MIGRATORY DISTANCE AND PREDATION RISK AS DRIVERS OF

BEHAVIORAL TRADEOFFS MADE BY PASSERINES

DURING FALL STOPOVER

By

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CHAPTER 1

A REVIEW OF BEHAVIORAL TRADEOFFS MADE UNDER

RISK OF PREDATION DURING MIGRATION

1.1. Introduction

Animals make behavioral tradeoffs between the conflicting demands of acquiring

energy and avoiding predators. Depending on contexts, individuals may optimize

behaviors to solve this problem. These tradeoffs are well studied during sedentary

periods of animals' lives. During migratory phases, however, the behavioral tradeoffs

between energy and risk are complicated by migratory schedules and the costs and

benefits of timely arrival to wintering or breeding grounds as well as uncertainty about

resources and risk as they move through unfamiliar areas. Although some individual

determinants of migratory behavior in the face of predation risk have been recognized,

we lack a synthesis that predicts what behaviors should arise in what populations and

environments. Here I will review research investigating how these constraints shape

behavioral decisions made under predation risk during migration and identify needs for

future research to construct a synthetic model of these behaviors.

1.2. Body Mass Regulation

The fitness of individuals is predicated on their ability to compromise between the

conflicting demands of avoiding starvation and avoiding predation. Carrying fat loads,

or energy reserves, is one way to guard against starvation but this may make individuals

more vulnerable to predation. Animals may minimize the likelihood of one risk by increasing the risk of a second (Dall 2010), so long as the relative intensity of the two risks is clear. During migration, when food availability and predation vary spatially, temporally, and independently across the migratory route, both the costs and benefits of carrying added mass are magnified.

An informative case study of this adaptive tradeoff is body mass regulation. Animals can guard against future starvation when resources are limited or unpredictable by carrying more fat reserves (Pravosudov and Grubb 1998). Resource stochasticity results in mass changes and size differences in many passerine species (Cuthill et al. 2000), corvids (Cucco et al. 2002) and insects (Leptidoptera: Leimar et al. 1994).

Any decrease in starvation risk by increasing fat reserves, however, also increases the risk of predation due to losses in maneuverability and escape speed (Lima 1986). Leaner birds have higher flight performance and predator evasion capabilities (McNamara and Houston 1987, Witter and Cuthill 1993). Kullberg et al. (1996) tested the escape flight angle and velocity of blackcaps (*Sylvia atricapilla*) with various fat loads after a staged merlin (*Falco columbarus*) attack. Heavier birds flew at both lower velocity and a lower angle in their escape attempts. Interestingly birds with the lowest fat took off 90° from the attack angle, possibly maximizing evasion. Results, however, have been mixed among species in similar experiments. Lind et al. (1999) showed heavier robins (*Erithacus rubecula*) escaped at a lower angle but with no difference in velocity. Conversely, fat load had a significant effect on sedge warblers' (*Acrocephalus schoenobaenus*) escape velocity but not angle when attacked (Kullberg et al. 2000).

Regardless, fat load decreased some aspect of flight performance across these studies. Whenever predation risk is larger than starvation risk, individuals should be relatively leaner (Houston et al. 1993, Macleod et al. 2007).

This pattern has been observed across multiple orders of birds. A four-decade long study of great tits (*Parus major*) at Wytham Woods, Oxforshire, England showed a switch in body mass regulation strategy (Gosler et al. 1995) by a songbird (order: Passeriformes). Sparrowhawks (*Accipiter nisus*) were absent at the start of this study (due to widespread pesticide use in the 1940s and 50s), leading to a very low winter predation rates for the tits relative to the rate of starvation. Populations of the predator and the concomitant risk of tit predation, however, rebounded during the study's last two decades. Great tits were significantly heavier when sparrowhawks were absent (and starvation risk outweighed predation risk) than when the hawk populations recovered (and predation risk outweighed starvation risk). Similar patterns of mass loss in the face of increased predation risk have been observed in western sandpipers (*Calidris mauri*; Ydenberg et al. 2004) and in mallards (*Anas platyrhychos*; Zimmer et al. 2010).

The appropriate strategy for mass regulation in the face of a given predation risk may be altered during migration due to increases in energetic demand during this activity. A study of eleven passerines species killed by predators (feral cats *Felis catus* and sparrowhawks) during migration, for instance, revealed that half of the victims were in the lower 20% body mass for their species (Dierschke 2003). Further, nearly 80% were in the lightest half. All birds need to build up energetic stores for sustained flight.

Lighter birds thus have increased need for foraging time to build up these stores relative to heavier birds, and the increase in foraging increases their exposure to predators. In support of this, Cimprich and Moore (2006) showed that fatter gray catbirds (*Dumetalla carolinensis*) waited longer to resume movement after a simulated predator attack than did leaner individuals. Dierschke (2003) suggests that the risk posed by increased foraging activity trumps any benefits in flight performance for lean birds.

1.3. Vigilance

Another behavioral tradeoff necessary to mitigate both predation and starvation risk occurs in vigilance (Lima and Dill 1990). Vigilance behaviors necessarily decrease foraging rates and subsequently reduce energy intake. Much as body mass regulation strategies are influenced by different predation risks, vigilance strategies are influenced by energetic demand (i.e. food deprived or satiated). Energetically stressed animals are less vigilant than satiated ones (Lima 1998). In birds and mammals, being in relatively better condition allowed individuals time for other diverse self maintenance behavior (Family: Sciuridae; Bachman 1993, Family: Muscicapidae; Cucco and Malacarne 1997, Family: Cervidae; Winnie and Creel 2007, Family: Macropodidae; Edwards et al. 2013). Consequently, these individuals had greater reproductive fitness or survival.

The relative costs of a given vigilance strategy, however, vary with past behaviors. For instance, if a food-deprived individual is subject to a long series of high risk events, repeated preference for vigilance over foraging will have even more deleterious effects as the costs of reduced foraging accumulate. The risk allocation

model (Lima and Bednekoff 1999) predicts that individual strategies minimize accumulated risk across longer periods. Risk varies temporally (e.g., tides: McIvor and Odum 1988, moonlight: Clarke 1983) as well as spatially (habitat: Brown 1988). Under the risk allocation model, individuals alter vigilance strategies across space and time and can thus compensate for losses from periods of sustained risk during periods of lower risk. It is unclear how such an optimization strategy would work for animals during migration. The success of risk mitigation is predicated upon an ability to predict or assess periods of high versus low relative risk. During migration, many species spend the majority of their time in novel habitats and may not have adequate information to mitigate risk in this way.

1.4. Habitat Selection

A third behavioral strategy to mitigate the competing risks of predation and starvation is habitat selection. In some environments, areas with the highest likelihood for foraging success are also areas with the highest predation risk (Walther and Gosler 2001). Dense habitat, for instance, can offer abundant plant resources, but impair predator detection (Metcalfe and Furness 1984). To mitigate this increase in risk, an animal foraging under such circumstances should be more vigilant, which decreases the net benefits of the habitat and alters the advantages of particular habitat preferences. In other environments the most productive foraging grounds may be in the open, but dense cover offers the most protection from predation (Lima and Dill 1990, Lind and Cresswell 2006). These conflicting scenarios emphasize that habitat selection strategies may vary

with available resources, physiological condition, and predator hunting behaviors (Repasky 1996).

The increased scale of movement for migratory animals can greatly alter both the habitats available to migrating individuals and the habitat selection strategies exhibited by populations. Antipredator behavior in migrating animals can cause individuals and groups to avoid entire stopover sites, rather than just habitat patches. For instance, western sandpipers commonly used Sidney Island, British Columbia for refueling during migration, when the island lacked predatory falcons. As raptor populations recovered (after a crash following pesticide use), predation risk on the island increased, refueling rates dropped dramatically, and birds remained for much shorter periods at the site (Ydenberg et al. 2004). Although this study did not quantify resource abundance, others have showed that patch use can be predator mediated regardless of foraging profitability (Feltmate et al. 1986, Wolfe and Summerlin 1989).

Migratory species may be more likely to show switches in habitat preferences across space and time because A) their larger scales of movement offer more options and B) the energetic demands of migration (and increases in foraging time) alter both the risks of starvation and predation. For instance, migrating bramblings (*Fringilla montifringilla*) switch from foraging in open fields to structured beech forests in years of beech mast (Lindstrom 1990). Predation rate is much lower in the forests than it is in the fields. In non-mast years, however, migrating birds cannot maintain adequate migratory condition in beech forests and must accept increased predation risk in the open fields. In mast years, however, birds switch to the beech forests even though

energy acquisition is lower than in the fields, because the ratio of predation to starvation risk changes enough to tip the scale.

1.5. Optimal Migration

Migration strategy itself has been posited as a solution to the competing risks of predation and starvation. Under this paradigm, different migratory strategies may simply be a cumulative set of evolutionarily modified behaviors that solve this tradeoff optimally for populations that are already committed to a migratory lifestyle: time selected and energy selected secondary levels of the migratory syndrome (Dingle 1996). Time selected migration should favor behavioral traits that minimize time spent on migration and is expected to arise in populations that move from limiting conditions on the breeding grounds to favorable wintering sites. Early arrival to wintering grounds, therefore, is advantageous and late arrival bares substantial costs. An energy minimizing strategy is favored in populations that move from favorable conditions on breeding grounds to wintering grounds that are limiting, thus early arrival bares no benefit (Alerstam and Lindström 1990, Minias et al. 2010).

Variation within populations and ecological conditions likely puts optimization strategies on a continuum (Houston 1998). As such, Alerstam and Lindström (1990) posit physiological and ecological rules that predict where a given population falls between two endpoints of migratory behaviors: a fast, time minimizing migration or an energetically efficient migration.   Migrations of time minimizers are characterized by shorter, infrequent stopovers and relatively faster refueling rates. Whereas migrations

of energy minimizers occur in smaller, frequent steps where individuals accumulate relatively lower fuel stores (Meltofte 1996).

Observed patterns of fuel deposition illustrate how time and energy minimization strategies shape individuals' behavioral tradeoffs between acquiring energy and avoiding predation during migratory stopover. Each extreme migration strategy predicts a different optimal fuel load, which reflects foraging intensity, upon departure from a stopover site. Gains in flight distance are positively associated with Departing Fuel Load (DFL), which is, in turn, determined by stopover duration and the local rate of energy acquisition, or site profitability (Hedenström and Alerstam 1997). The DFL is expected to be highest for time minimizers, as larger fuel stores allow for longer flight distances that in turn reduce the number of stopovers. Time minimizing birds will gain the maximum fuel available at a stopover site while energy minimizers will maintain some lower, fixed fuel level irrespective of availability. If, however, a stopover site does not provide large energy stores it would be more advantageous for time minimizers to skirt these sites and instead stop where high refueling rates are supported (Gudmundsson et al. 1991), thus maintaining their migratory schedule. While time minimizers require large fuel stores before departure to maximize flight distance, energy minimizers need only to reach the next stopover. Rather than depart a poor site early, they tradeoff time and consequently stay longer to attain their constant optimal fuel load (Bayly 2007).

High predation risk at stopover sites can undermine their resource profitability (Ydenberg et al. 2004), and therefore have similar effects on departure fuel loads for both time and energy minimizers. Few studies have tested how predation risk modulates foraging of time and energy minimizers (Hedenström 2008). The principles of site profitability apply, such that time minimizers would avoid high predation risk areas altogether to ensure acquisition of maximum fuel loads (Schmaljohann and Dierschke 2005). While, on the other hand, energy minimizers may exhibit more antipredator behavior and thus take longer to accumulate enough fat to leave. Duijns et al. (2009) found a time minimizing subspecies of bar-tailed godwit (*Limosa lapponica taymyrensis*) foraged at higher rates under increased risk than an energy minimizer (*L. l. lapponica*), accepting greater risk in favor of acquiring energy.

These few studies indicate that predation risk may influence the behavioral tradeoffs of time and energy minimizers differently, as well as independently of site profitability.   Additionally, minimizing total time on migration may simultaneously minimize total exposure to predation risk (Hedenström 2008) therefore mitigating predation risk may be more important for energy minimizers (Schmaljohann and Dierschke 2005).

1.6. Conclusions

As predation risk, migratory time budgets, and energy acquisition all interact, it can be difficult to determine the drivers of a given migratory strategy.   Mass regulation and vigilance are effective antipredator tactics but seem to be strongly determined by

individual variation in condition, which is difficult to measure or incorporate into a

comprehensive study. Habitat preferences are dependent on perceived costs and

benefits. Optimal migration provides a broad context for understanding factors

affecting birds' performance and the evolution of migratory behaviors. I believe,

however, that it lacks consistency in predicting how individuals tradeoff between energy

and time in relation to risk. Incorporating condition of known individuals and using

phylogenetic contrast to isolate differences in life history may improve how we assess

variation in migratory strategies.

CHAPTER 2

LONGER DISTANCE MIGRANT PASSERINES ARE MORE

AVERSE TO PREDATION RISK

DURING MIGRATION

2.1. Abstract

Migratory animals balance the energetic requirements of large-scale movement with the predation risk inherent in unfamiliar habitats. Optimality theory predicts that species migrating different distances prioritize time and energy differently, and the tradeoff between these two currencies shapes their response to predation risk. We conducted two investigations along the coast of Maine to determine the behavioral and population-scale responses of migrating birds to predation risk as a function of their migration distance. First, by observing bird activity in a field aviary before and after exposure to a predator call, we tested whether time-energy optimization correlated with migration distance in four Passerine species and whether this relationship changed with increased predation risk. Second, we used banding records of the same species to test whether different anti-predator behaviors explained size-corrected mass across nine sites varying in raptor abundance. Contrary to Optimality Theory, there were no differences in bird behavior by migration distance prior to predator exposure. Further, longer distance migrants were less active under increased risk relative to shorter distance migrants. At the population-scale, bird mass for all species decreased as

predator abundance increased, but mass loss was greater for longer distance migrants. We hypothesize that these individual and population-scale responses to risk may result from differential life expectancy. Longer distance migrants may be more risk averse to maximize future reproductive opportunities, while shorter distance migrants may prioritize current condition over long-term survival to avoid negative carryover effects on the subsequent breeding season.

2.2. Introduction

Migratory animals face the difficult task of balancing the energetic requirements of large-scale movement with the predation risk inherent in unfamiliar habitats. The stakes of striking a successful balance are high during migration because of the increased risks of predation and mortality relative to non-migratory periods (Sillett and Holmes 2002, Packer et al. 2005). Optimality theory suggests multiple behavioral solutions to the tradeoff between a fast migration and an energetically efficient migration in the face of risk (Alerstam and Lindström 1990). Our current understanding of how optimization operates among different species, however, is limited to correlative field descriptions. Here, we conducted a field experiment to test how relative predation risk alters the tradeoff between cryptic and activity in four species with different migratory constraints.

In general animals cannot maximize survival while simultaneously maximizing food acquisition due to a tradeoff between cryptic and active behaviors (Lima and Dill 1990). As a result, in these tradeoffs inactivity is associated with vigilance antipredator

behavior while activity is strongly correlated with foraging behavior (Cimprich et al. 2005). Although being vigilant reduces the probability of predation (FitzGibbon 1989, Sansom et al. 2009), it reduces foraging success in a wide variety of vertebrates (reviewed in Verdolin 2006). Further, this anti-predator behavior can cause individuals to avoid the most profitable foraging patches (Feltmate et al. 1986, Walther and Gosler 2001) or to avoid profitable patches during times of higher predation risk (Clark and Levy 1988, Cresswell and Quinn 2013).

Migrating animals face an additional constraint beyond energetic demand and survival: the time spent on migration. Thus, theory has explored how the selective forces of time and energy shape behavioral strategies of individuals on migration (Alerstam and Lindström 1990). Under this framework, individuals migrate at some point along the continuum between a fast migration and an energetically efficient migration. The utility of each currency varies by environment and species due to the relative costs of maximizing one currency at the expense of the others. Each species should exhibit a set of migratory behaviors that minimize the net cost of arriving late to the breeding or non-breeding grounds, engaging in risky behaviors while migrating, and arriving in poorer energetic condition.

Population experiencing more favorable conditions on their wintering grounds compared to their breeding sites benefit from early arrival in winter. As a result, their fall migrations are characterized by less frequent stopovers and departures with larger relative fuel loads to sustain longer flights (Newton 2008). Acquiring high fuel loads likely comes at a cost to vigilance and predation risk, and species that employ this

strategy are referred to as "time minimizers" (Hedenström and Alerstam 1997). A

hallmark of the time minimization strategy is the positive correlation between energy

acquisition rate and departure mass within populations. Individuals are expected to fuel

up as much as possible on high quality stopover sites to avoid the need to stop later, but

they should depart quickly from poor quality sites to avoid foraging inefficiency.

During fall migration "energy minimizers", on the other hand, generally move

from a surplus of resources on breeding grounds to limited resources on their wintering

grounds. They therefore benefit from late departure from breeding grounds and incur

no benefit from early arrival to wintering grounds. Consequently, their migratory

pattern consist of departure from stopover locations with a lower fuel load to maximize

flight efficiency at a cost to the number of stopover bouts (and time spent on stopover)

required to complete migration (Alerstam and Lindström 1990). Empirical evidence for

either strategy is uncommon, although time minimizers have been reported more often

for birds (reviewed by Alerstam 2011). These results may be biased, however, by the

selection of longer distance migrants for study.

In general, migration distance appears to correlate with optimization strategy.

From bird banding records, migration is relatively faster for longer distance migrants

(Ellegren 1993), suggesting that the costs of late arrival may be higher for species that

travel farther. A field study on a shorter distance migrant, however, (European robin,

Erithacus rubecula) showed support for both time and energy minimization (Dänhardt

and Lindström 2001). Although rate of mass gain and departure mass were not

positively correlated as time minimization predicts, the absolute values of both

characteristics resembled those of other reported time minimizers.

Optimization strategy also appears to vary by sex within a species, which is

expected when there are sex-specific time constraints (Ketterson and Nolan 1976,

Coppack and Pulido 2009) or migration distances (Komar et al. 2005, Nebel and

Ydenberg 2005). Compared to time minimizer male wheatears, females have similarly

high fuel departure mass but no correlation with acquisition rates, suggesting energy

minimization (Dierschke et al. 2005).

A few studies have examined how variation in predation risk influences the

tradeoff between optimization currencies en route (Lindstrom 1990, Schmaljohann and

Dierschke 2005, Duijns et al. 2009). Northern wheatears (*Oenanthe oenanthe*) did not

alter their time minimization strategy and only suffered slightly lower fuel deposition

rates under increased predation risk.   In contrast, migratory blackcaps (*Sylvia

atricapilla*) increased feeding rates when exposed to a model predator (Fransson and

Weber 1997). A time minimizing subspecies of bar-tailed godwit (*Limosa lapponica

taymyrensis*) accepted higher predation risk than an energy minimizing, shorter distance

subspecies (*L. l. lapponica)* (Duijns et al. 2009), favoring fuel intake. These results

suggests that varying predation risk and time constraints together place optimal

migration strategies on a continuum between safe/slow and risky/fast instead of

between distinct fast migration or an energetically efficient migration strategy (Hope et

al. 2014). The optimization strategies should then influence how risk is managed in a

particular environment.

To test whether migratory distance is associated with different behavioral solutions for minimizing time, energy, and predation risk on stopover, we conducted an aviary experiment on four wild, migrating songbird species. We asked three questions. First, do species that travel different migratory distances exhibit evidence for a different optimization between inactivity and activity? The energy- versus time-minimizer paradigm predicts that longer distance migrants would be more active than their counterparts to maximize fuel deposition rates (and conversely, minimize time until departure) and further, that they would carry more mass (relative to species-specific body size) than shorter distance migrants.

Second, we asked if species that travel different migratory distances show evidence for a different tradeoff between inactivity and activity under increased predation risk. If longer distance migrants are trying to minimize time more than shorter distance migrants, we predicted that they would accept more risk than shorter distance migrants and not decrease activity as much under increased risk of predation. With a lower time constraint, we expected shorter distance migrants to be more risk averse and less active under higher predation risk.

Third, do the size-corrected masses of migrating bird populations vary by stopover site and variation in predator frequency to reflect the behavioral tradeoffs of species that travel different distances under different predation risks. Raptors concentrate along coastlines during migration (Heintzelman 1975) creating spatial variation in risk between coastal and island stopover sites. Among our study locations, island sites report more accipiters and falcons than coastal or inland sites (results

below), suggesting greater risk to the songbird prey that use the islands. We predicted that shorter distance migrants would show a greater reduction in mass at sites with more avian predators than longer distance migrants, because time minimizing species should accept more risk (and give up fewer foraging opportunities as a result) during stopover.

2.3. Methods

2.3.1. Study Sites & General Design

We conducted aviary experiments at four sites during the autumnal songbird migration seasons of 2012 and 2013 in coastal Maine: Cross Island, Seawall, and two sites on the Schoodic Peninsula. Cross Island is a 603 ha island located 1 km offshore of Cutler, Washington County, Maine and is part of the Maine Coastal Islands National Wildlife Refuge. Seawall is a coastal headland on the southernmost point of Mount Desert Island, Hancock County. The Schoodic Peninsula lies 9 km to the east of Mount Desert Island in Hancock County. In 2012 we established an aviary site in the center of the peninsula, and in 2013 we moved our experiment 1-km to the southwest closer to the headland. The Schoodic Peninsula and Seawall sites were all within the boundaries of Acadia National Park. We operated all but the coastal Schoodic Peninsula site in 2012 and only the coastal Schoodic site in 2013. Each site consisted of spruce and hardwood mixed forest (dominated by *Picea* species with components of the genera *Abies, Larix, Betula, Acer,* and *Populus*) with mixed upland shrubs (e.g., *Alder, Aronia, Viburnum, Sorbus, Ilex*).

At each site we gathered behavioral data on individuals from four different species that we placed in a temporary aviary and exposed to either a predator call or a control birdcall. Our four species consisted of a longer and shorter distance migrant within each of two taxonomic families: yellow-rumped *(Setophaga coronata)* and blackpoll *(Setophaga striata)* warblers, and blue-headed *(Vireo solitarius)* and red-eyed *(Vireo olivaceus)* vireos. The two shorter distance migrants (yellow-rumped warbler and blue-headed vireo) winter in the greatest abundance in the southern Atlantic United States, while the most significant wintering populations of the two longer distance migrants (blackpoll warbler and red-eyed vireo) are in Central and South America (Hunt and Flashpohler 1998, Cimprich et al. 2000, DeLuca et al. 2013, Morton and James 2014).

2.3.2. Aviary Experiment

We placed a 5 m x 3 m x 3 m PVC-framed aviary, draped with 3.6-cm^2 mesh plastic netting in structurally and compositionally similar locations at each site between mid August and the end of October each year. Habitat within the aviaries was composed of dominant upland shrubs ranging within but not exceeding the height of the aviaries. Shrub density was similar among aviaries but, relative to surrounding habitat, were placed in less dense patches to avoid chronic visual obstruction of the subjects. Autumnal fruiting shrubs (e.g. *Aronia, Viburnum, Sorbus, Ilex*) are common at our sites and were included to replicate resource availability within each site. We selected birds captured from a passive mist-net array (at least 40 m from the aviaries at each site)

within six hours of sunrise on each day the nets were opened. Nets were not operated

when temperatures were below 7˚ C or above 24˚ C, under sustained or gusty winds

strong enough to bellow the nets, or under steady precipitation greater than a light mist

or drizzle. After banding, ageing, and measuring wing chord and mass, individuals were

placed into the aviary and allowed to acclimate for up to thirty minutes. Most

individuals attempted escape by frequently hopping or flying into the net walls.

Preliminary trials showed this behavior usually ceased between five and thirty minutes

after introduction into the aviary. Once a period of five minutes without an escape

attempt passed, the trial began. If the acclimation period lasted longer than thirty

minutes the trial was aborted and the bird was released.

Trials consisted of two, four-minute periods: Pre-treatment and Treatment.

During both periods, we recorded bird behavior to examine the tradeoffs in activity. An

observer dictated each bird's activities into a handheld, digital audio recorder (Roland R-

09HR) from a camouflaged burlap blind 6-8 m from the aviary. As our measure of

activity, we counted the number of perch changes separately for each period, as

movement is negatively correlated with vigilant behavior overall (Powell 1974). We

define a perch change as a movement via hop or flight that does not result in a net

encounter. We counted movements only over the time when the bird was visible in the

aviary and not engaged in or abutting the net wall. Hiding, or "freezing", is a common

response by songbirds to stress and predator attacks (Koivula et al. 1995) and would

limit total observation time. To reduce confounding effects of escape behavior (due to

stress of being confined) on our response of activity rate (due to response to a control

or predator cue) we also excluded the duration of escape attempts from the total observations time. To eliminate biased movement rates due to insufficient observation time, we only included individuals that were visible for at least 25% of both trial periods in our analyses. Among candidates for exclusion, we tested for biases in observation length among birds of both migratory distances and both treatment types in both periods.

Birds displayed a variety of natural behaviors both before and during the experimental trials. Gleaning and food-handling were relatively common behaviors for birds that had acclimated to the aviary. Both warbler species searched for and gleaned insects from the foliage inside the aviary, and in the case of yellow-rumped warblers, occasionally foraged on wax myrtle (*Myrica*) fruits. Vireos were more inclined to forage on insects within the aviary. On multiple occasions, a red-eyed vireo attacked and captured a dragonfly (*Odonata*). Food-handling times were not documented except for one vireo that handled a dragonfly from the acclimation period through the experimental trial: over twelve minutes. This individual was randomly selected to receive a predator treatment and it is included in this analysis.

During the Treatment period, the focal bird was exposed to either a simulated predator call or a neutral, heterospecific call. We used a merlin (*Falco columbarius*) call to simulate increased predator risk, as this species is common to all of our sites in fall and preys on small songbirds. Additionally, merlin presence can alter the foraging behavior of small passerines (Desrochers et al. 2002). American goldfinch (*Spinus tristis*), our control treatment, are also common on our study sites during fall migration,

but are not known to flock with or compete for food with any of our focal species. During the treatment period, calls were broadcast at 65-70 dB (measured at 1 m) in 30-second intervals (with 30 seconds of silence in between) from an Altec Lansing Orbit M, portable speaker and SanDisk Sansa, mp3 player hung 3 m away from the aviary and 4 m off the ground. We angled the speaker toward the aviary and positioned it on a different side than the observer. To avoid issues of treatment pseudoreplication (Kroodsma 1989), we randomly selected from one of four different predator or four different control calls for each treatment.

2.3.3. Statistical Analysis

2.3.3.1. Aviary Experiment

We performed all statistical analyses using R (version 3.0.1 R Development Core Team 2013). To examine the effect of migration distance on bird activity under increased predation risk, we constructed a generalized linear mixed model (package 'lme4') with counts of perch changes (hop or flight) modeled as a Poisson distribution with a log link function and an offset for the total observation time for each period. Maximum likelihood was used to estimate parameters with individual, site, and taxonomic family as random effects. We attempted to predict movement rates during the treatment phase as a function of the 3-way interaction between call type (predator or control), migration strategy (long versus short distance), and movement rate during the pre-treatment phase (to control for variation in baseline activity). We also tested for significance in the main effects and two-way interactions for each factor. We used the

Wald method to calculate 95% confidence limits. We used the ratio of the sum the

squared Pearson residuals to residual degrees of freedom to evaluate model fit.

To test the assumption that our focal individuals for the aviary study were in

similar physiological condition by migration distance and species, we examined the

differences among size-corrected body masses using residual mass from the linear

regression of wing chord to mass for each focal species. We used banding data from

nine banding sites (including our four sites) within a local migration monitoring network

(McCabe et al., *in review*) to parameterize the relationship between mass and wing for

each species, after first removing individuals with either mass or wing lengths that were

greater than three standard deviations from the mean. Protocol among banding sites

dictated wing chord as the primary body length measurement and was therefore

available for all sites and years.

2.3.3.2. Variation in Population Mass

To assess the trends in mass among migration strategies at different risk levels we

modeled size-corrected mass across nine sites from the larger migration monitoring

database. We used the same four focal species as in the aviary experiment, which

consisted of a longer and shorter distance migrant within each of two taxonomic

families: yellow-rumped *(Setophaga coronata)* and blackpoll *(Setophaga striata)*

warblers, and blue-headed *(Vireo solitarius)* and red-eyed *(Vireo olivaceus)* vireos. We

used a linear mixed effects model (package 'nlme') with restricted maximum likelihood

to estimate the two-way interaction between migration strategy (long versus short

distance) and banding site predator frequency, including main effects for each factor.

As we expect year may affect taxonomic family differently at each site we included year

nested within site nested within taxonomic family as random effects.

We calculated a predation risk by using the total number of raptors reported

from each banding site, divided by the total banding hours at each site. These raptor

families are common at our sites and are known to frequently prey upon passerine

species during migration (Sutton 1928, Page and Whitacre 1975, Thiollay 1982).

Banders at each site recorded opportunistic raptor observations only during hours the

mist nets were open.

2.4. Results

2.4.1. Aviary Experiment

We collected behavioral data from 105 birds. Only 62 were observed for at least 25% of

both sampling periods and included in this analysis. Among the 43 individuals that were

removed from the final dataset, the mean time available for calculating movement rate

was not different during Pre-treatment period for migratory distance (ANOVA: $F_{1,40}$ =

0.18, P = 0.67) or treatment type ($F_{1,40}$ = 2.17, P = 0.15). There were also no difference

in mean time available during Treatment period (migratory distance: $F_{1,40}$ = 0.76, P =

0.39, treatment type: $F_{1,40}$ = 0.01, P = 0.92). Among the 62 focal individuals, birds did

not differ in mean overall size-corrected body mass by migratory distance (N = 62, t_{59} =

0.52, P = 0.61). Baseline activity rate (rate of perch changes during the pretreatment

period) did not differ between species with different migratory distances (ß = -0.12 ±

0.08, *P* = 0.14). For all birds, activity changed between Pre-treatment and Treatment

periods (Table 1). There was also a significant 3-way interaction migration strategy,

treatment, and observation period.   Birds exposed to the control call did not change

their movement rates more than expected by the baseline increase over the entire trial

(Fig1a). Relative to their respective baseline activity rates, however, shorter distance

migrants increased their movement rates when exposed to a predator call while longer

distance migrants did not change their activity (Fig1b).

Our all species aviary model was slightly overdispersed, with a sum of squared

Pearson residuals to residual degrees of freedom ratio (SSP/rdf) of 2.9. Thus, marginal

significance of our Wald Z statistics may not be robust for inferences but our interest lies

mostly in the three-way interaction, which is significant (Table 1). Species-specific

patterns varied slightly compared to our full model, but sample sizes prohibited robust

estimates for each species that met model assumptions (Appendix A).

Variable	*Fixed Effects*		
	Est.	*SE*	*p value*
Intercept	-0.454	0.487	0.351
Treatment Merlin	0.751	0.653	0.250
Migration Distance Short	1.188	0.700	0.090
Period Broadcast	**0.337**	**0.118**	**0.004**
Treatment Merlin : Migration Distance Short	-1.000	0.940	0.288
Treatment Merlin : Period Broadcast	**-0.504**	**0.149**	**0.001**
Migration Distance Short : Period Broadcast	**-0.359**	**0.157**	**0.022**
Treatment Merlin : Migration Distance Short : Period Broadcast	**0.983**	**0.212**	**0.000**

Table 1. Parameter Estimates of Perch Changes Model. Maximum likelihood parameter
estimates and standard errors from model of perch changes of 62 experimental birds.
Parameters include treatment call type (American goldfinch or merlin), migratory
distance (long or short), and observation period (pre-broadcast or broadcast). Model
random effects include site, individual, and taxonomic family. Bold text indicates
parameter significance.
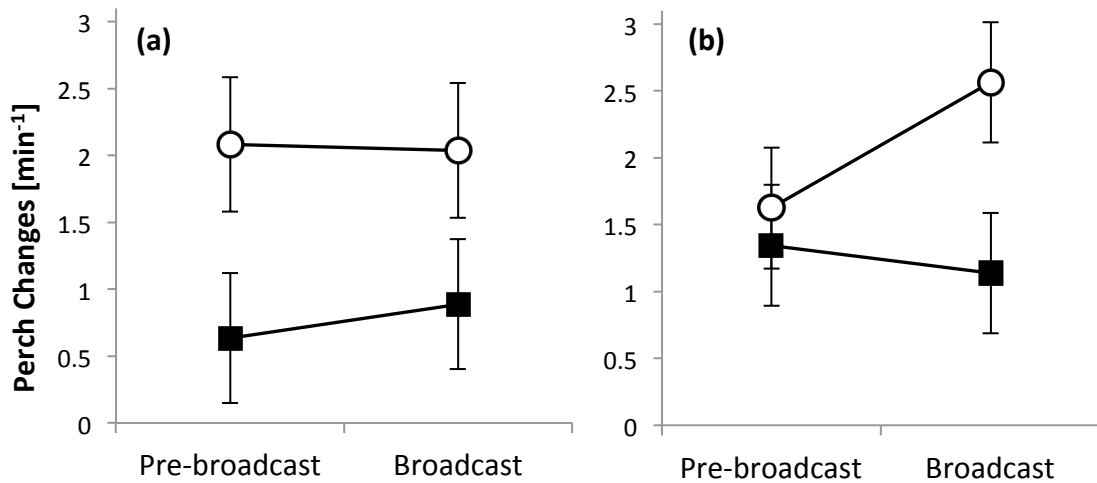
Figure 1. Model Predicted Perch Change Rates. Panels show the response of shorter (open circles) and longer (closed squares) distance migrant passerines to American goldfinch (a) and merlin (b) calls. Error bars represent SE of predicted values. Ratio of sum of squared Pearson residuals to residual degrees of freedom for our full model was 2.9, estimating slight overdispersion.

2.4.2. Variation in Population Mass

The overall condition of each of our focal groups decreased as Accipiter and Falcon frequency increased. For all birds, size-corrected mass was significantly under higher predation risk ($N = 5901$, $t_{11} = -4.88$, $P = 0.001$). We found no significant effect of migration distance on mass of our focal birds ($t_{5869} = -0.42$, $P = 0.7$). There are differences, however, within migratory distances such that when predator frequency is highest longer distance migrants carry less mass than when predators are minimal ($t_{5869} = 2.18$, $P = 0.03$; Fig. 2). Shorter distance migrants showed a similar change in mass among variation in predator frequencies but remained heavier than longer distance migrants when predators were most frequent.
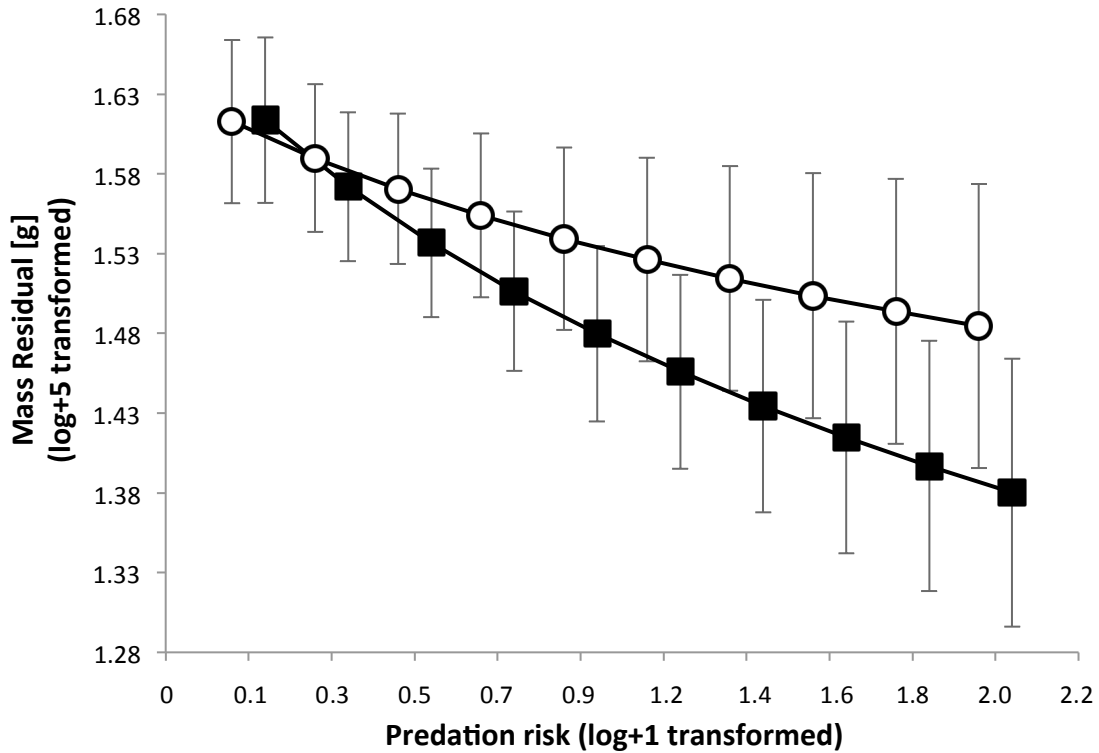
Figure 2. Changes in Size-corrected Mass Among Variation in Predation Risk. Model predicted mass residuals of shorter (open circles) and longer (closed squares) distance migrants from nine banding sites along the coast of Maine (2007-2013). Predation risk is the number of raptors reported during daily mist net operation at each banding site. Error bars represent 95% confidence intervals of the predicted means.

The trend in overall condition of our focal birds is also evident when compared to the

risk associated with individual sites. Mean mass residuals of longer distance migrants

were the same or less than those of shorter distance migrants at the four riskier sites.

They were the same or greater, however, at all five low-risk sites (Fig. 3).
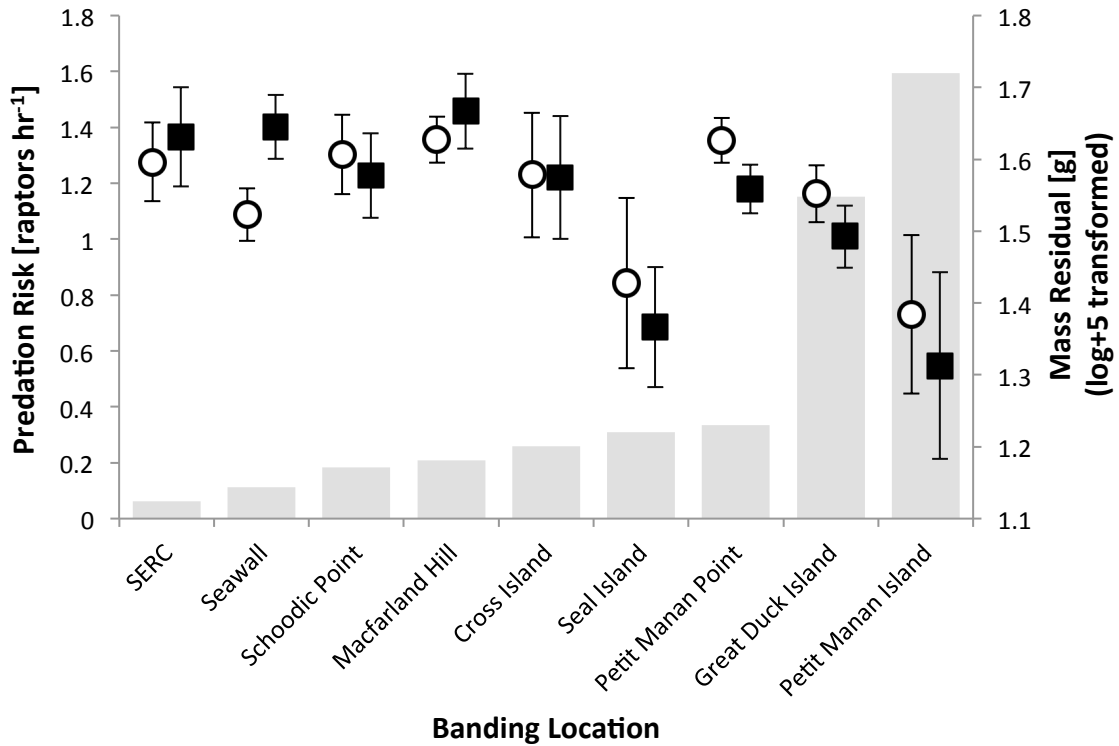
Figure 3. Changes in Size-corrected Mass by Banding Site Raptor Frequency. Model predicted mass residuals of shorter (open circles) and longer (closed squares) distance migrants at nine banding sites along the coast of Maine (2007-2013). Predation risk is the number of raptors reported during daily mist net operation. See Table 2 (Appendix C) for species totals for each site. Error bars represent 95% confidence intervals of the means.

2.5. Discussion

2.5.1. Aviary Experiment

Our focal birds did not demonstrate any differences in baseline activity related to

migration distance as expected by the time versus energy optimization paradigm. We

did detect, however, two distinct behavioral responses to increased predation risk

during fall migration. Activity rates changed with predation risk differently between

species with different migratory distance across two taxonomic families, although the

change was contrary to that predicted by optimization theory (Hedenström and Alerstam 1997). Relative to the control playback, longer distance migrants decreased activity rate and shorter distance migrants increased activity in response to a predator call.

Reduction in movements is a common response to an increase in risk (Lima and Dill 1990), and has been displayed by other passerines during fall migration (Cimprich et al. 2005). Under the time vs. energy paradigm, however, we would expect shorter distance migrants to reduce activity under increased predation risk, because they are less time constrained and generally exhibit lower masses upon departure relative to longer distance migrants (Hedenström and Alerstam 1997).

Similar increases in activity in the face of predation rate have been reported for migratory blackcaps and explained as a mechanism to facilitate movement away from danger (Fransson and Weber 1997). Further, Ferrari et al. (2009) explained such a counterintuitive response using the Risk Allocation Model (Lima and Bednekoff 1999); individuals exposed to longer bouts of high risk are more active and forage more intensely than those with lower prior risk exposure because of the effect of accumulated costs of delaying foraging. With wild, migrating birds we were unable to determine prior risk experiences, but it is possible that our shorter distance migrants had been present on the stopover site for longer than our longer distance migrants, that are conventionally thought of as more time-constrained. Even if this were true, however, we would have expected to see differences in baseline activity as well, instead of just differences following the short-term exposure to a predator call.

We suggest two alternative explanations for the difference in behavioral response to a predator call by longer versus shorter distance migrants: an adaptive response and a constrained response. First, the differences in behavioral response agree with the canon of work on risk aversion relative to life expectancy. Variation in survival affects the degree of risk a wide variety of animals take (Koops and Abrahams 1998, Candolin 1998, Ghalambor and Martin 2001). Longer lived animals are in general more cautious, because short-term costs are offset by anticipated longer term gains (Wolf et al. 2007). In passerines, longevity is positively correlated with migration distance (Møller 2007). Under this life history paradigm, we would predict that longer distance migrants should be more willing to pay short-term costs (in foraging success *and* migratory timing) for the longer term fitness gains provided by realizing greater expected longevity. This prediction is concordant with our observations in the aviary experiment.

Much work has supported this tradeoff between risk aversion and longevity when the cost is to a current breeding attempt and the gain is in future breeding (Stearns 1992, Martin 1995). For breeding birds, annual fecundity and adult survival are inversely related and correlated with species' migratory distances (Martin 1995, Ghalambor and Martin 2001). More fecund species, generally shorter distance migrants, are more active in the face of predation risk. Thus, they accept higher costs to current survival because the current reproductive event represents a greater percentage of their life-time fitness. The reverse is true for less fecund species with higher survival probabilities.

During migratory seasons, the fitness costs incurred by reducing migratory refueling rate or timing in the face of predation risk may be paid out through carryover effects to the subsequent breeding season. In our system, a more cautious mode of migration may lead to a timing lag in arrival on the nonbreeding grounds. Within neotropical migrant passerines, late arrivals can incur reproductive consequences the following breeding season (Saino et al. 2004, Rockwell et al. 2012), because changes to physiological condition resulting from migratory timing influence future reproductive prospects (Norris et al. 2004, Studds and Marra 2007). For shorter distance migrants, the subsequent breeding season represents a larger proportion of all future breeding opportunities relative to longer distance migrants. As a result, more cautious migratory behaviors, while they may result in the same immediate costs to migratory refueling rate and nonbreeding arrival time for all migratory birds, present a higher ultimate cost to shorter distance migrants in terms of lifetime fitness.

Second, the response of a species to predation risk during the migratory period may be constrained by selection for adaptive behaviors outside of this period. These across-situation behavioral correlations are known as behavioral syndromes (Sih et al. 2004).   Many studies show correlations for boldness among different contexts of sociality, breeding, and antipredator behavior (Ward et al. 2004, Moretz et al. 2007). Our results show that shorter distance migrants appear more bold under high predation risk than longer distance migrants. In the isolated context of our study, this response seems maladaptive, as increasing activity under predation risk only incurs greater costs. Boldness more generally, however, may be adaptive during the breeding season (e.g., if

the selection for boldness to provision nestlings in the face of predation risk was more

consistent for shorter than longer distance migrants: Dall et al. 2004) or during other

non-predation related behavioral interactions on migration (e.g., if competition during

foraging on stopover was higher in shorter than longer distance migrants). We find the

latter scenario less likely, however, as the difference in behavior was only expressed in

the face of increased predation risk. We found no evidence for a background difference

in overall boldness (especially since the aviary itself could be interpreted as a boldness

challenge). Regardless, if the advantage of boldness during any non-migratory context

was high enough to outweigh the costs of those behaviors in other contexts (like

migration), they could still provide a net adaptive advantage.

2.5.2. Variation in Population Mass

The mass averages of both migratory groups decreased as predation risk increased.

When predation risk was low, there was no difference in size-corrected mass between

species with different migratory strategies (Fig. 2). Under higher predation risk,

however, the mass of longer distance migrants was less than that of shorter distance

migrants. For longer distance migrants these results corroborate the behaviors we

observed in our aviary experiment. There too, movement rates were not different in

the pretreatment period but declined significantly for longer distance but not shorter

distance migrants when they were exposed to predator cue. We hypothesize that a

relatively negative behavioral response to increased risk in longer distance migrants

causes them to suffer losses in foraging opportunities and subsequently in mass (Sih 1982, Quinn 1997).

The increased activity of shorter distance migrants under high risk conditions may be a response to facilitate movement away from the high risk area (Fransson and Weber 1997), rather than to accumulate fuel reserves for a migratory movement, and thus display a reduction in mass. Blackcaps exposed to high predation risk in Frannson and Weber (1997), foraged at a higher rate but departed with less fat reserves than control birds. This suggests activity is not correlated with foraging but is a means of escaping predation risk. It is possible, however, that we were unable to detect such an escape tactic. This behavior would likely be a flight greater than the length or width of the aviary (5m x 3m), which, according to our protocol, would result in an aviary wall encounter and subsequently removed from our analysis. There were no differences in this behavior between migratory strategies or treatment type among these birds, leading us away from this conclusion. Instead, we might expect all birds to suffer some cost to condition for using sites with high predation risk (Gosler et al. 1995) but the tradeoffs should be relative to migration distance. Following our life history explanation of behavioral differences, longer distance migrants, being longer lived, tradeoff current costs for future gains: they behave more cautiously at a greater relative cost to physical condition. On the other hand, shorter distance migrants prioritize current fitness: they tolerate more risk to maintain current physiological condition.

The difference in condition of migratory birds in our study may be due to site characteristics rather than predator frequency alone. Petit Manan and Seal Islands

show the lowest mass for all birds, although they also have very different predator

frequencies (Fig. 3). Both islands do, however, lack significant habitat structure

similarly, and therefore they may not provide enough food resources for migrating birds

to maintain body mass. Conversely, birds on Great Duck Island, which has diverse

habitat and high predator frequency, maintain similar masses to low predation sites.

Habitat can also be a refuge from predators as well as a source of foraging resources,

however, and it's likely that the vegetative structure of an island interacts with both of

these determinants of bird condition.

Variation in neophobia between our focal migratory groups may also contribute

to variation in behavioral response to the novelty of our experimental aviary, and

possibly confound responses to predator calls. Aversion to novel contexts or objects

may be attributed to life history tactics (i.e. specialization or generalization; Greenberg,

1983), or in our study migratory distance, such that a groups' activity in the aviary is a

product of that groups latency to engage novel objects rather than an antipredator

mechanism. Greenberg (1989) found that differences in aversion between swamp

(*Melospiza Georgiana*) and song (*Melozpiza melodia*) occurred independently of

foraging under changes in predation risk associated with changes in cover. We find

neophobia unlikely to be an underlying factor in the behavioral responses to changes in

predation risk, as behavioral mechanisms displayed in our aviary experiment explain

population responses in mass changes by site. This supports our conclusion that

differences we found were reflective of differences in natural behavior.

We show here that variation in antipredator behaviors exists across populations of migratory animals with different migratory distances and those behaviors correlate with population-level responses in size-corrected mass. The results are consistent with greater risk aversion in longer-lived individuals but inconsistent with time versus energy minimization. Longer distance migrations appear more costly to current physiological condition, but we suggest the costs are balanced by the net benefit in survival to future reproduction opportunities. Further work testing for behavioral syndromes within and outside of the migratory season and quantifying the fitness costs to different strategies would help establish the evolutionary and ecological basis for behavioral variation during predatory-prey interactions.

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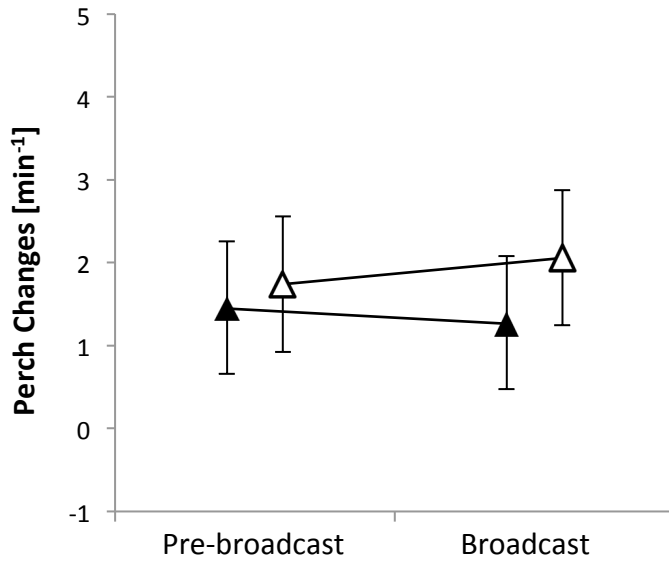**Appendix A.** Results of Aviary Experiment for Each Focal Species.
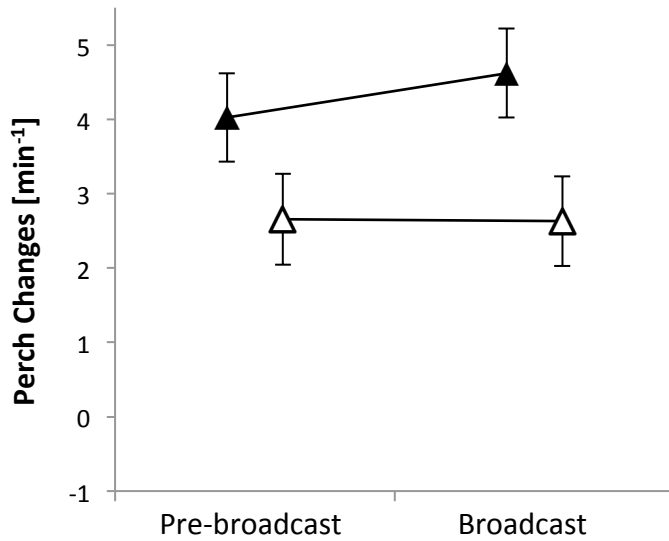
Figure 4. Model Predicted Perch Change Rates of Blue-headed Vireos (*Vireo solitarius*). Perch changes rates of blue-headed vireos (n=6) before and in response to American goldfinch (open triangles) and merlin (closed triangles) calls in an aviary experiment. Error bars represent SE of predicted values. Ratio of sum of squared Pearson residuals to residual degrees of freedom estimating dispersion was 1.2.
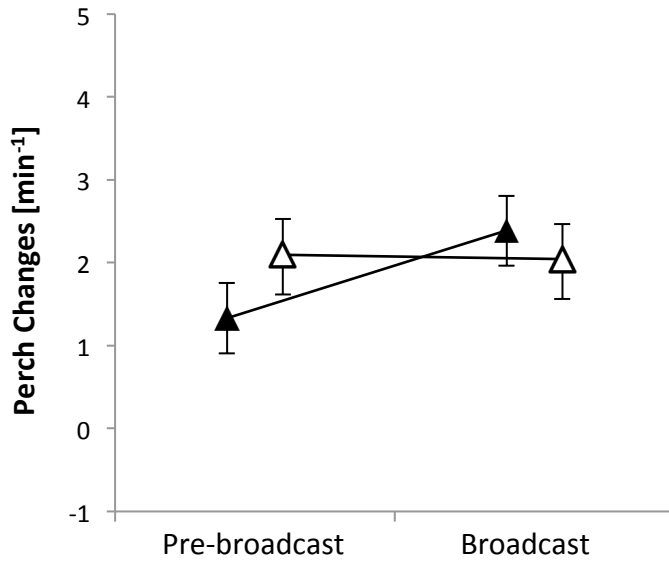
Figure 5. Model Predicted Perch Change Rates of Yellow-rumped Warblers (*Setophaga coronata*). Perch changes rates of yellow-rumped warblers (n=23) before and in response to American goldfinch (open triangles) and merlin (closed triangles) calls in an aviary experiment. Error bars represent SE of predicted values. Ratio of sum of squared Pearson residuals to residual degrees of freedom estimating dispersion was 2.9.
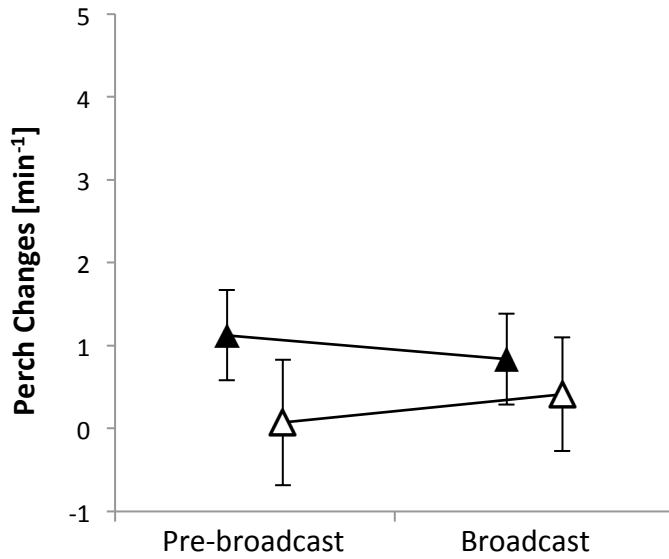
Figure 6. Model Predicted Perch Change Rates of Red-eyed Vireos (*Vireo olivaceus*). Perch changes rates of red-eyed vireos (n=16) before and in response to American goldfinch (open triangles) and merlin (closed triangles) calls in an aviary experiment. Error bars represent SE of predicted values. Ratio of sum of squared Pearson residuals to residual degrees of freedom estimating dispersion was 1.2.

Figure 7. Model Predicted Perch Change Rates of Blackpoll Warblers (*Setophaga striata*). Perch changes rates of red-eyed vireos (n=17) before and in response to American goldfinch (open triangles) and merlin (closed triangles) calls in an aviary experiment. Error bars represent SE of predicted values. Ratio of sum of squared Pearson residuals to residual degrees of freedom estimating dispersion was 5.8.
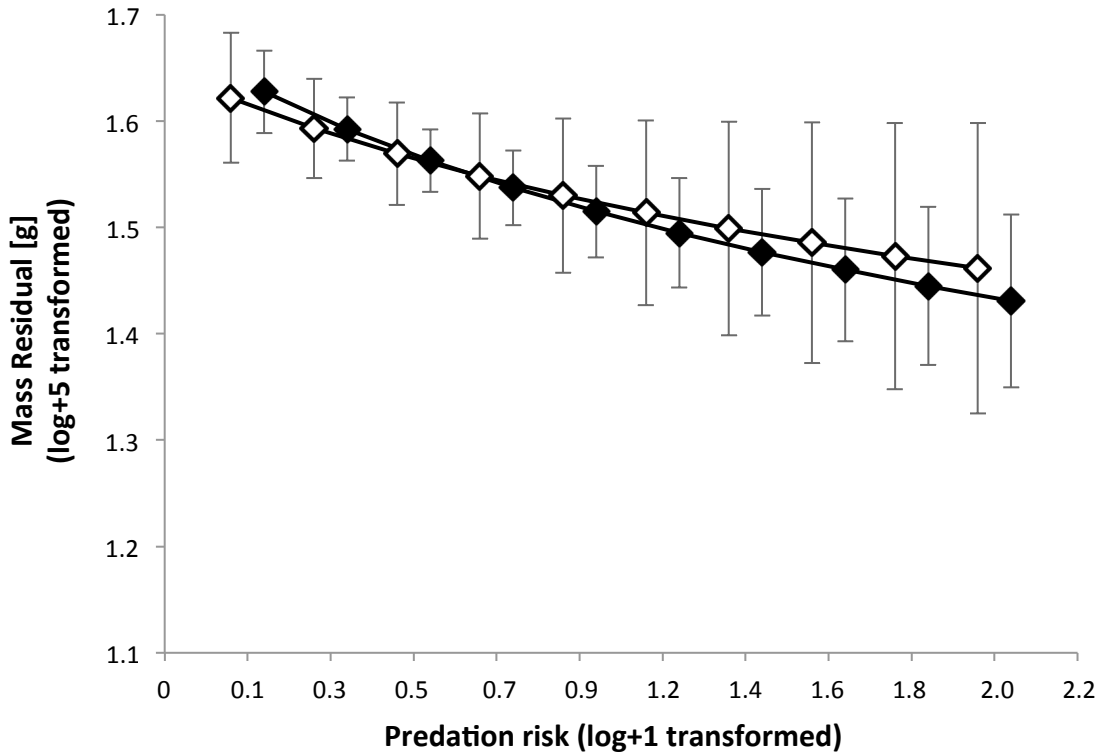
Figure 8. Size-corrected Mass of Focal Vireo Species Among Variation in Predation Risk. Model predicted mass residuals of blue-headed vireos (*Vireo solitaries*; n=220), a short distance migrant (open diamonds), and red-eyed vireos (*Vireo olivaceus*; n=878), a long distance migrant (closed diamonds), captured and banded at nine banding sites along the coast of Maine (2007-2013). Predation risk is the number of raptors reported during daily mist net operation at each banding site. Error bars represent 95% confidence intervals of the predicted means.
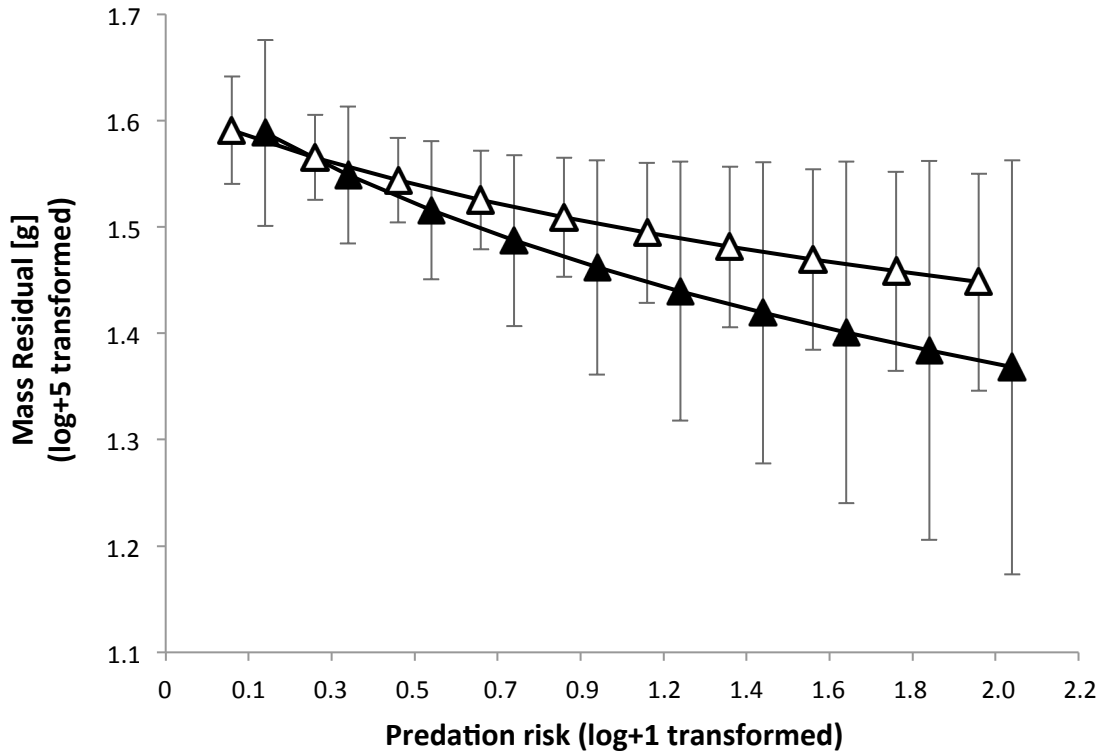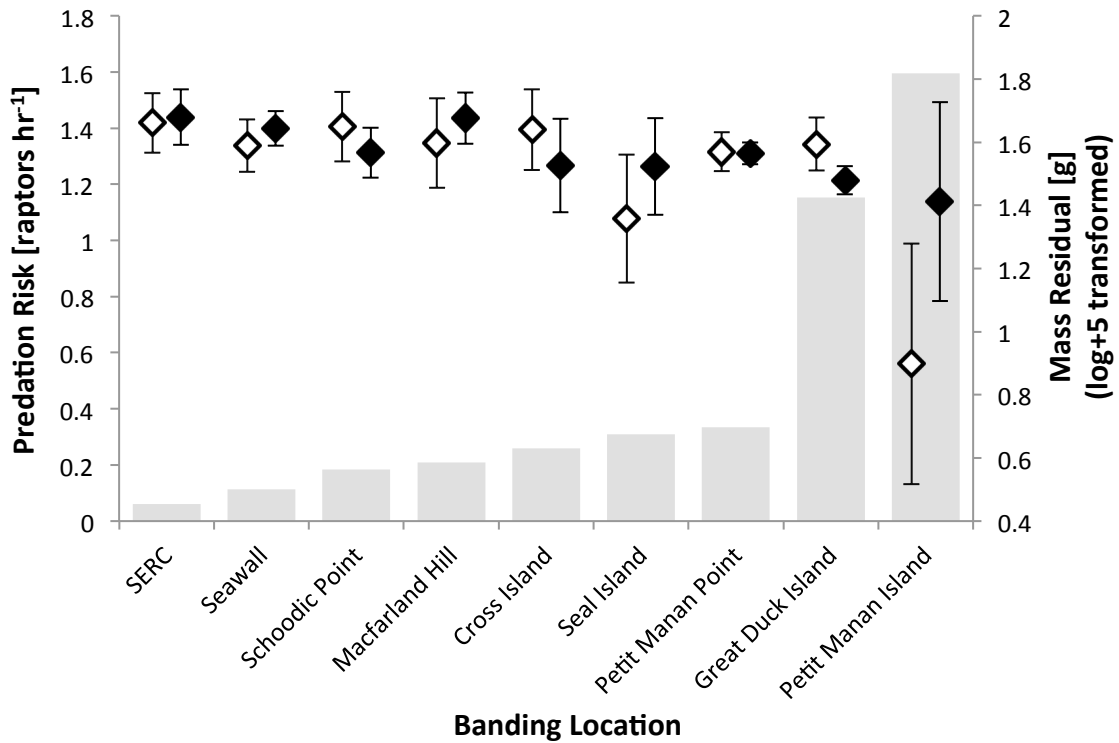
Figure 9. Size-corrected Mass of Focal Warbler Species Among Variation in Predation Risk. Model predicted mass residuals of yellow-rumped warblers (*Setophaga coronata*; n=4264), a short distance migrant (open triangles), and blackpoll warblers (*Setophaga striata*; n=539), a long distance migrant (closed triangles), captured and banded at nine banding sites along the coast of Maine (2007-2013). Predation risk is the number of raptors reported during daily mist net operation at each banding site. Error bars represent 95% confidence intervals of the predicted means.

Appendix C. Size-corrected Body Mass by Banding Location for Each Focal Species.

	Shorter Distance Migrants		Longer Distance Migrants		
	Blue-headed Vireo	*Yellow-rumped Warbler*	*Red-eyed Vireo*	*Blackpoll Warbler*	**Grand Total**
Cross Island	11	24	18	18	**71**
2012	11	24	18	18	**71**
Great Duck Island	31	294	202	31	**558**
2010	14	19	87	6	**126**
2011	17	275	115	25	**432**
Macfarland Hill	8	1570	60	58	**1696**
2010	2	599	30	13	**644**
2011	6	971	30	45	**1052**
Petit Manan Island	1	26	4	12	**43**
2009	1	26	4	12	**43**
Petit Manan Point	84	1415	329	209	**2037**
2010	27	166	130	48	**371**
2011	32	830	124	118	**1104**
2012	25	419	75	43	**562**
Schoodic Point	24	429	63	111	**627**
2013	24	429	63	111	**627**
Seawall	31	406	133	57	**627**
2010	9	94	56	15	**174**
2011	4	211	29	35	**279**
2012	18	101	48	7	**174**
SERC	26	84	52	12	**174**
2012	26	84	52	12	**174**
Seal Island	4	16	17	31	**68**
2007	4	16	17	31	**68**
Grand Total	**220**	**4264**	**878**	**539**	**5901**

Table 2. Focal Species Summary from Banding Sites Used in Body Size Analysis. Species totals from banding network database that were used in size-corrected mass analysis.

Figure 10. Size-corrected Mass of Focal Vireo Species by Banding Site Raptor Frequency. Model predicted mass residuals of blue-headed vireos (*Vireo solitaries*), a short distance migrant (open diamonds), and red-eyed vireos (*Vireo olivaceus*), a long distance migrant (closed diamonds), captured and banded at nine banding sites along the coast of Maine (2007-2013). Predation risk is the number of raptors reported during daily mist net operation. See Table 2 for species totals for each site. Error bars represent 95% confidence intervals of the means.
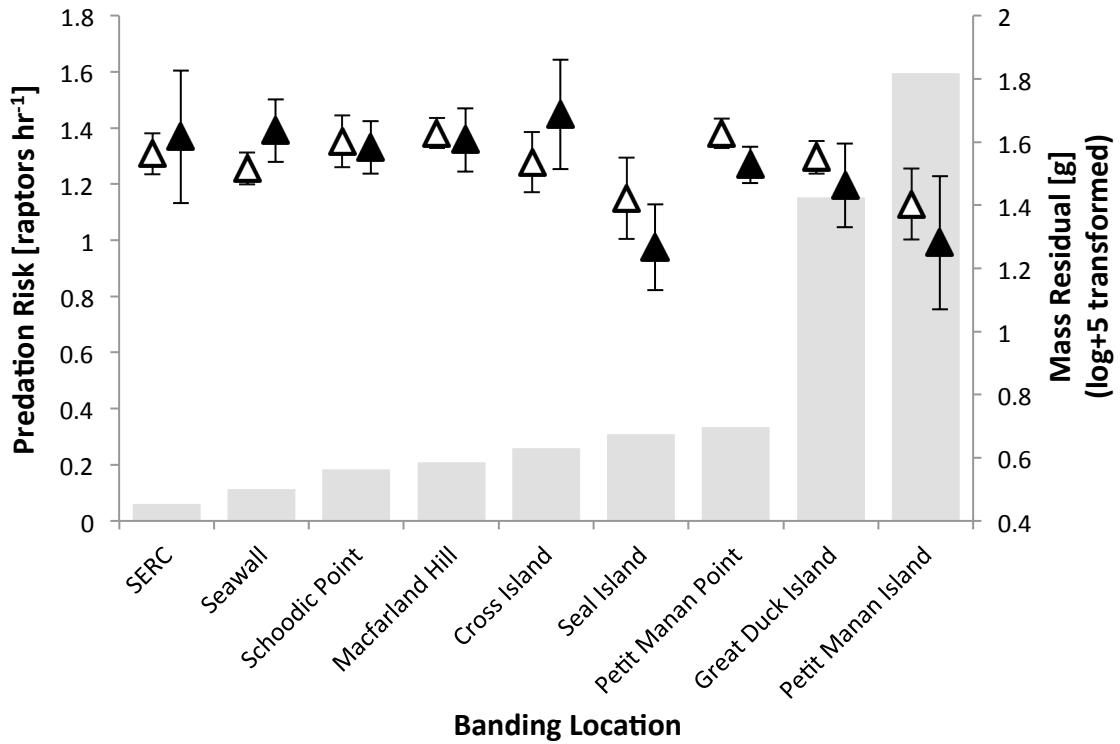
Figure 11. Size-corrected Mass of Focal Warbler Species by Banding Site Raptor Frequency. Model predicted mass residuals of yellow-rumped warblers (*Setophaga coronata*), a short distance migrant (open triangles), and blackpoll warblers (*Setophaga striata*), a long distance migrant (closed triangles), captured and banded at nine banding sites along the coast of Maine (2007-2013). Predation risk is the number of raptors reported during daily mist net operation. See Table 2 for species totals for each site. Error bars represent 95% confidence intervals of the means.

BIOGRAPHY OF THE AUTHOR

David Grunzel was born in Erie, Pennsylvania on March 14, 1985. He was raised there and graduated from Northwest Pennsylvania Collegiate Academy in 2003. He attended Washington & Jefferson College in Washington, Pennsylvania and graduated in 2008 with a Bachelor of Arts with a concentration in Biology. David worked as a biological science technician in California, Minnesota, Wyoming, New Hampshire, and Maine from 2008-2011 studying birds and mammals. He is a candidate for the Master of Science degree in Ecology and Environmental Science from the University of Maine in August 2014.