

The University of Southern Mississippi
The Aquila Digital Community

Honors Theses

Honors College

Spring 5-2019

Age-Related Tick Infestation Patterns in Springtime Migratory Passerines

Matthew Dunning
University of Southern Mississippi

Follow this and additional works at: https://aquila.usm.edu/honors_theses



Part of the [Ecology and Evolutionary Biology Commons](#)

Recommended Citation

Dunning, Matthew, "Age-Related Tick Infestation Patterns in Springtime Migratory Passerines" (2019).
Honors Theses. 657.
https://aquila.usm.edu/honors_theses/657

This Honors College Thesis is brought to you for free and open access by the Honors College at The Aquila Digital Community. It has been accepted for inclusion in Honors Theses by an authorized administrator of The Aquila Digital Community. For more information, please contact Joshua.Cromwell@usm.edu.

The University of Southern Mississippi

Age-Related Tick Infestation Patterns in Springtime Migratory Passerines

by

Matthew Dunning

A Thesis
Submitted to the Honors College of
The University of Southern Mississippi
in Partial Fulfillment
of Honors Requirements

May 2019

Approved by:

Michael Sellers, Thesis Adviser
Instructor of Biological Sciences

Frank R. Moore, Ph.D., Thesis Adviser
Professor Emeritus of Biological Sciences

Jake Schaefer, Ph.D., Director
School of Biological, Environmental, and
Earth Sciences

Ellen Weinauer, Ph.D., Dean
Honors College

Abstract

To test the hypothesis that younger migrants are more prone to arrive at stopover sites on the northern coast of the Gulf of Mexico with ticks than adult migrants, 2177 migratory passerines were screened for ticks at Gulf Coast sites in Texas and Louisiana. Fifty eight (2.7%) were infested with ticks with 28 (1.3%) being young birds and 30 (1.4%) being adult birds. The body condition of the birds was assessed to determine if tick infestation had negative consequences and if the severity of consequences varied between ages. I found no relationship of age with the prevalence of a tick attachment in any of the groups of birds. I also did not detect any consequences on body condition due to tick infestation, with the exception of the warbler group for which mean body mass was significantly lower in tick infested birds. Tick infestation does not seem to vary in young and old migrant birds and infestation alone does not seem to pose a major physiological cost to most migratory passerines.

Key Words: Neotropical migrants, stopover, passerine, tick, host-parasite interaction, ag

Acknowledgements

I would like to thank my advisors Michael Sellers and Dr. Frank Moore for their direction and support throughout this project. Thank you Michael for providing the inspiration for this project. Thank you Dr. Moore for allowing me to assist your lab over the years and for providing me with invaluable research experience. You both have had a major impact on my academic, professional, and personal life, and our interactions were one of the highlights of my experience at Southern Miss.

I am grateful to all the bird banders who collected data at the Louisiana and Texas sites. Thank you Dr. Emily Cohen for providing the 2013 Texas data, Michael Sellers for providing the 2010 Louisiana data, and Dr. T.J. Zenzal for providing the 2018 Louisiana data. All of your contributions made this project possible.

Table of Contents

List of Tables.....	vii
List of Figures.....	viii
List of Abbreviations.....	ix
Chapter 1: Introduction.....	1
Chapter 2: Literature Review.....	2
Chapter 3: Methods.....	5
Chapter 4: Results.....	8
Chapter 5: Discussion.....	10
Literature Cited.....	13

List of Tables

Table 1. The number of migratory birds sampled for ticks that were found to be either infested or non-infested.....	9
--	---

List of Figures

Figure 1. Common locations where immature ticks attach themselves to birds.....	2
Figure 2: Map of the banding location at Johnson’s Bayou, Louisiana.....	6
Figure 3: Map of the banding location at Mad Island March Preserve in Matagorda County, Texas.....	7

List of Abbreviations

AHY	After Hatch Year
ANOVA	Analysis of Variance
ASY	After Second Year
INBU	Indigo Bunting
SY	Second Year
USFWS	United States Fish and Wildlife Service
WOTH	Wood Thrush

Chapter I: Introduction

Migratory songbirds are known to be the host to a great many ectoparasites, including ticks. Ticks will often attach themselves to their avian host to take a blood meal before they transition to the next stage in their lifecycle. Birds act as a dispersal vehicle that can carry ticks over long distances and cross geographical barriers. I studied the relationships between tick infestations and the age of migratory songbirds caught on the northern coast of the Gulf of Mexico at Mad Island, Texas and Johnson's Bayou, Louisiana during the stopover period of their northward migration. These coastal locations were chosen because they provide the first opportunity to examine the presence of ticks and body condition of birds since their departure from the wintering grounds. The events and decisions that transpire at stopover sites can influence the survival and reproductive success of migrants; therefore, it is important to understand if tick parasitism has negative consequences to migration success and whether these consequences are evenly distributed across age class.

Through this project, I answered questions of how tick infestation is distributed across age classes in migratory passerines as well as the body conditions of parasitized vs. non-parasitized birds. I hypothesized that more ticks should be found on second-year (SY) birds than on after-second-year (ASY) birds. I also hypothesized that birds parasitized by ticks should have a poorer body condition than birds without ticks, and I speculated that the response to infestation should be more severe in ASY birds. The results of my study failed to support either hypothesis.

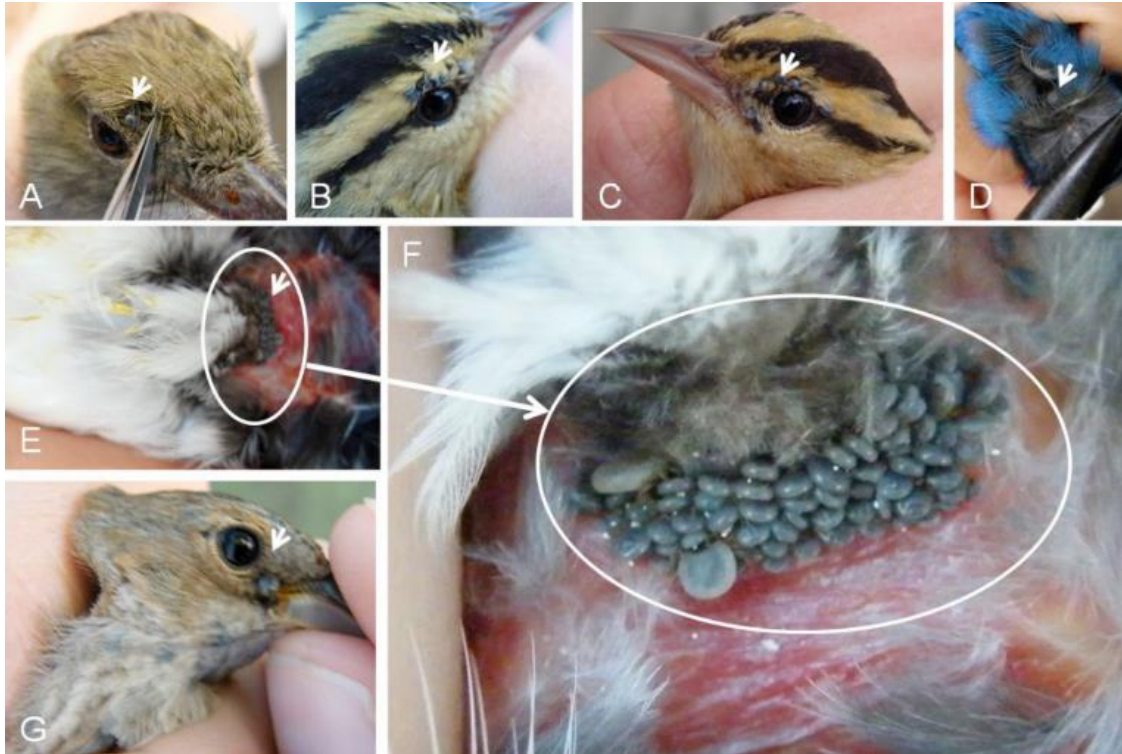


Figure 1: Common locations where immature ticks attach themselves to birds. (A) Acadian flycatcher (*Empidonax virescens*). (B and C) Worm-eating warbler (*Helmitheros vermivorus*). (D and G) Indigo bunting (*Passerina cyanea*). (E and F) Wood thrush (*Hylocichla mustelina*). (Courtesy of Michael Sellers; reproduced with permission.)

Chapter II: Literature Review

Millions of birds migrate between breeding, wintering, and stopover sites every year. Each phase of migration presents its own unique challenge that the birds must overcome. Decisions that birds make on their wintering grounds and stopover sites can have major consequences on survival during migration and reproductive success on the breeding grounds (Sherry and Holmes 1996). Only recently have researchers examined how migrants interact with their environment and other occupants prior to migration (Faabvovg et al. 2010; Sherry and Holmes 1996). One aspect of their migration that is still poorly understood is the parasitic interaction between tropical ticks and neotropical

migratory passerines, and the consequences of the interaction on the bird's body condition during migration.

Ticks require blood meals at different stages of their life, and birds will often serve as the host during the tick's nymph stage (James et al. 2011; Mukherjee et al. 2014). Ticks use a host-finding behavior known as questing, where they will position themselves at the tips of vegetation and wait for a host (Perret et al. 2004). Ticks can lay clutches of eggs in masses of up to 20,000; these clutches will hatch around the same time and have a clumped distribution (Sonenshine 1991; Mukherjee et al. 2014). A tick can remain on a host anywhere from a few hours to a few days once it attaches itself; furthermore, it takes approximately 18-24+ hours for a migratory bird to cross the Gulf of Mexico from the Yucatan, so it is likely that the ticks observed on a bird at a coastal stopover site came from Central and South America (Mukherjee et al. 2014; Bolus et al. 2017).

At least during the nesting season, birds exhibit avoidance behavior in their nest site selection when parasites are present, indicating that they can recognize parasites and will actively choose to avoid that area to nest (Oppliger et al. 1994; Loye and Carroll 1998). It may be the case that birds can recognize ticks and avoid that area for foraging at their wintering grounds. Birds compete individually for foraging territory on the wintering grounds and will tenaciously fight to maintain site dominance by arriving early and maintaining site fidelity (Stutchbury 1994). Previous studies have shown that older birds are more effective at claiming territory and that younger birds are socially subordinate during migration, so it is likely that the SY birds are subjected to poorer quality foraging habitat that contain more tick nests (Moore et al 2003; Stutchbury 1994).

Young birds are also still learning how to forage, so they may spend longer periods of time searching for food, and thus spend longer periods foraging (Franks and Thorogood 2018; Robinson and Holmes 1982; Wunderle 1991). Additionally, younger birds may depart the wintering grounds after older birds either because they cannot compete for breeding territory even with an early advantage or because they are too lean to attempt migration (Stewart et al. 2002). Regardless, the longer duration on the wintering grounds could increase the likelihood of a tick encounter and could be a temporal explanation if more SY birds have ticks. This is a possibility, particularly because the primary questing period for ticks coincides with the springtime migration of songbirds (Battaly et al. 1987). It may be more likely to find a tick on a younger bird because they may be encountering a parasite for the first time on the wintering ground and may not be familiar with different body maintenance behaviors like grooming, water bathing, dusting, and sunning (Clayton et al. 2010).

The basis of my hypothesis is previous research that studied tick infestations in migratory passerines. Mukherjee et al. (2014) and Cohen et al. (2015) collected ticks from migratory songbirds to investigate disease transmission between parasite and host. Both made observations about the frequency of infestation based on foraging guild (e.g. subcanopy/canopy, understory, ground) but neither mentioned age as a factor of infestation (Barrow et al. 2000). Other studies have addressed the hypothesis of an association between age and tick infestation but the results have been inconclusive. Scharf (2004) reported that a higher proportion of hatch-year birds were infested with ticks than their adult counterparts. A similar study by Gregoire et al. (2002) did not find a significant difference between tick prevalence and age but did find a difference in tick

load burden between ages, although this was mostly due to a lack of tick infestations in nestlings. However, comparisons cannot be drawn from these studies because the birds' breeding biology is different than their migration biology. For example, young birds may still depend on their parents for food even after they leave their altricial stage because they are inefficient foragers (Weathers and Sullivan 1989; Wunderle 1991). My interest in this study was the association between the age of migratory birds and tick infestation, and a study by Morris et al. (2007) found evidence of an increased proportion birds parasitized by ticks in the spring compared to the fall, so I therefore focused on springtime migrants at coastal stopover sites

Chapter III: Methods

Study area. During the spring migration season (March 15 - May 15) of 2010 and 2018, birds were captured and sampled for ticks on the northern coast of the Gulf of Mexico in Southwestern Louisiana (Johnson's Bayou, 29°45'N, 93°37'W) (Figure 2), and in Southeastern Texas at The Nature Conservancy's Clive Runnels Family Mad Island Marsh Preserve (Mad Island, 28°41'N, 96°6'W) (Figure 3). Johnson's Bayou's habitat consists of coastal woodlands (cheniers) and is critical to the rest and refueling of migratory birds because to the south is the Gulf of Mexico and to the north are unusable grassy marshes and wet prairies (Gauthreaux 1971, 1972). Mad Island has a similar chenier habitat and is also a critical stopover site for migratory birds. Mukherjee et al. (2014) did not find any ticks in the vegetation at the study site, most likely due to occasional flooding from the Gulf of Mexico.

Bird capture and tick removal. Birds were captured using mist-nets before they were brought to a central location for banding. Every captured bird was fitted with a U.S. Fish and Wildlife Service (USFWS) leg band. The age, sex, subcutaneous fat, muscle mass, wing chord, and mass (to the nearest 0.1g) were determined. The method detailed in Pyle (1997) was used to determine the age and sex; the method outlined by Helms and Drury (1960) was used to assess subcutaneous fat.

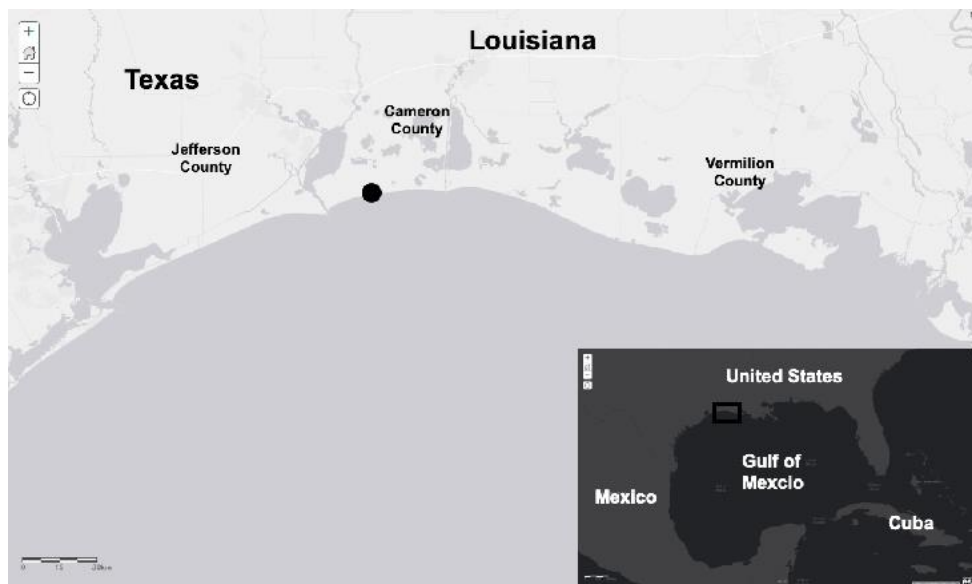


Figure 2: Map of the banding location at Johnson's Bayou, Louisiana. (Black dot) (Base map copyright ESRI.)

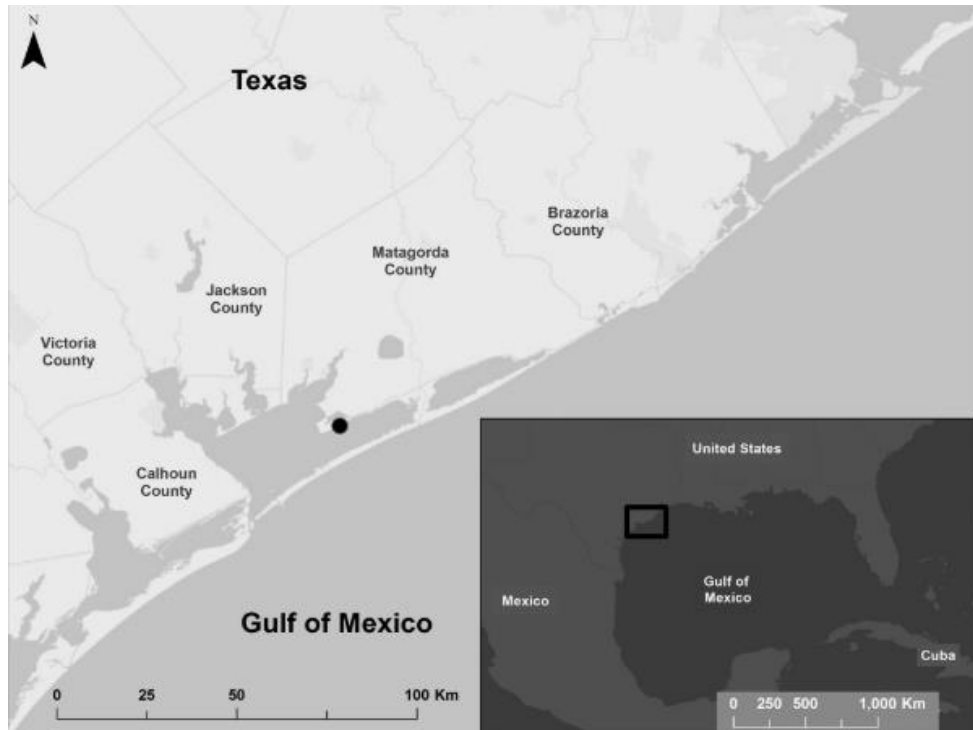


Figure 3: Map of the banding location at The Nature Conservancy's Clive Runnells Family Mad Island Marsh Preserve in Matagorda County, Texas (Black dot) (Cohen et al. 2015)

Birds were systematically searched for ticks by scanning the head, ear canals, nape, mandible, perimeter around the eyes, breast, and cloaca (Mukherjee et al. 2014; Cohen et al. 2015). A straw was used to part feathers by blowing a stream of air. Fine-tipped forceps were also used to part feathers, as well as remove ticks when they were discovered. The ticks were then placed in a vial with 70% ethanol to be used for later research studies.

Statistical analyses. One-Way Fisher's exact-tests were used to test the association between tick infestation and age classes. An analysis was conducted for each year individually, for each category of birds, and for every category combined between all years. Wood Thrushes (WOTHs) and Indigo Buntings (INBUs) had large enough samples to form their own category while species with similar phylogenetics and

ecologies were combined to form categories with testable sample sizes (*Catharus* thrushes, Warblers, and Tanagers). The categories were then broken down into SY (young) and ASY (older) age classes to test if age was correlated with tick infestation. After hatch year (AHY) birds were excluded from this study because all birds caught during spring migration are AHY.

Three-way contingency tables were used to determine if there were any correlations between age (SY and ASY), tick infestation (with tick and without tick), and body condition (lean and fat). Birds were considered lean if they had a fat score less than 2 while all birds with a fat score greater than or equal to 2 were considered fat (Helms and Drury, 1960)

A two-way analysis of variance (ANOVA) of age (SY and ASY) and tick infestation (with tick and without tick) on body condition, as measured by average body mass, was conducted for each group of birds except WOTH due to sample size problems. I tested for normality in all groups and found that warblers were the only group that needed a log₁₀ transformation to meet the assumptions of normality. Ovenbirds were excluded from the warbler group for these tests because they are slightly larger than the other warblers.

Chapter IV: Results

In total, 2177 SY and ASY birds were captured and sampled for ticks during 2010, 2013, and 2018. A total of 58 birds were found to have ticks, 28 SY and 30 ASY (Table 1). It was determined that tick infestation did not vary between ages in any category by using a Fisher's Exact test (WOTH, P=0.62; INBU, P=0.61; *Catharus*,

P=0.14; Warblers, P= 0.24; Tanagers, P=0.41). Additionally, another Fisher’s Exact test determined that tick infestation did not vary between age classes within each year sampled (2010, P=0.057; 2013, P=0.38; 2018, P=0.51). A final Fisher’s Exact test determined that tick infestation did not vary significantly between age class when all birds were combined (All, P=0.15).

It was determined that the differences between age, tick infestation, and body condition were not dependent on each other in most birds by using a three-way contingency table (WOTH, P=0.66; *Catharus*, P= 0.77; Warblers, P= 0.32; Tanagers, P=0.57). A significant difference was observed in INBU ($G^2=14.4$, $df= 4$, $P=0.0061$); however, further analysis showed that the difference was attributed to the interactions between age and body condition ($G^2=13.36$, $df= 1$, $P=0.0003$) and tick infestation was not significant in age or body condition ($P>0.05$).

The difference in body condition due to age was significant in Warblers, Thrushes, and Indigo Buntings (Warblers, two-way ANOVA $F_{3,1911}= 21.703$, $P<0.001$; *Catharus*, $F_{3,648}= 5.536$, $P<0.001$; INBU, $F_{3,1192}= 5.196$, $P= 0.0014$). In these groups, the ASY birds had a higher body mass average. Warblers were the only group where the difference in body condition was due to ticks ($F_{1,1911}= 0.023$, $P=0.025$). The warblers that had ticks were leaner than the warblers without ticks.

Species	Infested Totals			Non-infested Totals		
	SY	ASY	Total	SY	ASY	Total
WOTH	7	1	8	254	32	286
INBU	5	8	13	173	274	447
<i>Catharus</i>	7	4	11	402	94	496
Warblers	6	13	19	292	397	689
Tanagers	3	4	7	65	136	201
Total	28	30	58	1186	933	2119

Table 1: The number of migratory birds sampled for ticks that were found to be either infested or non-infested during the spring of 2010 and 2018 in Johnsons Bayou, Louisiana and the spring of 2013 in Mad Island, Texas.

Chapter V: Discussion

Migratory passerines arrived at spring stopover sites along the northern coast of the Gulf of Mexico carrying ticks that attached while the birds wintered in the Neotropics (Mukherjee et al. 2014; Cohen et al. 2015). The ticks were only partially engorged and the birds were examined shortly after arriving at the stopover site; therefore, it was concluded that the birds were infested prior to departure from their wintering site (Mukherjee et al. 2014; Cohen et al. 2015). Only 2-3% of birds were found to have ticks, which is likely a conservative number since banders may fail to detect 33% of ticks on birds (Ogden et al. 2008).

Tick infestation did not vary between older and younger migratory passerines, and thus my hypothesis was not supported by the results of the analyses. The lack of support for my hypothesis could be because the assumptions about the differences in behavior between older and younger birds were based on their wintering ecology. Migratory birds will become hyperphagic and broaden their foraging repertoire and substrate prior to migration to ensure they deposit enough fat stores to survive long-distance flights (Loria and Moore 1990; Wang and Moore 1997, 2005). This would nullify the previous assumption that older birds' claim to territory and superior foraging abilities would make them less likely to encounter a tick. Moreover, Moore and Simm (1986) provided evidence that migratory birds are more risk-prone foragers when their energy budget is below the budget required for survival. Both old and young birds may be willing to suffer the consequences of a tick infestation leading up to migration if it allows them to store enough fat deposits to complete their journey.

There is little evidence that body condition is impacted by the presence of ticks, thus my second hypothesis was not supported. Using fat scores as a measurement of body condition did not reveal much information about the overall condition of the bird. Coastal stopover sites are the first chance a bird gets to rest and refuel after a long, nonstop flight, so many of the birds arriving will be lean regardless of tick infestation (Loria and Moore 1990). Additionally, birds try to minimize the time spent at stopover sites, so the individuals with higher fat scores are likely to spend less time refueling or they may even skip stopping to continue their migration (Schaub et al. 2008).

Using average body mass revealed more information about the body condition of the birds but only provided limited support for my hypothesis. In most groups of birds, the average body mass was lower in SY birds than ASY birds. This is not surprising because several previous studies found similar body condition trends in migratory species at coastal stopover sites (e.g. Woodrey and Moore 1997). The warblers were the only group that experienced poorer body condition when infested with a tick. These results were not surprising given conflicting reports in the literature that ticks have a negative impact a bird's body condition (Galván et al. 2012; Norte et al. 2013; Heylen and Matthysen 2008; Mukherjee et al. 2014). Galván et al. (2012) examined how feather mites affect the body condition of passerines and found that there was little effect. Norte et al. (2013) found that birds exhibit an immunological response to tick infestations and that the responses can vary between ages but no noticeable differences in body condition were observed. Heylen and Matthysen (2008) did an experimental study that infested birds in a controlled setting, and the only negative impact observed was in haematocrit levels. Studies in a field setting have yielded similar results (e.g. Mukherjee et al. 2014).

Warblers, on average, have a lower body mass than the other birds studied, so they may be more sensitive to the negative effects of parasitism, like a lower haematocrit, thus explaining the poorer body condition in tick-infested individuals.

The results of this study provide some insight into the relationship between neotropical migratory passerines and tropical ticks and the effects of tick parasitism on the birds' body condition during stopover. Specifically, this study showed that there is no clear correlation between tick infestation and age during migration and that body condition is not impacted by tick parasitism in most birds. However, there are several confounding factors that my study design could not address. It is difficult to study seasonal interactions like tick parasitism while migrants are en route, because populations from different wintering locations may share the same stopover site (Paxton and Moore 2015). Sample sizes for birds with ticks are already low; obtaining samples of birds that had ticks and were able to be aged to SY or ASY presents its own unique challenges. It can be difficult and time consuming to age birds during migration, and bird banders may not have time to determine age. There could also be a sampling bias because mist netting is more likely to catch healthy, active individuals instead of the individuals that may be weak from tick parasitism (Valkiunas 2001). Alternatively, tick parasitism may not noticeably affect birds during migration. Stopover is not an ideal time to test for negative effects of parasitism on body condition because birds are immunosuppressed during migration, and any immune response to ticks would likely be suppressed (Owen and Moore 2008). Ticks and tick-borne pathogens share a long evolutionary history with birds, with birds likely being the first host to ticks (de la Fuente et al. 2015), so it is also

likely that birds have developed mechanisms to cope with the consequences of infestation (Nilsson et al. 2007).

Literature Cited

- Barrow, W.C., C.C. Chen, R.B. Hamilton, K. Ouchley, and T.J. Spengler. 2000. Disruption and restoration of en route habitat, a case study: The Chenier Plain. *Studies in Avian Biology* 20:71-87.
- Battaly, G.R., D.R. Fish, and R.C. Dowler. 1987. The seasonal occurrence of *Ixodes dammini* and *Ixodes dentatus* (Acari: Ixodidae) on birds in a Lyme disease endemic area of south-eastern New York state. *Journal of the New York Entomological Society* 95:461-468.
- Bolus, R.T., R.H. Diehl, F.R. Moore, J.L. Deppe, M.P. Ward, J.S. Smolinsky, and T.J. Zenzal. 2017. Swainson's Thrushes do not show strong wind selectivity prior to crossing the Gulf of Mexico. *Scientific Reports* 7:14280.
- Clayton, D.H., J.A.H. Koop, C.W. Harbison, B.R. Moyer, and S.E. Bush. 2010. How birds combat ectoparasites. *The Open Ornithology Journal* 3:41-71.
- Cohen, E.B., L.D. Auckland, P.P. Marra, and S.A. Hamer. 2015. Avian migrants facilitate invasions of neotropical ticks and tick-borne pathogens into the United States. *Applied and Environmental Microbiology* 81:8366-8378.
- de la Fuente, J., A. Estrada-Peña, A. Cabezas-Cruz, and R. Brey. 2015. Flying ticks: Anciently evolved associations that constitute a risk of infectious disease spread. *Parasites and Vectors* 8:538.
- Faaborg, J., R.T. Holmes, A.D. Anders, K.L. Bildstein, K.M. Dugger, S.A. Gauthreaux,...

- and N. Warnock. 2010. Conserving migratory land birds in the New World: Do we know enough? *Ecological Applications* 20:398-418.
- Franks, V.R. and R. Thorogood. 2018. Older and wiser? Age differences in foraging and learning by an endangered passerine. *Behavioral Processes* 148:1-9.
- Galván, I., E. Aguilera, F. Atiénzar, E. Barba, G. Blanco, J.L. Cantó,... and R. Jovani. 2012. Feather mites (Acari: Astigmata) and body condition of their avian hosts: A large correlative study. *Journal of Avian Biology* 43:001-007.
- Gauthreaux, S.A. 1971. A radar and direct visual study of passerine spring migration in southern Louisiana. *Auk* 88:343-365.
- Gauthreaux, S.A. 1972. Behavioral responses of migrating birds to daylight and darkness: A radar and direct visual study. *Wilson Bulletin* 84:136-148.
- Gregoire, A., B. Faivre, P. Heeb, and F. Cezilly. 2002. A comparison of infestation patterns by *Ixodes* ticks in urban and rural populations of the common blackbird *Turdus merula*. *Ibis* 144:640-645.
- Helms, C.W. and W.H. Drury. 1960. Winter and migratory weight and fat field studies on some north American buntings. *Bird-Banding* 31:1-40.
- Heylen, D.J.A. and E. Matthysen. 2008. Effect of tick parasitism on the health status of a passerine bird. *Functional Ecology* 22:1099-1107.
- James, M.C., R.W. Furness, A.S. Bowman, K.J. Forbes, and L. Gilbert. 2011. The importance of passerine birds as tick hosts and in the transmission of *Borrelia burgdorferi*, the agent of Lyme disease: a case study from Scotland. *Ibis* 153:293-302.
- Loria, D.E. and F.R. Moore. 1990. Energy demands of migration on red-eyed vireos,

- Vireo olivaceus*. Behavioral Ecology 1:24-35.
- Loye, J.E. and S.P. Carroll. 1991. Nest ectoparasite abundance and cliff swallow colony site selection, nestling development, and departure time. Annals of the Entomological Society of America 91:159-163.
- Moore, F.R and P.A. Simm. 1986. Risk-sensitive foraging by a migratory bird (*Dendroica coronata*). Experientia 42:1054-1056.
- Moore, F., S. Mabey, and M. Woodrey. 2003. Priority access to food in migratory birds: age, sex, and motivational asymmetries. In: Berthold P., E. Gwinner, E. Sonnenschein (eds) Avian migration. Springer, Berlin Heidelberg New York, pp 281–292.
- Morris, S.R., M.C. Ertel, and M.P. Wright. The incidence and effects of ticks on migrating birds at a stopover site in Maine. Northeastern Naturalist 14:171-182.
- Mukherjee, N., L. Beati, M. Sellers, L. Burton, S. Adamson, R.G. Robbins, F. Moore, and S. Karim. Importation of exotic ticks and tick-borne spotted fever group rickettsiae into the United States by migrating songbirds. Ticks and Tick-borne Diseases 5:127-134.
- Nilsson, J., M. Granbom, and L. Råberg. 2007. Does the strength of an immune response reflect its energetic cost? Journal of Avian Biology 38:488-494.
- Norte, A.C., D.N.C. Lobato, E.M. Braga, Y. Antonini, G. Lacorte, M. Gonçalves, ... and J.A. Ramos. 2013. Do ticks and *Borrelia burgdorferi* s.l. constitute a burden to birds? Parasitology Review 112:1903-1912.
- Ogden, N.H., L.R. Lindsay, K. Hanincová, I.K. Barker, M. Bigras-Poulin, D.F. Charron, ... and R.A. Thompson. 2008. Role of migratory birds in introduction and range

- expansion of *Ixodes scapularis* ticks and of *Borrelia burgdorferi* and *Anaplasma phagocytophilum* in Canada. *Applied and Environmental Microbiology* 74:1780-1790.
- Oppliger, A., H. Richner, and P. Christe. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit (*Pants major*). *Behavioral Ecology* 5:130-134.
- Owen, J.C. and F.R. Moore. 2008. Relationship between energetic condition and indicators of immune function in thrushes during spring migration. *Canadian Journal of Zoology* 86:638-647.
- Paxton, K.L. and F.R. Moore. 2015. Carry-over effects of winter habitat quality on en route timing and condition of a migratory passerine during spring migration. *Journal of Avian Biology* 46:495-506.
- Perret, J.-L., O. Rais, and L. Gern. 2004. Influence of climate on the proportion of *Ixodes ricinus* nymphs and adults questing in a tick population. *Journal of Medical Entomology* 41:361-365.
- Pyle, P. 1997. *Identification Guide to North American Birds: Part I Columbidae to Ploceidae*. Slate Creek, Bolinas.
- Robinson, S.K. and R.T. Holmes. 1982. Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918-1931.
- Scharf, W.C. 2004. Immature ticks on birds: Temporal abundance and reinfestation. *Northeastern Naturalist* 11:143-150.
- Schaub, M., L. Jenni, and F. Bairlein. 2008. Fuel stores, fuel accumulation, and the

- decision to depart from a migration stopover site. *Behavioral Ecology* 19:657-666.
- Sherry, T.W. and R.T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of neotropical-nearctic migrant birds. *Ecology* 77:36-48.
- Sonenshine, D.E. 1991. *The biology of ticks*. Oxford University Press, New York.
- Stewart, R.L.M., C.M. Francis, and C. Massey. 2002. Age-related differential timing of spring migration within sexes in passerines. *The Wilson Bulletin* 114:264-271.
- Stutchbury, B.J. 1994. Competition for winter territories in a neotropical migrant: The role of age, sex and color. *Auk* 111:63-69.
- Valkiūnas, G. 2001. Blood parasites of birds: sSe obstacles in their use in ecological and evolutionary biology studies. *Avian Ecology and Behavior* 7:87-100.
- Wang, Y. and F.R. Moore. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. *Auk* 114:236-278.
- Wang, Y. and F.R. Moore. 2005. Long distance bird migrants adjust their foraging behavior in relation to energy stores. *Acta Zoologica Sinica* 51:12-23.
- Weathers, W.W. and K.A. Sullivan. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs* 59:223-246
- Woodrey, M.S. and F.R. Moore. 1997. Moore. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695-707
- Wunderle, J.M. 1991. Age-specific foraging proficiency in birds. In *Current Ornithology*, D. M. Power, ed. pp 273–324. New York: Plenum Press.