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TRINITY COLLEGE

RAPTORS ON THE EAST COAST:
A SHIFT IN THE TIMING OF AUTUMN MIGRATION

BY

JASON M. BAIRD

A THESIS SUBMITTED TO
THE FACULTY OF THE DEPARTMENT OF BIOLOGY
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RAPTORS ON THE EAST COAST:
A SHIFT IN THE TIMING OF AUTUMN MIGRATION

BY
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TABLE OF CONTENTS

Abstract	1
Introduction	2
Avian Migration	3
Climate Change and the Phenology of Avian Migration	5
<i>Spring Migration</i>	5
<i>Autumn Migration</i>	6
Raptors	7
This Study	9
Methods	10
Results	15
Discussion	19
Red-tailed Hawk	19
Northern Harrier	20
Sharp-shinned Hawk	21
Broad-winged Hawk	22
Conclusion	23
Literature Cited	25

INDEX OF FIGURES AND TABLES

Figures

Fig. 1: Migration flyways in North America.	4
Fig. 2: Phenology mismatch in reproduction.	6
Fig. 3: Locations of three raptor migration count sites in eastern North America.	11
Fig. 4: Aerial photograph showing the terrain around three raptor migration count sites in eastern North America.	12
Fig. 5: Red-tailed Hawks delayed autumn migration by approximately five days over the period of 1976-2013 at three count sites in the northeastern US.	16
Fig. 6: Northern Harriers delayed autumn migration by approximately eight days over the period of 1976-2013 at three count sites in the northeastern US.	17
Fig. 7: Sharp-shinned Hawks advanced autumn migration by approximately six days over the period of 1976-2013 at Hawk Mountain.	17
Fig. 8: There was no significant shift of median passage date for the Broad-winged Hawk over the period of 1976-2013 at three count sites in the northeastern US.	18

Tables

Table 1: Geographic and temporal information for three raptor migration count sites in northeastern North America: Hawk Mountain in Pennsylvania and Quaker Ridge and Lighthouse Point in Connecticut.	11
Table 2: Natural history information for the four raptor species in this study.	13
Table 3: Results of the general linear models showing effects of factors on median passage date for four raptor species at three migration count sites in the northeastern US.	15
Table 4: Days per year of shift and total shift in median passage date for four raptor species at three migration count sites in the northeastern US.	16

ABSTRACT

I tested whether or not raptors on the east coast are shifting the timing of their autumn migration. I analyzed 38 years of passage data at three count sites across New England: Hawk Mountain, Quaker Ridge, and Lighthouse Point. I studied four raptors with diverse natural history traits: Red-tailed Hawk (*Buteo jamaicensis*), Northern Harrier (*Circus cyaneus*), Sharp-shinned Hawk (*Accipiter striatus*), and Broad-winged Hawk (*Buteo platypterus*). I also investigated possible factors associated with any documented shift, including climate, distance of migration, diet, and population trend. Long-distance migrants should advance their migration and short-distance migrants should delay their migration, as reported for numerous taxa, including raptors, in Europe. Raptors that feed primarily on birds should advance their migration. Species advancing their migration should advance it further in warm years, while species delaying their migration should delay it further in warm years. Finally, I predicted that species in decline would show little or no shift in migration timing; species unable to adjust to climate change may be at a disadvantage. The Red-tailed Hawk and Northern Harrier delayed their autumn migrations past these three count sites, while the Sharp-shinned Hawk advanced and the Broad-winged Hawk showed no shift in its migration phenology. Some of these results match my predictions based on the raptors' life history traits, but some do not, suggesting that North American raptors are responding to climate change differently from European raptors. The Broad-winged Hawk is the only raptor among the four species I studied that is not shifting and it is currently declining in population in the Northeast. This species may be more "hard-wired" to migrate at roughly the same time every year, and that inability to shift may be contributing to population decline.

INTRODUCTION

Climate change has been recognized as one of the greatest threats in the 21st century to ecosystems worldwide. Over the 20th century, the average global surface temperature has increased by 0.6 °C. This increase was the largest in at least the last 1000 years (Houghton et al. 2001). This change in climate has been coupled with a reduction in snow and ice coverage (Lemke et al. 2007) and changes in precipitation patterns across the globe. Current projections estimate a sea level rise of as much as 59 cm in the 21st century (Houghton et al. 2001). Climate change does not affect all areas evenly; average annual surface temperatures are increasing faster at high latitudes than at the equator (Keyser et al. 2002). Climate change is altering various aspects of animal and plant life history, especially in regions of greater climate shift, like the poles (Walther et al. 2002).

Plants and animals are displaying a variety of responses to climate change. Some are shifting in range or distribution; in the Northern Hemisphere, species' distributions are most commonly shifting farther north (Walther et al. 2002; Parmesan and Yohe 2003). Some species are retreating to higher elevations. For example, Wilson et al. (2005) documented a shift to higher elevations of the distribution of 30 species of butterflies in a Spanish mountain range. The authors suggested that such elevation shifts might lead to extinctions as warming causes ranges to shrink to mountaintops and then disappear. Each species has a certain optimum range of temperature and precipitation; range shifts are generally attributed to direct environmental changes in those parameters (Hoffman and Parsons 1997). Ranges are shifting irregularly among species leading to differences in community structure. In the Northern Hemisphere, more southerly species have been recorded shifting into northern areas faster than the northern species have retreated toward the North Pole (Walther et al. 2002). Invasions by alien species are becoming more common in some environments as species previously limited by temperature are colonizing areas that formerly were too cold for them (Stachowicz et al. 2002).

Climate change appears to be altering more than just the distribution of species. Researchers have noted correlations between climate and phenology, the timing of life events. For example, genetically identical deciduous trees and shrubs in Europe shed their leaves later in warmer years (Menzel and Fabian 1999); North American Tree Swallows (*Tachycineta bicolor*) are reproducing earlier (Dunn and Winkler 1999), and marmots

(*Marmota flaviventris*) in the Rocky Mountains are emerging from hibernation earlier (Inouye et al. 2000).

Avian Migration

Bird migration is one highly studied aspect of climate change ecology. Large collections of consistent, long-term data exist in both Europe and North America. These data sets have been used for various studies; for example, Tøttrup et al. (2006) studied shifts in autumn passerine migration over 28 years in Denmark. They found that long-distance migrants delayed their migration in warmer years while short-distance migrants advanced their migration in warmer years. Bensusan et al. (2007) studied raptor abundance during migration over 16 years at a migration hot spot at the Strait of Gibraltar. Filippi-Codaccioni et al. (2009) researched shifts in autumn raptor migration over a 27-year period using data from a raptor migration count site in France and showed that long-distance migrants are, in general, advancing their autumn migration – leaving their breeding grounds earlier.

Migration is the biannual travel of individual birds in spring and autumn to and from their wintering and breeding grounds. Birds in the Northern Hemisphere typically migrate south to warmer areas for the winter and return north to their breeding grounds for the summer breeding season, when food is abundant there. Migration is an adaptation for seasonal differences among ecosystems – moving between ecosystems allows migrants to take advantage of favorable conditions year-round (Pulido 2007). More specifically, migration allows birds to access breeding grounds at the time when food and other resources are at a maximum and to access warmer wintering grounds in other regions where sufficient resources are available.

In North America, birds typically migrate along one of several flyways that run north to south (Fig. 1). The most impressive migrants travel between hemispheres, allowing them to experience favorable conditions year-round. As an example, the Arctic Tern (*Sterna paradisaea*) migrates over 80,000 miles, from ice at the edges of Antarctica to Greenland (Egevang et al. 2009).

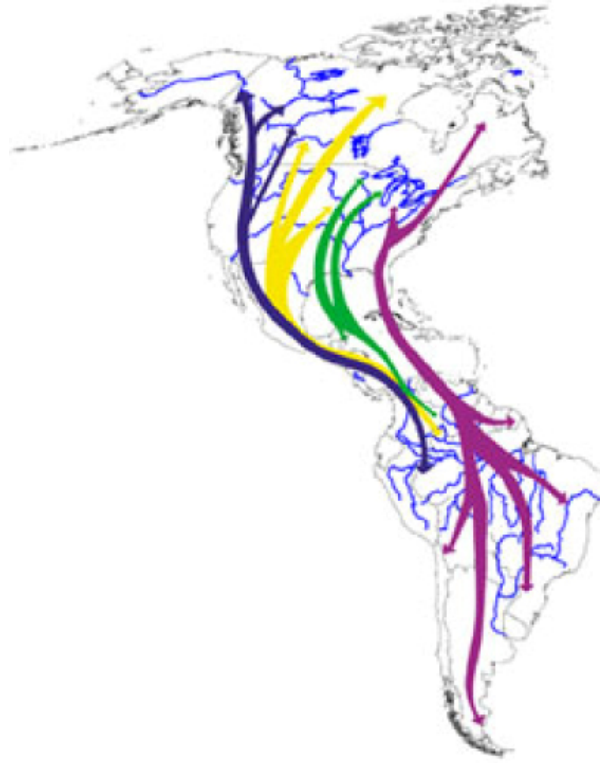


Fig. 1: Migration flyways in North America. Blue: Pacific Flyway. Yellow: Central Flyway. Green: Mississippi Flyway. Purple: Atlantic Flyway (New Jersey Audubon Society 2008).

Bird migration has been widely studied across the planet. Information on where, when, and how far birds travel during migration has been obtained using three primary techniques: banding and band recoveries (Clark et al. 2009), direct counting at specific count sites (Bildstein et al. 1998), and telemetry (Green et al. 2002). The first two methods have a long history in both Europe and North America. Scientific bird banding dates back to 1899 in Denmark and spread to the United States within three years (Marion and Shamis 1977).

Telemetry, using both VHF and satellite transmitters, is a more modern technique that focuses on individuals rather than populations, allowing researchers to track precise migration routes of individuals and to collect data on a number of other phenomena, such as flight routes, breeding and wintering zones, and migration stopovers. By way of examples, Green et al. (2002) examined the migration of Dark-bellied Brent Geese (*Branta bernicla*) in northern Europe, and Martell et al. (2004) studied the migratory routes and wintering sites of Ospreys (*Pandion haliaetus*) in North America.

Finally, a third common technique for studying migrants is, for the most part, only applicable for raptors. Our understanding of migration in birds of prey has been obtained primarily using data collected at migration count sites. These sites are typically situated on mountaintops and at other bottlenecks, points along migration routes where birds congregate drawing birders to count the migrants that fly by. Migrating raptors have been counted at the count site at Hawk Mountain in Pennsylvania since 1934 (Bildstein 2006). Data from Hawk Mountain have been used to analyze various aspects of migration, including nocturnal migration via radar sensing (Sielman et al 1981) and population trends (Bednarz et al. 1990). Likewise, the Strait of Gibraltar in Spain has long been a point of raptor observation; organized monitoring has been carried out at this site since the 1960s (Bensusan et al. 2007).

Climate Change and the Phenology of Avian Migration

Spring Migration

Many studies have documented associations between climate change and various aspects of avian migration. In many species, fewer individuals are migrating, and the individuals that are migrating aren't migrating as far, sometimes known as short-stopping (Lemoine and Böhning-Gaese 2003; Van Vliet et al. 2009). Perhaps most striking has been a well-documented shift in the timing of migration of many avian species across various taxa, including waterfowl (Lehikoinen 2009), raptors (Filippi-Codaccioni et al. 2009), passerines (Sokolov et al. 1998), and seabirds (Frederiksen et al. 2004). Many studies have reported advances in spring migration; in other words, birds are departing from wintering grounds and arriving on breeding grounds earlier than in the recent past (Sokolov et al. 1998; Kéry 2003; Lehikoinen et al. 2004; Møller et al. 2008; Lehikoinen 2009). In many regions, as spring becomes warmer, birds are shifting their behavior to take advantage of the additional resources available in early spring. Arriving at the breeding grounds earlier allows birds to secure better breeding territories and to breed earlier. Controlling good breeding territory is highly advantageous as it allows individuals to have higher nest success and to fledge more offspring successfully (Newton 1992). However, migrating and breeding earlier may also have negative consequences.

Lehikoinen (2009) documented a possible “mismatch” between the timing of hatching and the temperatures in which hatchlings are most likely to survive. Climate change

affects different seasons asymmetrically; a warmer spring doesn't necessarily mean a warmer summer. If birds are laying their eggs earlier in spring because temperatures are warmer, but summer is staying roughly the same temperature, then the eggs will hatch earlier into colder temperatures, possibly increasing the mortality rate of hatchlings (Fig. 2).

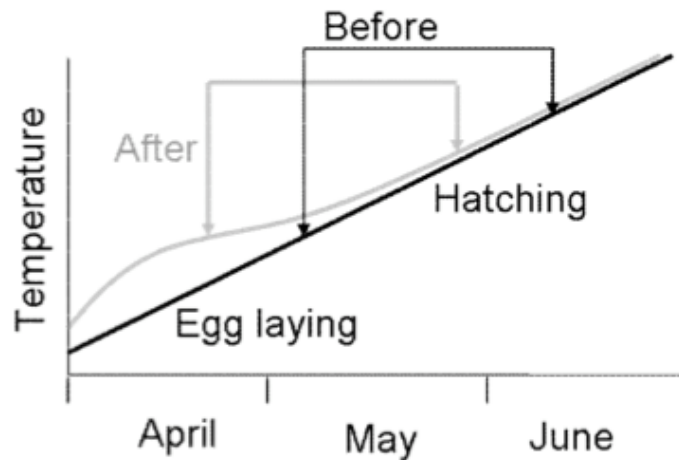


Fig. 2: Phenology mismatch in reproduction. Noted are times of egg laying and hatching before and after migration shift. Figure taken from Lehikoinen (2009).

Autumn Migration

While the advance in spring migration is well-documented for many bird species, shifts in the timing of autumn migration and possible associations with climate change are not as clear-cut and have received less study. In a European study on 65 small bird species, mostly passerines, Jeni and Kéry (2003) showed that some species are advancing their migration (departing the breeding grounds earlier in autumn), and some are delaying migration (departing the breeding grounds later). The authors suggested that whether a species advances or delays its migration is correlated with several aspects of its life history. Most notably, they found that long-distance migrants, defined as those that cross the Sahara desert during migration, are advancing their autumn migration (Jeni and Kéry 2003).

As temperatures warm and breeding dates advance, species finish breeding earlier, perhaps allowing them to leave the breeding grounds earlier. Earlier autumn migration can be advantageous in Europe because those species must pass across the Sahara desert, which gets progressively drier after September, and passing the Sahara before the dry season begins allows migrants to avoid potentially dangerous conditions (Jeni and Kéry 2003). Migratory birds must compete with resident species on their wintering grounds in addition to competing

with each other. Arriving on the wintering grounds earlier allows migrants to secure better territories. As a result, they will be more likely to survive the winter and be in ideal body condition for return migration to their breeding grounds in the spring (Filippi-Codaccioni et al. 2009).

Jeni and Kéry (2003) also reported that some short-distance migrant passerines delayed autumn migration. Unlike long-distance migrants that winter in tropical areas or even the alternate hemisphere, short-distance migrants spend the winter in areas that are often becoming more temperate due to climate change, perhaps enhancing their survival. Some short-distance migrants are delaying autumn migration or, in rare cases, are simply staying on the breeding ground year-round (Filippi-Codaccioni et al. 2009).

In contrast to studies that reported short-distance migrants showing a delay or no change in timing of autumn migration, Tøttrup et al. (2006) in a study of 22 species of passerines on the Baltic island of Christiansø found that many short-distance migrating species advanced their autumn migration by departing the breeding grounds earlier. If spring migration is advancing, and autumn migration is advancing as Tøttrup et al. (2006) suggest, then the time on the breeding grounds remains roughly constant. Perhaps birds that produce only one clutch annually only need a certain amount of time on the breeding grounds, regardless of when that time is taken. A general advance in autumn migration of short-distance migrants is uncommon among past research, however. Jeni and Kéry (2003) argued that species that can raise more than one brood in a summer are less likely to advance and more likely to delay their autumn migration, thus taking advantage of the effectively longer summer to raise additional broods.

Raptors

Raptors are relatively large birds specialized for predation, sometimes known as “birds of prey.” The categorization includes the order Falconiformes, which consists of diurnal raptors (family Accipitridae: hawks, eagles, falcons, and Old World vultures) and the family Cathartidae (New World vultures). Raptors have long wings for gliding, powerful eyesight for detecting prey at long ranges, and strong beaks and feet and sharp talons for killing and tearing apart prey. Raptors are found worldwide and feed on a variety of prey items; some generalist species feed on mammals, others feed primarily on other birds, and

some species specialize on specific types of birds, mammals, insects, or other prey (Bildstein 2006).

Sixty-two percent of all raptors migrate annually. In North America, the main migration routes run parallel to coasts, major mountain ranges, and major river valleys, and therefore run north-south. In Europe and Asia, many species migrating north-south concentrate in spectacular flights across major landmarks such as the Strait of Gibraltar and Elat in Israel (Bildstein 2006). Unlike passerines, which migrate mostly at night, raptors migrate primarily during the day, usually soaring by taking advantage of thermal air currents (Bildstein 2006).

Filippi-Codaccioni et al. (2009) and Lehikoinen (2009) reported that several European raptors, like most small birds, have advanced their spring migration over time. Lehikoinen (2009) showed that five species of raptors advanced their spring breeding date by 0.5 to 2.0 days per degree Celsius of local temperature increase during the month of egg-laying. Between the advance over time and the advance in specific warm years, Lehikoinen (2009) argued that climate change was correlated with earlier migration.

Filippi-Codaccioni et al. (2009) found that, like passerines, the long-distance migratory raptors they studied in Europe advanced their autumn migration in association with warming temperatures, while most short-distance migrants delayed their autumn migration under the same circumstances. These authors, reporting on raptor migration at the Organbidexka count site in France, found an average advance of 0.15 days per year between 1981 and 2008 for long-distance migrants such as the Western Marsh Harrier (*Circus aeruginosus*). In contrast, short-distance migrants, like the Common Kestrel (*Falco tinnunculus*) delayed their autumn passage across the Organbidexka count site. The only exception was a single short-distance migrant, the Eurasian Sparrowhawk (*Accipiter nisus*), which advanced its autumn migration significantly. This raptor was the only bird-eater among the studied short-distance migrants. Some raptors eat primarily passerines, many of which are advancing their autumn migration phenology based on temperature changes (Tøttrup et al. 2006), suggesting these raptors may be altering their migration timing along with their primary food source (Filippi-Codaccioni et al. 2009).

This Study

Autumn migration phenology is a little-studied topic in raptors, particularly in North America. The few studies that have addressed autumn migration were more commonly carried out in Europe and have shown a variety of results, each of which are highly dependent on species. Few studies have examined associations between autumn migration and climate change.

The primary objective of this study was to examine whether or not certain raptors on the east coast of North America are shifting the timing of their autumn migration and to identify possible factors associated with such shift. I sought specifically to determine if there is a shift in the median passage date for four raptor species counted over several decades at three raptor count sites in the northeastern United States. Using nearly four decades of count data from each site, I computed median passage dates – the date on which 50% of the raptors in a given autumn season had passed a count site – for the four species at the three count sites. Next, I determined whether there was a shift, either advance or delay, in the median passage date for each species at each site. Then, I investigated possible associations between the shifts and several environmental and biological variables. I made several predictions based on previous studies, which mostly focused on European raptors. First, I predicted that long-distance migrants, those raptors that winter in South America, should advance their autumn migration, as has been shown for long-distance migrant raptors in Europe (Lehikoinen 2009). Second, I predicted that the autumn migration phenology of short-distance migrants should remain unchanged, or perhaps be delayed (Filippi-Codaccioni et al. 2009). Finally, I predicted that short-distance migrants feeding mainly on other birds might advance their migration to follow their food sources, matching the explanation of Filippi-Codaccioni and colleagues (2009) for the Eurasian Sparrowhawk's behavior.

METHODS

I used daily counts of four migrating raptors at three well-known raptor count sites having at least 25 years of count data to investigate possible shifts in autumn passage by those raptors. These sites, all within the Atlantic Flyway, are Hawk Mountain Sanctuary in Pennsylvania and Lighthouse Point Park and Quaker Ridge Hawk Watch in Connecticut (Fig. 3). Raptor counting at these sites has occurred for several decades, beginning in 1934 at Hawk Mountain, in 1970 at Lighthouse Point, and in 1971 at Quaker Ridge, and continuing through 2013 at all three sites. Hawk Mountain's count site is located at the mountain's North Lookout; mountains forming wind corridors can be seen as streaks running southwest to northeast near Hawk Mountain (Fig. 4). The high speed of the winds flowing through the mountains makes Hawk Mountain an ideal location for hawks to migrate past. Lighthouse Point is situated on a peninsula that juts out into Long Island Sound; raptors migrate above the peninsula, avoiding the bodies of water that surround it. Similar to Hawk Mountain, Quaker Ridge's namesake coastal ridge drives air upward in thermals that allow migrating raptors to gain elevation rapidly.

Each count site is manned daily for raptor counts between roughly August 20th and November 20th, weather and volunteers permitting. At Hawk Mountain, one or two employees organize and supervise counts each day aided by a number of trained volunteers and employees of the site who assist with the counts. Counting at Hawk Mountain typically takes place between 0800 and 1700 daily (Bednarz et al. 1990). Counting at Lighthouse Point is carried out daily from the parking lot at Lighthouse Point Park, CT, starting at 0700 and continuing until the hawks stop flying (Hawk Count 2013; New Haven Bird Club 2014). At Lighthouse Point, one dedicated volunteer supervises other volunteers every day (Zagorski 2013). Since 1985, one paid, full-time hawk watcher has manned Quaker Ridge, supported by a varying number of trained volunteers that staff the site on weekends. Quaker Ridge's count site is on the grounds of the Greenwich Audubon Center, and counting occurs usually between 0900 and 1700 (Audubon Greenwich 2013).

Each site lacks complete data for its early years. Thus, my analysis of each site's dataset included only years for which, of the 61 days in September and October, fewer than 12 days (<20%) lacked any data. Omitting years with 12 or more days lacking data resulted in available count data for the years between 1940 and 2013 for Hawk Mountain, between

1980 and 2013 for Lighthouse Point, excluding 1982 and 1983, and between 1986 and 2013 for Quaker Ridge, excluding 1996 and 2012 (Table 1). However, the most recent period of global climate change includes only years from 1976 onwards (Ring et al. 2012); therefore, I did not include data from years before 1976 in my study.

Table 1: Geographic and temporal information for three raptor migration count sites in northeastern North America: Hawk Mountain in Pennsylvania and Quaker Ridge and Lighthouse Point in Connecticut.

<i>Site</i>	Years Available	Period Analyzed	State	Latitude (°N)	Longitude (°W)	Elevation (m)
<i>Hawk Mountain</i>	1934-2013	1970-2013	PA	40.6	76.0	464
<i>Lighthouse Point</i>	1970-2013	1980-2013	CT	41.3	72.9	13
<i>Quaker Ridge</i>	1971-2013	1986-2013	CT	41.1	73.7	155

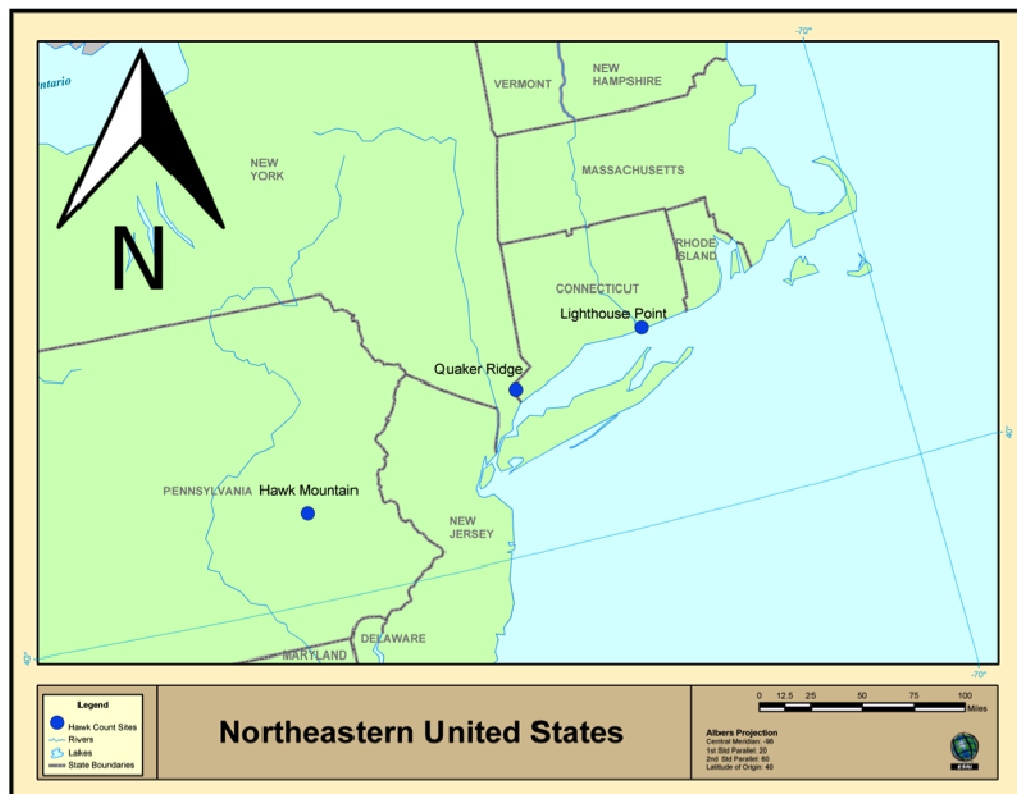


Fig. 3: Locations of three raptor migration count sites in eastern North America.



Fig. 4: Aerial photograph showing the terrain around three raptor migration count sites in eastern North America.

I studied a group of four raptor species with diverse ecological and morphological traits chosen because they are a relatively diverse group of common migrants in the Northeast, and all have sufficient count numbers at the three count sites. The four raptors I studied were the Red-tailed Hawk (*Buteo jamaicensis*), Northern Harrier (*Circus cyaneus*), Sharp-shinned Hawk (*Accipiter striatus*), and Broad-winged Hawk (*Buteo platypterus*; Table 2). For these species, I obtained information on diet, migration distance, and body size from Cornell Lab of Ornithology's *Birds of North America* series (Bildstein and Meyer 2000; Preston and Beane 2009; Goodrich et al. 2014; Smith et al. 2014). I classified the raptors into three categories based on diet: species that primarily eat birds, species that primarily eat mammals, and species that eat a mix of the two (Table 2). I used the *Birds of North America* definitions of short- and long-distance migrants: species that migrate more than 1,500 km are long-distance migrants and species that don't are short-distance migrants. Body size of each species was the average mass of male and female adults in the northeastern United States in autumn. I obtained information on the population trend (percent change over the period

1966 - 2011) of each species in New England/mid-Atlantic coast regions from the Breeding Bird Survey (Sauer et al. 2014).

Table 2: Natural history information for the four raptor species in this study. Long distance migrants are species for which at least some individuals migrate from North America to South America. Short-distance migrants winter primarily in Central America or at points farther north.

Species	Body Size (g)	Migration Distance	Diet	1966-2011 Population Trend (% change over entire period)	95% Confidence Intervals
<i>Red-tailed Hawk</i>	1134.4	Short	Mammals	3.7	2.8, 4.7
<i>Northern Harrier</i>	506.5	Long	Mix of birds and mammals	-0.4	-4.3, 3.1
<i>Sharp-shinned Hawk</i>	140.5	Long	Birds	1.8	-2.3, 5.9
<i>Broad-winged Hawk</i>	398.9	Long	Mammals	-0.5	-2.2, 1.3

To look for shifts in migration phenology of each species over time, I used median passage date, the date in a given year when 50% of the total individuals of a given species counted that year had passed the count site. Other common measures of passage date, such as the date on which a species is first recorded at a count site, are inaccurate due to their variability (Lehikoinen et al. 2004). For each raptor, I used a general linear model (GLM) with median passage date as the dependent variable and with year, site, and the North Atlantic Oscillation (NAO) index, as independent variables. The NAO is a climatic phenomenon in the North Atlantic Ocean that controls the strength and direction of westerly winds and storm tracks across the North Atlantic and thus is believed to have an impact on the weather over much of eastern North America (National Climatic Data Center 2014). The NAO index has varied in the past 60 years between -3.5 and 3.5, with an average monthly value of -0.3. In years when the NAO index is relatively high, the east coast of the United States experiences a warm winter, and in years when the NAO index is relatively low, the east coast of the United States experiences a cold winter (Climate Prediction Center Internet Team 2005). Förchhammer et al. (2002) showed that the NAO index, as well as spring

temperatures, is correlated with the timing of spring migration in six species of European birds. Therefore, I used the NAO index and year as representatives of climate change to examine whether or not birds shift their autumn migration in response to changing temperatures. In this study, for each year of count data, I obtained the NAO index from the Oceanic and Atmospheric Administration's Climate Prediction Center (Climate Prediction Center Internet Team 2005). Finally, I examined associations between each species' diet, migration distance, and population trend and any shift found in median passage date.

I used SYSTAT v. 8.0 (SPSS, Chicago, Illinois) for all statistical analyses and considered statistical significance at $\alpha = 0.1$.

RESULTS

I found a year effect on median passage date for the Red-tailed Hawk and the Northern Harrier (Table 3) and for the Sharp-shinned Hawk ($t=2.39$, $P=0.07$). The Red-tailed Hawk (Fig. 5) and the Northern Harrier (Fig. 6) delayed migration by approximately five and eight days, respectively, over the study period of 1976-2013 at the three study sites (Table 4). I found a site effect and an effect of the interaction between site and year for the Northern Harrier but not for the Red-tailed Hawk (Table 3). In contrast, the Sharp-shinned Hawk advanced its migration by approximately six days over the same time period at Hawk Mountain (Fig. 7). Insufficient numbers of Sharp-shinned Hawks passed by Lighthouse Point and Quaker Ridge for long-term analysis of their migration phenology. Unlike the other raptors, the Broad-winged Hawk showed no significant shift in median passage date at any of the three sites (Tables 3 and 4, Fig 8).

I found an apparent association between the NAO index and the median passage date only for the Northern Harrier (Table 3). In years with higher NAO index values (warmer winters), the Northern Harrier passed the three count sites later than in years with lower NAO index values. For the other three species, I found no association between the NAO index and median passage date (Table 3; Sharp-shinned Hawk: $\rho=-0.12$, $P=0.55$).

Table 3: Results of the general linear models showing effects of factors on median passage date for four raptor species at three migration count sites in the northeastern US. Data reflect the time period 1976-2013.

<i>Species</i>	<i>Independent</i>	<i>d.f.</i>	<i>F</i>	<i>P</i>
<i>Red-tailed Hawk</i>	<i>Year</i>	1	4.43	0.04
	<i>NAO</i>	1	1.28	0.26
	<i>Site</i>	2	2.26	0.11
	<i>Site x Year</i>	2	2.24	0.11
<i>Northern Harrier</i>	<i>Year</i>	1	30.63	0.00
	<i>NAO</i>	1	15.90	0.00
	<i>Site</i>	2	2.94	0.06
	<i>Site x Year</i>	2	2.86	0.06
<i>Broad-winged Hawk</i>	<i>Year</i>	1	1.02	0.32
	<i>NAO</i>	1	0.01	0.91
	<i>Site</i>	2	0.02	0.98
	<i>Site x Year</i>	2	0.02	0.98

Table 4: Days per year of shift and total shift in median passage date for four raptor species at three migration count sites in the northeastern US. Data reflect the time period 1976-2013. No data (ND) are available on shift of the Sharp-shinned Hawk at Lighthouse Point and Quaker Ridge because insufficient numbers of these hawks passed that count site during the study period.

<i>Species</i>	Advance or Delay	Hawk Mountain (38 years)	Lighthouse Point (30 years)	Quaker Ridge (27 years)	Total Shift (Days, Average of three sites)
<i>Red-tailed Hawk</i>	Delay	0.07	0.25	0.23	5
<i>Northern Harrier</i>	Delay	0.40	0.12	0.23	8
<i>Sharp-shinned Hawk</i>	Advance	-0.17	ND	ND	6
<i>Broad-winged Hawk</i>	No Shift	0.06	0.04	0.06	1

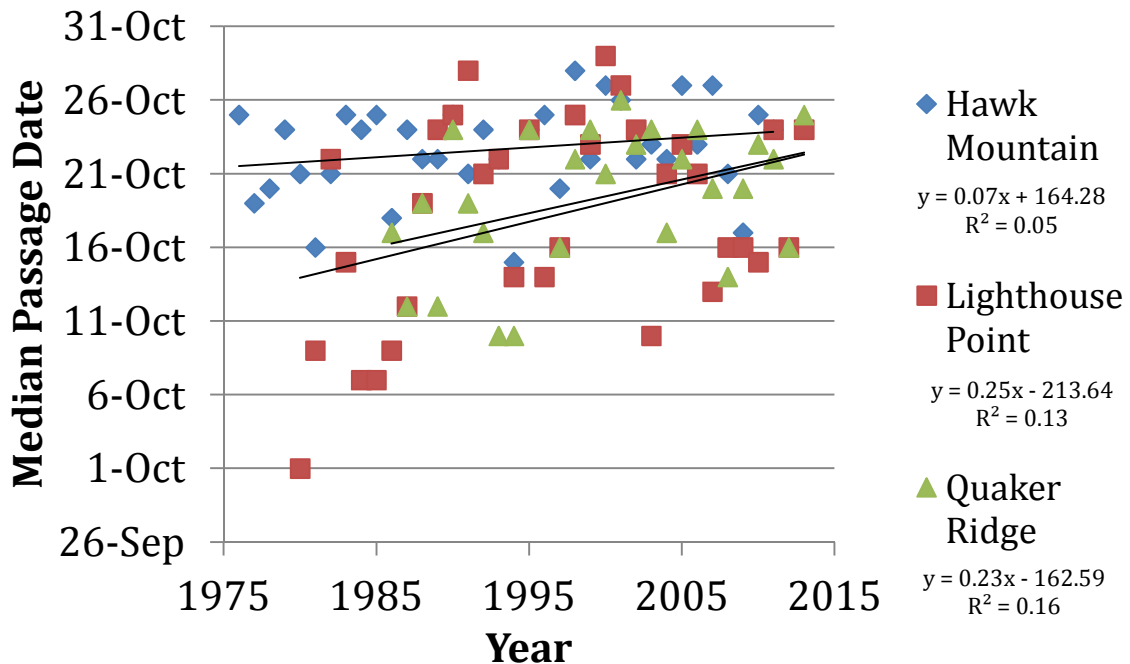


Fig. 5: Red-tailed Hawks delayed autumn migration by approximately five days over the period of 1976-2013 at three count sites in the northeastern US. Slope of each equation is equal to the average days of shift per year for that site.

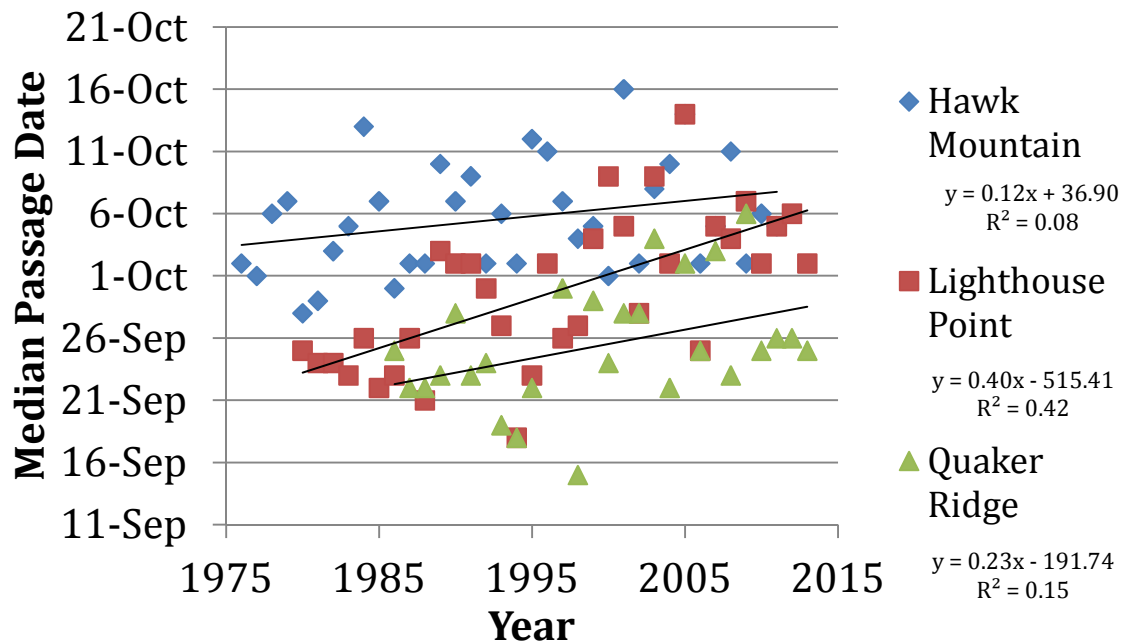


Fig. 6: Northern Harriers delayed autumn migration by approximately eight days over the period of 1976-2013 at three count sites in the northeastern US. Slope of each equation is equal to the average days of shift per year for that site.

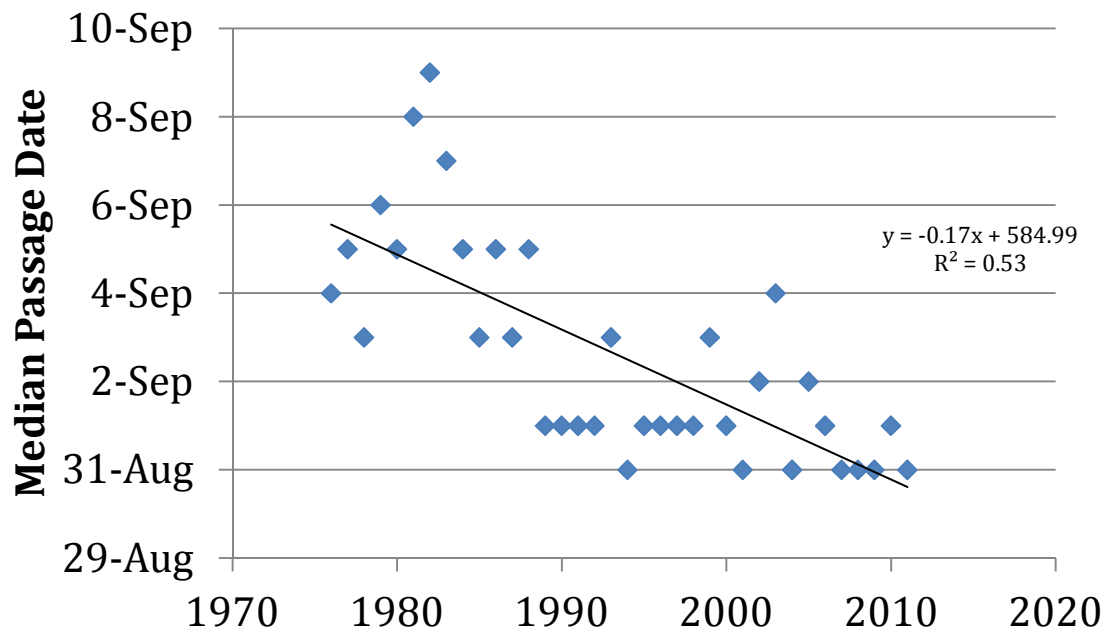


Fig. 7: Sharp-shinned Hawks advanced autumn migration by approximately six days over the period of 1976-2013 at Hawk Mountain. Slope of each equation is equal to the average days of shift per year for that site.

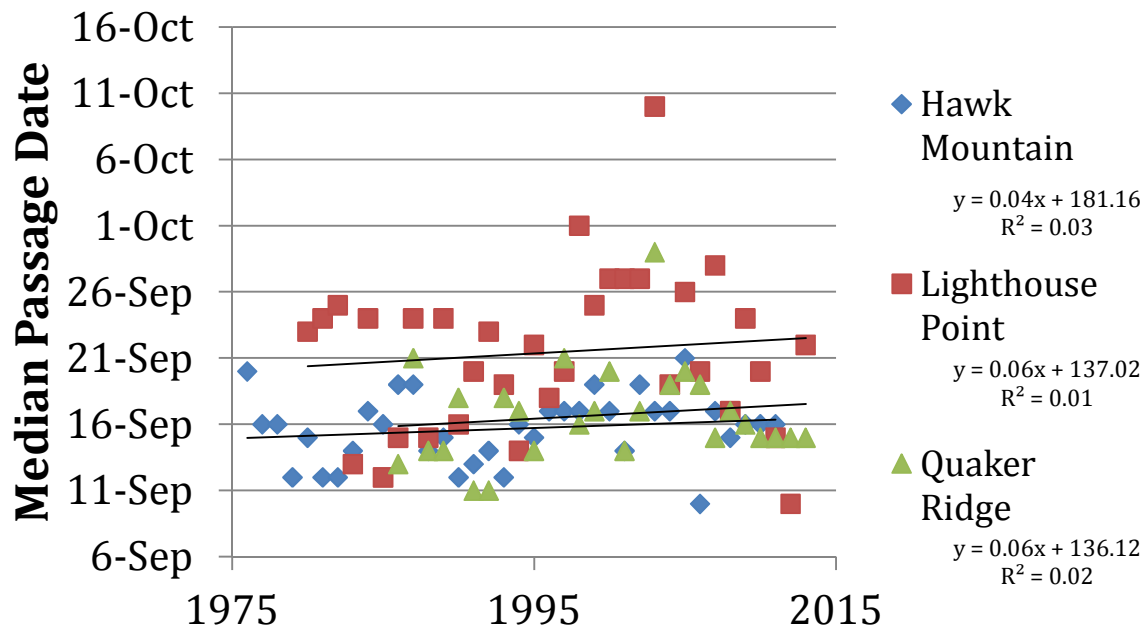


Fig. 8: There was no significant shift of median passage date for the Broad-winged Hawk over the period of 1976-2013 at three count sites in the northeastern US. Slope of each equation is equal to the average days of shift per year for that site.

DISCUSSION

The four raptor species I analyzed displayed a variety of shifts in migration phenology over the past 40 years. Two species delayed their autumn migration, one advanced its autumn migration, and one showed no shift. There is a distinct lack of literature on autumn migration phenology in North American raptors. Therefore, comparing these results to European studies is the first step in understanding how American raptors may be responding to climate change.

Red-tailed Hawk

The Red-tailed Hawk delayed its autumn migration by approximately five days over the 38 years of study at the three count sites. Site was almost a significant factor as well; the delay in migration was much less pronounced at Hawk Mountain than at Quaker Ridge or Lighthouse Point.

The Red-tailed Hawk in eastern North America is a short-distance partial migrant; not every individual in the eastern population migrates, and those that do migrate relatively short distances. The species is not generally considered a trans-equatorial migrant, though there have been a few reports of Red-tailed Hawks as far south as Colombia (Preston and Beane 2009). Migration to South America is the exception rather than the rule; most breeders in the United States and Mexico actually are residents (Preston and Beane 2009). Short-distance raptor migrants in Europe are generally delaying their autumn migration (Filippi-Codaccioni et al. 2009), so the Red-tailed Hawk's delay in autumn migration timing is similar to the pattern seen in European species.

The Red-tailed Hawk's main food sources include small- and medium-sized mammals such as mice, rabbits, and hares, relatively sedentary birds such as the Ring-necked Pheasant (*Phasianus colchicus*; Giudice and Ratti 2001), Northern Bobwhite (*Colinus virginianus*; Brennan 1999), and snakes (Preston and Beane 2009). None of those taxa migrate regularly, and therefore each is available as a food source more or less year-round. Filippi-Codaccioni et al. (2009) suggested that some raptors may be advancing their migration to match an advance in the migration of their passerine food sources (Filippi-Codaccioni et al. 2009). The Red-tailed Hawk's lack of reliance on migratory food sources suggests that food availability is not driving the shift in its autumn migration phenology.

Instead, the Red-tailed Hawk's delay in autumn migration may be a response to climate change. If that were the case, a possible benefit to this delay would be a reduction in mortality rates. Staying on the breeding grounds longer to gather resources after breeding allows for better body condition when eventually beginning migration (Jeni and Kéry 2003), and remaining on the breeding grounds later in the fall is made possible by warmer fall temperatures associated with climate change. Reduced migration distance is a common response to climate change. A delay in autumn migration coupled with a reduction in migration distance may also allow short-distance migrants to arrive on the breeding grounds earlier in the spring (Jeni and Kéry 2003), which would result in the various benefits associated with earlier breeding.

Northern Harrier

The Northern Harrier delayed its autumn migration over the 38 years of study at the three count sites by approximately eight days. For the Northern Harrier, site also had a significant effect on median passage date. The delay at Hawk Mountain was less notable than at the other two sites, which are situated 0.5-0.7 degrees of latitude farther north than Hawk Mountain and 2.3 to 3.1 degrees farther east. The birds may pass Hawk Mountain later than the other two sites due to the difference in latitude; Hawk Mountain is farther south than Quaker Ridge or Lighthouse Point, so autumn passage should be slightly later. The landscape around Hawk Mountain is also more rural than the landscape around the other two sites. Perhaps the density of resident hawks in the urban areas near Quaker Ridge and Lighthouse Point results in migrants moving past those areas faster than raptors that are migrating across a more rural landscape.

Migration in the Northern Harrier is partial but often long-distance; some individuals occasionally winter as far south as the Andes Mountains of Venezuela (Smith et al. 2011). Long-distance raptor migrants in Europe are typically advancing their autumn migration (Filippi-Codaccioni et al. 2009). Jeni and Kéry's (2003) explanation for this advance is that long-distance migrants are avoiding the earlier onset of the dry season in the Sahara Desert associated with climate change. My finding of a significant delay in the Northern Harrier's autumn passage dates is opposite to findings in European studies of long-distance migrating raptors. Long-distance migrants in the United States don't have to contend with the heat and

dehydration of the Sahara, but instead must travel over long distances over land around the Caribbean and Gulf of Mexico. Raptors rely on thermals to migrate and cannot migrate over water for long distances (Bildstein 2006). Perhaps the absence of such a large, inhospitable landform in eastern North America allows more flexibility in timing of migration. A delay in the timing of autumn migration may benefit the Northern Harrier by allowing for better body condition when migrating and earlier return to the breeding grounds (Jeni and Kéry 2003) and may be possible due to warmer fall temperatures associated with climate change, as suggested above for the Red-tailed Hawk. The Northern Harrier is migrating significantly later in years with a high NAO index (warm years) as well, further suggesting that the harrier's advance in autumn migration is a response to climate change.

The Northern Harrier's diet is comprised of a variety of mammals, reptiles, frogs, and birds, including migratory species. Individuals in the northern part of the Northern Harrier's range rely almost exclusively on *Microtus* voles. The Northern Harrier engages in "leap-frog" migration, with individuals from the northern part of the range wintering farther south than individuals living in more temperate areas (Smith et al. 2011). The individuals that migrate the farthest are, therefore, those that rely most heavily on small mammals as a food source. Individuals passing by the three count sites in my study are likely from northern populations; thus, they likely rely heavily on small mammals. As mammals are available as a food source year-round (Filippi-Codaccioni et al. 2009), diet may not play a significant role in timing of the Northern Harrier's autumn migration at the three count sites in my study.

Sharp-shinned Hawk

The Sharp-shinned Hawk advanced its autumn migration by approximately six days over the study period of 38 years at Hawk Mountain. Because there were not enough data at the other two sites for analysis, I was unable to examine the differences in median passage dates among sites for the Sharp-shinned Hawk.

The Sharp-shinned Hawk is a partial long-distance migrant; some individuals in its populations remain on the breeding grounds year-round, and others winter as far south as Panama (Bildstein and Meyer 2000). European studies reported that long-distance raptor migrants have advanced their autumn migration, allowing the raptors to arrive earlier on the wintering grounds and secure better territory, and possibly to track climate change-driven

ecological changes during migration more easily (Filippi-Codaccioni et al. 2009). My analysis indicated that the Sharp-shinned Hawk displayed a shift similar to that described for European long-distance migrants. Thus, this hawk likely benefits from the same advantages noted in other studies: acquiring better wintering grounds and possibly migrating earlier in spring.

Jeni and Kéry (2003) proposed that breeding only requires a certain length of time; because most studied species of avian migrants are advancing their spring migration, they are capable of leaving earlier in the fall. Leaving earlier in the fall can be advantageous because it allows birds to secure better wintering territory on arrival, resulting in better conditions for spring migration. Filippi-Codaccioni et al. (2009) proposed that the Eurasian Sparrowhawk is advancing its autumn migration to match its passerine food sources, many of which are also advancing their migration in response to warmer temperatures (Förchhammer et al. 2002). It is likely that the Sharp-shinned Hawk, which primarily preys on smaller birds, is responding similarly.

Broad-winged Hawk

The Broad-winged Hawk showed no shift in the timing of autumn migration at the three study sites. Site also was not correlated with median passage date. The Broad-winged Hawk is a long-distance migrant. Unlike the other three study species, it is a complete migrant; all continental hawks leave the breeding grounds during winter, and some migrate as far south as Brazil and Peru (Goodrich et al. 2014). In Europe, long-distance raptor migrants typically advance their autumn migration, but a lack of advance or delay has also been reported (Filippi-Codaccioni et al. 2009).

The Broad-winged Hawk, like the Red-tailed Hawk, eats primarily mammals, though amphibians, insects, and juvenile birds are also common food sources (Goodrich et al. 2014). While the availability of juvenile passerines is dependent on the timing of their parents' migration and reproduction, this food source forms a minority of the Broad-winged Hawk's diet. Therefore, the Broad-winged Hawk's lack of shift in autumn migration is unlikely to be dependent on the migration of its prey.

However, many raptor species that do not depend heavily on migratory species for prey are showing a shift in the timing of autumn migration, at least in Europe, to match

ecological changes due to climate change. These species include the Western Marsh Harrier (*Circus aeruginosus*), Black Kite (*Milvus migrans*), and European Honey Buzzard (*Pernis apivorus*) studied by Filippi-Codaccioni et al. (2009), and the Northern Goshawk (*Accipiter gentilis*) studied by Lehikoinen (2009). The fact that the Broad-winged Hawk is not shifting its migration is puzzling.

It is possible that the Broad-winged Hawk, as a long-distance complete migrant, is “hard-wired” to migrate every year at the same time, making a shift in the timing of its migration unlikely. Other species apparently have some degree of plasticity related to migration; for example, the Northern Harrier delays its migration in years with warm average winter temperatures (relatively high NAO index). However, the Broad-winged Hawk does not appear to shift its migration based on the NAO, site, or year, suggesting that it may not exhibit the degree of plasticity shown by other species.

Lack of plasticity in migration phenology may be a problem for species that do not exhibit a shift in response to climate change. Several European studies have noted that bird species not showing a phenology response to climate change are often in decline (Lehikoinen et al. 2006; Møller et al. 2008; Filippi-Codaccioni et al. 2009). Breeding Bird Survey data for eastern North America suggest that the Broad-winged Hawk is declining in the region (Sauer et al. 2014). Possible threats to the species include hunting on wintering grounds and habitat degradation at both breeding and wintering grounds. However, reforestation in the northeastern United States may be increasing the Broad-winged Hawk’s potential breeding range (Goodrich et al. 2014), so how changes in habitat are affecting the Broad-winged Hawk’s populations is unclear. The apparent lack of response in migration to climate change may be another possible threat to the Broad-winged Hawk, especially if climate change may be affecting other factors important to the hawk such as the availability of food resources, the temperatures while young are in the nest, and the frequency and/or severity of inclement weather.

CONCLUSION

Many studies have shown that a number of avian taxa have shifted the timing of migration in the recent past, and some have shown that migration timing is correlated with temperature (Förchhammer et al. 2002) or climate indices (Lehikoinen 2009), suggesting that

the shift is a response to climate change. Three of the four raptor species I studied showed a shift in the timing of their autumn migration over the 38 years of the study period at the three northeastern United States count sites. The finding of a strong year effect for all three species suggests the shifts may reflect a response to climate change. A delay in autumn migration may be useful to reduce migration mortality rates and is possible because of warmer autumn temperatures due to climate change. An advance in autumn migration may be useful to allow individuals to secure better wintering territory and return to the breeding ground earlier, as well as to match the shifting ecology of their prey. The more puzzling result, however, is the apparent lack of shift by the Broad-winged Hawk. Other studies have shown that birds failing to adjust their migration phenology to changes in temperature are more often in decline than those that are adapting. It is possible that the Broad-winged Hawk is “hard-wired” to migrate at a given time, and, over time, a lack of shift in phenology could impact the species’ population persistence.

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