown to under-

estimate prevalence when compared with PCR (Fallon and Ricklefs, 2008) and therefore my study represents one of the few to accurately measure infection on arrival. Since parasites typically retreat to the spleen and liver during the wintering period (Valkiunas, 2005), dry season studies typically record little infection among migrants even though on arrival infection may be quite high. Despite an infection rate of nearly one half early in the season, malarial prevalence did not interact with other mechanisms to affect territory acquisition.

This study cannot rule out the negative consequences associated with Malaria since I only sampled individuals able to reach the wintering grounds. If malarial infection is high during breeding and fall migration, the effects of these parasites may have large impacts on survival. Furthermore, although infection did not seem to affect the measure of interest (i.e. territory acquisition), PCR is able to detect the slightest of infections. It is possible that parasitic load rather than prevalence could have been highly variable and an important factor influencing early social competition. Future studies should examine both the effects of parasitic prevalence using a simple PCR screen followed by qPCR parasitic load measurements to quantify the level of infection (Bentz et al. 2006). To test the effects of malaria on autumn territory acquisition an experimental treatment of these parasites could be performed in a subset of birds. Studies which experimentally treat avian infection are often better able to predict the associated costs of disease (Atkinson et al. 2000; Merino et al. 2000).

### *Energetic Condition and Survival*

In this study the body condition of juvenile birds was significantly lower than adults and as predicted the body condition of territory owners was higher than that of non-territorial birds. Body condition was measured following territory acquisition and therefore may have reflected both the cumulative costs of migration and autumn social competition as well as the conditions

following territory acquisition. Regardless of territory status HY birds were in poorer condition than adults which could have been due to less effective foraging at stopovers, slower migration speeds, and reduced fat deposition when leaving the breeding grounds (Wunderle, 1991; Ellegren, 1993; Heise and Moore, 2003). For instance, Yong et al. (1998) discovered that immature Wilson's Warblers captured during fall migration had fewer fat stores and were less likely to cope with habitat alterations, both of which resulted in longer stopover periods.

The poor body condition of HY birds would put them at a disadvantage when attempting to acquire winter territory which was reflected in the greater number of HY non-territorial birds. In addition to poor condition and perhaps social subordination of juveniles (e.g. Stutchbury 1994, Marra, 2000), migratory distance may have been a factor affecting territorial status. Since non-territorial HY birds had longer migration distance they may have been exposed to greater costs (e.g. increased exposure to habitat alteration, competition at stopover sites etc.) that could carry-over to non-breeding and impact territory acquisition.

Measures of corticosterone were taken following social competition and therefore represent levels of stress associated with territorial status. In this study both baseline and elevated CORT titres were not associated with the other factors and did not differ with territorial status during the month of October. Marra and Holberton (1998) found that regardless of habitat type, early wintering American Redstarts had baseline CORT titres at similar concentrations as well as substantial increases in elevated CORT titres following handling. In spring, however, individuals in poor quality habitat had higher levels of baseline CORT, and were unable to mount a strong elevated response. Perhaps a similar pattern exists among territorial and non-territorial birds whereby only later in the season are the cumulative costs of being non-territorial detected via a stress mediated response. While not significant, baseline

CORT titres of wanderers were higher than those of sedentary birds. The reduced foraging rate and poorer body condition among wanderers may have triggered this response which would likely intensify throughout the wintering period (Marra and Holberton, 1998). Since no pattern was observed in the acute corticosterone response it is possible that the effects of higher baseline stress had not yet become detrimental to survival (Kitaysky et al. 2003).

### *Conclusion*

Since survival was 100% over the study period and insect availability among space use strategies did not differ, several conclusions regarding this stage of the wintering period can be made. The early arrival transition period coincides with the later part of the wet season which may be indirectly beneficial for non-territorial birds. It is believed that over the course of the wintering period insect resources become more limited, which may in turn influence levels of territory aggression (Smith, 2011b). In the case of non-territorial birds this could cause a further reduction in body condition. Therefore, the early stages of wintering may represent low costs of wandering, since non-territorial birds' food resources are greatest and defence from conspecifics is reduced. In this study the proportion of floaters was greater than previous mid-winter estimates and individuals were actively seeking territory early in the season. Future studies should investigate spatial use pattern throughout the entirety of the overwintering cycle so that changes in territory defence, insect abundance, foraging pattern, and most importantly proportion of wanderers can be monitored.

This study illustrates the importance of a multivariate approach since multiple factors contributed to autumn territory acquisition. Although territory acquisition appeared to be influenced by age and relative breeding origin, elsewhere on the wintering grounds other

mechanisms may be at work. In addition to variation at geographically distinct wintering areas it is expected that patterns of territory acquisition will differ across habitat (both degraded and pristine). Fine scale mapping of migratory connectivity (Stutchbury et al. 2009), combined with studies of how habitat quality affects different wintering populations is needed to assess how extensive habitat loss and alteration in the tropics will impact the population dynamics of migratory birds. Understanding where unique breeding populations winter and the fitness consequences of arrival date, will give us strong predictive power in assessing which wintering regions are most vulnerable and thus should be targets for conservation efforts.

## References

- Angelier, F., Holberton, R.L., and Marra, P.P. 2009. Does Stress Response Predict Return Rate in a Migratory Bird Species? A Study of American Redstarts and their Non-Breeding Habitat. *Proceedings of the Royal Society B*, 276: 3545-3551.
- Angelier, F., Tonra, C.M., Holberton, R.L., and Marra, P.P. 2010. How to Capture Wild Passerines Species to Study Baseline Corticosterone Levels. *Journal of Field Ornithology*. 151: 415-422.
- Astheimer, L. B., Buttemer, W. A., and Wingfield, J. C. 1992. Interactions of Corticosterone With Feeding, Activity and Metabolism in Passerine Birds. *Ornis Scandinavica*, 23: 355–365.
- Atkinson, C.T., Dusek, R.J., Woods, K.L., Iko, W.M. 2000. Pathogenicity of Avian Malaria in Experimentally-Infected Hawaii Amakihi. *Journal of Wildlife Diseases*, 36: 197-204.
- Barlow, J., Haugaasen, T., and Peres, C.A. 2002. Effects of Ground Fires on Understory Bird Assemblages in Amazonian Forests. *Biological Conservation*, 105: 157-169.
- Basu, P. 2006. Seasonal and Spatial Patterns in Ground Foraging Ants in a Rainforest in the Western Ghats, India. *Biotropica*, 29: 489-500.
- Bearhop, S., Hilton, G.M., Votier, S.C., and Waldron, S. 2004. Stable Isotope Ratios Indicates that Body Condition in Migrating Passerines is Influenced by Winter Habitat. *Biological Sciences*. 271: 215-218.
- Bentz, S., Rigaud, T., Barroca, M., Martin-Laurent, F., Bru, D. , Moreau, J., and Faivre, B. 2006. Sensitive Measure of Prevalence and Parasitaemia of Haemosporidia from European Blackbird (*Turdus merula*) Populations: Value of PCR-RFLP and Quantitative PCR. *Parasitology*, 133: 685-692.
- Borger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., and Coulson, T. 2006. Effects of Sampling Regime on the Mean and Variance of Home Range Size Estimates. *Journal of Animal Ecology*, 75: 1393-1405.
- Bowen, G.J., Wassenaar, L.I., and Hobson, K.A. 2005. Global Application of Stable Hydrogen and Oxygen Isotopes to Wildlife Forensics. *Oecologia*, 143: 337-348.
- Brown, D. R., and Long, J. A. 2006. Experimental Fruit Removal Does not Affect Territory Structure of Wintering Hermit Thrushes. *Journal of Field Ornithology*. 77: 404–408.
- Brown, D.R., and Long, J.A. 2007. What is a Winter Floater? Causes, Consequences, and Implications for Habitat Selection. *The Cooper Ornithology Society*. 109: 548-565.
- Brown, D.R., and Sherry, T.W. 2008. Alternative Strategies of Space Use and Response to Resource Change in a Wintering Migrant Songbird. *Behavioral Ecology*. 19: 1314-1325.

Brown, D.R., Stouffer, P.C., and Strong, C.M. 2000. Movement and territoriality of wintering Hermit Thrushes in southeastern Louisiana. *Wilson Bulletin*. 112: 347–353.

Brown, J.L. 1969. Territorial Behaviour and Population in Birds a Review and Re-evaluation. *Wilson Bulletin*. 81: 293-329.

Buskirk, R.E., and Buskirk, W.H. 1986. Changes in Arthropod Abundance in a Highland Costa Rican Forest. *American Midland Naturalist*. 95: 288-298.

Chamberlain, C.P., Blum, J.D., Holmes, R.T., Feng, X., Sherry, T.W., and Graves, G.R. 1997. The Use of Isotope Tracers for Identifying Population of Migratory Birds. *Oecologia*, 109: 132-141.

Davidar, P., and Morton, E.S. 2006. Are Multiple Infections More Severe for Purple Martins (*Progne subis*) than Single Infections? *The Auk*. 123: 141-147.

Ellegren, H. 1993. Speed of Migration and Migratory Flight Lengths of Passerines Birds Ringed During Autumn Migration in Sweden. *Ornis Scandinavica*, 24: 220-228.

Fallon, S.M., Ricklefs, R.E., and Swanson, B.L., and Bermingham, E. 2003. Detecting Avian Malaria: An Improved PCR Diagnostics. *Journal of Parasitology*, 89: 1044-1047.

Fallon, S.M., and Ricklefs, R.E. 2008. Parasitemia in PCR-Detected Plasmodium and Haemoproteus Infections in Birds. *Journal of Avian Biology*, 39: 514-522.

Garvin, M.C., Marra, P.P., and Crain, S.K. 2004. Prevalence of Hematozoa in Overwintering American Redstarts (*Setophaga ruticilla*): No Evidence for Local Transmission. *Journal of Wildlife Diseases*, 40: 115-118.

Garvin, M.C., Szell, C.C., and Moore, F.R. 2006. Blood Parasites of Nearctic-Neotropical Migrant Passerine Birds During Spring Trans-Gulf Migration: Impact on Host Body Condition. *Journal of Parasitology*. 92: 990-996.

Greenberg, R., and Salewski, V. 2005. Ecological Correlates of Wintering Social Systems in New World and Old World Migratory Passerines in R. Greenberg and P. P. Marra, editors. *Birds of two worlds: ecology and evolution of migration*. Johns Hopkins University Press, Baltimore.

Heise, C.D., and Moore, F.R. 2003. Age-Related Differences in Foraging Efficiency, Molt, and Fat Deposition of Gray Catbirds Prior to Autumn Migration. *The Condor*, 105: 496-504.

Hobson, K.A. 2005. Stable Isotopes and the Determination of Avian Migratory Connectivity and Seasonal Interactions. *The Auk*. 122: 1037-1048.

Hobson, K.A., and Wassenaar, L.I. 1997. Linking Breeding and Wintering Grounds of Neotropical Migrants Songbirds Using Stable Hydrogen Isotope Analysis of Feathers. *Oecologia*, 109: 142-148.



Holmes, R.T., Sherry, T.W., and Reitsma, L. 1989. Population Structure, Territoriality, and Overwinter Survival of Two Migrant Warbler Species in Jamaica. *Condor*. 91: 545-561.

Hooge, P.N., and Eichenlaub, B. 2000. Animal Movement Extension to ARCVIEW, version 2.0. Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage. [Online.] Available at [alaska.usgs.gov/science/biology/spatial/gistools/index.php/](http://alaska.usgs.gov/science/biology/spatial/gistools/index.php/).

Howell, D.L., and Chapman, B.R. 1997. Home Range and Habitat Use of Red-Shouldered Hawks in Georgia. *Wilson Bulletin*, 109: 131-144.

James, F.C., and Shugart, H.H. 1970. A quantitative Method of Habitat Description. *Audubon Field Notes*, 24: 727-736.

Jones, J., Norris, R.D., Girvan, K.M., Barg, J.J., Kyser, K.T., and Robertson, R.J. 2008. Migratory Connectivity and Rate of Population Decline in a Vulnerable Songbird. *The Condor*, 110: 538-544.

Kahn, N.W., and St. John, J., and Quin, T.W. 1998. Chromosome-Specific Intron Size Differences in the Avian CHD Gene Provide an Efficient Method for Sex Identification in Birds. *Auk*, 115: 1074-1078.

Kelly, J.F. 2006. Stable Isotope Evidence Links Breeding Geography and Migration Timing in Wood Warblers (Parulidae). *Auk*, 123: 431-437.

Kitaysky, A.S., Kitaishkaia, E.V., Piatt, J.F., Wingfield, J.C. 2003. Benefits and Costs of Increased Corticosterone Secretion in Seabird Chicks. *Hormone Behaviour*. 43: 140-149.

Kokko, H. 1999. Competition for Early Arrival in Migratory Birds. *Journal of Animal Ecology*. 68: 940-950.

Koronkiewicz, T.J., Sogge, M.K., Van Ripper III, C., and Paxton, E.H. 2006. Territoriality, Site Fidelity, and Survivorship of Willow Flycatchers Wintering in Costa Rica. *The Condor*, 108: 558-570.

Latta, S.C., and Faaborg, J. 2002. Demographic and Population Responses of Cape May Warblers Wintering in Multiple Habitats. *Ecology*. 83: 2502-2515.

Lefebvre, G., and Poulin, B. 1996. Seasonal Abundance of Migrant Birds and Food Resources in Panamanian Mangrove Forests. *The Wilson Bulletin*. 108: 748-759.

Levings, S.C. 1983. Seasonal, Annual, and Among-site Variation in the Ground Ant Community of a Deciduous Tropical Forest: Some Causes of Patchy Species Distributions. *Ecological Monographs*, 53: 435-455.

Levings, S.C., and Windsor, D.M. 1984. Litter Moisture Content as a Determinant of Litter Arthropod Distribution and Abundance During the Dry Season on Barro Colorado Island, Panama. *Biotropica*, 16: 125-131.

- Lopez, G., and Moro, M.J. 1997. Birds of Aleppo Pine Plantation in South-East Spain in Relation to Vegetation Composition and Structure. *The Journal of Applied Ecology*. 34: 1257-1272.
- Lozano, G.A., Perreault, S., and Lemon, R.E. 1996. Age, Arrival Date, and Reproductive Success of Male American Redstarts *Setophaga ruticilla*. *Journal of Avian Biology*. 27: 164-170.
- Lynch, J.F., Morton, E.S., and Van Der Voort, M.E. 1985. Habitat Segregation Between the Sexes of Wintering Hooded Warblers (*Wilsonia citrina*). *Auk*. 102: 714-721.
- Marra, P.P. 2000. The Role of Behavioral Dominance in Structuring Patterns of Habitat Occupancy in a Migrant Bird During the Non-Breeding Period. *Behavioural Ecology*, 11: 299-308.
- Marra, P.P., and Holberton, R.L. 1998. Corticosterone Levels and Indicators of Habitat Quality: Effect of Habitat Segregation in a Migratory Bird During the Non-Breeding Season. *Oecologia*. 116: 284-292.
- Marra, P.P., Sherry, T.W., and Holmes, R.T. 1993. Territorial Exclusion by a Long-Distance Migrant Warbler in Jamaica: A Removal Experiment with American Redstarts (*Setophaga ruticilla*). *The Auk*. 110: 565-572.
- Marra, P.P., Hobson, K.A., and Holmes, R.T. 1998. Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. *Science*. 282: 1884-1886.
- Mazerolle, D.F., and Hobson, K.A. 2005. Estimating Origins of Short-Distance Migrant Songbirds in North America: Contrasting Influences from Hydrogen Isotope Measurements of Feathers, Claws, and Blood. *The Condor*, 107: 280-288.
- McGlynn, T.P., Sallnas, D.J., Dunn, R.R., Wood, T.E., Lawrence, D., and Clark, D.A. 2007. Phosphorus Limits Tropical Rain Forest Litter Fauna. *Biotropica*, 39: 50-53.
- Merino, S., Moreno, J., Sanz, J.J., and Arriero, E. 2000. Are Avian Blood Parasites Pathogenic in the Wild? A Medication Experiment in Blue Tits (*Parus caeruleus*). *Proceedings: Biological Science*, 267: 2507-2510.
- Moller, A.P., de Lope, F., and Saino, N. 2004. Parasitism, Immunity, and Arrival Date in a Migratory Bird, the Barn Swallow. *Ecology*. 85: 206-219.
- Morton, E.S. 1976. The Adaptive Significance of Dull Coloration in Yellow Warblers. *Condor*, 78: 423.
- Morton, E.S., Lynch, J.F., Young, K., and Mehlhop, P. 1987. Do Male Hooded Warblers Exclude Females from Nonbreeding Territories in Tropical Forest? *The Auk*. 104: 133-135.
- Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W., and Ratcliffe, L.M. 2004. Tropical Winter Habitat Limits Reproductive Success on the Temperate Breeding Grounds in a Migratory Bird.

Proceedings of the Royal Society B. 271: 58-64.

Norris, R.D., Marra, P.P., Bowen, G.J., Ratcliffe, L.M., Royle, A.J., and Kyser, K.T. 2006. Migratory Connectivity of a Widely Distributed Songbird, the American Redstart (*Setophaga ruticilla*). Ornithological Monographs, 61: 14-28.

Ornat, L.A., and Greenberg, R. 1990. Sexual Segregation by Habitat in Migratory Warblers in Quintana Roo, Mexico. Auk, 107: 539-543.

Parr, C.L., and Chown, S.L. 2001. Inventory and Bioindicator Sampling: Testing Pitfall and Winkler Methods with Ants in a South African Savanna. Journal of Insect Conservation, 5: 27-36.

Parrish, J.D., and Sherry, T.W. 1994. Sexual Habitat Segregation by American Redstarts Wintering in Jamaica: Importance of Resource Seasonality. The Auk. 111: 38-49.

Pyle, P. 1997. Identification Guide to North American Birds. Bolinas, California. Slate Creek Press.

Rappole, J.H. AND Tipton, A.R. 1991. New Harness Design for Attachment of Radio Transmitters to Small Passerines. Journal of Field Ornithology, 62: 335-337.

Rappole, J.H., Ramos, M.A., and Winker, K. 1989. Movements and Mortality in Wintering Wood Thrushes. Auk. 106: 402-410.

Reitsma, L., Hunt, P., Burson, S.L., and Steele, B.B. 2002. Site Fidelity and Ephemeral Habitat Occupancy: Northern Waterthrush Use of Puerto Rican Black Mangroves During the Non-Breeding Season. Wilson Bull, 114: 99-105.

Royle, J.A., and Rubenstein, D.R. 2004. The Role of Species Abundance in Determining Breeding Origins of Migratory Birds with Stable Isotopes. Ecological Applications, 14: 1780-1788.

Samuel, M.D., Pierce, D.J., and Garton, E.O. 1985. Identifying Areas of Concentrated Use within the Home Range. Journal of Animal Ecology, 54: 711-719.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., and Gitzen, R.A. 1999. Effects of Sample Size on Kernel Home Range Estimates. Journal of Wildlife Management, 63: 739-747.

Sherry, T.W., and Holmes, R.T. 1996. Winter Habitat Quality, Population Limitation, and Conservation of Neotropical-Nearctic Migrant Birds. Ecology. 77: 36-48.

Silverin, B. 1998. Behavioural and Hormonal Responses of Pied Flycatchers to Environmental Stressors. Animals Behaviour, 55: 1411-1420.

Smith, J.A., Reitsma, L.R., and Marra, P.P. 2011a. Multiple Space-Use Strategies and Their Divergent Consequences in a Nonbreeding Migratory Bird (*Parkesia noveboracensis*). The

Auk. 128: 53-60.

Smith, J.A.M., Reitsma, L.R., and Marra, P.P. 2011b. Influence of Moisture and Food Supply on the Movement Dynamics of a Nonbreeding Migratory Bird (*Parkesia noveboracensis*) in a Seasonal Landscape. *The Auk*. 128: 43-52.

Smith, S. 1978. The Underworld in a Territorial Sparrow- Adaptive Strategy for Floaters. *American Naturalist*, 112: 571-582.

Smith, S.M. 1984. Flock Switching in Chickadees: Why be a Winter Floater? *American Naturalist*. 123: 81-98.

Sogge, M.K., Koronkiewicz, T.J., Van Ripper III, C., and Durst, S.L. 2007. Willow Flycatcher Non-Breeding Territory Defense Behavior in Costa Rica. *The Condor*, 109: 475-480.

SPSS. 2010. SPSS 19.0 for Windows. Release 19.0.0. SPSS, Inc., Chicago, IL.

Strobel, B.N., and Boal, C.W. 2010. Red-Shouldered Hawk Nesting Habitat Preference in South Texas. *Journal of Fish and Wildlife Management*, 1: 33-37.

Strong, A.M. 1999. Effects of Food Abundance on Non-Breeding Habitat Quality for Two Species of Ground-Foraging Neotropical Migrant Warblers. New Orleans, Tulane University, PhD dissertation.

Strong, A.M. 2000. Divergent Foraging Strategies of Two Neotropical Migrant Warblers: Implications for Winter Habitat Use. *The Auk*, 117: 381-392.

Strong, A.M., and Sherry, T.W. 2000. Habitat-Specific Effects of Food Abundance on the Condition of Ovenbirds Wintering in Jamaica. *Journal of Animal Ecology*. 69: 883-895.

Strong, A.M., AND Sherry, T.W. 2001. Body Condition of Swainson's Warblers Wintering in Jamaica and the Conservation Value of Caribbean Dry Forests. *The Wilson Bulletin*. 113: 410-418.

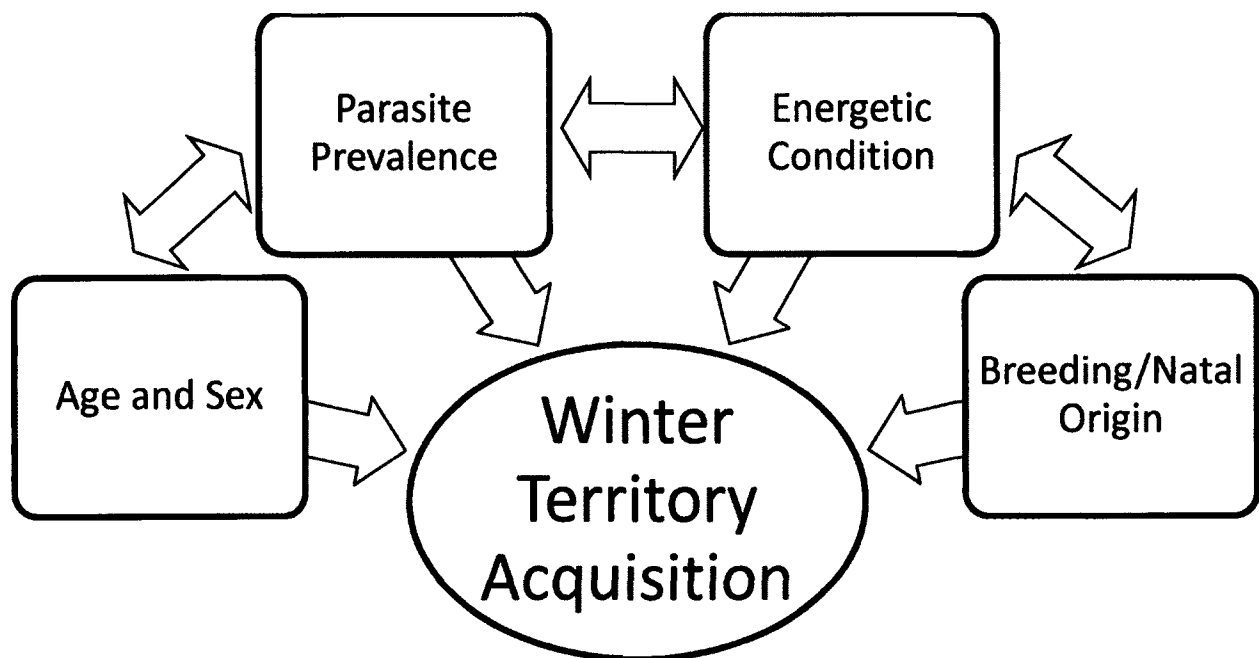
Studds, C.E., and Marra, P.P. 2005. Nonbreeding Habitat Occupancy and Population Processes: An Upgrade Experiment with a Migratory Bird. *Ecology*. 86: 2380-2385.

Stutchbury, B.J.M. 1994. Competition for Wintering Territories in a Neotropical Migrant: The Role of Age, Sex and Color. *The Auk*. 111(1): 63-69.

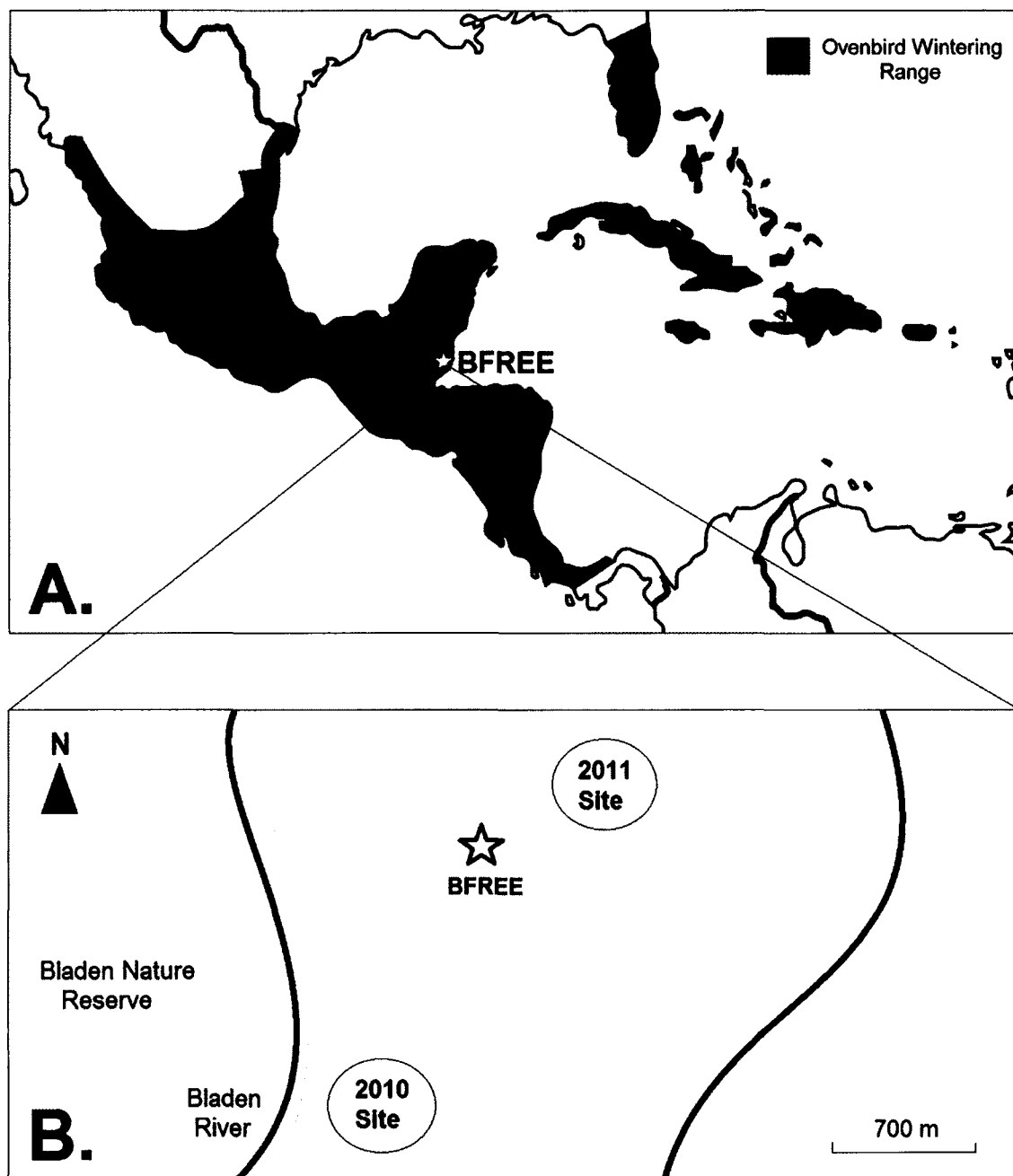
Stutchbury, B.J.M., Tarof, S.A., Done, T., Gow, E., Kramer, P.M., Tautin, J., Fox, J.W., and Afanasyev, V. 2009. Tracking Long-Distance Songbird Migration by Using Geolocators. *Science*. 323: 896.

Townsend, J.M., Rimmer, C.C., and McFarland, K.P. 2010. Winter Territoriality and Spatial Behavior of Bicknell's Thrush (*Catharus bicknelli*) at Two Ecologically Distinct Sites in the Dominican Republic. *The Auk*. 127: 514-522.

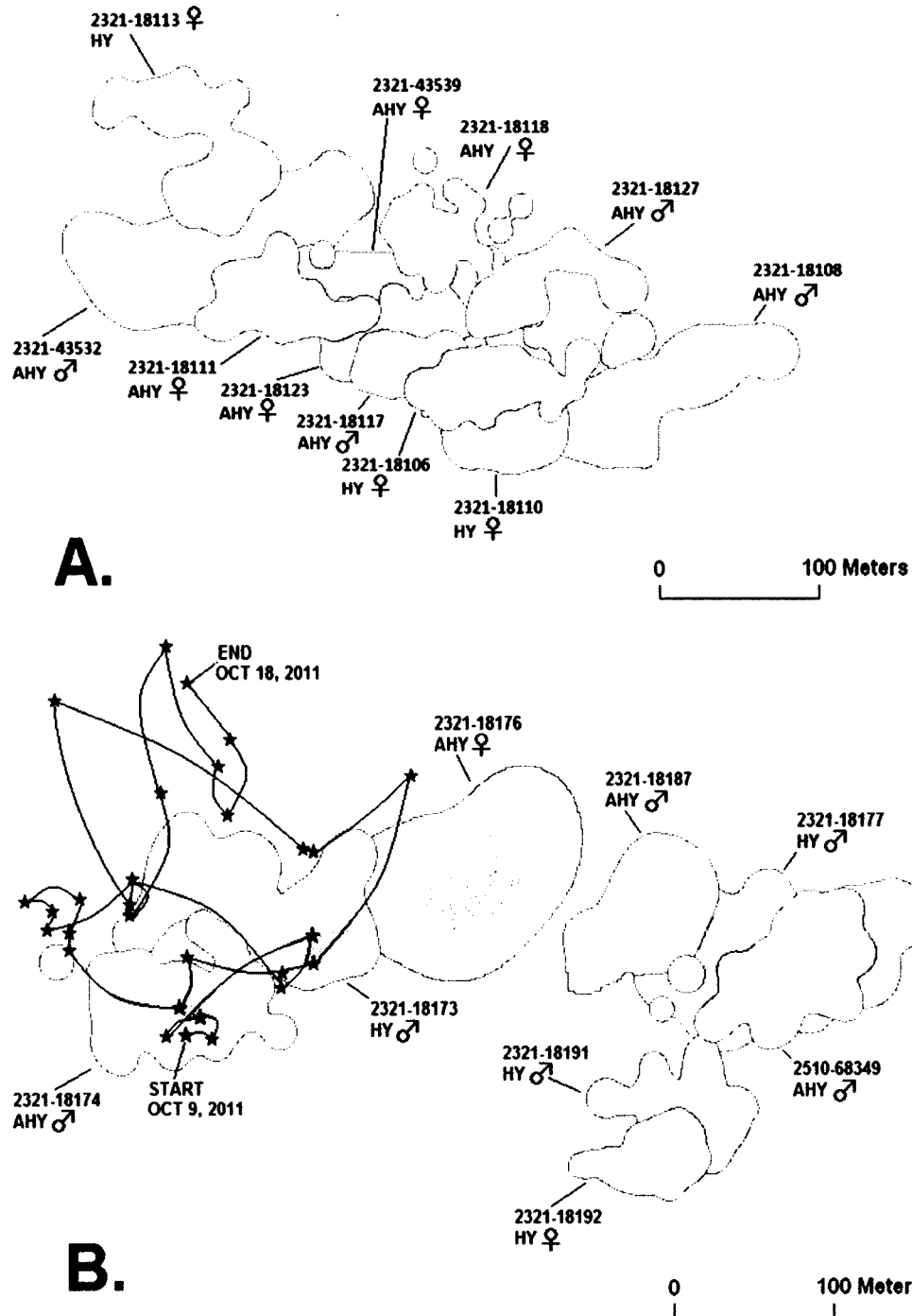
- Valkiunas, G. 2005. Avian Malaria Parasites and Other Haemosporidia. CRC Press, Boca Raton, Florida.
- Van Horn, M.A., Donovan T.M. 1994. Ovenbird. In: Poole, A., Gill, F. The Birds of North America, No. 88. The Acad. of Nat. Sci., Philadelphia and The American Ornithologists, Washington, D.C. pp 1–22
- Washburn, B.E., Millsbaugh, J.J., Faaborg, J., and Schultz, J.H. 2002. Using a Commercially Available Radioimmunoassay to Quantify Corticosterone in Avian Plasma. *The Condor*, 104: 558-563.
- Wassenaar, L.I., and Hobson, K.A. 2001. A Stable Isotope Approach to Delineate Geographical Catchment Areas of Avian Migration Monitoring Stations in North America. *Environmental Science and Technology*, 35: 1845-1850.
- White, G.C., and Garrott, R.A. 1990. Analysis of Wildlife Radio-Tracking Data. San Diego, California. Academic Press.
- Wingfield, J.C., Matt, K.S., and Farner, D.S. 1984. Physiologic Properties of Steroid-Hormone Binding Proteins in Avian Blood. *General and Comparative Endocrinology* 53: 281-292.
- Wingfield, J.C., Vleck, C.M, and Moore, M.C. 1992. Seasonal Changes in the Adrenocortical Response to Stress in Birds of the Sonoran Desert. *Journal of Experimental Zoology*, 264: 419-428.
- Winker, K. 1998. The Concept of a Floater. *Ornitologia Neotropical*. 9: 111–119.
- Winker, K., Rappole, J.H., and Ramos, M.A. 1990. Population Dynamics of the Wood Thrush in Southern Veracruz, Mexico. *The Condor*. 92: 444-460.
- Wolda, H. 1988. Insect Seasonality: Why? *Annual Review of Ecology and Systematics*. 19: 1-18.
- Woodley, S.K., and Moore, M.C. 1999. Female Territorial Aggression and Steroid Hormones in Mountain Spiny Lizards. *Animal Behaviour*, 57: 1083-1089.
- Worton, B.J. 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, 70: 164-168.
- Wunderle, J.M. 1991. Age-Specific Foraging Proficiency in Birds. *Current Ornithology*, 8:273-324.
- Yong, W., Finch, D.M., Moore, F.R., and Kelly, J.F. 1998. Stopover Ecology and Habitat Use of Migratory Wilson's Warblers. *The Auk*, 115: 829-84



**Figure 1.** Multiple factors proposed to influence autumn territory acquisition.



**Figure 2.** A) The study location and wintering range (adapted from Van Horn and Donovan, 1994) of Ovenbird (*Seiurus aurocapillus*). B) A different site was used each year of the study and separated by over 2.5 kilometers.

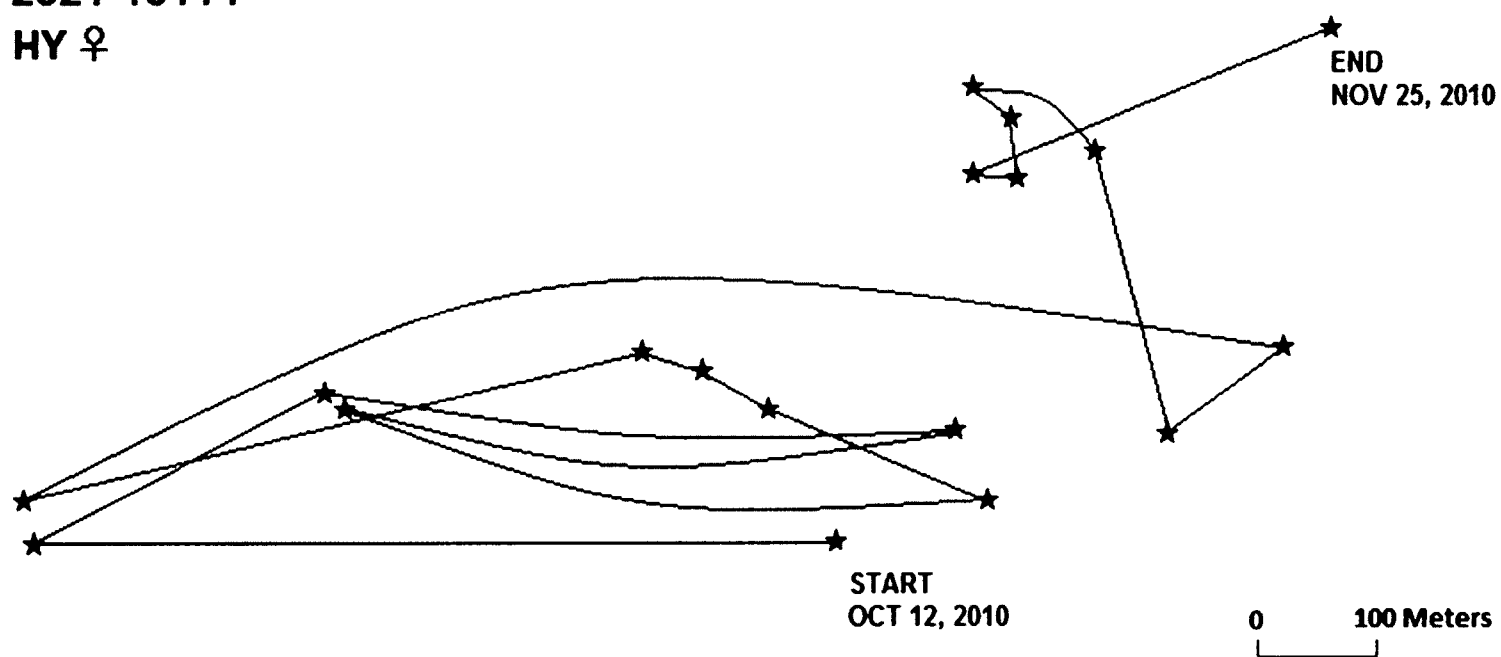


**Figure 3.** A) Fixed home ranges of 11 sedentary Ovenbird in Belize Oct-Nov 2010. Home range size is represented by 90% fixed kernel utilization distributions (UD) and core areas (grey centres) are represented by 50% fixed kernel UD. B) Fixed home ranges of 8 sedentary Ovenbird and the movement of a short distance wanderer (Band ID: 2321-18175) in fall 2011. (★) are locations on different days connected from starting point to endpoint. Tracking was performed in different locations during each year of the study.



**2321-18114**

**HY ♀**

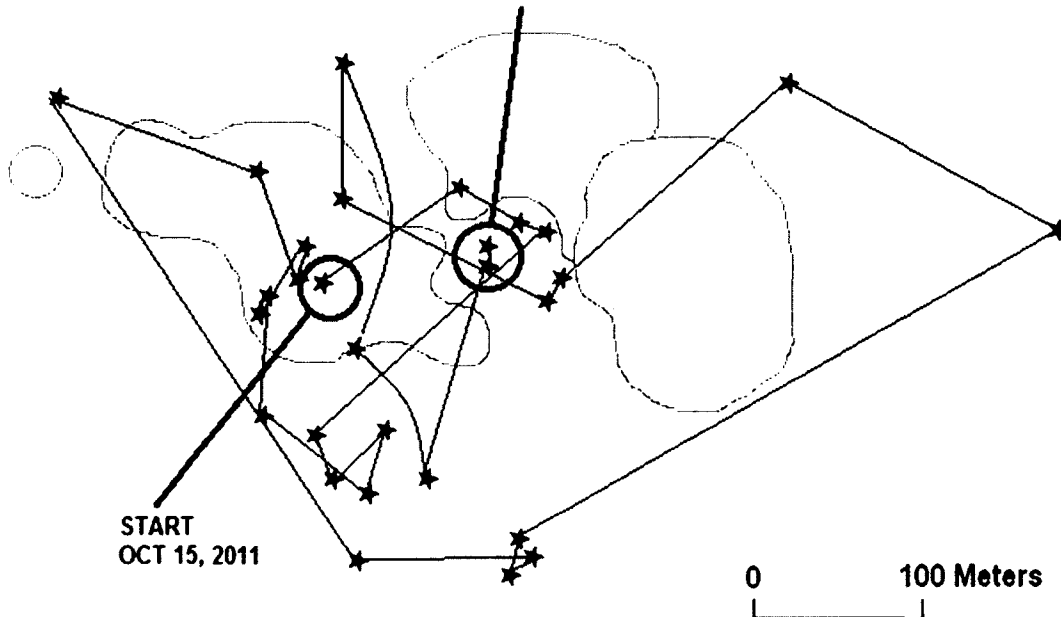


**Figure 4.** Sample movement pattern of a long distance wanderer (Band ID: 2321-18114) in fall 2010. (★) are locations on different days connected from starting point to endpoint.

2321-18185  
HY ♀

TERRITORY ACQUISITION  
OCT 26, 2011

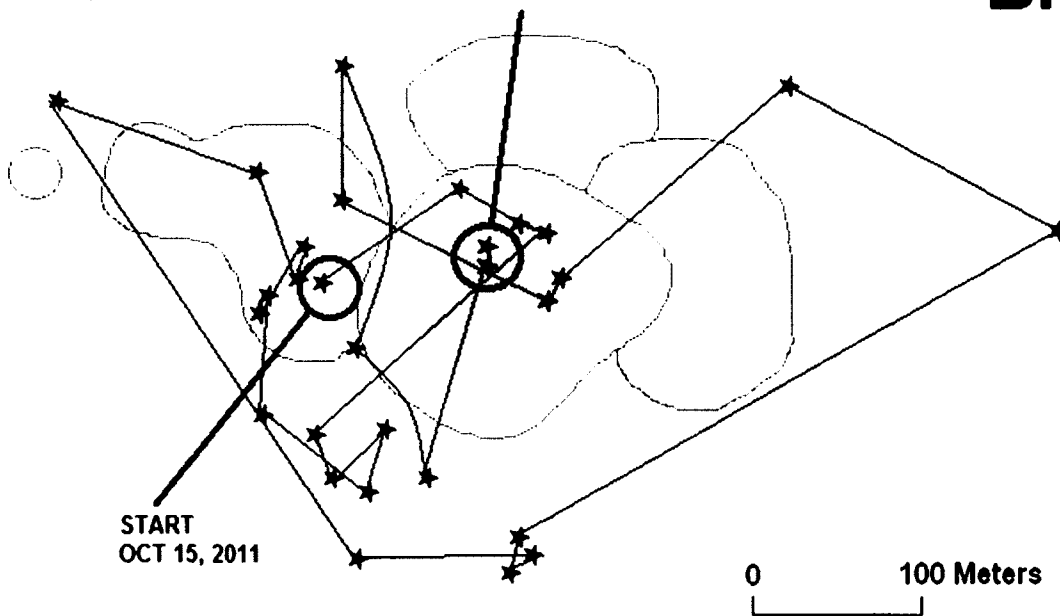
**A.**



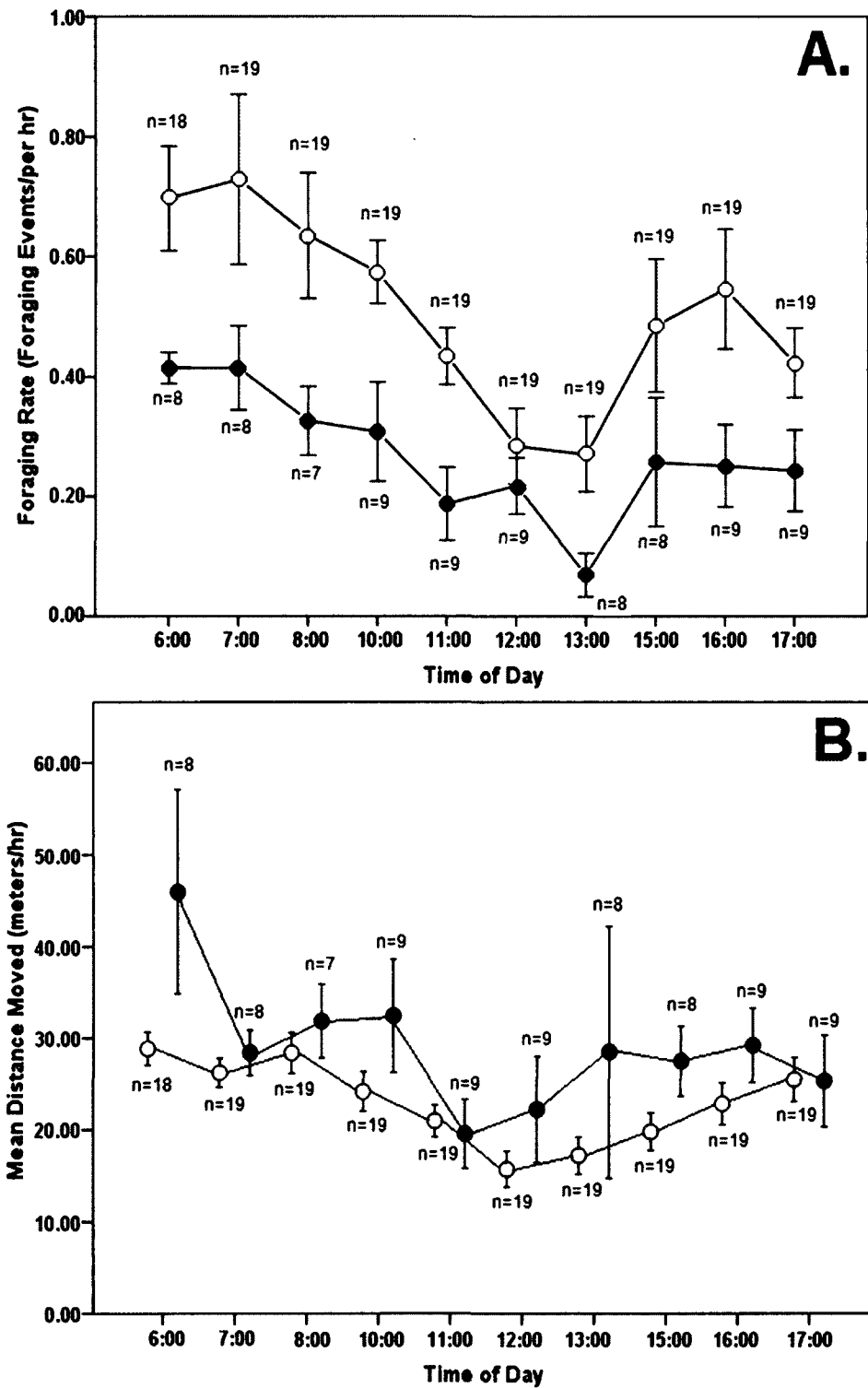
2321-18185  
HY ♀

TERRITORY ACQUISITION  
OCT 26, 2011

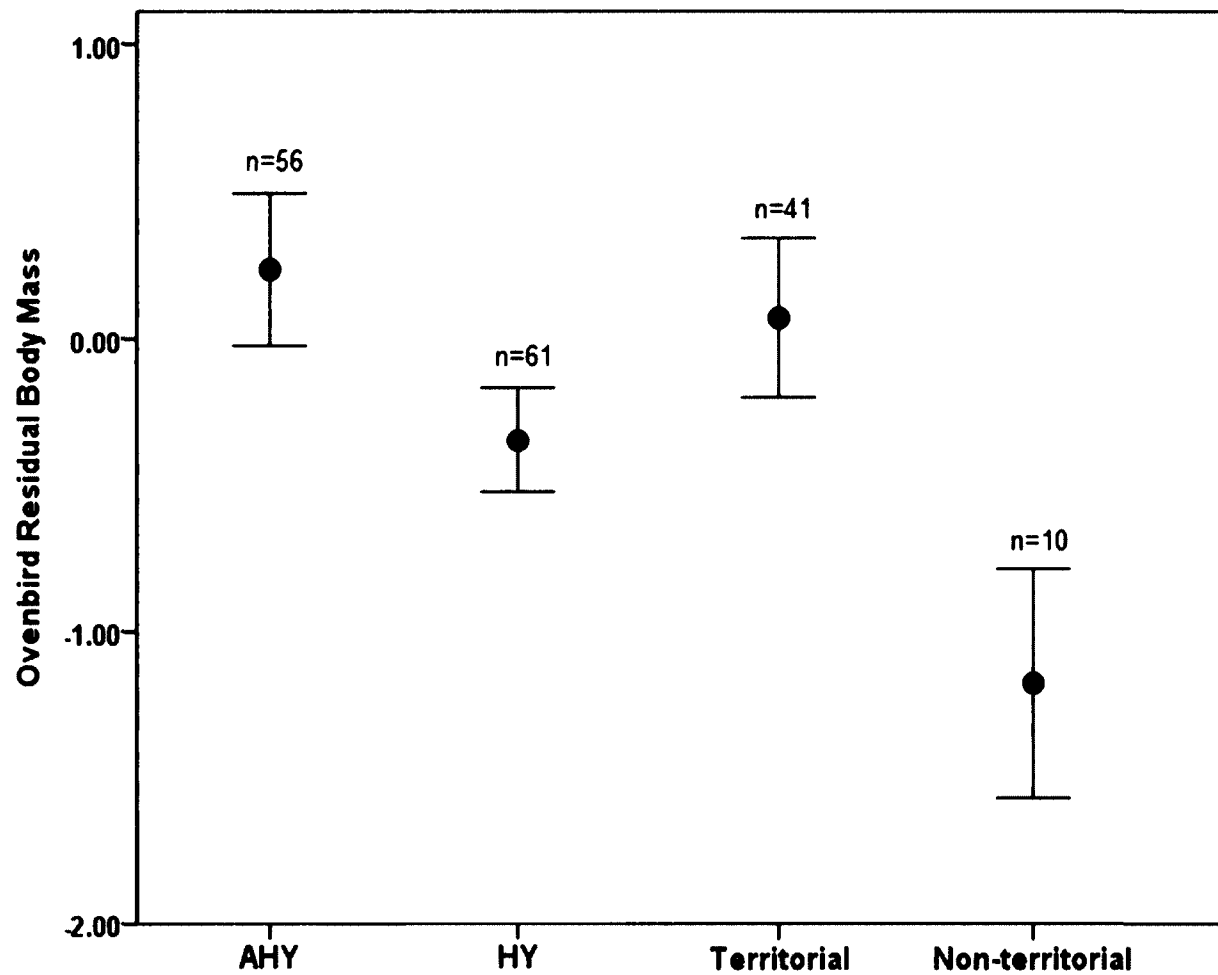
**B.**



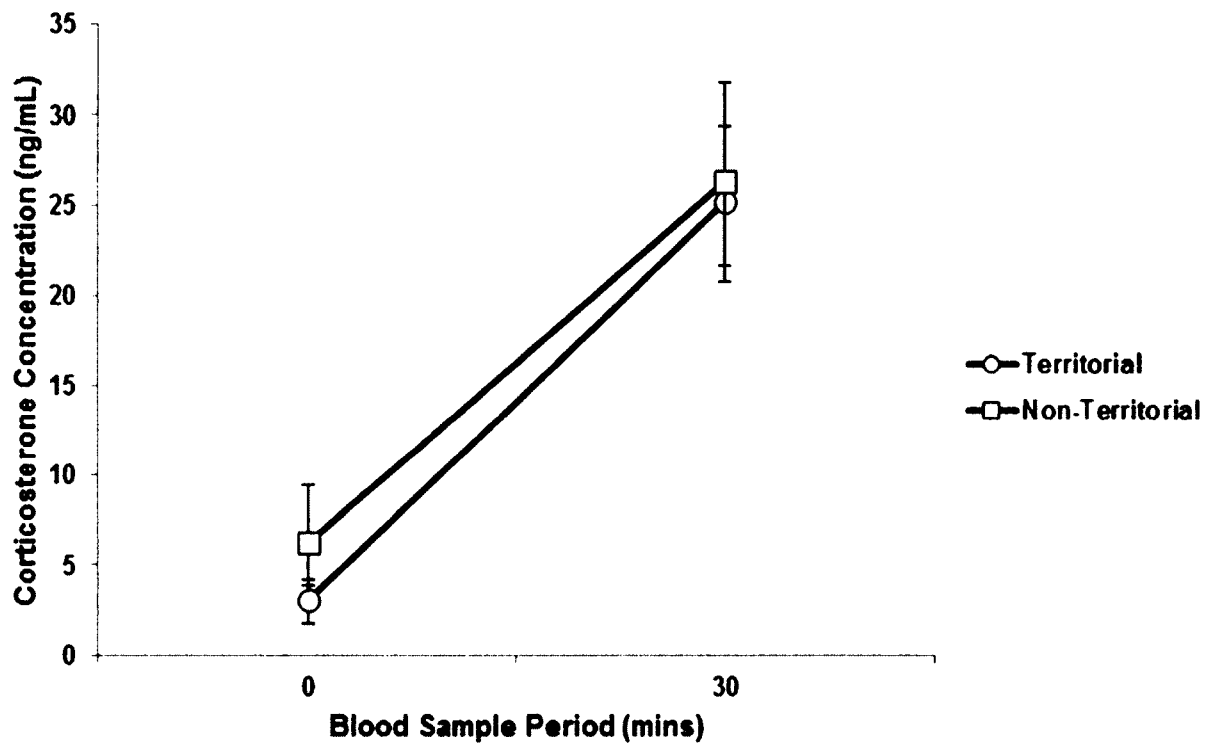
**Figure 5. A)** Short distance wanderer's movements (Band ID: 2321-18185) prior to territory acquisition in fall 2011. (★) Show 2-3 location points per day, and irregular ovals show territory boundaries of sedentary birds during the wanderer's movements. **B)** The territory shown with a core area (grey centre) was claimed by the wanderer and generated using points acquired after October 26, 2011.



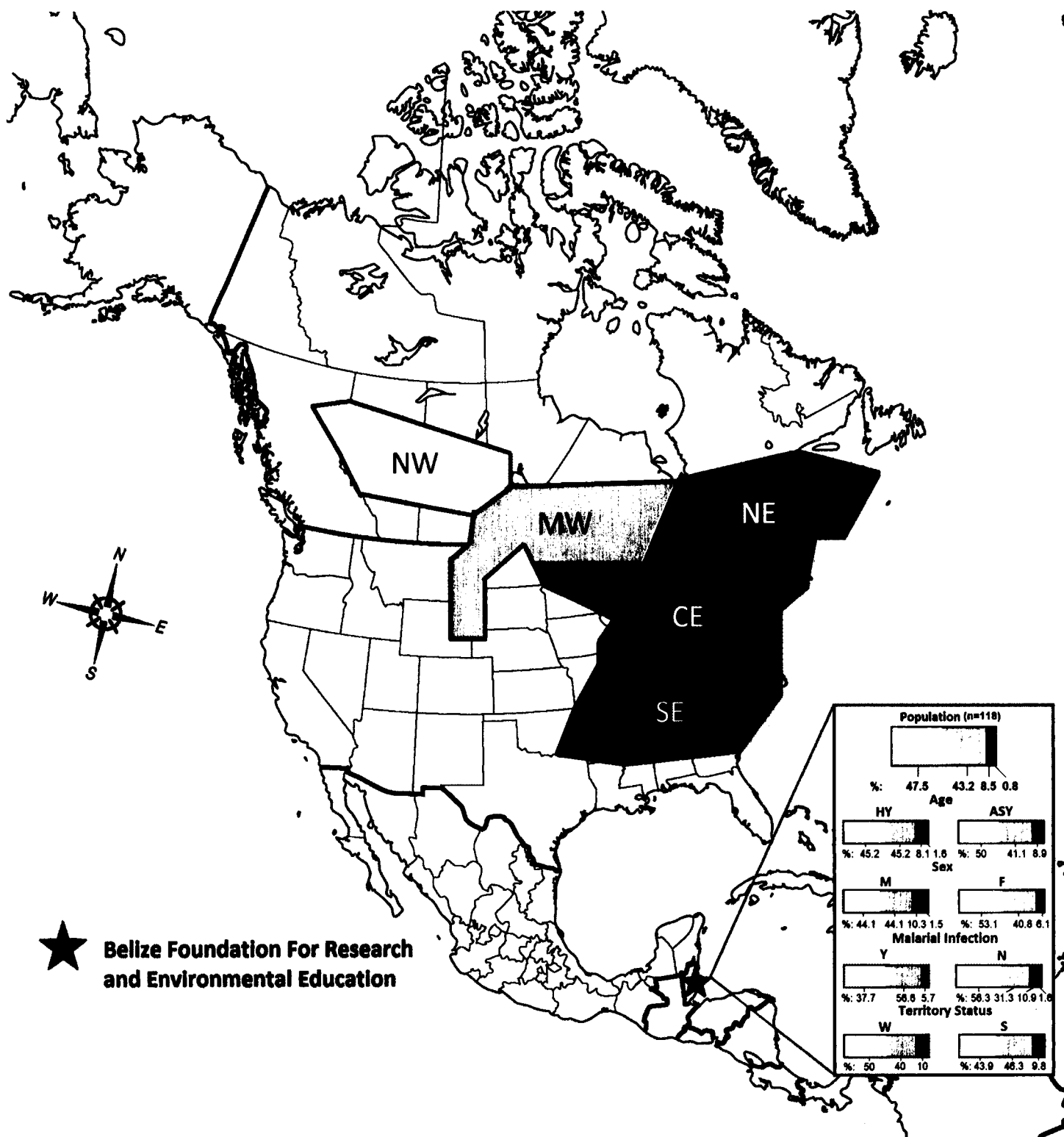
**Figure 6. A)** The foraging rate of sedentary birds (open circles) was significantly higher than that of wanderers (filled circles). Foraging rate of wintering Ovenbirds was greatest in the morning and lowest in the early afternoon. **B)** Mean distance moved changed with time of day but did not differ with spatial use strategy. Values are expressed as mean and standard error.



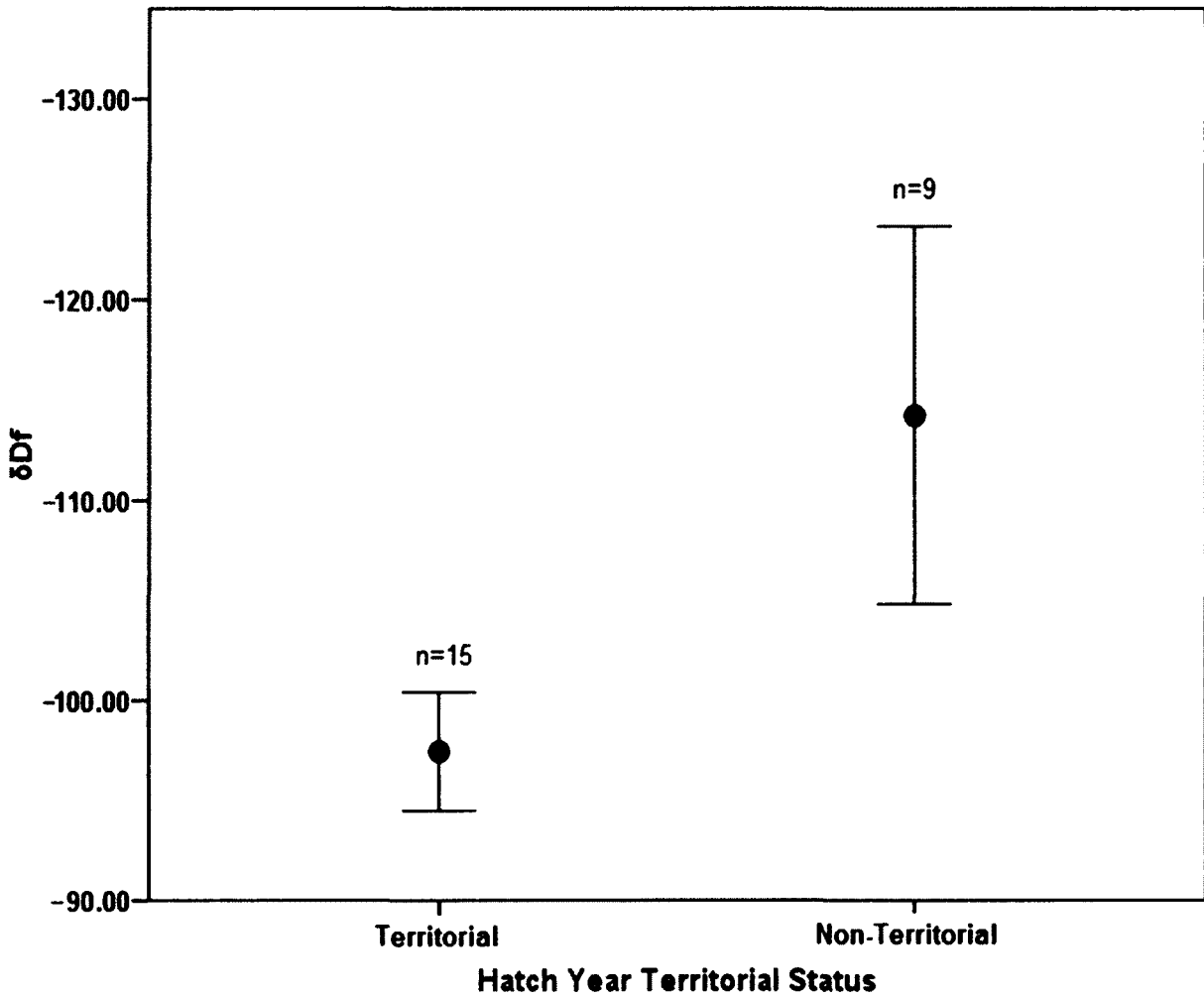
**Figure 7.** Residual body mass of Ovenbirds (observed body mass – predicted body mass) compared across age and territory status. Values are expressed as mean and standard error.



**Figure 8.** Baseline (0 min sample) and elevated (30 min sample) corticosterone titres compared among territorial strategy. Territorial birds are represented by circles (baseline: n=19. elevated: n=25) and non-territorial birds are represented by squares (baseline: n=8. elevated: n=8). Values are expressed as mean and standard error.



**Figure 9.** The breeding region of Ovenbird was divided into geographic bins based on data available from the Breeding Bird Survey and prior knowledge of North American patterns of  $\delta D$  in precipitation. Bars represent the relative proportion of individuals belonging to a breeding region within the entire population and among the factors of age, sex, malarial infection, and territory status.



**Figure 10.**  $\delta D$  of Ovenbird P1 feather compared with territorial status (territorial or non-territorial) at the final wintering ground location.

**Table 1.** Summary data of home range, core use, and % neighbour overlap for wintering Ovenbird (Oct-Nov 2010, 2011). Values are expressed as mean and standard error.

	<i>N</i>	Home Range (ha) Area (90% UD)*	Core Use Area (50% UD)*	Range (at 90% UD)	MCP**	% Neighbour Overlap (90% UD)*	% Neighbour Overlap (50% UD)*
<b>Average Sedentary</b>	31	1.05 ± 0.11	0.25 ± 0.03	0.48 - 3.11	1.23 ± 0.21	47.41 ± 6.67	14.46 ± 5.24
Adult Male	11	0.91 ± 0.11	0.21 ± 0.03	0.48 – 1.44	1.19 ± 0.39	41.40 ± 12.52	13.66 ± 7.35
Hatch Year Male	8	1.47 ± 0.32	0.32 ± 0.06	0.72 - 3.11	1.53 ± 0.39	48.16 ± 11.39	15.19 ± 11.69
Adult Female	7	1.00 ± 0.25	0.27 ± 0.09	0.51 – 2.34	1.30 ± 0.59	71.66 ± 14.11	25.23 ± 15.49
Hatch Year Female	5	0.76 ± 0.14	0.18 ± 0.05	0.56 – 1.29	0.73 ± 0.13	25.50 ± 9.06	0
<b>Average Wanderer</b>	9	7.40 ± 2.62		2.79 - 13.14	2.86 ± 1.05		

\* UD = Utilization Distribution

\*\*MCP = Minimum Convex Polygon



**Table 2.** Summary data of Ovenbird age and sex compared with the entire sample population (all birds banded) and spatial use strategy.

		Overall Sample Population (n=118)	Spatial Use Strategy (n=51)	
			Sedentary	Wanderer
Age	HY	62	15	9
	AHY	56	26	1
Sex	Male	68	23	4
	Female	50	17	6

**Table 3.** *Plasmodium* and *Haemoproteus* infection rate (%) of the entire sample population (n=118) was compared with age and sex classes. Infection rate (%) was also compared with spatial use strategy (n=51).

		% infected (n=54)
<b>Age</b>	<b>AHY</b>	55.5 (n=30)
	<b>HY</b>	44.4 (n=24)
<b>Sex</b>	<b>Male</b>	64.8 (n=35)
	<b>Female</b>	35.2 (n=19)
		% infected (n=24)
<b>Space Use Strategy</b>	<b>Sedentary</b>	83.3 (n=20)
	<b>Wanderer</b>	16.6 (n=4)