

Avian Responses to Different Anthropogenic Disturbances and Habitats

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by

Lara Kazo
Bachelor of Science
University of Rhode Island, 2016

Director: David Luther, Professor
Department of Environmental Science and Policy

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George Mason University
Fairfax, VA

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DEDICATION

I would like to thank the many friends, relatives, and supporters who have made this happen. I would especially like to thank my Scottish Terrier, Sir Guster Burton Kazo, for keeping me sane during the last three years.

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ABSTRACT

AVIAN RESPONSES TO DIFFERENT ANTHROPOGENIC DISTURBANCES AND HABITATS

Lara Kazo, MS

George Mason University, 2021

Thesis Director: Dr. David Luther

To determine how habitat disturbance impacts avian communication and species diversity, I analyzed data on mixed species flocks from (1) a self-collected, short term study in urban Northeastern Virginia and (2) a long-term study of forest fragments in the lowland Amazon near Manaus, Brazil (the Biological Dynamics of Forest Fragments Project). The second chapter examines how animals avoid predation in the presence of relatively loud anthropogenic noise. Field experiments were conducted to assess if the effectiveness of alarm calls, that warn about predators, is reduced in the presence of anthropogenic noise. Any changes to alarm calls can be extremely detrimental to the overall fitness of bird populations, as these calls aid in the ability of birds to avoid predation and to communicate with heterospecifics. The third chapter examines the effects of forest fragmentation on the body condition of understory birds of the Brazilian Amazon. This project aims to further the knowledge of how increased fragmentation may negatively impact the fitness of essential species, as there is limited information on the

impacts on fragmentation on the health of birds. Understanding the effects on bird health provides direction on the best conservation practices for fragmented habitats.

CHAPTER ONE

Introduction

Human activities have created worldwide declines in species (Pereira et al. 2010, Rands et al. 2010, Pimm et al. 2014, Vos et al. 2015, Haddad et al. 2015, Ceballos et al. 2017, Pfeifer et al. 2017, IPBES 2019, Ceballos et al. 2020). In North American, there has been a 30% decrease in bird populations since the 1970's (Rosenberg et al. 2019) and species declines continue worldwide (WWF 2020). Reasons for bird declines are both universal and species-specific, and the causes are numerous. They include deforestation, collisions with human structures and vehicles, indirect poisonings through chemical pollution, disruptions by light pollution or anthropogenic noise, displacement by invasive predators, declines due to climate change and illegal wildlife trade, and losses due to habitat degradation and fragmentation (Butchart et al. 2010, BirdLife International 2018, Rosenberg et al. 2019). Many of these threats are nuanced or interactive, with smaller threats exacerbating more pervasive threats.

The leading cause of biodiversity loss worldwide is habitat destruction and fragmentation (Pereira et al. 2010, Rands et al. 2010, Pimm et al. 2014, Vos et al. 2015, Haddad et al. 2015, Ceballos et al. 2017, 2020). Forest biomes in particular are being cleared, fragmented, and degraded at an alarming rate (Song et al. 2018), negatively impacting forest biodiversity. Nearly $\frac{3}{4}$ of the 6680 mammals, birds, and amphibians assessed as Threatened (Vulnerable, Endangered, or Critically Endangered) or Near Threatened on the IUCN Red List occur in forests (IUCN 2021). Fragmentation not only

reduces the amount of available habitat for native species it also increases the potential for edge effects, predation events, and generally degrades the available resources (Haddad et al. 2015, Pfeifer et al. 2017).

Often concomitant with fragmentation is an increase in human activity or occupancy near remaining forest patches. Proximity of humans to avian habitats increases the likelihood of compounding the types of disturbances bird's encounter. One such disturbance is human-generated noise, particularly from vehicle traffic, construction, or other types of sounds likely to exceed the decibels of naturally produced sounds. Recently, avian biologists and other scientists have begun to consider anthropogenic noise as a form of habitat degradation. Anthropogenic noise can make it more difficult for animals to communicate via acoustic signals, to detect predators, or to maximize foraging efficiency, all of which can reduce population size. For birds that remain near urban soundscapes, anthropogenic traffic sound can interfere with bird ability to communicate territory boundaries, as well as to display mating and alarm calls (Ware et al. 2015, Templeton et al. 2016, Jung et al. 2020). Ultimately, loud anthropogenic noise can cause decreases in richness of bird species (Perillo et al. 2017, Manzanares Mena and Macías Garcia 2018). However, its impacts on habitat use, population persistence, and species survival haven't been quantified for most species and are likely to differ greatly from behavioral changes generated by deforestation or fragmentation.

It is essential to understand how bird populations will be impacted by these and other anthropogenic to develop best conservation practices to aid in overall bird health

and diversity. While all disturbances to birds need to be further researched in order to gain in-depth knowledge on impacts to bird population and individuals, during this thesis I focused on two main disturbances: anthropogenic noise and habitat fragmentation. The goals of this research were to determine exactly how these anthropogenic stressors effect birds

CHAPTER TWO

An investigation into the effect of anthropogenic noise on the efficacy of avian alarm calls in mixed species flocks in Northern Virginia

Abstract

Animals use alarm calls to alert both conspecifics and heterospecifics of potential dangers. Anthropogenic noise can disrupt and reduce the salience of acoustic communication signals including alarm calls. To examine if alarm calls are impeded by anthropogenic noise, we recorded local alarm calls of the tufted titmouse, *Baeolophus bicolor*, a sentinel species, and conducted playback experiments to mixed species flocks along an anthropogenic noise gradient in Northern Virginia. We observed behavior of mixed species flock members, including *Poecile carolinensis*, *Cardinalis cardinalis*, *Sitta carolinensis*, and *Thryothorus ludovicianus*, before and after alarm call exposure along an anthropogenic noise gradient to assess the responses of individuals to alarm calls under different amounts of anthropogenic noise. Vigilance and fleeing behavior increased and foraging behavior decreased after alarm call presentation both in noisy and quiet sites. Foraging behavior decreased and fleeing behavior increased more rapidly as anthropogenic noise increased such that birds at louder sites demonstrated an elevated response to alarm calls with heightened predator response behaviors compared to birds at relatively quieter locations. Our results indicate that while species are still able to hear

and respond to alarm calls in areas of heightened anthropogenic noise, birds inhabiting areas with high levels of anthropogenic noise are more vigilant.

Introduction

Anthropogenic noise can interfere with and alter many aspects of animal behavior, including communication (Chan et al. 2010, Luther and Gentry 2013, McGregor et al. 2013, Kern and Radford 2016). More specifically, anthropogenic noise can make it more difficult for animals to detect and discriminate acoustic signals (Chan et al. 2010, Luther and Gentry 2013, Kern and Radford 2016, Damsky and Gall 2017). While the vast majority of studies on the influence of anthropogenic noise on acoustic communication focus on signals for long range communication, less attention has been given to short range communication signals such as contact calls and alarm calls.

Many species have developed alarm calls to warn conspecifics and heterospecific species of potential dangers from predation (Munn 1986, Hollén and Radford 2009). Heterospecific species often gather together in mixed-species flocks, consisting of at least two species foraging together (Harrison and Whitehouse 2011, Magrath et al. 2015, Pollock et al. 2017, Zou et al. 2018) and spend prolonged periods of time together benefiting from shared resources of food, water, and safety (Sridhar et al. 2009, Zou et al. 2018). In mixed-species flocks, conspicuous alarm calls create a signaling system to alert conspecific and heterospecific species to potential dangers, thus creating antipredator protection that extends beyond the calling species (Templeton and Greene 2007). Recognition of heterospecific specific alarm calls is an effective antipredator strategy

(Seyfarth and Cheney 1990, Templeton and Greene 2007, Fallow et al. 2013, Magrath et al. 2015, Grade and Sieving 2016, Potvin et al. 2018). In many mixed species flocks, a specific species, referred to as a sentinel species, uses alarm calls to warn all other flock members about potential dangers (Munn 1986, Magrath et al. 2015). Alarm calls provide vital information regarding predatory threats, such as location, species and size (Seyfarth and Cheney 1990, Suzuki 2014), permitting receivers time to select a course of action, such as fleeing or vigilance responses (Kern and Radford 2016). These alarm calls are so fundamental to many species that there is evidence of worldwide convergent evolution of alarm calls; such that the calls are extremely similar regardless of taxonomy or which continent species inhabit (Gyger et al. 1987).

In areas with relatively high levels of human background noise, individuals may be unable to communicate or detect predators as easily as in locations with lower levels of background noise (Goodwin and Podos 2013, McClure et al. 2017). Many animals modify their behavior in the presence of anthropogenic noise by changing the amplitudes, frequencies, or note selection of their calls and songs to compensate for interference of background noise effects (Luther 2009, Luther and Gentry 2013, Brumm and Zollinger 2014). Alarm calls are especially important for survival: adaptation of alarm calls to compensate for anthropogenic noise could reduce the strength of antipredator responses (Potvin et al. 2014).

Alarm calls tend to occur at frequencies of 6 - 9 kHz, which are higher than the level of relatively low-frequency anthropogenic noise (Zhou et al. 2019), generally 1 - 3 kHz (Estabrook et al. 2016, Mason et al. 2017). Alarm calls also tend to occur at higher

frequencies than bird songs, and in frequency ranges that are difficult for avian and mammalian predator species to detect, which can typically hear best between 4 - 5 kHz (Klump et al. 1986, Seyfarth and Cheney 1990). Finally, avian alarm calls tend to be quieter than bird songs since they are intended for relatively close-range communication (Klump et al. 1986, Magrath et al. 2007, Potvin et al. 2018). For these reasons one might assume that alarm calls would not be as affected by anthropogenic noise as the frequency range of the alarm calls occurs outside the range of anthropogenic noise. However, the intense amplitude of some anthropogenic noise can interfere with the detection of acoustic signals regardless of their frequency range or amplitude (Klump et al. 1986, Chan et al. 2010, Luther and Gentry 2013).

Animals have a variety of responses to alarm calls. Vigilance in response to alarm calls is commonly observed as a solid stance with head upwards, as if to better observe any potential predator (Zhou et al. 2019). This reaction is considered alert as the relaxed posture is typified as having the head down below body level, ideal for foraging (Quinn et al. 2006). Vigilance can also be observed as a freeze response (Magrath et al. 2007), which means birds are seen with eyes open, motionless and occasionally crouched (Gabrielsen et al. 1985). In areas of high anthropogenic noise, vigilance has been more frequently observed than in areas with less anthropogenic background noise (Damsky and Gall 2017, Zhou et al. 2019). The flee response is the abrupt escape and search for shelter when a predator is present (Leavesley and Magrath 2005, Zhou et al. 2019). Fleeing occurs either immediately after alarm calls, or after a brief stance of vigilance (Leavesley and Magrath 2005, Fallow et al. 2013). Relatively loud anthropogenic noise could cause

interference with the detection and discrimination of alarm calls which would create latency in flee response as individuals do not respond to antipredator warning at the same rate as non-interference alarm calls (Damsky and Gall 2017). When anthropogenic noise disrupts alarm calls, receivers may not receive the caller information that provides details on the type and location of a predator (Kern and Radford 2016). When unable to hear or understand details of an alarm call, receivers are in greater danger of predators than if able to hear alarm calls (Kern and Radford 2016). For species in areas of relatively loud anthropogenic noise, such as highways, lack of received predator warning could create higher predation rates (Templeton et al. 2016).

The tufted titmouse (*Baeolophus bicolor*) provides a model system for testing hypotheses regarding noise interference and alarm calls. *Baeolophus bicolor* is a common non-migratory Paridae in eastern deciduous forests in the midwestern and eastern United States (Brawn and Samson 1983). It is found in low elevations in mature deciduous woods or pasture areas and is common in eastern suburban zones throughout the eastern United States (Ehrlich and McLaughlin 1988, Lutmerding and Love 2019). Paridae species are known to have high vigilance and aggressive behavior, incite mobbing of predator species, and display complex communication system (Schmidt et al. 2008). North American woodland birds of the Paridae (parids) produce alarm calls upon which over 30% of other forest species rely for warning about the presence of potential predators (Leavesley and Magrath 2005).

In the mid-Atlantic region of the U.S., tufted titmice travel with wintering mixed-species flocks, often comprised of Carolina chickadee (*Poecile atricapillus*), Northern

cardinal (*Cardinalis cardinalis*), white-breasted nuthatch (*Sitta carolinensis*), Carolina wren (*Thryothorus ludovicianus*) and other species (Sullivan 1985). Previous studies indicated that various flock obligates such as Northern cardinals, White-breasted nuthatches and Carolina wrens respond to titmice alarm calls (Damsky and Gall 2017). Other terrestrial species such as eastern chipmunks are likewise known to flee when alarm calls of titmice are heard (Schmidt et al. 2008). Calls of titmice contain information about the type of predator thereby giving risk-based specificity (Courter and Ritchison 2010). Alarm calls of titmice have a broadband “dee- dee-dee” sound and are relatively low frequency calls, between 2 to 4 kHz, with the possibility of some notes reaching up to 8 kHz, and low in amplitude “seet”, roughly 4 kHz (Schmidt et al. 2008). However, researchers have not studied how mixed-species flocks will respond to these calls in areas with high levels of anthropogenic noise.

To determine whether louder anthropogenic noise lessens the response of mixed species flock members to alarm calls of a sentinel species, the tufted titmouse, we conducted playback experiments of alarm calls to mixed species flocks at locations with varying amounts of anthropogenic noise. We predicted that greater anthropogenic noise impacts the ability of animals to detect and respond to alarm calls from other species, and thus, a diminished response in the presence of relatively louder anthropogenic noise. In areas that are relatively quiet in terms of anthropogenic noise, we predict that receivers should respond to alarm calls immediately after the alarm call was played, with immediate predator response behaviors (fleeing, vigilance, etc.). In contrast, we predicted

that responses to alarm calls should be slower and less frequent in areas with relatively loud anthropogenic noise.

Methods

Study site

Research was conducted at locations in Fairfax county in northern Virginia and were selected based on a spectrum of relatively quiet to relatively loud anthropogenic noise that ranged from 30 dB to 70 dB. Ambient noise levels were taken at each site using the National Institute for Occupational Safety and Health (NIOSH) Sound Level Meter, an iOS platform application (The National Institute for Occupational Safety and Health (NIOSH) 2019). Noise measurements were taken for 30 seconds from each of the four cardinal directions, and the average readings in each direction were recorded and averaged. Experiments were conducted between 0700 and 1400 hours from February 12 to March 5, 2020.

Alarm Call Recordings

Alarm calls, consisting of several “seet” notes, were recorded from seven different tufted titmouse individuals. Alarm calls were recorded from birds in mixed species flocks in Northern Virginia in the winter of 2020. Recordings were made with a Marantz PMD 660 and a Sennheiser ME 66 shotgun microphone. Background noise at the location and time of alarm call recording ranged from 30 dB to 80 dB, although there were no significant differences in the minimum or mean frequency of alarm calls from

locations with different levels of background noise ($t_6=-93.58$, $p=1.003$). Recordings were manipulated in RavenPro5 to remove background noise by filtering out sounds below and above the alarm calls. Noises below 2 kHz and over 10 kHz were removed. Frequencies and amplitudes of call notes were not changed in order to stay true to wild alarm call.

Playback Experiment

We played recorded alarm calls of the tufted titmouse to mixed species flocks along an anthropogenic noise gradient. At each playback location, mixed species flocks were located and observed to have at least one tufted titmouse as well as heterospecific species consisting of at least two of the following species: Carolina chickadee, Northern cardinal, white-breasted nuthatch, Carolina wren, downy woodpecker (*Picoides pubescens*), or song sparrow (*Melospiza melodia*). Observed flocks consisted of a range of two to six species and two to thirty total individuals.

We compared the frequency of behavioral responses to alarm calls of each of species before and after experimental playbacks. Before playbacks began, focal baseline behavior was observed for one minute. Previously recorded alarm call of tufted titmouse was randomly selected and played for one minute at 61 dB. Observed individuals' behavior was observed and recorded during the one-minute playback as well as ten minutes after the alarm call was played. Observed behaviors included: the amount of time feeding, number of fights, number of vocalizations, amount of vigilance (portion of time with head raised and alert) and the number of times fleeing to hiding spots, as well as the

latency of response for each behavior above. We also documented the amount of time until a bird returned to the baseline behaviors seen before playback of the alarm calls.

Analysis

All statistical analyses used R statistical packages (R Core Team 2020, R Development Core Team 2008) and Tableau software (Tableau Software, LLC 2021). We used paired t-tests of the behavioral response variables using the R statistical package `data.table` (Dowle and Srinivasan 2019) to determine differences in behaviors of individuals before and after playback presentation. To assess the effect of anthropogenic noise on responses we conducted linear regression in R using the `lmer` (function *lmer*) model package. To assess the effect of anthropogenic noise on responses we used regression in R to run a ‘intercept only model’ using the function `abline` (function *abline*).

Results

Background noise ranged from 30 dB to 74 dB at the time of playback when we conducted playback experiments and observed responses on 24 mixed species flocks. All species responded to the experimental alarm calls with a predator response behavior, though species differed in the specific behaviors displayed (Table 1). The majority of behaviors, such as singing, preening, sitting, or the number of alarm calls, did not change after experimental alarm calls regardless of the level of background noise; however, three bird behaviors (foraging, vigilance and fleeing) significantly changed after experimental alarm call presentation (Table 2). Vigilance and fleeing behavior increased after exposure

to alarm calls. Vigilance behavior significantly increased from 0% before to 44% of a bird's time after alarm call presentation ($t_{26} = -3.820$, $p = 0.0007$). Fleeing behavior increased from 0.003% to 9% of a bird's time after alarm call presentation ($t_{26} = -6.154$, $p < 0.01$). Contrary to our prediction, fleeing responses increased with increasing background noise ($R^2 = 0.28$, $p = 0.028$) (Figure 1a). Foraging behavior was reduced after exposure to alarm call ($t_{26} = 2.815$, $p = 0.009$) such that prior to alarm call presentation foraging behavior averaged 36% of a bird's time while after alarm call presentation foraging was reduced to only 8% of their time. Foraging behavior did not show significant change in areas with louder background noise ($R^2 = 0.013$, $p = 0.657$) (Figure 1b). Vigilance behavior did not change significantly with louder background noise levels ($R^2 = 0.023$, $p = 0.685$) (Figure 1c).

Discussion

Birds responded to alarm calls regardless of the level of background noise. However, the effect of anthropogenic noise on avian responses to alarm calls was nuanced as the level of background noise did not affect the amount of vigilance or foraging, but fleeing responses increased at louder sites. Thus, when presented with alarm calls in locations with relatively loud anthropogenic noise, birds tended to flee more quickly rather than remain and be vigilant of possible predators as they did in quieter locations.

Consistent with previous alarm call research, birds in our flocks spent less time foraging after alarm calls (Lima and Valone 1986, Baack and Switzer 2000). In their examination of yellow-bellied marmots, Carey and Moore (1986) discovered there was a reduction in foraging rates after an alarm call. In addition, Bhattacharjee et al. (2019) used individual modeling to show that there is a decrease in foraging behaviors after most alarm communications. As reduction in foraging behavior after an alarm call is supported throughout the literature it is also held that birds would be more likely to flee or be vigilant once alerted to a potential danger. An increase in vigilance and fleeing is supported by the body of evidence that alarm calls produce a predator response (Bradbury and Vehrencamp 2011). Leavesley and Magrath (2005) and Zhou et al. (2019) indicate that birds are more likely to flee after an alarm call than from other communication signals.

Louder anthropogenic noise affected responses to alarm calls in terms of variations in fleeing behaviors. With higher background noise levels, species fled more readily than those in lower noise areas. There was a decline in foraging behavior in areas with higher background noise, but the decrease was insignificant. In general foraging tends to decrease in areas with higher anthropogenic noise as increased vigilance behavior reduces the amount of time available for foraging (Ware et al. 2015). In the enclosure experiments of Ware et al. (2015), noise was manipulated to assess the tradeoff of vigilance and feeding in the presence of anthropogenic noise, however the study birds did not have the opportunity to flee since it was an enclosed space. In the case of the wild populations in our study, individuals fled quickly in response to an experimental alarm

call. However, when in relatively quieter locations, birds may remain vigilant and observe potential threats longer before fleeing (Evans et al. 2018).

As alarm calls carry specific details of predator type and location (Kern and Radford 2016) in areas where anthropogenic noise might make detecting and discriminating alarm calls more difficult, it is possible that individuals are more likely to flee when an alarm call is detected. Decision making is a key component of anti-predatory behavior (Shettleworth 2009) and the decision to flee or remain vigilant may depend on the relative background noise to alarm call ratio. Morris-Drake et al. (2017) and Jung et al. (2020) found increases in anti-predator behaviors, such as vigilance and fleeing, and a reduction in foraging along with increases in anthropogenic noise, consistent with our results. Vigilance increases with higher anthropogenic noise (Rabin et al. 2006, Kern and Radford 2016), however, Meillère et al. (2015) suggested that in areas of increased noise levels birds may compensate for the difficulty of detecting predators by fleeing more readily. It is probable that increased vigilance ultimately leads to more frequent fleeing (Morelli et al. 2019). Such findings could explain the decision to flee rather than remain vigilant in situations with heightened anthropogenic noise.

All species do not respond uniformly to alarm calls (Petrelli et al. 2017). For example, downy woodpeckers and white-breasted nuthatches in our study were less likely to flee or become vigilant after alarm calls. However, the passerine species in our flocks, Carolina wrens, Carolina chickadees and northern cardinals, increased in vigilance behavior, stopped foraging, and fled more frequently after hearing alarm calls. Differences in responses to alarm calls can be based on factors such as foraging guild,

foraging behavior, distance to the alarm call, and the type of threat (Martínez and Zenil 2012, Petrelli et al. 2017). Petrelli et al. (2017) also found that songbird responses to predators can be species-specific. Certain species, such as ground dwelling birds, fled more frequently in noisy environments while canopy species showed a lower rate of fleeing in noisier environments. However, even within a guild, species can have varying responses to predator stimuli (Petrelli et al. (2017). Species-specific differences in response to alarm calls may explain how previous studies have found varied results of mixed species flocks detecting and responding to alarm calls in the presence of anthropogenic noise.

Contrary to our results, Zhou et al (2019) found that birds were less likely to flee or be vigilant in areas with louder background noise. In addition, Grade and Sieving (2016) and Templeton et al. (2016) found that species did not respond to alarm calls in the presence of loud anthropogenic noise. Some possible explanations for these differences include the study species, the duration of the study, and the type of background noise. Zhou et al. (2019) examined wild superb fairy-wrens (*Malurus cyaneus*) in Australia and experimentally tested how overlapping noise would affect their response to alarm calls, by playing background noise (which included both anthropogenic and background bird calls) in a frequency between 6 - 10kHz which overlapped with the fairywren alarm calls which range from 8.6 - 9.5 kHz. Birds did not respond to calls when presented with noise that overlapped in frequency but did respond to alarm calls when non-overlapping noise was presented (2 - 6kHz). In these cases, birds fled in a fashion similar to our own results.

Similar to our study, Grade and Sieving (2016) used alarm calls of the tufted titmouse and examined northern cardinal responses but found no response from cardinals to alarm calls in ‘noisy areas’ (greater or equal to 50dBA). However, in the ‘quieter areas’ (less than or equal to 49.9.dBA), over half of the birds did respond to alarm calls. One main difference between our study and Grade and Sieving (2016) is that their study took place in May and July during the cardinal breeding season while our study was in February and March during the non-breeding season. North American mixed species flocks tend to reduce or disperse during the breeding season, which can make them less receptive to flock-associated behaviors (Farley et al. 2008, Gentry et al. 2019). It is possible that a change in season with a reduction in the number of mixed flock individuals or sentinel species results in a diminished response to heterospecific alarm calls. Templeton et al. (2016) used recorded traffic noise and played alarm calls when there was a break in actual traffic. It is possible that by removing the visual cue of cars, birds were less likely to flee than in an area with both high noise levels and high visual stimuli. Birds are known to use visual cues when in the presence of a predator, along with auditory and chemical cues (Devereux et al. 2006, Saavedra and Amo 2020). Lack of visual stimuli (in this case cars) may cause a reduction in the alarm state of individual birds. We suspect methodological differences could explain many of the different findings between our studies and those of Grade and Sieving (2006) and Templeton et al. (2016).

In conclusion, we found that high levels of anthropogenic noise create a heightened predator response behavior. Contrary to our prediction, individuals were more

likely to respond quickly with a predator response behavior to alarm calls in areas with increased anthropogenic noise.

Acknowledgments

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Tables and Figures

Table 2.1

Number of predator response behaviors of each species after tufted titmouse (*Baeolophus bicolor*) alarm was played both in relatively quiet and relevantly loud noise areas.

Species	Total Vigilance Count	Total Fleeing Count	Notes
Downy Woodpecker (<i>Picoides pubescens</i>)	0	1*	Downy Woodpecker did flee after alarm call, though it was not immediate. * Unknown if fleeing was based on alarm call itself, or other outside influences.
Carolina Wren (<i>Thryothorus ludovicianus</i>)	74	16	All individuals fled after exposure to alarm calls. 34% fled immediately while 66% of individuals became vigilant before fleeing
Northern cardinal (<i>Cardinalis cardinalis</i>)	94	15	92% of individuals became vigilant after alarm calls. Fleeing was seen after a time of vigilance behavior with 83% of individuals fleeing after a period of vigilance.
Carolina chickadee (<i>Poecile carolinensis</i>)	0	1	Species fled after alarm call without a small period of vigilance previously
White-breasted nuthatch (<i>Sitta carolinensis</i>)	6	3	All individuals became vigilant after alarm call with 66% fleeing after period of vigilance
Song sparrow (<i>Melospiza melodia</i>)	17	4	All individuals became vigilant after alarm call with 66% fleeing after period of vigilance

Table 2.2

Results of statistical comparison of before and after behavior reactions to tufted titmouse (*Baeolophus bicolor*) alarm call 2020 using paired t-tests.

Variable	Mean±SE		t	p
	Before Alarm Call	After Alarm Call		
Foraging	3.48±0.72	1.37±0.59	2.82	0.009*
Flying	107±0.23	1.78±0.59	-1.35	0.19
Sitting	3.44±0.68	2.26±1.04	1.23	0.23
Alarm Call	0.04±0.04	0.26±0.17	-1.29	0.21
Song	1.37±0.39	1.82±1.1	-0.48	0.64
Vigilance	0	7.22±1.89	-3.82	0.0007*
Fleeing	0.04±0.04	1.48±0.24	-6.16	1.65E-06*
Preening	0.22±0.22	0.22±0.22	NA	NA

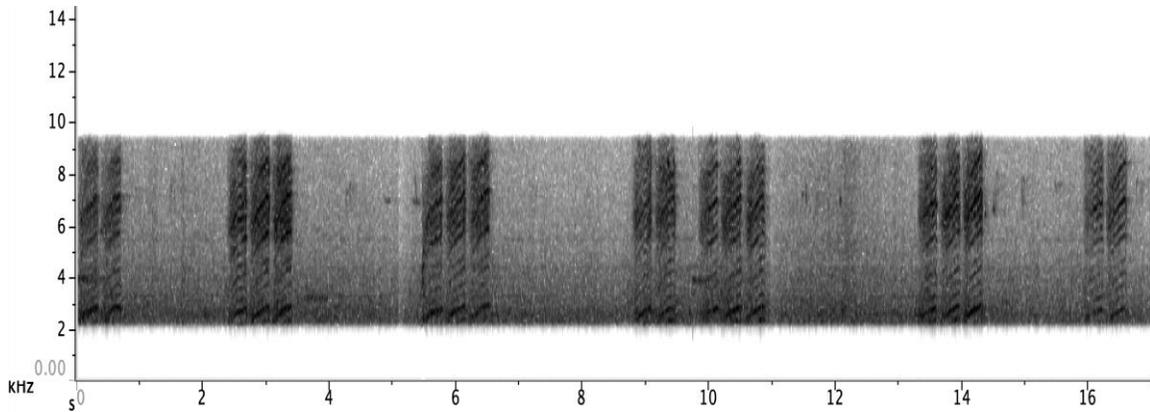


Figure 2.1

Spectrogram of tufted titmouse (*Baeolophus bicolor*) “seet” alarm call. Low anthropogenic noise d from 2 kHz and high anthropogenic noise over 9.5 kHz was removed to allow for no background noise interference. Noise between each alarm call was also removed between playbacks. Created using RavenPro5.

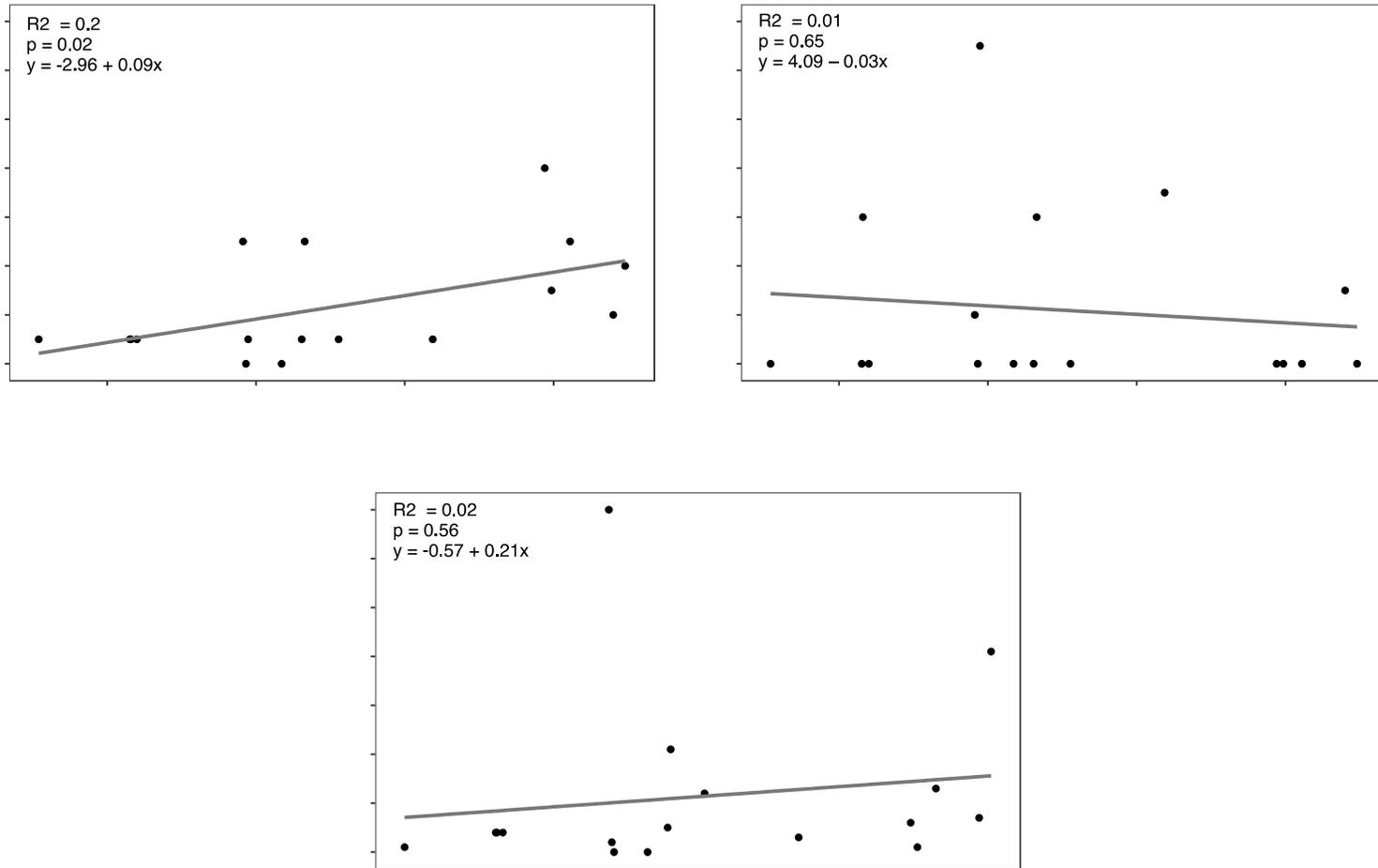


Figure 2.2
 Linear regressions of behavioral responses 1a) fleeing, 1b) foraging and 1c) vigilance in response to alarm calls in the presence of varying amounts of anthropogenic noise.

CHAPTER THREE

Effects of forest fragmentation on body condition of understory birds at the Biological Dynamics of Forest Fragments Project in Amazonia

Abstract

Deforestation and habitat fragmentation are chief drivers of biodiversity loss. Understanding how these disturbances impact the species that remain in disturbed habitats is important to global conservation efforts. While studies have been conducted on birds that leave habitat fragments, the impact on species that remain is largely unexplored. We hypothesized that species that remain in habitat fragments will experience a decline in health as fragments are known to contain poorer quality habitats in comparison to undisturbed habitats. The effect of forest fragmentation on health of birds was assessed from data collected at the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon. Mist-net data from understory species caught before and after fragmentation events at the BDFFP was analyzed to determine impacts on body condition, which was used as a determinant of health. Contrary to our predictions, we found that insectivorous species that remained in fragments gained weight. Furthermore, frugivores maintained a stable weight and had no significant weight change. Weight gains in insectivores may be due to increased food sources in the form of arthropods that benefit from fragmentation. Understanding weight gain and stable weight

state in avian species may provide insights on species' susceptibility to forest fragmentation. Further studies on body condition of individuals that remain in fragments and the ultimate consequences of fluctuations in body condition is needed to better understand why some individuals and species are more susceptible to forest fragmentation than others.

Introduction

Habitat destruction and fragmentation are the leading causes of biodiversity loss worldwide (Pereira et al. 2010, Rands et al. 2010, Pimm et al. 2014, Vos et al. 2015, Haddad et al. 2015, Ceballos et al. 2017, 2020). Globally, 20% of forests are found within 100m of a forest edge and 70% within 500m (Haddad et al. 2015, Pfeifer et al. 2017). Understanding the impact of fragmentation on terrestrial community structure is imperative for the management and restoration of degraded habitats (Bierregaard and Lovejoy 1989, Malcolm 1994, Fletcher 2005, Broadbent et al. 2008, Pfeifer et al. 2017).

Immediately after fragment isolation, animal diversity and abundance temporarily increase (Bierregaard and Lovejoy 1989). As habitat is destroyed, refugee birds flee inward to remaining habitat, which provide protection and resources for survival (Andr n 1994, Laurance et al. 2007, Korfanta et al. 2012). Fragments quickly become crowded with new refugees competing for territory and food resources (Korfanta et al. 2012, Blake and Loiselle 2016, Evans et al. 2017, Newmark et al. 2017). The initial increase in abundance is followed by species loss from fragments with strong area effects (Stouffer et al. 2006, Korfanta et al. 2012).

While many species become locally extinct in fragments, some individuals remain, and little is known about the quality of their persistence in the fragmented landscape. Specific health indicators such as feather growth and parasite load can be used to determine how fragmentation affects the health of bird species. Habitat fragmentation can lead to higher nest predation, brood parasites, and increased predator exposure for species that remain in fragments (Ambuel and Temple 1983, Brittingham and Temple 1983, Andren 1992, Robinson et al. 1995, Brearley et al. 2013). For example, *Glyphorynchus spirurus* and *Psuedopipra pipra* have lower feather growth rates in fragments than in continuous forest, indicating a nutritional deficiency in fragments compared to continuous forest (Stratford and Stouffer 2001, Hernández-Palma and Stouffer 2018).

Anthropogenic habitat changes can create adverse environments for survival, such as fewer food resources or increased predation, that can affect body condition (Daszak et al. 2001, Shochat et al. 2002, Acevedo-Whitehouse and Duffus 2009, Gaston et al. 2014, Willems et al. 2021, Ditmer et al. 2021). Significant weight loss is often an indicator of a health disparity in wildlife species (Sainsbury et al. 2001, Mathews et al. 2006, Robbins 2012, Ryser-Degiorgis 2013). Generally, studies compare individuals in fragmented habitats to individuals in nearby continuous habitat to infer how body condition has been affected by fragmentation. However, for a more accurate assessment of how fragment isolation affects body condition, researchers should track individual body condition before and after fragment isolation. Here, we assessed changes in body weight of

understory birds before and after fragmentation at the Biological Dynamics of Forest Fragments Project (BDFFP) in rainforest habitat in the central Amazon.

Despite heterogeneity in resources and diversity, the Amazon rainforest historically contained some of the largest areas of intact forest and was characterized by minimal climate fluctuations and disturbance (Cheng et al. 2013). Thus, disturbances, such as fragmentation, can have adverse impacts on species that have evolved to live in contiguous, stable habitat. We predicted that birds will lose weight after fragment isolation and that birds remaining in smaller fragments will have greater weight loss due to loss of high quality habitat as compared to birds in larger fragments (Hernández-Palma and Stouffer 2018). We also predicted that birds would lose weight after fragment isolation regardless of sex, as both males and females will be equally affected by the loss of resources. This research will fill a knowledge gap regarding how species respond to forest fragmentation. Such information will be critical to our understanding of the effects of fragmentation on avian health.

Methods

Study site and field techniques

The BDFFP in central Amazonia, is approximately 80 kilometers north of the city of Manaus in the state of Amazonas, Brazil, is the largest and longest fragmentation study in the world (Laurance et al. 2018). Forest fragments at the BDFFP were first isolated in the early 1980s (Bierregaard and Lovejoy 1989) and reisolated in 2013. Our analysis

focuses on forest understory avian species captured in mist nets in each of the five 1ha, four 10ha, and two 100ha fragments at the BDFFP.

Birds in the rainforest understory were captured with mist nets before and after fragment isolation in 1, 10, 100 ha fragments and continuous forest at the BDFFP. Mist nets were set in lines of 8 nets in 1ha and 16 nets in the areas that were to be fragmented into 10 ha and 100 ha fragments. Nets were roughly 2.5m tall with the bottom trammel of the nets set at ground level. One line of nets (8 or 16 nets) was open per day and nets were open from 0600 to 1400 (Bierregaard and Lovejoy 1989). Birds within fragments were sampled before and after the initial fragment isolation 1979-1983 and 1985-1988, respectively, as well as before and after the most recent fragment isolation in 2013 and 2014 respectively. As a control, birds in nearby continuous forest were sampled for weight changes in 2011 and 2012, as control forest was not sampled during the same period as fragments. All bird data comes from the dry season, June to October, and wet season birds' collections were removed before analysis.

Each bird captured in the mist nets was banded with an individual number, and recaptures of the same individuals were recorded. Avian mass in the 1980s was measured using analog spring scales, often to the nearest 0.25 or 0.5g, but since 2010, mass has been measured with an electronic balance to the nearest 0.1g. While the instrument was different in these two-time frames, the instrument before and after isolation was the same in each respective decade, thus our results of weight differences before and after fragment isolation comparisons are not an artifact of different sampling techniques. At the time of capture, birds were identified to species and sexed as male, female, or sex unknown. All

young birds were removed from the dataset prior to our analysis as they could be expected to gain weight more rapidly than adults and could bias results. Birds were also divided into two broad foraging guilds: frugivore or insectivore. The size of the fragment where captured (1, 10, or 100ha) was also noted.

Analyses

Individual changes in weight

In the first analysis, we assessed the effect of fragment isolation on individual birds. Mist net captures were filtered to identify individual birds that were captured and recaptured in the same fragment before and after fragment isolation. Changes in weight of individual birds was assessed with paired t-tests using the R statistical package *data.table* (Dowle and Srinivasan 2020) version 1.13.2. Due to low sample sizes of species recaptured after fragment isolation, we grouped individuals by foraging guild, sex, and the fragment size in which they were captured to assess how each variable affected change in weight after fragment isolation. As a control, we compared individuals recaptured in continuous forest in 2011 and 2012 to assess if they also exhibited changes in weight. Statistical analyses were conducted using R studio (R Core Team 2020).

Population level changes in weight

In the second analysis, we assessed the effect of fragment isolation on populations of three bird species commonly caught in mist nets both before and after fragment isolation. Two species were insectivorous, *Willisornis poecillisonis* and *Glyphorynchus spirurus*, and one species was a frugivore, *Psuedopipra pipra*. These three species were

selected to assess how fragment isolation affected weight differentially between the sexes and according to fragment size within a species. Additionally, species were chosen to compare possible differences between insectivores and frugivores. To compare means of weight before and after fragmentation, an unpaired two-samples Wilcoxon test was used to compare the weights of all individuals, each sex, and each fragment size of each species before and after fragmentation. Linear mixed models (LMM) (function *lmer*) from the R package *lme4* (Bates et al. 2015) was used. The Wilcoxon test compared mean weights before and after fragmentation within specific fragment sizes or sexes independently, while LMMs assessed differences between different fragment sizes and the sexes. Fixed effects in LMM were before or after fragmentation, sex, and fragment size. Band number was a random effect, and weight was the response variable. Models were built for each of the three species before and after the initial isolation event which took place between 1981- 1993. We tested different combinations of additive effects and interactions between effects, and the model with the lowest AICc and the majority of the AIC weight was chosen as the best model. The package *performance* (functions *check_model*) (Lüdtke et al. 2020) generate plots to check that data met all LMM assumptions and to check residuals.

Results

Individual changes in weight

Out of the 3,466 bird mist net captures in the 1980s, only 25 adult individuals with reported weights were captured in the same location before and after fragment

isolation. Between 2013 and 2014, 48 adult individuals were recaptured in the same fragment before and after fragment isolation out of 567 birds captured in total. In the years 2011 to 2012, 476 individuals were caught in mist nets in the continuous forest, but only 18 adults were recaptured in the same net lines after one year. There was a significant change in weight of birds before and after fragment isolation, both in the initial fragment isolation event of the 1980s ($t_{25} = -2.329$ $p=0.02$) and in a subsequent isolation event in 2013 ($t_{48} = -2.84$ $p=0.006$) (Figure 1). In addition, insectivores had significant weight changes after fragment isolation in the 1980s ($t_{22} = -2.31$, $p=0.03$) and in the 2013 fragment isolation event ($t_{28} = -2.35$, $p=0.02$). Frugivores had no significant weight changes in 2013 ($t_{19} = -1.56$, $p=0.14$) and there were too few individuals to test in the 1980s. There were insufficient numbers of individuals recaptured after fragment isolation in 10ha fragments to assess before and after weight changes at the individual level. However, in the 100ha fragments, there were significant weight changes in the 1980s ($t_{18} = -2.9$, $p=0.009$) (Table 1). Neither time period found significant weight changes in males before compared to after fragment isolation in 1980s males ($t_9 = -1.94$, $p=0.088$), and 2013 males ($t_{12} = -0.1$, $p=0.92$) and there were insufficient numbers of females recaptured after fragment isolation to properly assess individual weight changes. Birds that were recaptured in fragments gained weight after fragment isolation (Table 1). There were no significant weight changes in individuals captured in the control continuous forest in 2011 and recaptured in 2012 ($t_{18} = 0.67$, $p= 0.5$) (Table 1).

Population changes in weight

One hundred and seventy *Willisornis poecilinotus* were caught in mist nets in the fragments between 1981 and 1993. Based on results from an unpaired two-samples Wilcoxon test, *Willisornis poecilinotus* showed a significant weight difference before and after fragmentation ($W = 170$, $p = <0.001$), and the pattern held for subgroups of males ($W=98$, $p=0.02$), females ($W=70$, $p=0.008$), 10ha ($W=57$, $p=0.04$) and in 100ha ($W=113$, $p=0.02$) fragments (Table 2). In addition, results from the LMM indicate a significant weight difference between birds in 10ha and 100ha fragments ($p = 0.03$), but not as an interaction with fragment isolation (Table 4). The lack of a significant interaction term indicates the differences in weight between fragment sizes (birds are larger in 100ha than 10ha fragments) is not related to fragment isolation. *Glyphorynchus spirurus* was caught 160 times between 1981 and 1993, and Wilcoxon tests revealed significant differences in weight before and after fragment isolation ($W=160$, $p=2.51E-05$), as well as in subgroups of 10ha ($W=85$, $p=0.0002$) and 100ha fragments ($W=75$, $p=0.02$) all gaining weight (Table 2). *Glyphorynchus spirurus* are not sexually dimorphic, thus we were unable to compare weight changes between sexes. Results from LMM showed there was no significant difference between fragment sizes in terms of *Glyphorynchus spirurus* weight (Table 4). *Psuedopipra pipra* was caught 85 times and showed no significant weight difference before and after fragmentation according to the unpaired two-samples Wilcoxon test. LMM indicated a significant difference in weights between the sexes for *Psuedopipra pipra* ($p=0.0001$), with females being heavier than males. Again, there was

no significant interaction term indicating the differences in weight between the sexes was not related to fragment isolation (Table 3).

Discussion

Following forest fragment isolation during the 1980s and in 2013, birds that remained in fragments had significant weight increases. The increase in weight contradicted our predictions that nutritional loss in forest fragments would create health disparities. After a fragmentation event, many species become locally extinct from fragments, (Bierregaard and Lovejoy 1989, Bierregaard, et al. 1992, Gascon et al. 1999a, Stratford and Stouffer 1999, Antongiovanni and Metzger 2005, Ewers and Didham 2006, Stouffer et al. 2006) and lack of food resources is expected in forest fragments and is considered a primary reason for such local extinctions (Burke and Nol 1998, Zarette et al. 2000, Irwin 2007). Our research suggests the few birds that do persist in habitat fragments after isolation are not only able to endure but also to gain weight, while birds in continuous forest in the same time frame did not lose or gain weight.

Fitness can be linked to habitat quality and resource availability (Pulliam 2000, Johnson 2007) with food availability being a major determinant of habitat quality (Grüebler et al. 2018). Though certain species persist in habitats that lack nutritional quality by traveling outside home ranges for food resources (Tremblay et al. 2005), we doubt that is the case for the birds in our study as they don't cross the matrix before the second-growth forest has reached a certain level of maturity (Stouffer and Bierregaard 1995, Powell et

al. 2013). However, there are a number of behaviors and factors that may explain why species gained weight in recently isolated forest fragments.

Lack of food resources can cause a choice between the care of an individual's self-needs versus reproduction needs, indicating that in a habitat in poor condition, species will use more resources for self-survival than ensuring survival of their young (Martin 1987, Newton 1998, Gruebler et al. 2018). As nest success is known to decrease in areas with increased fragmentation (Herkert et al. 2003, Newmark and Stanley 2011, Gruebler et al. 2018), it is possible that birds remaining in fragments use the limited nutritional resources on self-survival, thereby increasing in weight and no or little expenditures go to reproductive efforts. Additionally, forest fragments can have fewer avian blood parasites than birds in continuous forest (Laurance et al. 2013). A decrease of parasites should improve the health of those species that can persist in the fragments and could lead to improved body condition.

Certain species are known to take advantage of fragmentation events to out-compete others (Reitz and Trumble 2002, Henry et al. 2007, Liao et al. 2013, Jessen et al. 2018). Buchmann et al. (2013) suggests that bird species may have plastic responses to fragmentation by expanding home ranges in poor habitats to find resource that otherwise may have been neglected. Species which are able to out-compete on both a interspecific and intraspecific level may use this 'expansion response' (Ims et al. 1993, Buchmann et al. 2013) to increase foraging territories. Species remaining in fragments after isolation are likely to have outcompeted individuals that either fled or perished. Thus, weight gain after fragment isolation could be a benefit from a lack of competition allowing for a

wider foraging niche. As many species are lost during fragmentation (Stouffer et al. 2006, Korfanta et al. 2012) and in poor habitats (Shochat et al. 2002), there may be opportunities for broader niches for those that can remain in the fragments imminently after fragmentation (MacArthur et al. 1972, Wright 1980, Sinclair and Pech 1996).

Insectivorous birds were most likely to gain weight after fragment isolation compared to birds in other guilds. Understory and terrestrial insectivores are known to be highly affected by fragmentation, with many insectivores fleeing fragments or becoming locally extinct in small fragments (Bierregaard and Lovejoy 1989, Bierregaard, et al. 1992, Gascon et al. 1999, Stratford and Stouffer 1999, Antongiovanni and Metzger 2005, Ewers and Didham 2006, Stouffer et al. 2006, Stouffer et al. 2006; 2011; 2020). The prevailing wisdom has been that birds in fragmented habitat must overcome a lack of food resources (Burke and Nol 1998, Zanette et al. 2000, Irwin 2007), competition (Rolstad 1991) and increased predation (Brittingham and Temple 1983, Andren 1992, Robinson et al. 1995). For a complete understanding of why insectivores gained weight after fragment isolation, we need to understand the response of their prey, insects and arthropods, to fragment isolation. For example, an increase in insect abundance could account for an increase in insectivore body weight. Like birds and other taxonomic groups, insects and arthropods do not respond uniformly to forest fragment isolation in the Amazon (Vasconcelos and Bruna 2012). Didham et al. (1998) found that abundance of leaf-litter beetles increased in smaller fragments and around fragment edges, which is consistent with Barrera et al. (2015) who found that leaf cutter ants increase in species richness and abundance around fragment edges and in the interior of smaller forest

fragments. An increase in beetle and ant abundance may be associated with the increased weight of *Glyphorhynchus spirurus* and *Willisornis poecilinotus* after fragment isolation of forest fragments as examinations of *G. spirurus* and *W. poecilinotus* stomach contents indicate that beetles are a main prey item for *G. spirurus* species (Marantz et al. 2020), with beetles, ant larva and cockroaches being important for *W. poecilinotus* (Zimmer et al. 2020).

Weight gains after fragment isolation should be interpreted cautiously as they do not necessarily indicate increased fitness. For example, *W. poecilinotus* exhibits reduced survival within the first 5 years after fragment isolation while *G. spirurus* and *P. pipra* have slightly increased survival shortly after fragment isolation (Wolfe et al. 2020). *G. spirurus* and *P. pipra* are known to have resiliency in light of fragment isolation and readily use edge habitat and the matrix once it reaches a certain level of maturity (Powell et al. 2016), while *W. poecilinotus* is known to be more sensitive to forest fragmentation and is either lost from forest fragments or stays in the interior of the fragments (Stouffer et al. 2011).

Conclusion

Understanding how fragmentation affects the health of birds is important for conservation efforts in landscapes where human disturbance occurs. However, survival and reproductive success should also be investigated for a fuller picture of the condition and fitness of individuals that remain in fragments after isolation. Further studies on body condition of individuals that remain in fragments and the ultimate consequences of

fluctuations in body condition will help reveal why some individuals and species are more susceptible to forest fragmentation than others.

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Tables and Figures

Table 3.1

Individual weights (grams) before and after forest fragment isolation in the 1980s, re-isolation in the 2010s, and continuous forest in the 2010s. Results from paired t-tests are broken down by sex, foraging guild, and fragment size. Statistical tests were not conducted on subgroups with fewer than 6 individuals.

Variable	Years	Number of Individuals	Mean±SE (grams)		t value	p value
			Before Fragmentation	After Fragmentation		
All						
Individuals		25	23.38±2.88	24.26±2.84	-2.323	0.03*
Male		9	17±1.84	18.17±1.82	-1.94	0.09
Female		3	18.8±3.35	19.67±3.48		
Insectivore	1981-1993	22	23.82±3.14	24.64±3.01	-2.31	0.03*
Frugivore		3	20.17±8.19	21.5±10.25		
10ha		7	26.5±8.54	27±8.05	-0.48	0.65
100ha		18	22.17±2.46	23.19±2.59	-2.91	0.01*
All						
Individuals		47	19.84±1.89	20.31±1.97	-2.85	0.006*
Male		12	17.01±2.37	17.15±2.43	-0.10	0.92
Female		4	27.15±14.25	28.23±14.96		
Insectivore	2013-2014	28	19.80±2.35	20.32±2.46	-2.36	0.03*
Frugivore		19	20.02±3.37	20.43±3.51	-1.56	0.14
1ha		9	18.23±3.17	14.93±1.81	1.05	0.32
10ha		13	20.72±3.97	23.25±4.31	-1.36	0.19
100ha		24	20.59±2.93	21.12±3.07	-0.41	0.68
All						
Individuals		18	20.02±1.89	17.49±2.33	0.67	0.50
Male	Continuous Forest	2	16.3±0.2	16.8±0.5		
Female		5	18.36±4.87	14.7±1.56		
Insectivore	2011-2012	15	19.96±1.88	17.18±2.42	0.66	0.52
Frugivore		2	20.5±10.9	20.35±10.75		

Significant differences are indicated by an asterisk.

Table 3.2

Population level responses in weight of *Willisornis poecilinotus*, *Glyphorynchus spirurus*, and *Psuedopipra pipra* before and after forest fragment isolation in the 1980s. Results are from unpaired two-samples Wilcoxon tests. *Glyphorynchus* could not be divided by sex as they are not sexually dimorphic.

Variable	Species	Number of Individuals	W	P	% change
All Individuals		170	2427.5	<0.001*	5.46%
Male	<i>Willisornis poecilinotus</i>	98	884.5	0.03*	4.59%
Female		70	341	0.008*	7.51%
10ha		57	276.5	0.04*	2.50%
100ha		113	1021.5	0.02*	5.71%
All Individuals	<i>Glyphorynchus spirurus</i>	160	1645.5	<0.001*	6.44%
10ha		85	387	<0.001*	7.52%
100ha		75	419.5	0.02*	5.95%
All Individuals	<i>Psuedopipra pipra</i>	85	731.5	0.45	3.02%
Male		22	44.5	0.82	1.57%
Female		51	302.5	0.92	0.08%
10ha		31	124	0.79	-0.83%
100ha		54	245.5	0.27	5.27%

Significant differences are indicated by an asterisk.

Table 3.3

AIC table for each species, LMM tested with band number as a random term. Cut represents before and after fragment isolation, while type represents the size of the fragment 10ha or 100ha.

Species	LMM model	AICc	Δ AICc	AICc wt.
<i>Willisornis poecilinotus</i>	wt ~ cut + type	600.37	0	0.42
	wt ~ cut*type	601.5	1.12	0.24
	wt ~ cut	602.5	2.36	0.13
	wt ~ cut + sx + type	602.73	2.51	0.12
	wt ~ type	604.71	4.33	0.05
	wt ~ cut + sx	605.45	5.07	0.03
	wt ~ sx	610.13	9.76	0
<i>Glyphorynchus spirurus</i>	wt ~ cut	549.88	0	0.69
	wt ~ cut + type	552.21	2.34	0.21
	wt ~ cut*type	553.9	4.02	0.09
	wt ~ type	560.2	10.33	0
<i>Psuedopipra pipra</i>	wt ~ sx	311.06	0	0.56
	wt ~ cut + sx	312.11	1.05	0.33
	wt ~cut +sx +type	314.4	3.34	0.11
	wt ~ cut	322.56	11.49	0
	wt ~ type	322.89	11.84	0
	wt ~ cut + type	324.72	13.66	0
	wt ~ cut*type	325.31	14.24	0

Table 3.4

Model output for the best LMM for each of the three species: *Willisornis poecilinotus*, *Glyphorynchus Spirurus*, *Psuedopipra pipra*. Cut represents before and after fragment isolation, while type represents the size of the fragment 10ha or 100ha.

Species		β Estimate	Standard Error	df	t-value	p-value
<i>Willisornis poecilinotus</i>	Intercept	16.14	0.30	76.74	52.50	<2e-16*
	cut	0.73	0.27	116.74	2.72	0.008*
	type	0.71	0.31	79.58	2.2	0.03*
<i>Glyphorynchus Spirurus</i>	Intercept	13.51	0.21	118.03	65.04	< 2e-16*
	cut	0.85	0.25	127.31	3.39	0.0009*
<i>Psuedopipra pipra</i>	Intercept	10.82	0.45	54.57	24.21	<2e-16*
	sex	1.61	0.42	62.92	3.87	0.0001*

Significant differences are indicated by an asterisk.

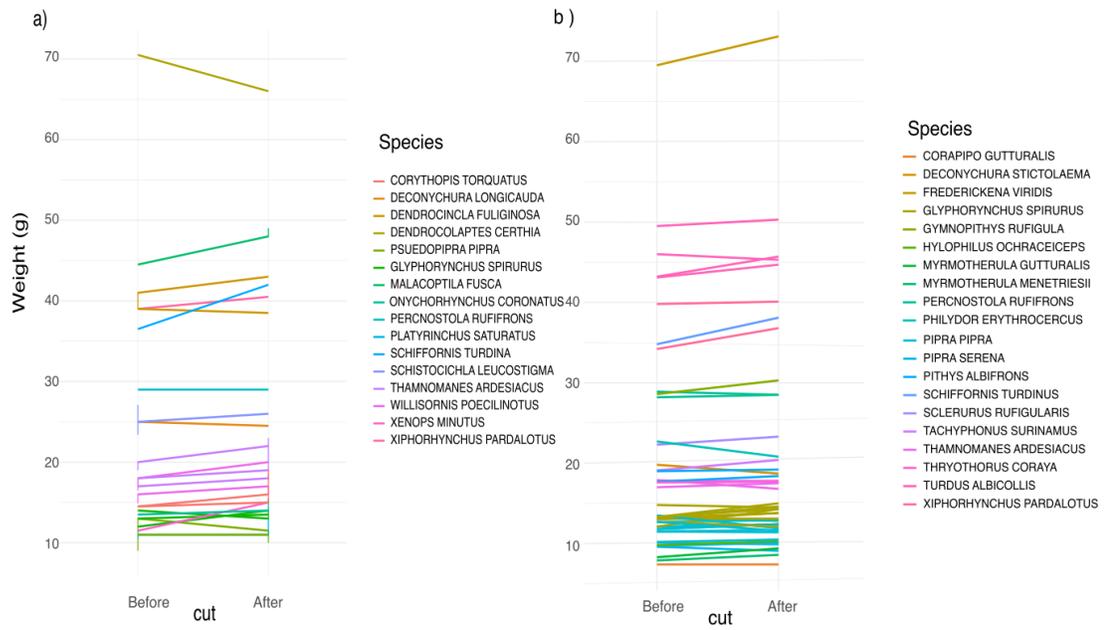
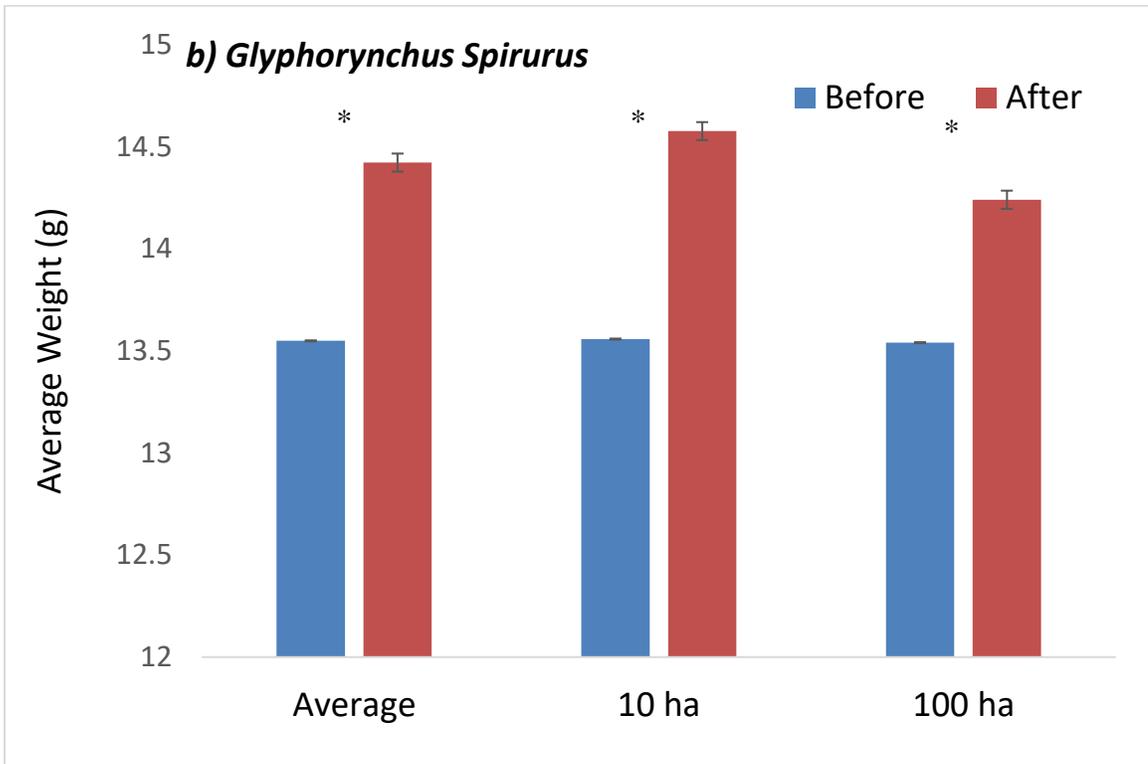


Figure 3.1

Changes in the weight of individual birds captured before and after fragment isolation in the a) 1980s and b) 2013. When considered together, birds on average significantly gained weight after both fragment isolation events.



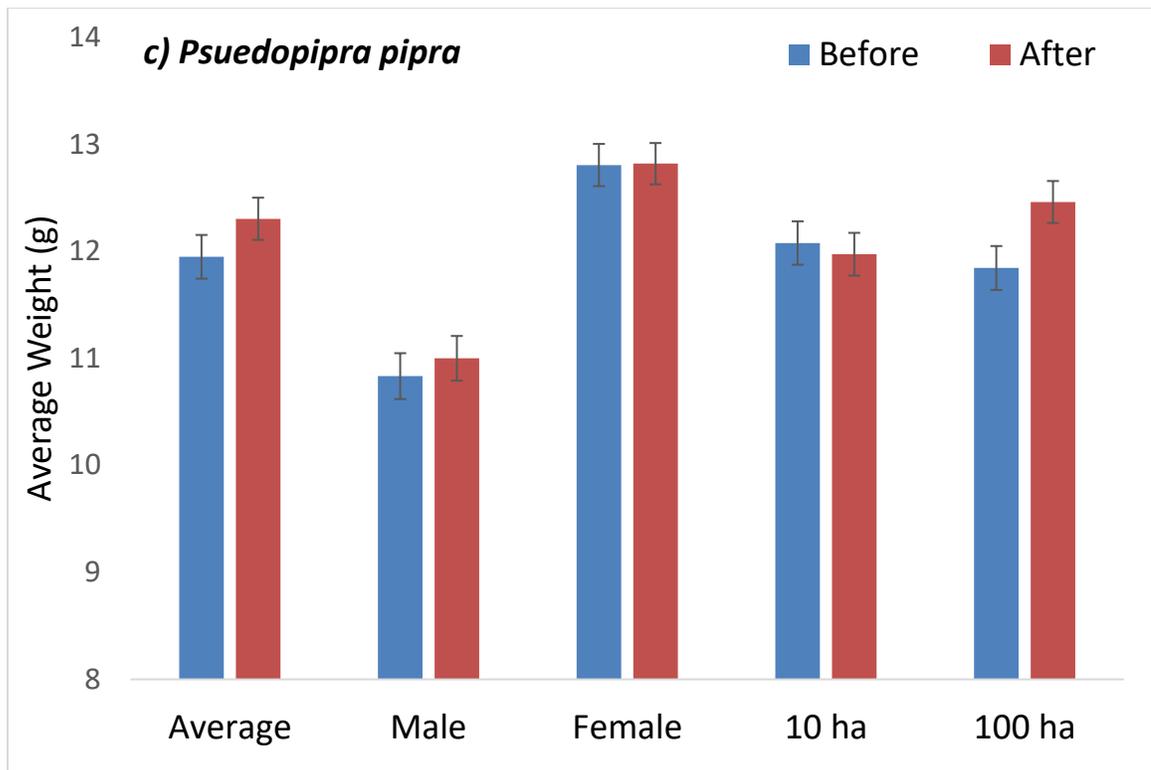


Figure 3.2

Individual species weight responses of a) *Willisornis poecilinotus* b) *Glyphorynchus spirurus* and c) *Psuedopipra pipra* to fragment isolation. Comparative differences between all individuals of a species with subpopulations based on gender and fragment size. Significant differences indicated by asterisk.

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BIOGRAPHY

Lara Kazo graduated from University of Rhode Island, in 2016 with a B.S. in Wildlife Biology. She was employed as a zookeeper, wildlife vet tech, and nature instructor before receiving her Master of Science in Environmental Science and Policy from George Mason University in 2021.