

PATTERNS AND DRIVERS IN COUNTS OF MIGRATORY RAPTORS AT HAWK  
MOUNTAIN SANCTUARY, USA

by

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## DEDICATION

To my mama, the biggest supporter of my wildest aspirations in life.

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## ABSTRACT

Understanding the mechanisms driving biodiversity patterns amidst an era of global environmental change is the core of modern ecological research. The magnitude of biodiversity losses associated with anthropogenic activities has prompted resource managers and ecologists alike to identify strategies to address conservation issues. Broadly, two types of approaches are employed to answer ecological research questions: 1) single-species and 2) ecosystem-based approach. Single-species approaches are often useful to elucidate mechanisms driving population trajectories of individual species. On the other hand, ecosystem-based approaches can help in identifying general patterns that may be useful for multi-species management.

Here, I used both approaches in assessing broad-scale patterns and mechanisms driving count trends of migrating raptors recorded at Hawk Mountain Sanctuary (HMS), Pennsylvania. In the first chapter, I used a hierarchical breakpoint model to identify the assemblage-wide and species-specific timing of the shifts in count trends. Then I evaluated if changes in trend directionality of counts were linked to species' traits (body size, population size, migratory behavior, tolerance to human presence, DDT (dichlorodiphenyltrichlorethane) susceptibility, habitat or dietary specialization). I found that an assemblage-wide shift in counts occurred around 1974, and this timing was common among 14 of the 16 species in the assemblage. Moreover, I found that habitat specialization appeared to explain the synchronous positive and negative count trends of multiple species. Other traits that I evaluated were not consistently associated with either

types of trends. The temporal shift in trends in 1974 emphasized the relative importance of DDT, an organochlorine known to have adversely influenced several wildlife species and was banned in the US around the 1970s, in driving population dynamics of raptor species. However, because the counts of species susceptible to DDT were highly variable after 1974, this may suggest that a suite of additional factors, acting together, affected the recovery of species from DDT-associated declines. Additionally, the potential role of habitat specialization in count trends may suggest important linkages between habitat use and demography.

In the second chapter, I used a generalized linear mixed-effects model to assess the relationships between changes in the count totals and total proportional cover of major land-use types in nine states located in the northeastern US (Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont). The hierarchical modelling approach that I used allowed me to identify average and species-specific responses to the proportional cover of forested and urban area. These land-use variables were not associated with overall raptor counts. However, species-specific responses were variable and significant. I found that counts of northern goshawk, American kestrel, rough-legged hawk, sharp-shinned hawk, and red-tailed hawk were positively associated with forest cover. On the other hand, turkey and black vultures, bald eagle, and peregrine falcon were positively associated with urban cover. Moreover, red-shouldered hawk, broad-winged hawk, and northern harrier were not significantly associated with forest cover but were negatively associated with urban cover. Merlin and Cooper's hawk exhibited similar non-significant associations to forest but positive associations with urban cover. Finally, golden eagle and osprey were not



significantly associated with either land-use variables. These results provided insights on the potential influence of land-use changes on the demography of migrating raptors. Thus, these findings may be useful in improving our predictions of the population trajectories of these species in future landscape scenarios.

These results illustrate the utility of evaluating species-level and assemblage-wide patterns in long-term count data. In this case, it allowed me to identify general patterns in counts of migrating raptors and gain detailed insights on the responses of individual species to land-use changes. In doing so, I was able to better understand the potential drivers of their ecological dynamics. By integrating information from these two approaches, we can expect to obtain a better understanding of natural systems and consequently, increase the probability of successful conservation outcomes.

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## LIST OF ABBREVIATIONS

BBS	Breeding Bird Survey
DDT	dichlorodiphenyltrichloroethane
HMS	Hawk Mountain Sanctuary
IBA	Important Bird Area
LULC	land-use and land cover
MLU	major land-uses
USA	United States of America

CHAPTER ONE: SHARED FUNCTIONAL TRAITS EXPLAIN SYNCHRONOUS  
LONG-TERM TRENDS IN COUNTS OF MIGRATORY RAPTORS

**Abstract**

Assessing long-term shifts in faunal assemblages is important to understand the consequences of ongoing global environmental change. One approach to assess drivers of assemblage changes is to identify the traits associated with synchronous shifts in trend directionality among species. Our research identified traits influencing 72 years of trends in assemblage structure of migrating raptors recorded in northeastern United States of America (USA). Migrating raptors were counted following a standardized protocol, each autumn, for 72 years. I used a hierarchical breakpoint model to identify the temporal shift in count trends. Then I evaluated if changes in trend directionality of counts, based on differences between pre- and post- breakpoint slopes ( $\Delta\delta$ ), were linked to species' traits (body size, population size, migratory behavior, tolerance to human presence, DDT susceptibility, habitat or dietary specialization). I used a correlation analysis to evaluate the association between trend directionality and allometric and demographic traits. Then, I calculated the probabilities of observing positive and negative  $\Delta\delta$ s given each type of functional trait. I documented a shift in count trends at about 1974 for 14 of 16 species of migrating raptors. Eight of the nine species with negative change in counts ( $\Delta\delta < 0$ ) were habitat specialists, and all seven species with positive change in counts ( $\Delta\delta > 0$ ) were habitat generalists. No other traits were consistently associated with positive or negative change in counts. This approach allowed the identification of fundamental ecological



processes that may be driving population trends. In this case, habitat specialization was a key factor associated with changes in trend directionality, suggesting important linkages between habitat use and demography. This information will be useful in identifying general patterns to improve predictions of biodiversity trends in changing ecosystems.

### **Introduction**

Assessing long-term shifts in faunal assemblages is important to understand the consequences of ongoing global environmental change (McGill et al., 2015).

Examination of time-series data on ecological assemblages can provide us with information on ecosystem processes (Dornelas et al., 2014). Often, changes in ecosystem dynamics are driven by shifts in community composition and population density (Spaak et al., 2017). Thus, simultaneously assessing the trends of multiple species in an assemblage can help us identify drivers of variations in community composition.

Changes in species assemblages are often identified by assessing trends of diversity indices and patterns of species' functional traits (Naeem et al., 2012). Specifically, the functional structure of an ecosystem can be evaluated by quantifying the distribution of functional traits or by assessing changes in the trait identities of the species in an assemblage (Diaz and Cabido, 2001; Tilman et al., 1997). Thus, trait-based ecology can be useful in obtaining a more mechanistic understanding of ecosystem dynamics (McGill et al., 2006).

Long-term count data on wildlife populations are central to efforts in understanding changes in ecosystem dynamics. For example, 33 years of count data on fish populations were used to identify the impacts of anthropogenic stress and biotic factors on the organizational patterns of a fish assemblage in France (Kuczynski et al.,

2017). Long-term monitoring surveys for birds were also key in identifying widespread population declines of North American avifauna (Rosenberg et al., 2019).

Raptors are top predators that strongly influence the population dynamics of a broad range of species in terrestrial communities. Specifically, raptors may limit the numbers of their prey items, such as small mammals and gamebirds (Terraube and Bretagnolle, 2018; Valkama et al. 2005). Moreover, because migrating raptors are sensitive to disturbances in their breeding, stopover, and overwintering sites, they are good candidates for predicting the ecosystem-level impacts of environmental change over large spatial scales (Bildstein, 2006; Therrien et al., 2012; Cruz et al., 2019).

Here, I assessed the temporal patterns of species' counts and the functional trait composition of the assemblage of migrating raptors recorded at Hawk Mountain Sanctuary (HMS) in Pennsylvania, USA. HMS maintains the world's longest-running raptor migration monitoring program, with records of autumn flights from 1934 to the present day (Therrien et al., 2012). I used a breakpoint model to identify the timing of directional changes in assemblage-wide and species-specific raptor counts. I expected this model to capture two distinct processes driving count trends before and after the ban of DDT, an agricultural pesticide known to have adversely influenced several bird species, including raptors (Ratcliffe, 1970). Then, I looked for support for the hypothesis that synchronous shifts in count trends were associated with shared species' traits. Specifically, I evaluated if variation in count trends was linked to characteristics such as body size, population size, migratory behavior, tolerance to human presence, DDT susceptibility, dietary and habitat specialization. This approach allowed me to identify fundamental ecological processes that may be driving count trends of migrating raptors

during a period of increasing natural and anthropogenic stress.

## Methods

### Study site

The Appalachian Mountains are a major corridor for migrating raptors. This mountain range spans > 3,000 miles, from Newfoundland and Quebec in Canada, to Alabama in the southeastern United States (Goodrich and Smith, 2008). HMS straddles the Kittatinny Ridge, which transects eastern Pennsylvania from northern New Jersey to Maryland. The ridge is recognized as a Global Important Bird Area (IBA) for the bird migration occurring along its slopes (Audubon, 2018). Large numbers of outbound migrating raptors from southeastern Canada and New England states concentrate at HMS each autumn because of its geography (Bildstein, 2006). Since 1934, monitoring of spring and autumn raptor migration has been consistently conducted at a single location at HMS.

### Migration count data

Counts of migrating raptors have been collected at HMS by trained staff and volunteers following consistent protocols (Barber et al., 2001). Here, I used annual autumn count data collected between 15 August and 15 December over the years 1946 to 2018, the period in which monitoring efforts were consistent across all years for all species except for turkey (*Cathartes aura*) and black (*Coragyps atratus*) vultures. Systematic counts of those species only began in the 1970s. I focused our analyses on the 16 most commonly recorded species: black vulture, turkey vulture, osprey (*Pandion haliaeetus*), golden eagle (*Aquila chrysaetos*), northern harrier (*Circus cyaneus*), sharp-shinned hawk (*Accipiter striatus*), Cooper's hawk (*A. cooperii*), northern goshawk (*A. gentilis*), red-shouldered hawk (*Buteo lineatus*), broad-winged

hawk (*B. platypterus*), red-tailed hawk (*B. jamaicensis*), rough-legged hawk (*B. lagopus*), bald eagle (*Haliaeetus leucocephalus*), American kestrel (*Falco sparverius*), merlin (*F. columbarius*), and peregrine falcon (*F. peregrinus*). Other species were occasionally recorded at HMS, but too infrequently to be included in the analyses.

## Data Analysis

### Breakpoint model for count trends

I evaluated temporal patterns in the count data of migrating raptors using a hierarchical breakpoint model, also called a piecewise regression model. This approach is used to evaluate non-linear relationships and to assess sudden ecological changes that result from anthropogenic impacts (Brilleman et al., 2017; Roopsind et al., 2018; Toms and Lesperance, 2003). Newer methods of implementing this model enable estimation of the timing of the breakpoint and of slopes before and after the breakpoint (Beckage et al., 2007). Here, I used a breakpoint model where the intercept, breakpoint, and pre- and post- breakpoint slopes were allowed to vary for each species. The model had the form:

$$Y_{ij} \sim \text{Negative Binomial}(\mu_{ij}, \varphi) \quad (\text{Eqn.1})$$

$$\log(\mu_{ij}) = \begin{cases} \beta_{0j} + \beta_{1j} * (X_{ij} - \tau_j) + \log(K_i), & X_{ij} \leq \tau_j \\ \beta_{0j} + \beta_{2j} * (X_{ij} - \tau_j) + \log(K_i), & X_{ij} > \tau_j \end{cases} \quad (\text{Eqn.2})$$

In the equations above,  $Y_{ij}$  is the total number of recorded individuals of species  $j$  at a given year ( $X_{ij}$ ), which follows a negative binomial distribution with a mean ( $\mu$ ) and an overdispersion parameter ( $\varphi$ ). I modelled the response variable with the following parameters:  $\hat{\beta}_{0j}$ , the species-specific intercept (mean count when other parameters are constant),  $\hat{\beta}_{1j}$ , the species-specific slope before the breakpoint (pre-breakpoint slope),  $\tau_j$ , the species-specific breakpoint year (the year in which the count trend shifts),  $\hat{\beta}_{2j}$ , the slope after the breakpoint (post-breakpoint slope), and  $K$ , the offset term used to account

for differences in total observation days, which were log-transformed, for each year (Hilbe, 2010; see Supporting Information).

I rescaled the values for year by centering each variable on the mean and dividing by two standard deviations (Gelman, 2008). By standardizing year in this manner, I allowed the intercept to be centered in the time series. In Eqn. 2, I further centered the year around the breakpoint ( $X_{ij} - \tau_j$ ) to ensure that the deterministic model was continuous at the intercept.

I implemented the model in a Bayesian framework with weakly-informed priors, following current best practices (Brilleman et al., 2017; Gelman et al., 2008; McElreath, 2020). I based parameter estimates from the breakpoint model on four chains of 5500 iterations with 4000 iterations for warm-up period, resulting in 1500 posterior draws for each parameter from each chain (6000 total). I assessed model convergence and mixing of chains through visual inspection and by using the Gelman-Rubin (Gelman and Rubin, 1992) diagnostic ( $\hat{R}$ ). I performed posterior predictive checks to evaluate deviations of model-generated data from the observed data. I interfaced to Stan using the ‘rstan’ package to fit our model in R (R Core Team, 2018; Stan Development Team, 2019).

I estimated species-specific estimates for intercept, pre- and post-breakpoint slope, and breakpoint year by drawing them from the global distribution of each parameter (Royle and Dorazio, 2008). I report all parameter estimates on their original scale (i.e., years, counts of raptors). For each species, I calculated the difference between the estimates of the pre- and post- breakpoint slopes (hereafter the “ $\Delta\delta$ ”) at each iteration to identify trend directionality. Specifically, I classified  $\Delta\delta$  values as either indicative of a

positive change in counts ( $\Delta\delta > 0$ ; positive difference between pre- and post- breakpoint slopes), or of a negative change in counts ( $\Delta\delta < 0$ ; negative difference between pre- and post- breakpoint slopes).

#### Assessments on assemblage composition

I performed post-hoc tests to evaluate our hypothesis that shared traits may be associated with the synchronous count trends of species. I organized species according to traits (allometric, demographic, and functional) based on information in Birds of North America accounts (Rodewald, 2015) and Partners in Flight (2019) databases (Table 1.1).

I created a reference plot wherein the mean  $\Delta\delta$  values for each species were ranked in ascending order. This plot was used to visualize species' ranks based on magnitude of rate changes, and as reference against which to compare similar plots based on species' traits. I evaluated our hypotheses for how traits relate to  $\Delta\delta$ s using statistical tests as described below.

I plotted  $\Delta\delta$  values of species in ascending order based on (a) their average body mass (g), and (b) the estimate of their population size in US and Canada. I compared the order of the species in these plots with the order of species in the reference plot, and we assessed rank-based associations between the  $\Delta\delta$  and trait using a Spearman's rank correlation test ( $r$ ). I then evaluated the similarity of the order of species in these plots to the order in the reference plot. I interpreted a Spearman's correlation coefficient ( $r$ ) of  $> 0.60$  as indicative of an association between the trait and the trend directionality.

I sorted species based on their migratory behavior, tolerance to human presence, susceptibility to DDT, dietary, and habitat specialization (Table 1.1; Table A.1). I described species based on their migratory behavior as either a complete (i.e., species in

which > 90% of all individuals routinely migrate), or a partial migrant (i.e., species in which < 90% of all individuals routinely migrate). I described species based on their acceptance of human presence as tolerant (i.e., nests in human-perturbed landscapes), or intolerant (i.e., nests far from human-perturbed landscapes). I described species based on DDT susceptibility as susceptible (i.e., documented reproductive impairment in response to presence of DDT in the environment), or not susceptible (i.e., no documented response to presence of DDT in the environment). I described species as diet specialists or generalists based on the diversity of their diet (as reviewed by Sherrod, 1978; Therrien et al., 2017). I classified species with diet diversity index values > 1 as generalists, and < 1 as specialists. I described species as habitat specialists (i.e., associated with stable or homogeneous habitats), or habitat generalists (i.e., associated with disturbed and heterogeneous habitats). See Appendix A for additional details on my methodology for classifying species.

For each of the two classifications of a functional trait, I calculated the probability of observing positive and negative change in counts using species-specific estimates of  $\Delta\delta$ . Because the Bayesian models incorporated pre- and post- breakpoint slopes as species-level random effects, I was able to calculate 6000 posterior samples of  $\Delta\delta$  for each species. Using these posterior samples, I obtained probabilities of a positive or negative change in count trends by dividing the frequency of positive or negative  $\Delta\delta$  posterior draws by the total number of posterior draws for all  $\Delta\delta$  values for each species. By separating species into functional trait categories, I was able to calculate probabilities of negative or positive change for a given trait type. For example, I obtained the probability of a species being a generalist and having a positive change in counts by

dividing the frequency of positive  $\Delta\delta$  posterior samples of generalists by the total number of posterior samples for all positive and negative  $\Delta\delta$  values of generalists.

## Results

### Temporal trends of the assemblage of migrating raptors

The assemblage-wide breakpoint year was around 1974 (Table 1.2). Moreover, the mean breakpoint year for most species occurred during the period, 1970-1978. The exceptions were merlin and Cooper's hawk, species that had mean breakpoint years of 1968 and 1966, respectively.

In general, raptor counts were declining prior to the breakpoint and increasing after the breakpoint (Table 1.2). However, estimates for pre- and post- breakpoint slopes varied substantially among species (Fig. 1.2, Fig. A2). Northern goshawk and red-shouldered hawk showed the greatest negative change in count trends and bald eagle and the two vulture species showed the greatest positive change in count trends (Table 1.2, Fig. 1.1). The 95% credible intervals (CI) of  $\delta_1$  and  $\delta_2$  did not overlap each other for all species except osprey and red-tailed hawk (Table 1.1). For turkey vulture, bald eagle, golden eagle, and peregrine falcon, slope estimates were negative before the breakpoint (negative  $\delta_1$  and 95% CI not overlapping zero) and positive after the breakpoint (positive  $\delta_2$  and 95% CI not overlapping zero; Table 3). In contrast, for sharp-shinned hawk, northern goshawk, red-shouldered hawk, rough-legged hawk, and American kestrel, the slope estimates were positive before the breakpoint and negative after the breakpoint. For black vulture, Cooper's hawk, and merlin, the 95% CI of the slope estimates overlapped zero before the breakpoint but were positive after the breakpoint. In contrast, for northern harrier, broad-winged hawk, and red-tailed hawk, opposite trends were observed (95% CI



of pre-breakpoint slope estimates overlapped zero, but post-breakpoint trend estimates were negative). Finally, for the osprey, the slope estimates before the breakpoint were positive, but 95% CI of post-breakpoint slope estimates overlapped zero.

#### Drivers of patterns in assemblage composition

Rankings by body mass (Fig. 1.3a) did not match the observed assemblage patterns (Fig. 1), and there was poor correlation between the two data sets ( $r = 0.49$ ), indicating that body mass was not associated with the observed assemblage structure. However, we observed some species-specific relationships between body mass and  $\Delta\delta$ . The two smallest species (American kestrel and sharp-shinned hawk) both had negative change in counts. On the other hand, the three largest species (black vulture, golden and bald eagles) all had positive change in counts.

Rankings by estimates of population size (Fig. 1.3b) also did not match the observed assemblage patterns (Fig. 1.1), and there was very poor correlation between the two data sets ( $r = 0.013$ ), indicating that population size was not associated with the observed assemblage structure. However, we did observe some species-specific relationships between population size and  $\Delta\delta$ . Specifically, the three species with the smallest population estimates (peregrine falcon, and golden and bald eagles) all had positive change in counts.

Migratory behavior did not appear to explain the observed distribution of positive and negative  $\Delta\delta$  values of all species in the assemblage (Figs. 1.1, 1.4a). Despite the fact that the probability of observing negative change in counts was high for complete migrants (> 99%), the probability of observing negative change in counts was still 45% for partial migrants. As such, although complete migrants appear to be experiencing

population declines, overall assemblage-wide trends were not explained by migratory behavior.

Tolerance of human presence also did not appear to explain the observed distribution of positive and negative  $\Delta\delta$  values of all species in the assemblage (Figs. 1.1, 1.4b). Again, despite the fact that the probability of observing negative change in counts was high for intolerant species (83%), the probability of observing negative change in counts for tolerant species was still 38%, indicating that being tolerant of humans did not guarantee positive change in counts. As such, although intolerant species appear to be experiencing population declines, overall assemblage-wide trends also were not explained by tolerance of human presence.

DDT susceptibility did not appear to explain the observed distribution of positive and negative  $\Delta\delta$  values of all species in the assemblage (Figs. 1.1, 1.4c). In this case, the probability of observing negative change in counts was very high for non-susceptible species (93%) and moderately high 46% for susceptible species. As such, populations of both susceptible and non-susceptible species appear to be in decline in a manner not explained by DDT susceptibility and, thus, overall assemblage-wide trends were not explained by DDT susceptibility.

Diet specialization also did not appear to explain the observed distribution of positive and negative  $\Delta\delta$  values of all species in the assemblage (Figs. 1.1, 1.4d). The probability of observing negative change in counts was at intermediate levels for both generalists (67%) and specialists (48%). As such, trends for neither group were associated with dietary specialization and overall assemblage-wide trends were not explained by diet specialization.

In contrast to all the other potential trait predictors we evaluated, habitat specialization did appear to explain the observed distribution of positive and negative  $\Delta\delta$  values of all species in the assemblage (Figs. 1.1, 1.4e). In this case, the probability of observing negative change in counts was high among specialists (> 99%), and very low for generalists (10%). These patterns show that most specialist populations experienced negative change in counts over time and that most generalist populations experienced positive change in counts. The fact that no other trait shows similar patterns suggests a strong role for habitat specialization in driving assemblage-wide trends in counts.

## **Discussion**

### Temporal patterns of an assemblage of migrating raptors

Community-wide analyses of temporal patterns in wildlife assemblages can be used to identify common factors driving large-scale biodiversity changes. With growing concern about biodiversity loss, there is a need to better understand how shifts in abundance at the species-level can impact assemblages and ecosystems. Here, the synchronized temporal patterns of multiple species with shared functional traits suggest that broad-scale drivers may be shaping the assemblage structure.

A prominent hypothesis used to explain changes in raptor abundance in North America is the presence of DDT in the environment (Bednarz et al., 1990; Rosenberg et al., 2019). The effects of this toxicant were wide-ranging and pervasive, resulting in the decline of non-target species such as raptors (Ratcliffe, 1970). The assemblage-wide shift in trends that I detected in the early 1970s is synchronous to the policy change controlling the use of DDT. This synchrony illustrates the likely significant role that DDT played in the changes in the counts of some species within the assemblage I studied. However, after

the breakpoint year, the counts of species susceptible to DDT were highly variable (Table 3), suggesting that a suite of additional factors acting together affected the recovery of species from DDT-associated declines.

Other environmental policies were implemented around the same time as the DDT ban. These included ratification of the Migratory Bird Treaty Act and implementation of a law protecting hawks in Pennsylvania (Paehlke, 1995). These statutes, which criminalize the persecution of raptors in North America (Bildstein, 2008), may have contributed to positive change in counts for some species, thus influencing the assemblage-wide trends we observed.

#### Shared traits of species with synchronous trends

The complex and dynamic nature of assemblages makes it difficult to identify general laws or common ecological factors shaping them. Thus, there is often more evidence for the drivers of population dynamics of one or a few species, rather than for multi-species communities (Simberloff, 2004). In general, species' responses to abiotic pressures can be determined by their traits (Pacifci et al., 2017). My results suggest that some characteristics shared among species influence assemblage-wide patterns in count data.

The trait that seemed most influential in driving trends in HMS raptor count data was habitat specialization. I infer that the landscape changes in the northeastern US in the past four centuries (Adams et al., 2019; NOAA, 2010; Thompson et al., 2013) have driven shifts in the availability of certain habitat types and, consequently, influenced raptor count trends. In particular, positive trends in counts of synanthropic species such as Cooper's hawk, red-tailed hawk, peregrine falcon, merlin, bald eagle, and turkey and

black vultures may be linked to their lack of specialization and their associated ability to thrive in heterogeneous environments such as urban areas (Curtis and Rosenfield, 2006; Millsap et al., 2004).

Negative count trends of habitat specialists in the assemblage may also be linked to their narrow habitat niche. The specialists I evaluated were either forest-dependent species such as northern goshawk, red-shouldered hawk, sharp-shinned hawk, and broad-winged hawk, or those associated with open habitats like American kestrel and northern harrier. For these taxa, on-going landscape changes in the northeastern US appear to be a driver of negative trends in count data.

#### Other potential drivers of trends in raptor counts

Biotic factors such as species interactions, shifts in distribution, food availability, migration phenology and migratory behavior may have also influenced count data for some species. However, these did not appear important in driving assemblage-wide patterns. For example, regional trends of counts of osprey at inland northeastern US sites are significantly declining (Brandes et al., 2016; Crewe et al., 2016). However, Breeding Bird Survey (BBS) data suggest stable trends in North America (Sauer et al., 2017). These conflicting trend estimates may suggest that inland osprey population levels are either stabilizing or are regulated by other environmental factors (Farmer et al., 2008). In fact, species interactions also may matter for osprey, as increasing numbers of bald eagles can limit the nesting success of this and other piscivore species (Cruz et al., 2019). Similarly, predation by larger accipiters coupled with landscape changes may contribute to the increased mortality of American kestrel (Farmer et al., 2006). Finally, for scavengers such as black and turkey vultures, increases in road density, which increase

the preponderance of carrion along roads, may have benefitted their populations (Kirk and Mossman, 1998).

Shifts in distribution are potentially driving changes in counts for some species as well. For example, the positive change in counts of both species of vultures may be attributed to the northward expansion of their breeding ranges (Buckley, 1999; Kirk and Mossman, 1998). Moreover, change in migratory behavior may have also driven changes in count trends for the red-tailed hawk (Paprocki et al., 2017). Consistent with my results, there have been significant declines in the counts of red-tailed hawk monitored in northeastern hawk watch sites (Brandes et al., 2016; Crewe et al., 2016). However, BBS data suggests positive or stable trends in the US (Link and Sauer, 2002). Presumably, red-tailed hawk in the east are exhibiting migratory short-stopping or are experiencing breeding population declines in eastern Canadian provinces (Paprocki et al., 2017). Finally, shifts in migration timing (i.e., delay in migration phenology) may have an impact on the observed count trends (Therrien et al., 2017).

### **Conclusions**

Ongoing global change is often associated with the reorganization of ecological communities and assemblages. Thus, ecologists are challenged to make better predictions of the impacts of interacting anthropogenic stressors. My results illustrate the utility of a trait-based approach in evaluating assemblage-wide trends and compositional patterns. By classifying species into ecological groups, we identified traits that influenced count trends of some species. This suggests that trait-based assessments may be useful in multi-species conservation planning.

With existing risks and vulnerabilities magnified by anthropogenic stressors, it is

important to develop conservation strategies that address conservation concerns for multiple species. Thus, community ecologists are calling for more research using approaches focused on functional traits that allow for the mechanistic understanding of species assemblages (McGill et al., 2006). Analyses such as our breakpoint modeling approach, that identify correlations between species' abundance trajectories and functional traits, can provide a foundation for mechanistic hypotheses in community ecology.

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Tables

**Table 1.1. Allometric, demographic, and functional traits of 16 species recorded at Hawk Mountain Sanctuary, Pennsylvania. Data are from Birds of North America accounts (Rodewald, 2015) and Partners in Flight (2019) databases.**

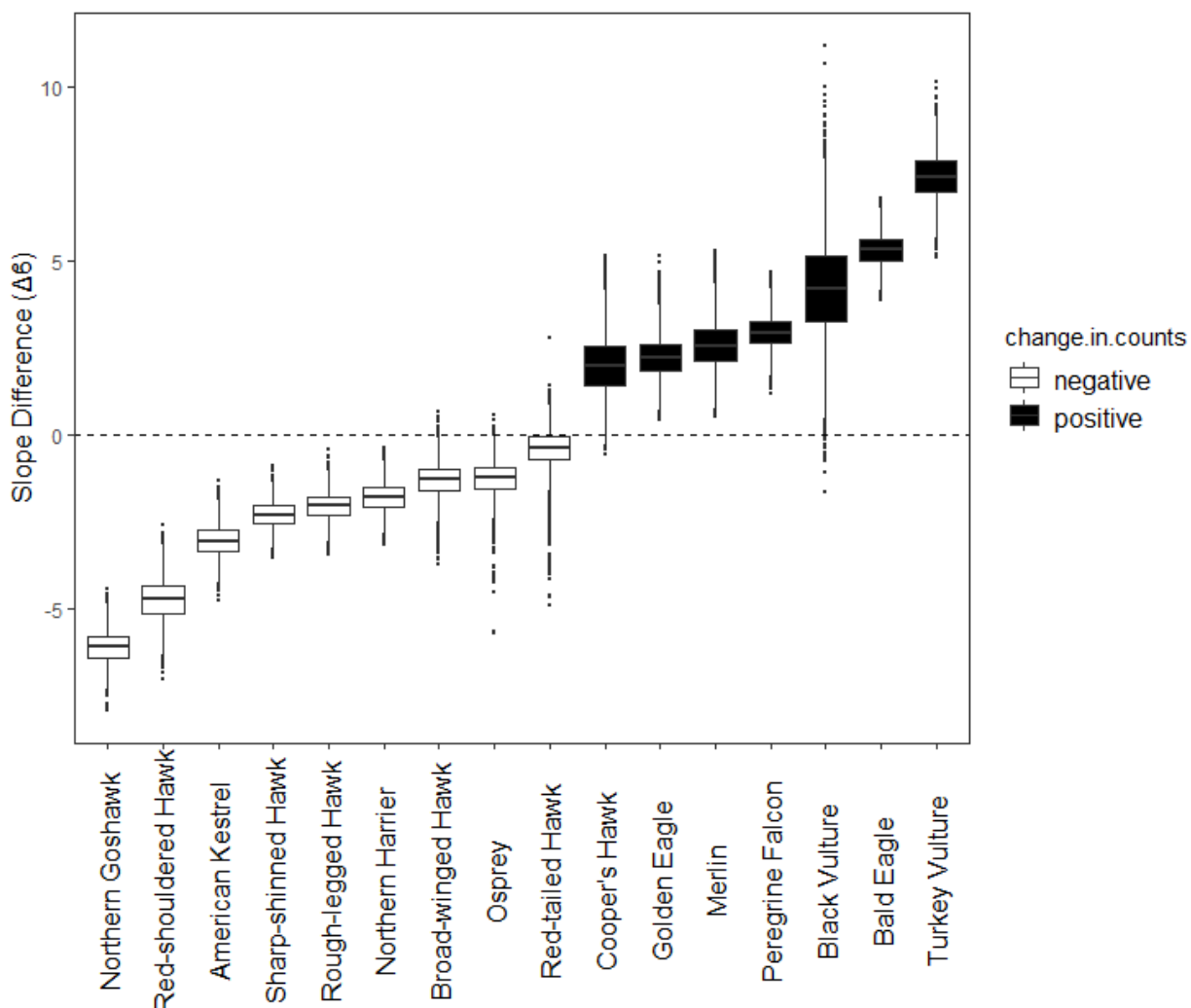
Species	Ave. Body Mass(g)	Pop. Estimate (millions)	Habitat	Diet	Migratory Behavior	Anthropogenic Tolerance	DDT susceptibility
Turkey Vulture	1425	8.40	Generalist	Specialist	Partial	Tolerant	Susceptible
Black Vulture	1640	1.90	Generalist	Specialist	Partial	Tolerant	Susceptible
Osprey	1570	0.40	Specialist	Specialist	Complete	Tolerant	Susceptible
Bald Eagle	4790	0.20	Generalist	Generalist	Partial	Tolerant	Susceptible
Northern Harrier	447	0.82	Specialist	Generalist	Partial	Intolerant	Susceptible
Sharp-shinned Hawk	166	0.41	Specialist	Specialist	Partial	Intolerant	Susceptible
Cooper's Hawk	452	0.84	Generalist	Generalist	Partial	Tolerant	Susceptible
Northern Goshawk	990	0.21	Specialist	Generalist	Partial	Intolerant	Susceptible
Red-shouldered Hawk	625	1.80	Specialist	Generalist	Partial	Tolerant	Susceptible
Broad-winged Hawk	397	1.80	Specialist	Generalist	Complete	Intolerant	Not susceptible
Red-tailed Hawk	1126	2.80	Generalist	Specialist	Partial	Tolerant	Not susceptible
Rough-legged Hawk	951	0.30	Specialist	Specialist	Complete	Intolerant	Not susceptible
Golden Eagle	4200	0.063	Generalist	Specialist	Partial	Intolerant	Susceptible
American Kestrel	116	2.80	Specialist	Specialist	Partial	Tolerant	Susceptible
Merlin	222	1.60	Generalist	Specialist	Partial	Tolerant	Susceptible

Peregrine Falcon	794	0.04	Generalist	Specialist	Partial	Tolerant	Susceptible
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**Table 1.2. Estimates of breakpoint year and pre-( $\delta_1$ ) and post-( $\delta_2$ ) breakpoint slope for count data from 16 species recorded at Hawk Mountain Sanctuary, PA. Estimates provided are posterior means and associated 95% credible intervals in square parentheses, derived from a Bayesian hierarchical breakpoint model.**

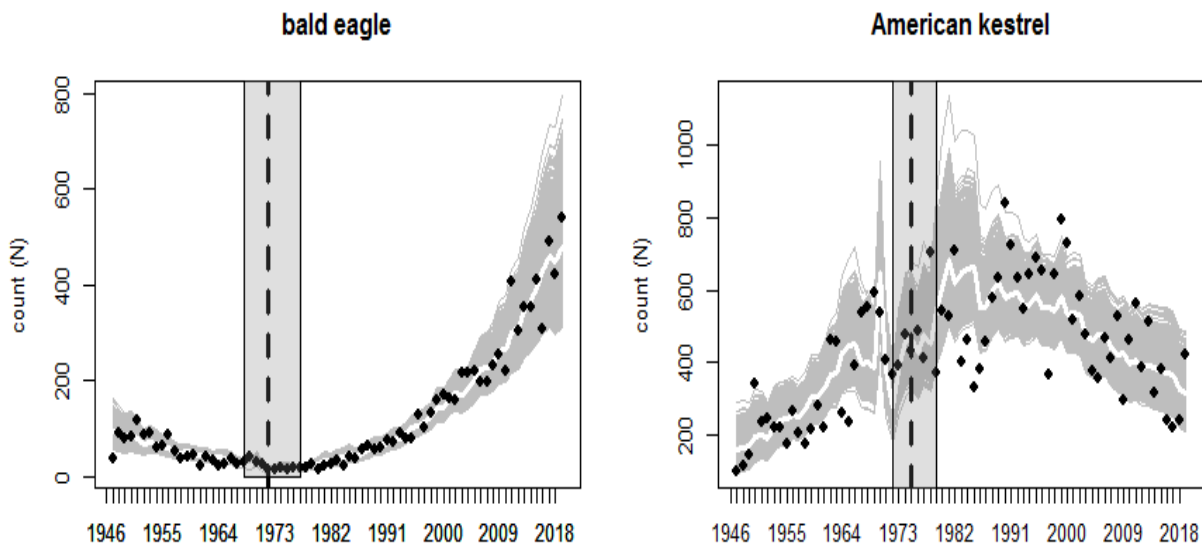
Species	Mean breakpoint year [CI]	Slope Estimates [CI]	
		$\beta_1$	$\beta_2$
Cooper's Hawk	1966 [1960, 1974]	-0.91 [-2.43, 0.38]	1.06 [0.72, 1.38]
Merlin	1968 [1961, 1974]	-0.76 [-2.23, 0.34]	1.82 [1.48, 2.18]
Golden Eagle	1970 [1963, 1978]	-1.23 [-2.50, -0.32]	0.99 [0.67, 1.35]
Black Vulture	1972 [1959, 1983]	-2.03 [-4.77, 0.65]	2.16 [1.51, 2.83]
Broad-winged Hawk	1972 [1964, 1980]	0.32 [-0.37, 1.22]	-0.99 [-1.31, -0.68]
American Kestrel	1972 [1968, 1977]	2.05 [1.30, 2.86]	-1.03 [-1.40, -0.67]
Turkey Vulture	1972 [1970, 1976]	-4.11 [-5.18, -3.08]	3.30 [2.71, 3.89]
Northern Goshawk	1972 [1971, 1974]	3.84 [3.13, 4.60]	-2.29 [-2.65, -1.93]
Peregrine Falcon	1975 [1971, 1980]	-1.57 [-2.31, -0.86]	1.37 [0.93, 1.84]
Bald Eagle	1975 [1972, 1979]	-2.53 [-3.32, -1.77]	2.79 [2.35, 3.26]
Red-shouldered Hawk	1976 [1961, 1989]	1.84 [0.89, 2.92]	-2.92 [-3.80, -2.20]
Osprey	1976 [1966, 1991]	0.78 [0.19, 1.49]	-0.47 [1.15, -0.02]
Red-tailed Hawk	1976 [1970, 1983]	-0.41 [-1.05, 0.52]	-0.82 [-1.31, -0.43]
Northern Harrier	1978 [1971, 1986]	0.48 [-0.06, 1.12]	-1.32 [-1.84, -0.87]
Rough-legged Hawk	1978 [1972, 1984]	0.83 [0.23, 1.48]	-1.24 [-1.70, -0.86]
Sharp-shinned Hawk	1978 [1974, 1983]	1.25 [0.77, 1.73]	-1.07 [-1.50, -0.66]
Assemblage-wide	1974 [1970, 1978]	-0.15 [-1.19, 0.87]	0.10 [-0.77, 1.01]

## Figures

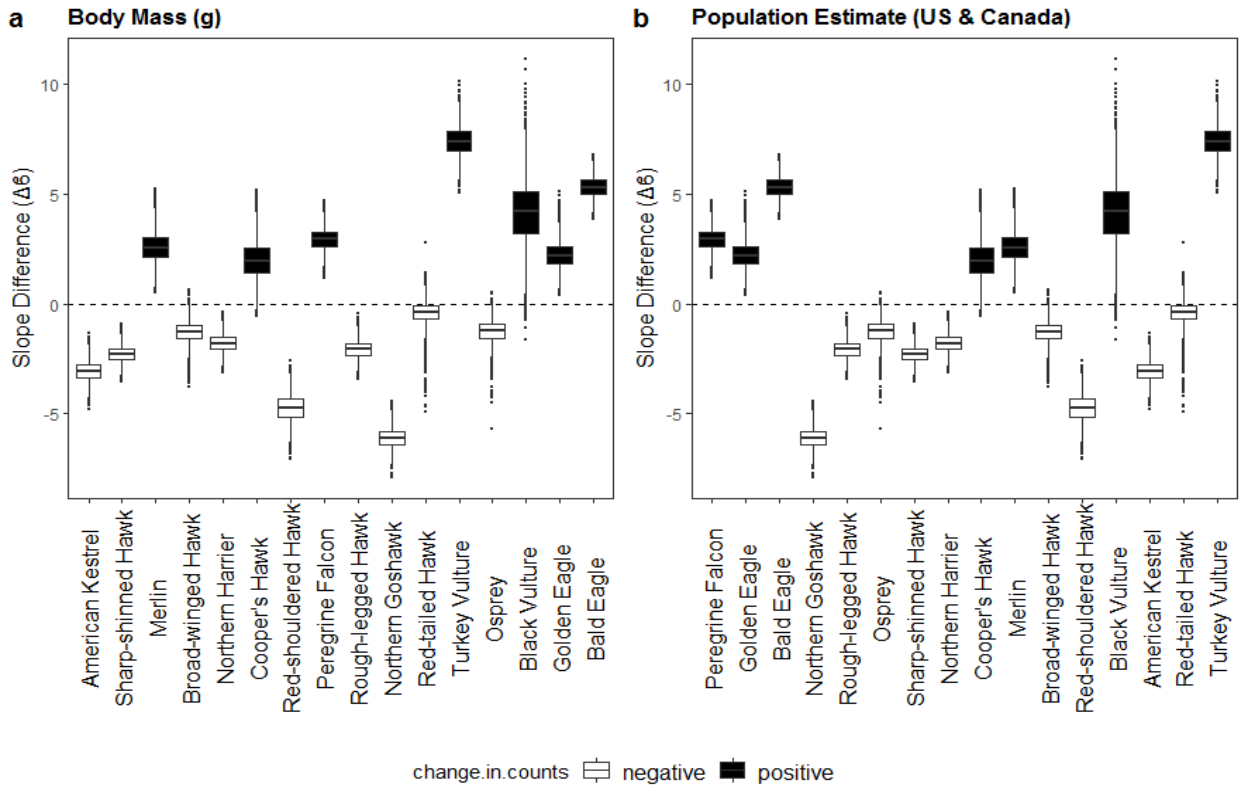


**Fig.1.1.** Mean difference between the estimates of pre- and post-breakpoint slopes for all species recorded at Hawk Mountain Sanctuary, Pennsylvania. Boxes delineate first to third quartiles, the thick black line with boxes shows the median, and 'whiskers' represent minimum and maximum observations within 1.5 times of the upper and lower quartiles. Thus, for each species, 100% of the uncertainty in estimated slope differences is accounted for in the boxplot.

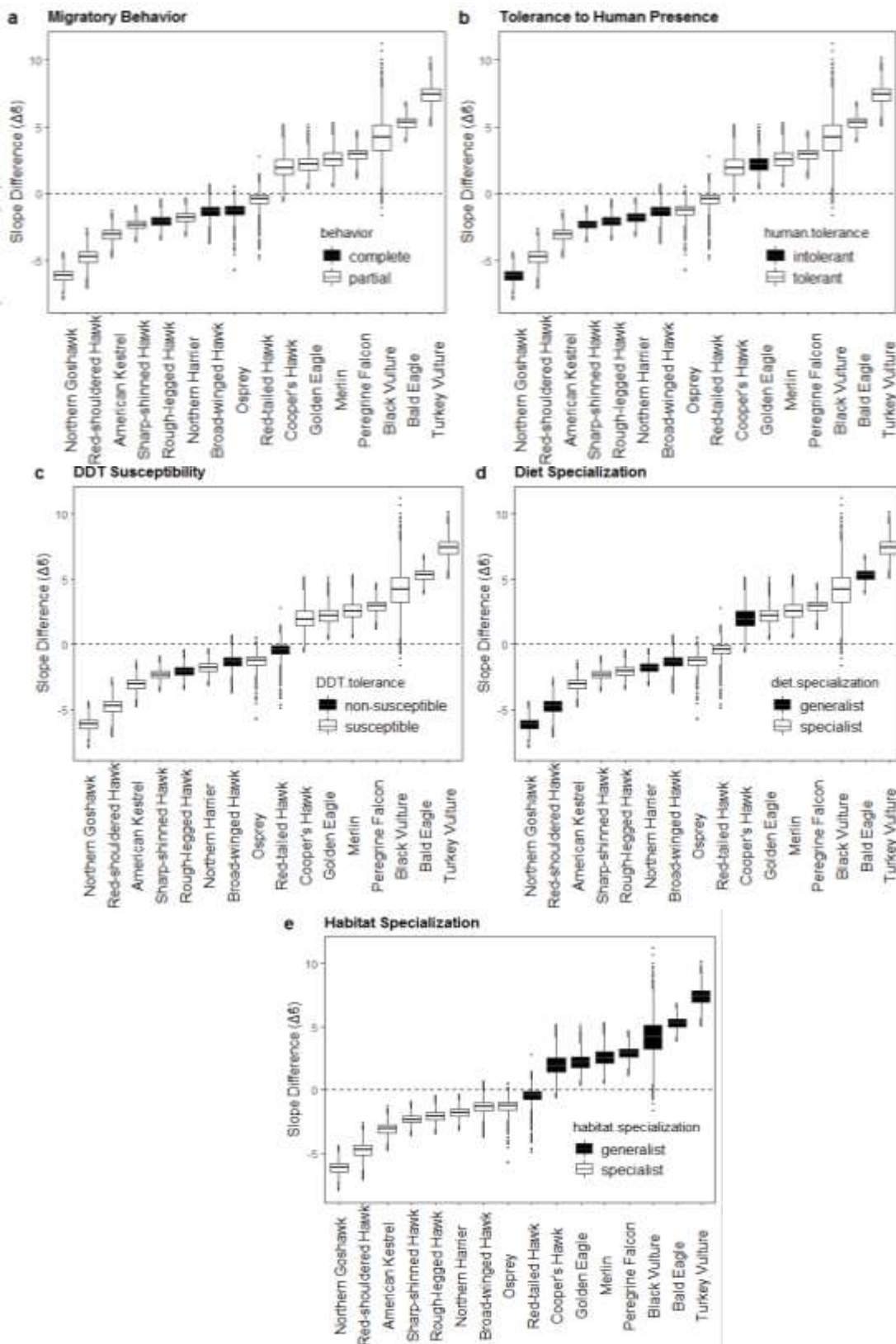




**Fig.1.2. Long-term count trends of species recorded at Hawk Mountain Sanctuary from 1946 to 2018. Bald eagle trends are similar to those of black and turkey vultures, Cooper’s hawk, golden eagle, merlin, and peregrine falcon. American kestrel trends are similar to those of sharp-shinned hawk, northern goshawk, northern harrier, broad-winged, red-tailed, red-shouldered, and rough-legged hawks, and osprey. White lines are mean predicted counts and each grey line is one of the 6000 draws of the posterior distribution of parameters, accounting for both sampling and parameter uncertainty. Dashed vertical line indicates mean breakpoint year and the vertical shaded region indicates 95% credible interval for the estimate of the breakpoint year.**



**Fig.1.3.** Mean difference between modeled estimates of pre- and post-breakpoint slopes for all species recorded at Hawk Mountain Sanctuary, Pennsylvania. Species are sorted based on a) allometry (body mass), and b) demography (population size). For explanation of box plots see Fig. 1.1.



**Fig.1.4.** Mean difference between the estimates of the pre- and post-breakpoint slopes for all species recorded at Hawk Mountain Sanctuary, Pennsylvania. Species are sorted based on a) migratory behavior, b) tolerance to human presence, c) DDT susceptibility, d) diet specialization, and e) habitat specialization. For explanation of box plots see Fig. 1.1.

CHAPTER TWO: LINKING LAND-USE CHANGES TO LONG-TERM TRENDS IN  
COUNTS OF MIGRATING RAPTORS IN NORTHEASTERN USA

**Abstract**

Land-use and land cover changes (LULC) may drive shifts in biodiversity patterns. Thus, it is important to evaluate the responses of wildlife populations to land-use transitions that may result in habitat alteration. I obtained long-term datasets on the observed abundance of migrating raptors at Hawk Mountain Sanctuary (HMS), Pennsylvania collected annually, and the proportional cover of major land-uses in the northeastern US collected at five-year intervals. Then, I applied a generalized linear mixed-effects model to evaluate the relationships between these two processes. Specifically, I assessed the effects of the changes in the total proportional cover of forested and urban area for the states of Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, and Vermont on raptor counts at HMS. Total raptor counts were not significantly influenced by the amount of area of either forest or urban cover, but species-specific responses were significant and highly variable. Counts of northern goshawk, American kestrel, rough-legged hawk, sharp-shinned hawk, and red-tailed hawk were positively associated with forest cover. On the other hand, turkey and black vultures, bald eagle, and peregrine falcon were positively associated with urban cover. Moreover, red-shouldered hawk, broad-winged hawk, and northern harrier were not significantly associated with forest cover but were negatively associated with urban cover. Merlin and Cooper's hawk exhibited similar non-

significant associations with forest but exhibited positively associations with urban cover. Finally, golden eagle and osprey were not significantly associated with either land-use variable. Because migrating raptors are particularly vulnerable to land-use changes occurring in their breeding, stopover, and overwintering sites, evaluating their responses is important to understand their relationships with their environment. By assessing species' responses to land-use changes, we can make better predictions of their population trajectories in future landscape scenarios.

### **Introduction**

Shifts in land-use and land cover (LULC) patterns are common factors associated with biodiversity loss and change (Sala et al., 2000). Species extinctions due to loss of suitable habitats often result in impairments of ecosystem functions (Aronson et al., 2014). With the present rate at which extinctions are occurring, there is a strong incentive among ecologists to understand how species respond to anthropogenic stressors, and to use this information to address contemporary conservation issues (Lindenmayer et al., 2007).

The landscape in the northeastern United States (US) has been altered by anthropogenic activities. Until the 1650s, the region was largely forested. However, with the implementation of intensive logging and agricultural clearing, it became predominantly open fields (Donahue, 2007). Forest cover reached its lowest around the end of the 19<sup>th</sup> century, at which point agricultural expansion moved towards the western US and industrialization spread in the eastern US. Since then, farmlands have been abandoned, urban areas have sprawled, and previously open areas have naturally reforested (Irland, 1999). However, current landscapes appear to have reached a peak of

reforestation, and land conversions for urban development now appear to be outpacing forest growth (Drummond and Loveland, 2010).

Land-use changes such as agricultural expansion and urbanization can alter ecosystem dynamics (Margules and Pressey, 2000). Specifically, transitions in land-use patterns alter distributions of some species (Evans et al., 2011). This occurs because the novel environments created by habitat change may be unsuitable for some species but beneficial for others (Melles et al., 2003). Thus, in contemporary landscapes that are often heterogeneous in nature, species that possess traits associated with adaptability to a broad range of environmental conditions often succeed (Le Bagousse-Pinguet et al., 2017; Bonier et al., 2007).

Raptors are good indicators of change in environmental conditions because of their wide spatial distribution and role in ecosystem function (Bildstein, 2006; Newton, 1979). Declines of some raptor populations have been associated with land-use transformations that reduce foraging habitats, abundance of prey items, and availability of suitable nest sites (Buij et al., 2013; Tapia et al., 2017). However, there are raptors that have successfully adapted to novel conditions brought about by land-use changes. For example, some species respond positively to urbanization by utilizing human-made infrastructure and exploiting novel food resources such as roadkill (Curtis and Rosenfield, 2006, Millsap et al., 2004). Similarly, agricultural and managed lands benefit some species, as these areas create new types of foraging and breeding habitats (Cardador et al., 2011).

Here, I explored the potential links between the changes in land-use patterns in the northeastern US (Connecticut, Maine, Massachusetts, New Hampshire, New Jersey,

New York, Pennsylvania, Rhode Island, Vermont) documented at five-year intervals since 1945 and the observed abundance of migrating raptors at Hawk Mountain Sanctuary (HMS), Pennsylvania over that same time period. Specifically, I assessed the relationships of the total proportional cover of forest and urban areas in aforementioned states with count data. This information will be useful for conservation planning along known migration routes and breeding grounds for North American raptors utilizing the Atlantic Flyway.

## **Methods**

### Study site

In the eastern US, about 500 bird species use the Atlantic Flyway, stretching from eastern Canadian provinces to southern states (Audubon, 2018). Several hawk watch sites monitor the passage of avian migrants along this flyway. Each autumn, large numbers of outbound migrating raptors that breed in southeastern Canada and in some states in the northeastern USA concentrate at HMS because of its orography (Bildstein, 2006). Since 1934, raptor migration monitoring has been conducted annually at the same location at HMS.

### Data Sources

#### Raptor migration count data

Migration count data are annually collected at HMS by trained staff and volunteer counters using systematic techniques described elsewhere (Barber et al., 2001). I used 72 years of autumn hawk count data collected from 1946-2018 at HMS. I included counts for 16 commonly observed species: black vulture (*Coragyps atratus*), turkey vulture (*Cathartes aura*), osprey (*Pandion haliaeetus*), golden eagle (*Aquila chrysaetos*), northern harrier

(*Circus cyaneus*), sharp-shinned hawk (*Accipiter striatus*), Cooper's hawk (*A. cooperii*), northern goshawk (*A. gentilis*), red-shouldered hawk (*Buteo lineatus*), broad-winged hawk (*B. platypterus*), red-tailed hawk (*B. jamaicensis*), rough-legged hawk (*B. lagopus*), bald eagle (*Haliaeetus leucocephalus*), American kestrel (*Falco sparverius*), merlin (*F. columbarius*), and peregrine falcon (*F. peregrinus*).

#### Land-use variables

I selected data on land-use variables that I expected were important to the observed abundance of migrating raptors and that were suitable metrics of forest availability, agricultural expansion and urbanization. I limited the spatial scale of these land-use variables to the states of Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, and Vermont, as data for these states are readily accessible and all are part of the Atlantic Flyway. Estimates of forested, agricultural, and urban area for each state were obtained from the Major Land Use (MLU) reports prepared by the United States Department of Agriculture Economic Research Service and its predecessor agencies (USDA-ERS; Reuss et al., 1948; Wooten, 1953; Frey, 1973; Daugherty, 1992; Lubowski et al., 2006; Bigelow and Borchers, 2017). These have been published at 5-year intervals since 1945. The dataset included six categories of land-use: 1) cropland, 2) grassland, pasture and range, 3) forested area, 4) special uses, 5) urban area, and 6) other uses. I combined the estimates for cropland with grassland, and pasture and range into a single estimate for agricultural land, because I was interested in assessing the impacts of open areas in general. I retained the classification of other land-use types.



I calculated proportional cover by dividing the total area used for each major land-use type by the total land area for all nine states. Given that the two datasets were collected at different temporal scales (every five years vs every 1 year), I assigned to each year of count data the land-use data reported for the prior five-year period. Then, I assessed multicollinearity among the land-use variables using Pearson's correlation coefficient and I based inference on models with uncorrelated predictors ( $r < 0.5$ ).

### Data Analysis

#### Hierarchical models for species' response to land-use variables

I fitted hierarchical generalized linear models to assess the potential relationship between raptor counts and land-use variables. The hierarchical structure of the models allowed for independent variation in the estimates of slope for each land-use variable, and of intercept for each species (Pollock et al., 2012). The models had the form:

$$Y_{i,j} = NB(\mu_{i,j}, \delta^2) \quad (\text{Eqn. 1})$$

$$\mu_{i,j} = \exp(\alpha + \alpha_{SP}) + \beta_I * \text{year} + (\beta_2 + \alpha_{SP}) * \text{land-use}_{[l]} + \log(K) \quad (\text{Eqn. 2})$$

In equation 1,  $Y_{i,j}$  is the response variable (number of recorded individuals) for the  $i$ th species at year  $j$ , and it follows a negative binomial distribution with a mean ( $\mu$ ) and an overdispersion parameter ( $\delta^2$ ). The base linear model for the counts (Eqn. 2) has an intercept ( $\alpha$ ) that varies for each species ( $\alpha_{SP}$ ), a slope coefficient for year ( $\beta_I$ ), a vector of slope estimates ( $\beta_2$ ) that varies by species ( $\alpha_{SP}$ ) for each land-use variable  $l$ , and an offset term for observation effort ( $K$ ), which was a log-transformation of the number of days when counts were conducted in each year. With this modelling framework, I obtained estimates of the response of each species to changes in each land-use variable.

I created a set of hierarchical models with no correlated variables and conducted model selection using leave-one-out cross validation (package ‘loo’; Vehtari et al., 2019). In all models, year and the offset term (observation effort) were retained. I implemented these models in a Bayesian framework using the ‘rstanarm’ package in R (R Core Team, 2018; Goodrich et al., 2020). I used weakly informed (default) priors for the slope, intercept, and the covariance matrix. The parameter estimates were based on four chains of 5000 iterations, of which 1000 iterations were for a warm-up period. I assessed model convergence and mixing of chains through visual inspection and common diagnostic tools such as  $\hat{R}$  and the effective sample size (Gelman and Rubin, 1992).

I evaluated the different responses of each species to variation in each land-use variable. Because the hierarchical models allowed the intercepts and slopes to vary for each species and land-use variable, respectively, I was able to obtain 4000 posterior samples of each slope estimate for each species. If the 95% credible intervals for those slope estimates did not overlap zero, I interpreted the estimate as a significantly positive or negative response of a species to change in a given land-use variable. I also interpreted the coefficient estimates for the association between species-specific counts with land-use variables as indicative of the magnitude of the association (i.e., a positive or negative response to a given land-use type).

## Results

There were 1,330,325 raptors counted during the autumn migration period at HMS from 1946 to 2018, with approximately 18,500 counted yearly. Preliminary evaluations of the trends in the proportional cover of forest, agricultural, and urban areas suggest that agricultural cover was highly correlated to forest ( $r = -0.76$ ) and urban ( $r = -$

0.88) cover. In general, urban cover increased, and agricultural cover decreased linearly over time (Fig. B1). On the other hand, forest cover increased until the 1970s and since then, it has stabilized at around 60% proportional cover.

Among all models developed, those that performed best had main predictors for year, forested, and urban area (Table 2.1). Of the remaining three models, that with urban cover had the best predictive performance, and the model with forest cover had the worst predictive performance.

#### Association between raptor counts and land-use variables

The mean effect of year ( $\beta_{\text{year}} = 0.1 [-0.2, 0.3]$ ), forest ( $\beta_{\text{forest}} = -1.4 [-9.9, 7.1]$ ), and urban ( $\beta_{\text{urban}} = 2.5 [-8.4, 13.6]$ ) cover on overall total raptor counts were not significant. However, species-specific responses to change in land-use were highly variable and often significant. Of the 16 species evaluated, five (northern goshawk, American kestrel, rough-legged hawk, sharp-shinned hawk, and red-tailed hawk) were positively associated with the forest cover and negatively associated with urban cover (Fig. 2.1). In contrast, four species (turkey vulture, black vulture, bald eagle, and peregrine falcon) were negatively associated with forest cover but positively associated with urban cover (Fig. 2.2). Finally, seven species had non-significant responses to forest cover (Fig. 2.3). Of these, two (merlin, Cooper's hawk) had significant positive responses to urban cover, three (red-shouldered hawk, broad-winged hawk, and northern harrier) had significant negative responses to urban cover, and the remaining two (golden eagle, osprey) showed no response to either variable.

Among the species that were positively associated with forest cover, northern goshawk exhibited the strongest positive response. This species also exhibited the

greatest negative response to urban cover. On the other hand, among the species that were negatively associated with forest cover, turkey vulture exhibited the strongest response. Moreover, this species also exhibited the greatest positive response to urban cover. Finally, among species that had non-significant responses to forest cover but were significantly influenced by urban cover, merlin exhibited the greatest positive response, and broad-winged hawk the greatest negative response.

### **Discussion**

The effects of anthropogenic activities such as land-use changes are often accompanied by changes in the abundances of wildlife species. Here, I showed the utility of long-term data in assessing the effects of large-scale disturbances on a suite of raptor species in a broad geographical area. I found that species-specific counts, but not total counts of all species, were associated with forest and urban cover.

Most raptor populations monitored at HMS breed in the northeastern US and eastern Canada and overwinter as far south as South America (Ferguson-Lees and Christie, 2001). Similar to northeastern US landscapes, land-use patterns in Canada and South America also have undergone recent transitions. In Ontario, there have been steep declines in the amount of area utilized for agriculture since the late 20<sup>th</sup> century (Smith, 2015). However, since the 1930s, many agricultural landscapes have been converted to urban uses (Muller and Middleton, 1994). In other parts of Canada, especially eastern provinces and the Maritimes, the rate of logging activity substantially increased in the 20<sup>th</sup> century (Smith, 2000). Similarly, deforestation is prominently occurring in South America, where several species of migrating raptors overwinter. Many forest stands in that region are being converted to pasture lands and other forms of agricultural land-use

types (de Sy et al., 2015). It is therefore possible that urban development and loss of old-growth forests in both breeding and overwintering habitats may be influencing population dynamics of migrating species that depend on them. Thus, examining the associations between land-use changes occurring both at a broader spatial scale, or specifically in regions where migrants nest and where they overwinter, may be useful in understanding the spatial correlates of raptor migration count data.

I detected different effects of reforestation in the northeastern USA on raptor species counted at HMS. Counts of sharp-shinned hawk and northern goshawk responded positively to increasing forest cover in the region. However, there is growing evidence that population and site-specific trends for both species are negative (Brandes et al., 2016, Crewe et al., 2016). These contradictory patterns may be explained by the ecological difference between shifts in forest structure versus shifts in forest cover. In fact, old-growth forest and mixed-age stands in the region have, in many cases, been replaced by predominantly younger and regenerating stands. Additionally, in eastern Canada, mixed and deciduous forests have replaced coniferous forests (Boucher et al., 2009). Future analyses that incorporate forest structure or age may provide additional insight into the details of how landscape change influences these forest-dependent species.

Similarly, the effects of land conversions for urban development may vary among species. Counts of open country species like the American kestrel and rough-legged hawk declined with increasing forest cover, and these species appear to have declining population trends (Brandes et al., 2016, Crewe et al., 2016). In this case, the conversion of pastures to urban areas and the reforestation of abandoned farmlands may be associated with the declining trends in their counts at HMS. In fact, farmlands in the

northeastern US have either been largely reforested or developed, reducing the availability of favorable foraging and stopover locations for these species (Farmer and Smith, 2009).

Counts of synanthropic species that are generally adaptable to habitat changes, such as turkey and black vultures, bald eagle and peregrine falcon, are positively correlated to change in urban cover. Populations of these species are generally stable or increasing in the Appalachian Mountains and the eastern Breeding Bird Survey (BBS) region (Sauer and Link, 2011). Potentially, the ability of these species to adapt to heterogeneous environments in urban areas and their lack of dependence on forests contributed to their success in modern landscapes. Both species of vultures and the bald eagle are scavengers. For these species, urbanization may have been advantageous in part because it led to increased availability of food resources (Millsap et al., 2004; Novaes and Cintra, 2015). Increased availability of nesting structures such as buildings and avian prey items may have also been beneficial for the peregrine falcon (Kettel et al., 2019).

For several other species, the impacts of the shifts in forest cover seem less important than the continued increase in urban cover. Red-shouldered hawk, broad-winged hawk, and northern harrier all responded negatively to urban cover. This might suggest that land conversions for urban development may be a bigger threat to these species than the loss of old-growth forests. This may be because converting lands into developed areas often results in a perpetual loss of the forested habitat as development limits the regrowth of vegetation in areas with permanent structures (Meyer and Turner, 1992). In contrast, agricultural land-use may allow secondary succession to occur (Marks, 1983; Wright and Fridley, 2010).

A confounding factor in our analysis is that changes in behavior may influence count data. For example, it is counterintuitive that counts of red-tailed hawk exhibit negative responses to urban cover, given what we know about the species' biology. This is a generalist species that often nests in urban areas, and there is also evidence that the breeding status of this species is stable or increasing in the region (Sauer and Link, 2011). Count data do not show such a pattern. An explanation for this pattern could be that, although indices of their population trends are increasing, red-tailed hawk populations have changed their migratory behavior. In this scenario, if more individuals choose to overwinter in food-rich urban areas where they breed, counts at hawk watch sites may reflect downward trends despite increasing populations overall (Paprocki et al., 2017).

### **Conclusions**

Changes in the population dynamics of wildlife are often driven by a suite of interacting factors such as land-use change. In fact, the availability of suitable habitat can be associated with shifts in the population trends of several species. Thus, it is important to understand the consequence of environmental changes that alter the structure of habitats that species utilize. Moreover, in the case of migratory species, there is relevance to assessing the effects of land-use changes occurring at broad spatial scales.

During migration, raptor species are exposed to a suite of anthropogenic threats that may adversely impact their survival and consequently, their population dynamics. With these implications, an understanding of the relationships between their observed abundance and changes in land-use patterns is important. By examining their responses to anthropogenic threats, we can gain insights on the causal processes driving their trends.

Using this information, we can improve our predictions of their population trajectories under future landscape scenarios.

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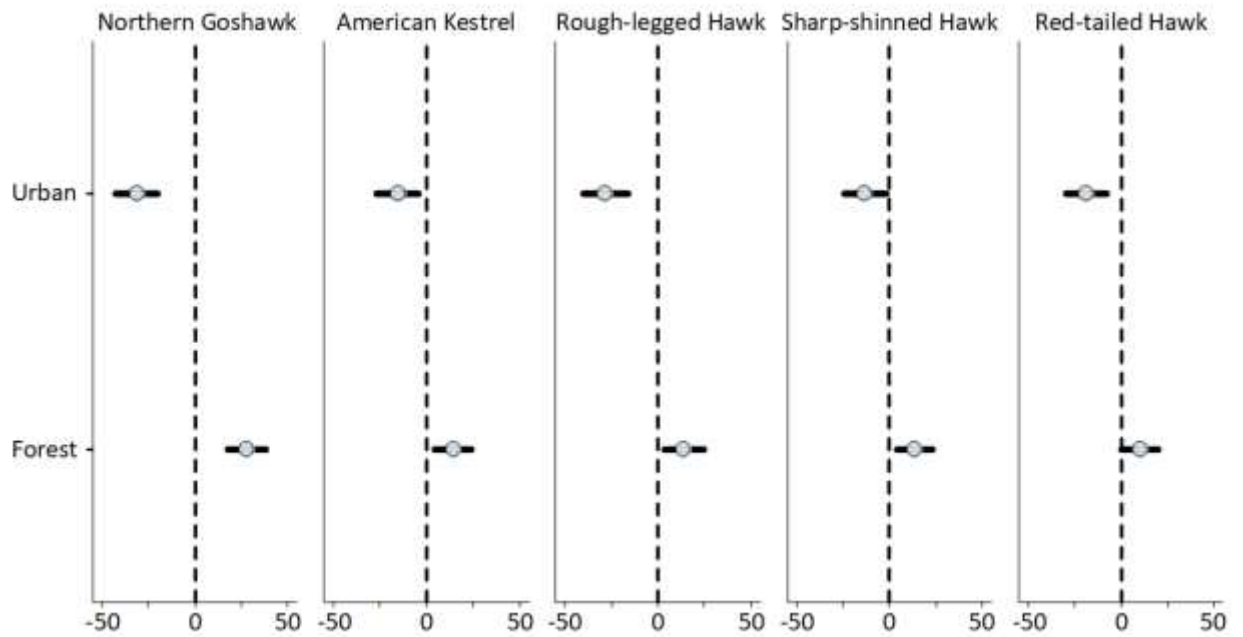
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## Tables

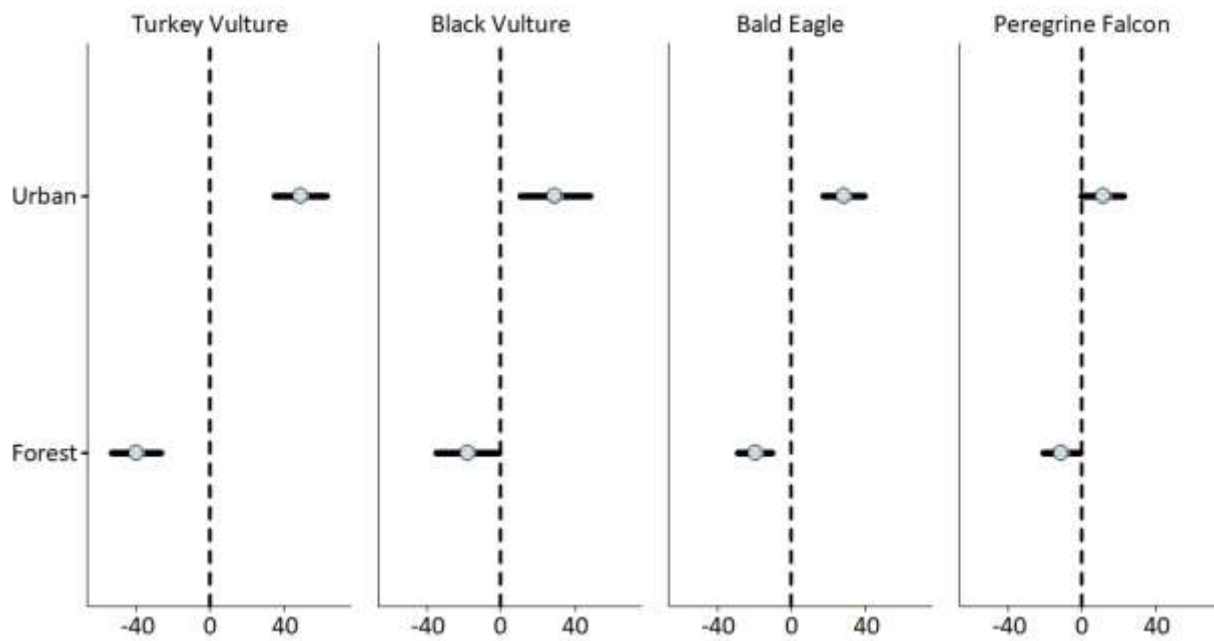
**Table 2.1. Models to evaluate associations between raptor counts at Hawk Mountain Sanctuary (Pennsylvania, USA) from 1946 to 2018 and the total proportional cover of major land-use types in northeastern USA.**

Model	LOOIC $\pm$ SE
$\text{count} \sim \beta_{\text{year}} + \beta_{\text{forest, species}} + \beta_{\text{urban, species}} + \log(\text{H})$	13509.4 $\pm$ 135.3
$\text{count} \sim \beta_{\text{year}} + \beta_{\text{urban, species}} + \log(\text{H})$	13833.4 $\pm$ 135.1
$\text{count} \sim \beta_{\text{year}} + \beta_{\text{agricultural, species}} + \log(\text{H})$	13956.7 $\pm$ 133.8
$\text{count} \sim \beta_{\text{year}} + \beta_{\text{forest, species}} + \log(\text{H})$	13994.5 $\pm$ 131.2

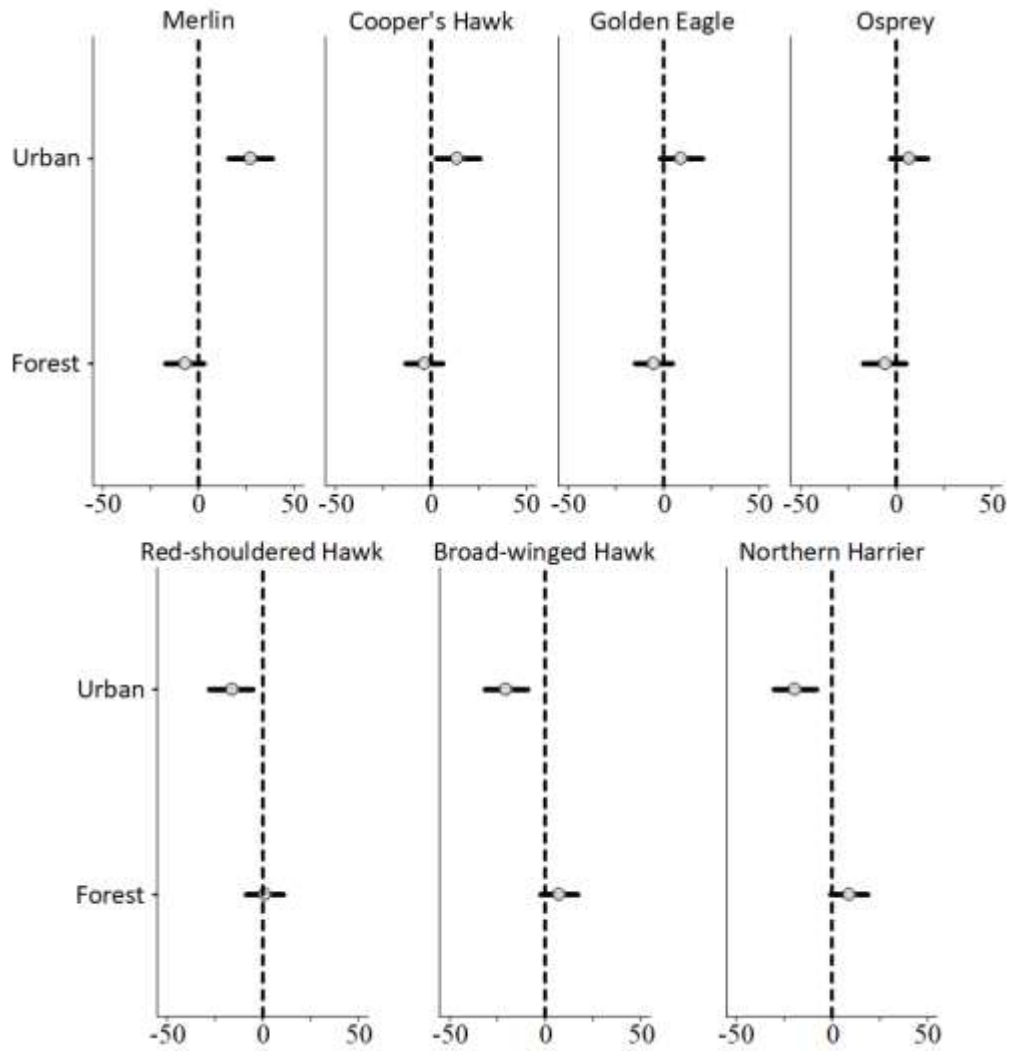
## Figures



**Fig. 2.1.** Coefficient estimates of a suite of raptor species with similar positive responses to forested and negative responses to urban land cover in northeastern USA. Light blue dots indicate mean slope estimates and dark blue lines account for 95% Credible Intervals of the estimates. All estimates are drawn from a global distribution of slope estimates for each land-use variable.



**Fig. 2.2.** Coefficient estimates of a suite of raptor species with similar positive responses to urban and negative responses to forested area in northeastern USA. For explanation of coefficient plots, see Fig.2.1.



**Fig. 2.3.** Coefficient estimates of a suite of raptor species with similar non-significant responses to forested and variable responses to urban area. Two species exhibited positive and two exhibited non-significant responses to urban area (top panel). Other species exhibited negative response to urban cover. For explanation of coefficient plots, see Fig.2.1.



## APPENDIX A

**Supplementary Methods**

### Classification of species based on functional traits

I used the following methodology to classify species based on functional traits. First, I conducted a literature review to gather information on functional characteristics of the 16 species in the assemblage. From this review, I created a classification framework by which each species was assigned into a functional trait type (Table A.1). Then, I obtained expert input by sending the actual scores for each species (Table 1.1) to a team of early-career raptor biologists and tenured experts in the field (hereafter referred to as “reviewers”) and sought their opinion on the accuracy of the assignment of each species to each trait type. In cases where the assignment of the species to a trait type did not receive a unanimous approval from the reviewers, I assigned species to a category based on the opinion of the majority.

I used data on migration from Bildstein (2006) to describe migratory behavior. I described species as tolerant if their nesting structures are located in urban/suburban areas and farmlands, and intolerant if located in forests/forest edges or open grass/shrublands. I described species as susceptible if at least one published case on its DDT-linked decline was reported (e.g., agency report, journal article), and non-susceptible if none was found. In sorting species based on their diet specialization, I used scores provided by Sherrod (1978) to describe species with a diet diversity index  $> 1$  as generalists and those with index values  $< 1$  as specialists. Finally, I described species as habitat generalists if their breeding sites are in homogeneous environments or if terrestrial vegetation types they occupied are similar and contiguous (e.g., occupies open to semi-open areas or mixed forests), and specialist, if otherwise (e.g., occupies a mix of forest edge, urban, and/or coastal areas).

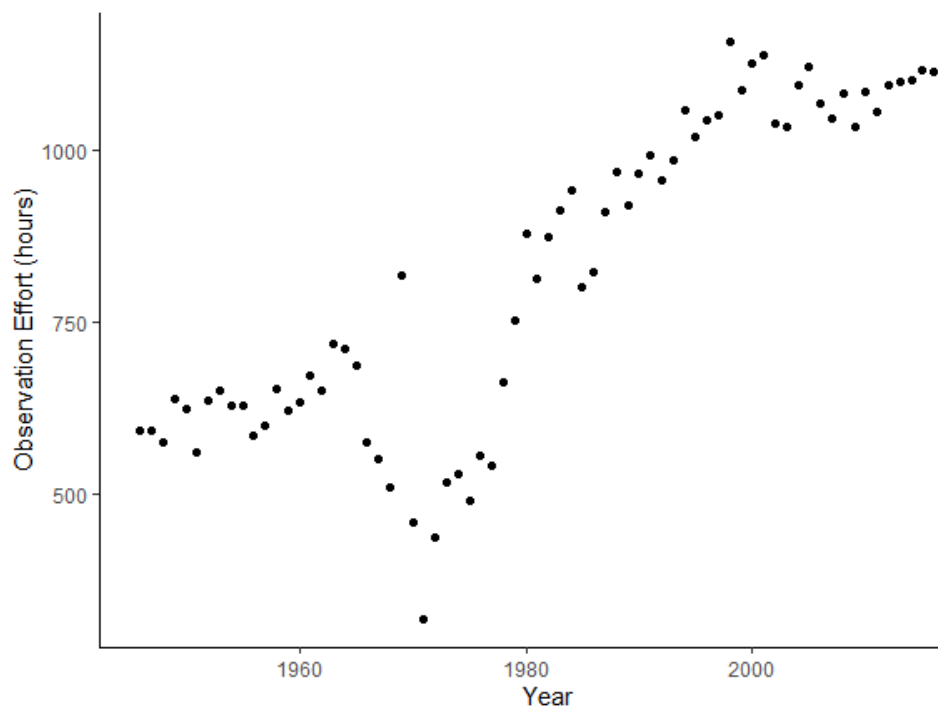
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**Table A.1. Matrix for classification of species based on functional traits. For each functional trait, I provide the two binary categories that were assigned to each species, a description for each trait type, and references from which information was derived.**

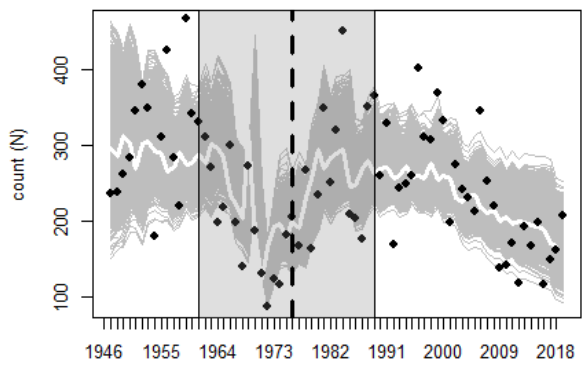
<b>Functional trait</b>	<b>Trait type</b>	<b>Score</b>	<b>Description</b>	<b>Reference</b>	
Migratory behavior	complete	1	> 90% of individuals in the population annually migrate	Bildstein, 2006	
	partial	0	< 90% of individuals in the population annually migrate		
Tolerance to human presence	tolerant	1	nesting structures in human-perturbed landscapes	Rodewald, 2015	
	intolerant	0	nesting structures away from human-perturbed landscapes		
Known DDT susceptibility	susceptible	1	with > 1 reported cases of DDT-associated reproductive impairment	Porter and Wiemeyer, 1969; Henny and Wight, 1972; Joiris and Delbeke, 1985; Risebrough and Peakall, 1988	
	non-susceptible	0	with no reported cases of cases of DDT-associated reproductive impairment		
Diet specialization	generalist	1	high species diversity of prey items	Sherrod, 1978; Therrien et al., 2017	
	specialist	0	low species diversity of prey items		
Habitat specialization	generalist	1	occupies homogeneous environment during breeding season	Rodewald, 2015	
	specialist	0	occupies heterogeneous environment during breeding season		

## Supplementary Figures

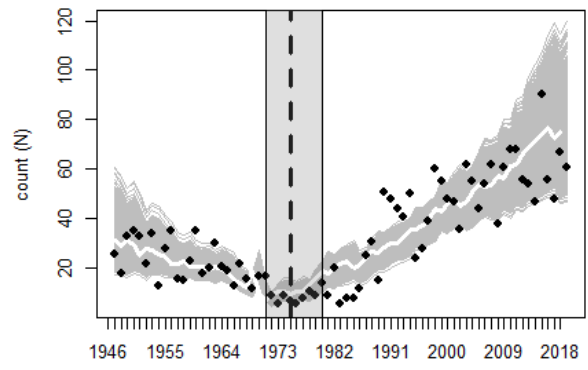


**Fig. A.1.** Observation effort (in hours) during annual raptor migration monitoring at Hawk Mountain Sanctuary, PA from 1946 to 2018.

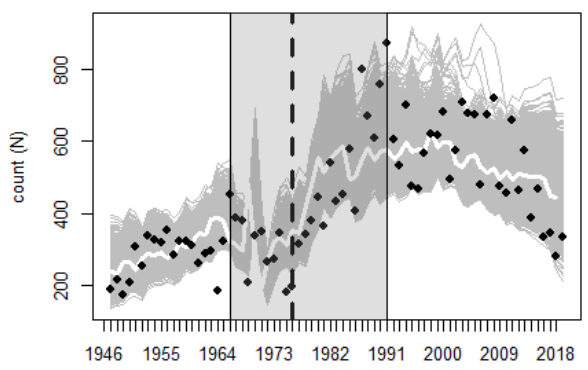
**red-shouldered hawk**



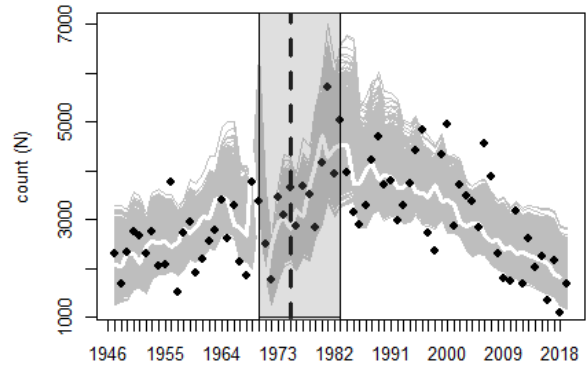
**peregrine falcon**



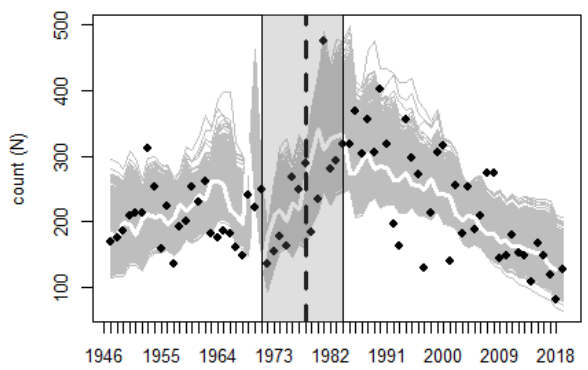
**osprey**



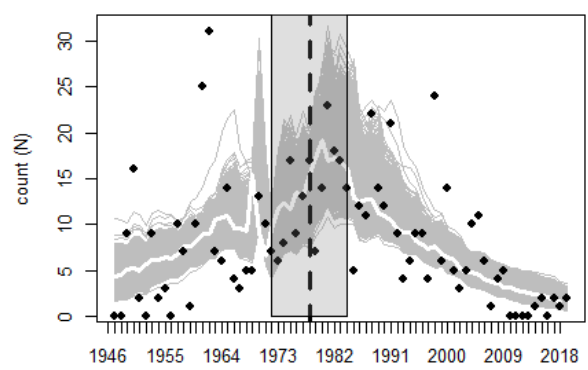
**red-tailed hawk**

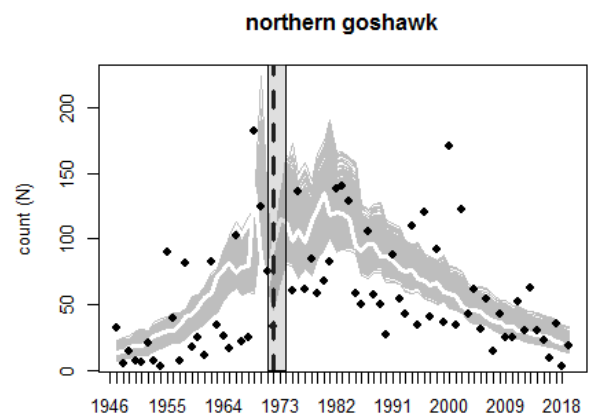
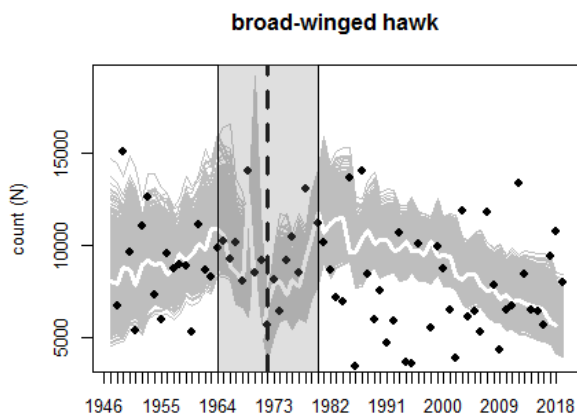
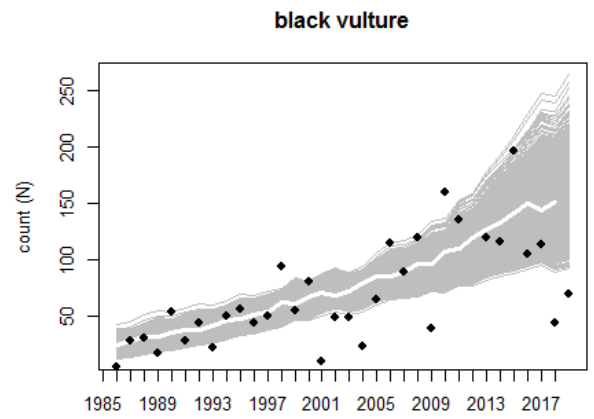
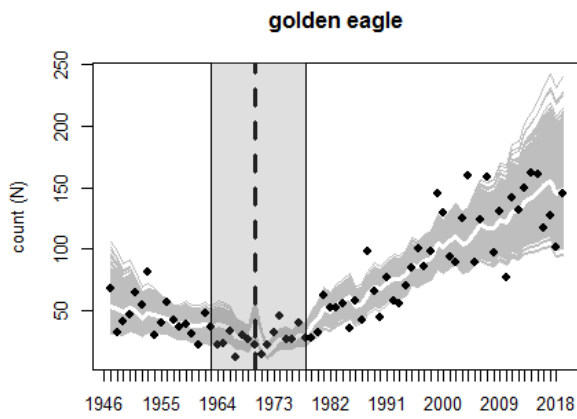
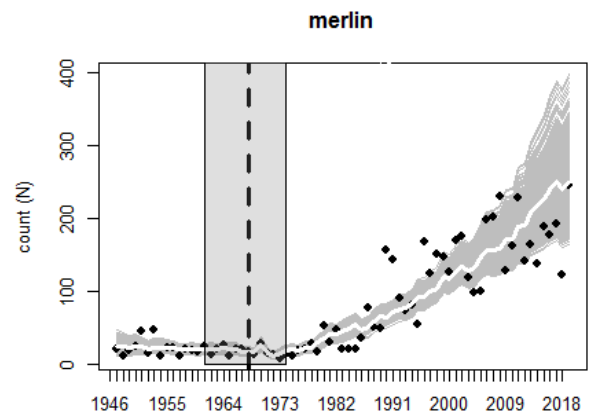
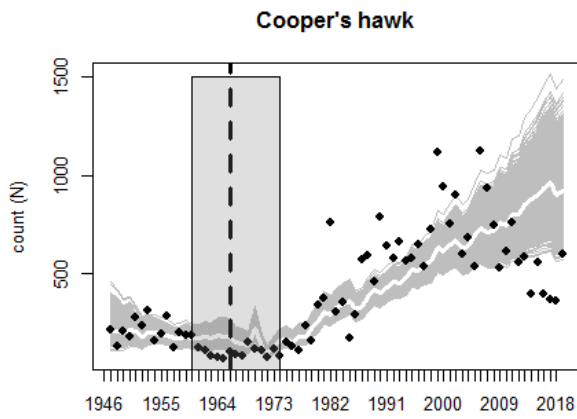


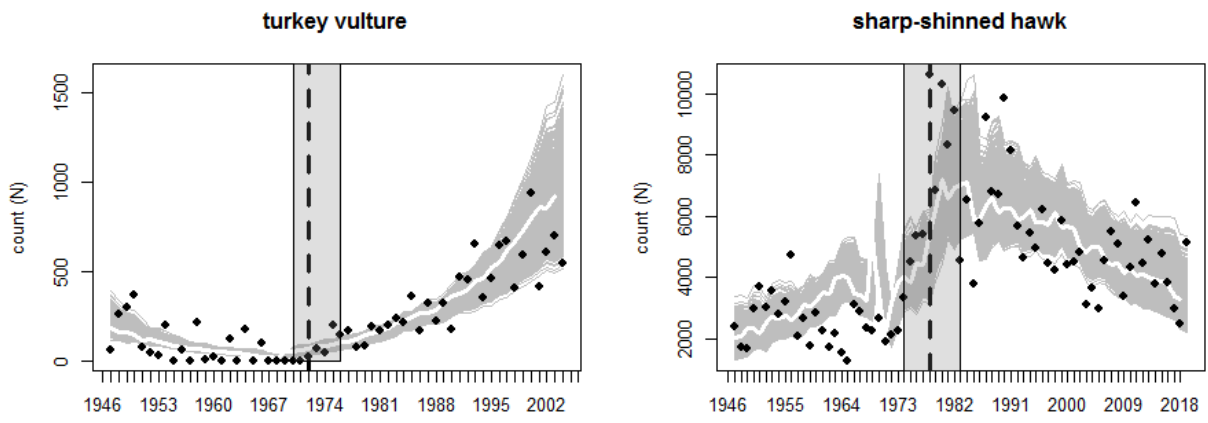
**northern harrier**



**rough-legged hawk**





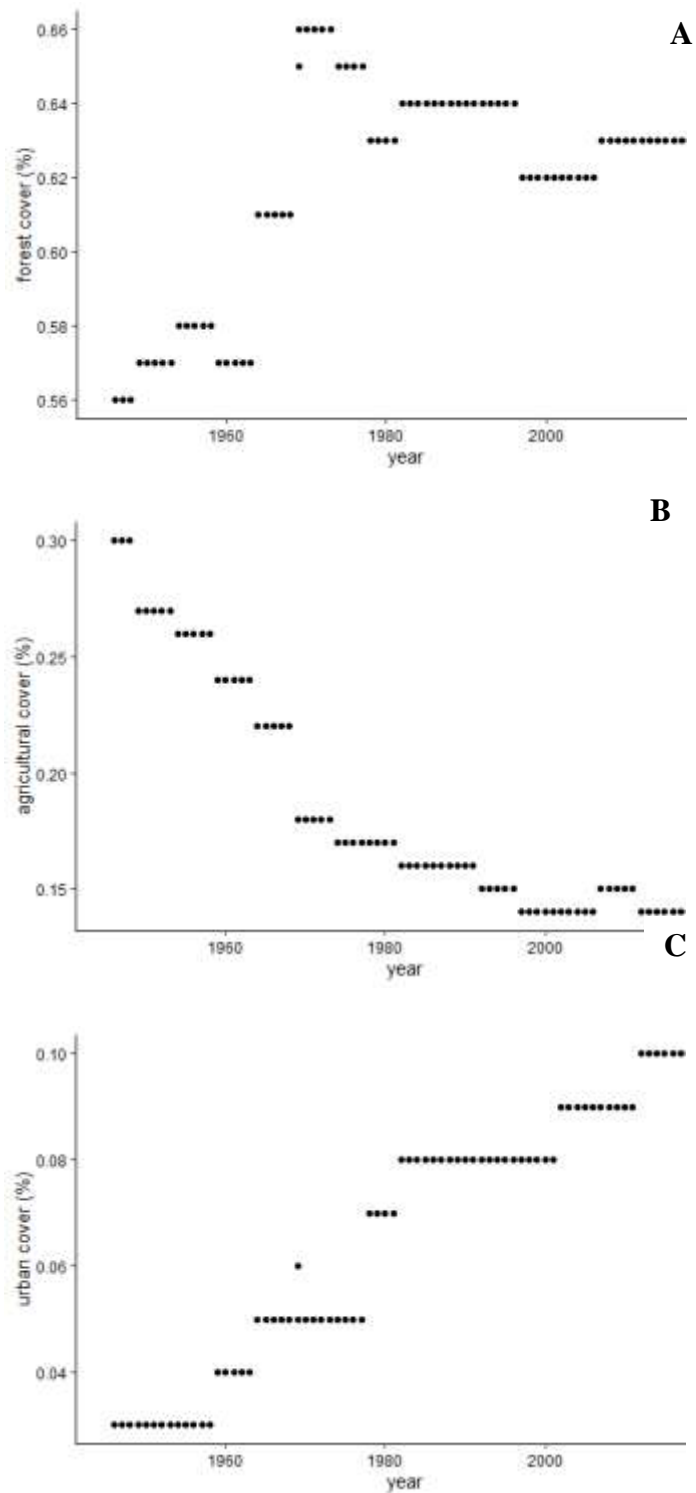


**Fig. A.2.** Long-term trends in counts of individual species recorded at Hawk Mountain Sanctuary from 1946 to 2018. White lines are mean predicted counts and each grey line is one of the 6000 draws of the posterior distribution of parameters, accounting for both sampling and parameter uncertainty. Dashed vertical line indicates mean breakpoint year and the vertical shaded region indicates 95% credible interval for the estimate of the breakpoint year.



## APPENDIX B

**Supplementary Figures**



**Fig. B.1.** Long-term trends of the total proportional cover of a) forested, b) agricultural, and c) urban areas in nine northeastern US states from 1946 to 2018.