

# Shared functional traits explain synchronous changes in long-term count trends of migratory raptors

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Editor: Catherine Sheard

## Abstract

**Aim:** 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 count trends among species. Our research identified traits influencing trends in 73 years of count data on migrating raptors recorded in the north-eastern USA.

**Location:** Pennsylvania, USA.

**Time period:** 1946–2018.

**Major taxa studied:** Birds of prey/raptors.

**Methods:** Migrating raptors were counted during autumn, following a standardized protocol. We used a hierarchical breakpoint model to identify when count trends shifted and to assess the role of traits in driving these trends before and after the breakpoint. Specifically, we quantified the probability of the direction (PD) of an effect of body mass, habitat or dietary specialization, migratory behaviour and susceptibility to dichlorodiphenyltrichloroethane (DDT) on count trends.

**Results:** We documented an assemblage-wide mean shift in count trends of migrating raptors in 1974. In general, species that exhibited negative count trends before the breakpoint exhibited positive count trends afterwards. We found that traits associated with resource use (diet and habitat specialization) had high probabilities of affecting count trends, pre- and post-breakpoint (> 90%). Moreover, the direction of their effects differed during both periods. Unexpectedly, other traits we evaluated, including DDT susceptibility, had relatively weaker associations with count trends.

**Main conclusions:** Trait-based frameworks have promise for testing generalized assumptions about drivers of population trajectories. Historically, DDT was considered a key driver of changes in raptor population trends. However, our analysis suggests that other factors were also relevant. Moreover, the positive association between count trends and generalist behaviour depended on the temporal context. This result has implications for other settings where demographic trends can be linked to traits and help to identify drivers of biodiversity change.

## KEYWORDS

breakpoint model, global environmental change, north-eastern USA, species assemblages, traits

## 1 | 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 assemblage-wide time series data can provide 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 to identify drivers of variations in assemblages.

Changes in species assemblages can be driven by species-specific responses to disturbance, environmental conditions and biotic interactions. Often, these species-specific responses are determined by functional traits (Moullot et al., 2013). When environmental perturbations adversely impact populations of species possessing certain traits, they provide evidence of the role of interspecific trait variation in shaping the community response to a disturbance (Haddad et al., 2008). Thus, trait-based approaches are increasingly being used to obtain a predictive understanding of ecosystem dynamics (McGill et al., 2006). However, despite the surge in ecological research focused on trait-based ecology, there are few empirical studies that explore the associations between traits and population trends over long time periods.

Long-term count data on wildlife populations are central to efforts to understand changes in ecosystem dynamics. This is because assessment of the indices of population trends of multiple species can allow for the identification of ecological patterns and hypothesis testing on the general mechanisms underlying population-level variations (Nagy et al., 2017). 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., 2018). Long-term monitoring surveys for birds were also key in identifying widespread population declines of North American avifauna (Rosenberg et al., 2019). Furthermore, some long-term data sets, such as those on raptor migration, have been used to detect organochlorine contamination and help to inform management decisions for affected species (Bednarz et al., 1990).

Raptors are top predators that strongly influence the population dynamics of a broad range of species in terrestrial communities, sometimes even limiting the numbers of their prey items (Terraube & Bretagnolle, 2018). Moreover, migrating raptors are sensitive to disturbances in their breeding, stopover and overwintering sites (Bildstein, 2006). Thus, because of their ecological roles and sensitivity to anthropogenic threats, raptors are good candidates for assessing the ecosystem-level impacts of environmental change over large spatial scales (Bildstein, 2006).

Here, we assessed the temporal patterns of species-specific trends in counts and the association between species traits and trends 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 programme, with records of autumn flights from 1934 to the present day (Bildstein, 2006). Species that are regularly counted on this site include northern breeders, such as the peregrine falcon

and osprey, from Greenland and extreme northern Québec, and the turkey vulture, Cooper's hawk and red-shouldered hawk, which breed > 2,500 km to the south in the mid-Atlantic states (Bildstein, 2006). Thus, count data collected at HMS are reflective of the trends of species occurring at a large spatial scale.

As is the case for raptor populations worldwide, trends in species monitored at HMS have fluctuated substantially, some so much that they have been helpful in identifying global conservation problems [e.g., dichlorodiphenyltrichloroethane (DDT) was identified as a problem in part because of trends in counts of bald eagles at HMS; Bildstein, 2006]. Here, we used a hierarchical breakpoint model to identify the timing of directional changes in assemblage-wide and species-specific raptor count trends and to assess the role of species traits in driving changes in these trends. Earlier research has suggested the presence of a response in count trends to the banning, within the USA, of DDT, an agricultural pesticide thought to be the primary factor adversely influencing populations of several bird species, including raptors (Ratcliffe, 1970). We then quantified the probability of the direction (PD) of the effect of various species traits on raptor count trends. This allowed us to evaluate whether species characteristics, such as body mass, dietary or habitat specialization, migratory behaviour and DDT susceptibility, were linked to variation in changes in count trends. This approach allowed us to identify ecological factors that might be driving count trends of migrating raptors during a period of increasing natural and anthropogenic change.

## 2 | METHODS

### 2.1 | Study site

The Appalachian Mountains are a major corridor for migrating raptors in North America. This mountain range spans > 4,800 km, from Newfoundland and Quebec in Canada to Alabama in the south-eastern USA (Goodrich & 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 Pennsylvania, 2018). Large numbers of outbound migrating raptors from south-eastern 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 conducted consistently at HMS at a single location. That said, because of the different meteorological and demographic drivers of migratory behaviour, spring counts are low and variable, and autumn counts are generally considered more useful in assessing population trends (Bildstein, 2006).

### 2.2 | 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, we used count data collected annually between 15 August and 15 December over 73 years, from 1946 to 2018, a 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 both vulture species began only in the 1980s. Given that turkey vultures were recorded in substantial numbers in prior years, we have included data for them from the start of the surveys. We focused our analyses on the 16 most commonly recorded species: black vulture, turkey vulture, osprey (*Pandion haliaetus*), golden eagle (*Aquila chrysaetos*), northern harrier (*Circus cyaneus*), sharp-shinned hawk (*Accipiter striatus*), Cooper's hawk (*Accipiter cooperii*), northern goshawk (*Accipiter gentilis*), bald eagle (*Haliaeetus leucocephalus*), red-shouldered hawk (*Buteo lineatus*), broad-winged hawk (*Buteo platypterus*), red-tailed hawk (*Buteo jamaicensis*), rough-legged hawk (*Buteo lagopus*), American kestrel (*Falco sparverius*), merlin (*Falco columbarius*) and peregrine falcon (*Falco peregrinus*). Other species were occasionally recorded at HMS, but too infrequently to be included in the analyses (< 10 per season).

### 2.3 | Species traits

To determine which characteristics of birds might be associated with count trends, we evaluated a suite of traits that are ecologically relevant (Gregory & Gaston, 2000), associated with a species' extinction risk (Julliard et al., 2004), and which are good indices of their exposure to human pressures (Owens & Bennett, 2000). We included three traits that we treated as continuous variables (size, diet and habitat specialization) and two traits we treated as categorical variables (migratory behaviour and DDT susceptibility). For the three continuous variables, we obtained species-specific values for the average body mass of adults (Ferguson-Lees & Christie, 2001), diet diversity index (Therrien et al., 2017) and the number of "level 2" habitat types occupied during the breeding season (*sensu* BirdLife International, 2020). We described species based on their migratory behaviour as either a complete or a partial migrant (Supporting Information Appendix S1, Methods and Table S1). Finally, we described species based on their known susceptibility to DDT as susceptible (i.e., documented reproductive impairment from DDT; sources given in Supporting Information Appendix S1, Table S1) or not susceptible (i.e., no documented reproductive impairment from DDT). Although we would have preferred to describe migratory behaviour and DDT susceptibility as continuous rather than categorical variables, we know of no reasonable continuous metric for these parameters that has been measured for all species.

### 2.4 | Data analysis

#### 2.4.1 | Hierarchical breakpoint model

We 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 nonlinear relationships, including assessments of sudden ecological changes that result from anthropogenic impacts (Roopsind et al., 2018; Toms & Lesperance, 2003). Our breakpoint model is an extension of a generalized linear mixed model (GLMM), with species-level random effects that enable quantification of assemblage-wide patterns from multispecies count data (Brilleman et al., 2017; Ovaskainen et al., 2017). However, our modelling approach goes beyond the GLMM framework by estimating the timing of the breakpoint from the data as a nonlinear function (Equation 2). Explicit estimation of breakpoint timing enables more robust inference about temporal changes, including propagation of uncertainty on when the breakpoint occurred through to other parameters in the model (Beckage et al., 2007). Our model had the following form:

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

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

$$\beta_{1j} = \beta_1 + \sum_{a=1}^5 (T_{aj} * \theta_{1a}) \quad (3)$$

$$\beta_{2j} = \beta_2 + \sum_{a=1}^5 (T_{aj} * \theta_{2a})$$

In Equation 1,  $Y_{ij}$  is the  $i$ th year-specific observation for the  $j$ th species (total number of recorded individuals), which follows a negative binomial distribution with a mean ( $\mu$ ) and an overdispersion parameter ( $\varphi$ ; for justification of the use of negative binomial distribution, see Appendix S1 Methods). We modelled the response variable with the following parameters (Equation 2):  $\beta_{0j}$ , the species-specific intercept (mean count when other parameters are constant);  $\beta_{1j}$ , the species-specific slope before the breakpoint (pre-breakpoint slope);  $X_{ij}$ , the  $i$ th year for species  $j$ ;  $\tau_j$ , the species-specific breakpoint year (the year in which the count trend shifts);  $\beta_{2j}$ , the slope after the breakpoint (post-breakpoint slope); and  $K$ , the offset term used to account for differences among years in total observation days (Hilbe, 2010). The species-specific estimates for the slope before and after the breakpoint were modelled as a function of the global (i.e., assemblage-wide average) estimate of the pre- ( $\beta_1$ ) or post- ( $\beta_2$ ) breakpoint slope and the effect of the species-specific trait  $T_{aj}$  with the parameters  $\theta_{1a}$  and  $\theta_{2a}$ , where  $\theta$  is a vector of five parameter estimates (one for each trait) that was allowed to vary per time period (i.e., before and after the breakpoint; Equation 3). We assessed potential correlations among traits using Pearson's correlation test to ensure that the correlations of these traits were low ( $|r| \leq .7$ ; Dormann et al., 2013; for correlation matrix, see Supporting Information Appendix S1, Table S2).

We allowed the intercept, pre- and post-breakpoint slopes and breakpoint to vary by species because we assumed that different species in the assemblage might have had different initial abundances

and trajectories during both time periods (pre- and post-breakpoint). We also allowed the trait effects to vary temporally, with separate parameters for pre- and post-breakpoint effects, because variation in the traits driving synchronous count trends might be driven by a species' phenotypic plasticity and local adaptation to prevailing environmental conditions (Anderson et al., 2014).

Our modelling framework allows us to estimate simultaneously both count trends over time and the impacts of species traits on these trends. This approach is potentially more robust than indirect functional analyses that rely on post hoc tests. To facilitate interpretation of the effects estimated from our model, we standardized variables by centring each value on the mean and dividing them by two standard deviations (i.e., we standardized the year and trait values; Gelman, 2008). This standardization also enables direct comparisons of the relative effect size of continuous and categorical variables.

#### 2.4.2 | Model implementation and diagnostics

We implemented the model in a Bayesian framework and gave all parameters weakly informative, normally distributed priors with a mean of zero and a variance of 10 (Gelman et al., 2008; McElreath, 2020). We used a separation strategy to decompose the variance-covariance matrix of the random effects. This allowed us to specify priors for the correlation matrix with a Lewandowski-Kurowicka-Joe (LKJ) distribution, and the standard deviation terms for the random effects with a Cauchy-distributed prior, with a location of zero and a scale of 2.5 (Brilleman et al., 2017; Lemoine, 2019).

We based parameter estimates from the breakpoint model on four chains of 2,500 iterations, each with 1,250 iterations used for the warm-up period, resulting in a total of 5,000 posterior draws for each parameter estimate. We assessed model convergence and mixing of chains through visual inspection and by using Gelman and Rubin's (1992) diagnostic ( $\hat{R}$ ; Supporting Information Appendix S1). We performed posterior predictive checks to evaluate deviations of model-generated data from the observed data. After fitting our breakpoint model, we conducted validation exercises to assess the role of phylogenetic relationships and first-order temporal autocorrelation in parameter estimation (for more details on the validation exercises, see Supporting Information Appendix S1). We interfaced to Stan using the "rstan" package to fit our model in R v.3.6.2 (R Core Team, 2019; Stan Development Team, 2019).

#### 2.4.3 | Model interpretation

We report all estimates on their original scale (i.e., years and counts of raptors). We interpreted species-specific estimates of the slopes and the effect of each trait, pre- and post-breakpoint, with the probability of direction (PD). The PD quantifies the probability of a directional effect of the predictor on the response variable (i.e., either positive or negative; Makowski et al., 2019). The PD represents

evidence for an effect (i.e., rejecting the null hypothesis) and can be viewed as the Bayesian counterpart of frequentist  $p$ -values. However, in contrast to  $p$ -values, the PD is directly interpretable as the probability that an effect is positive or negative. Here, we evaluated the probability of observing positive or negative count trends for each species and of observing positive or negative effects of each trait for each of the two time periods.

### 3 | RESULTS

#### 3.1 | Temporal trends of the migratory raptor assemblage

The mean assemblage-wide breakpoint year was 1974 [95% credible interval (CI): 1970, 1979]. For most species, the estimated mean breakpoint year was around the same time period, the exceptions being Cooper's hawk and merlin, which had earlier breakpoints (Table 1). Moreover, the probability (PD) of the assemblage-wide count trend being positive, either before [ $P(\beta_1 \geq 0) = .42$ ] or after [ $P(\beta_2 \geq 0) = .48$ ] the breakpoint, was weak and uncertain. Generally, species that had a high probability of exhibiting positive count trends before the breakpoint had a high probability of exhibiting negative count trends after the breakpoint (Figures 1 and 2; Supporting Information Appendix S1, Tables S3 and S4; Figures S1 and S2). Moreover, we found no evidence for either phylogenetic signal or first-order autocorrelation in our modelled parameters (Figures S3 and S4).

Before the species-specific breakpoints, osprey, red-tailed hawk, sharp-shinned hawk, rough-legged hawk, American kestrel and northern goshawk each had a high probability of exhibiting a positive count trend [ $P(\beta_{1j} \geq 0) \geq .99$ ; Figure 2]. During this same period, broad-winged hawk [ $P(\beta_{1, \text{broad-winged hawk}} \geq 0) = .79$ ] and northern harrier [ $P(\beta_{1, \text{northern harrier}} \geq 0) = .94$ ] each had a lower probability of exhibiting positive count trends. On the contrary, pre-breakpoint count trends for golden eagle, peregrine falcon, bald eagle and black and turkey vultures all had a high probability of being negative [ $P(\beta_{1j} \leq 0) \geq .95$ ]. Merlin [ $P(\beta_{1, \text{merlin}} \leq 0) = .88$ ] and Cooper's hawk [ $P(\beta_{1, \text{Cooper's hawk}} \leq 0) = .87$ ] both had a lower probability of exhibiting negative count trends.

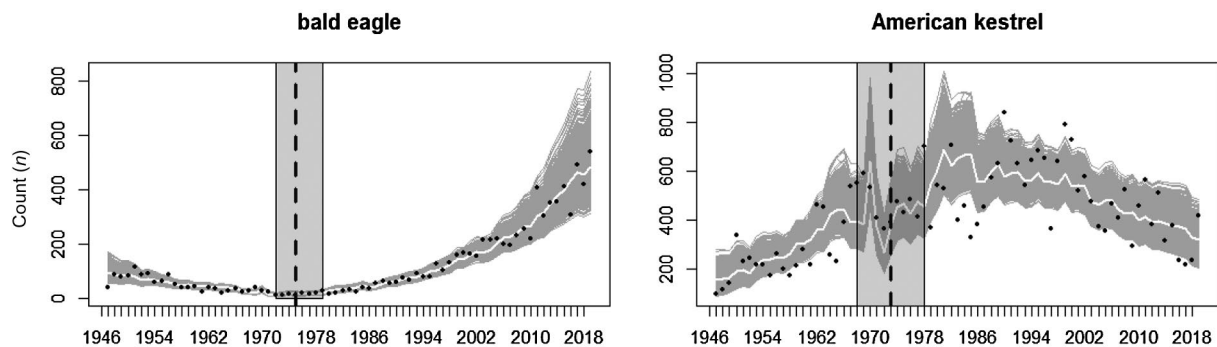
After the breakpoint, all the species with negative trends before the breakpoint had a high probability of exhibiting a positive count trend [ $P(\beta_{2j} \geq 0) \geq .99$ ]. This was true even for the two species, merlin and Cooper's hawk, for which the pre-breakpoint probability of a negative count trend was lower. Likewise, after the breakpoint, count trends had a high probability of being negative [ $P(\beta_{2j} \leq 0) \geq .99$ ] for all the species that had positive count trends before the breakpoint. Again, this was true even for species that had a lower probability of positive count trends before the breakpoint (broad-winged hawk and northern harrier).

The one species whose count trend did not appear to switch signs between the two periods was the red-shouldered hawk. During both periods, this species had a high probability of exhibiting negative

**TABLE 1** Estimated mean breakpoint year in count data, with 95% credible intervals, and traits of 16 species recorded at Hawk Mountain Sanctuary, Pennsylvania.

Species	Breakpoint year [CI]	Average body mass (g)	Dietary diversity	Habitat types	Migratory behaviour	DDT susceptibility
Turkey vulture	1973 [1970, 1976]	1,425	1.48	9	Partial	Susceptible
Black vulture	1975 [1963, 1986]	1,640	1.48	9	Partial	Susceptible
Bald eagle	1975 [1972, 1979]	4,790	1.02	11	Partial	Susceptible
Peregrine falcon	1976 [1972, 1981]	794	0.25	16	Partial	Susceptible
Golden eagle	1972 [1963, 1981]	4,200	0.42	9	Partial	Susceptible
Cooper's hawk	1966 [1960, 1974]	452	1.05	4	Partial	Susceptible
Merlin	1967 [1960, 1974]	222	0.69	6	Partial	Susceptible
Red-shouldered hawk	1977 [1962, 1990]	625	1.48	3	Partial	Susceptible
Broad-winged hawk	1972 [1962, 1979]	397	1.46	3	Complete	Non-susceptible
Northern harrier	1979 [1972, 1987]	447	1.23	7	Partial	Susceptible
Osprey	1979 [1967, 1993]	1,570	0.02	15	Complete	Susceptible
Red-tailed hawk	1976 [1970, 1984]	1,126	0.98	11	Partial	Non-susceptible
Sharp-shinned hawk	1978 [1974, 1983]	166	0.33	9	Partial	Susceptible
Rough-legged hawk	1979 [1973, 1986]	951	0.57	5	Complete	Non-susceptible
American kestrel	1972 [1968, 1978]	116	0.80	11	Partial	Susceptible
Northern goshawk	1972 [1971, 1974]	990	1.05	4	Partial	Susceptible

Note: Average body mass data are from the study by Ferguson-Lees and Christie (2001). Dietary diversity represents the dietary diversity index provided by Therrien et al. (2017). Habitat types is the number of "level 2" habitat types occupied during the breeding season (BirdLife International, 2020). Migratory behaviour is either partial or complete, and species are either susceptible or non-susceptible to DDT (for sources, see Appendix S1, Table S1). DDT = dichlorodiphenyltrichloroethane.



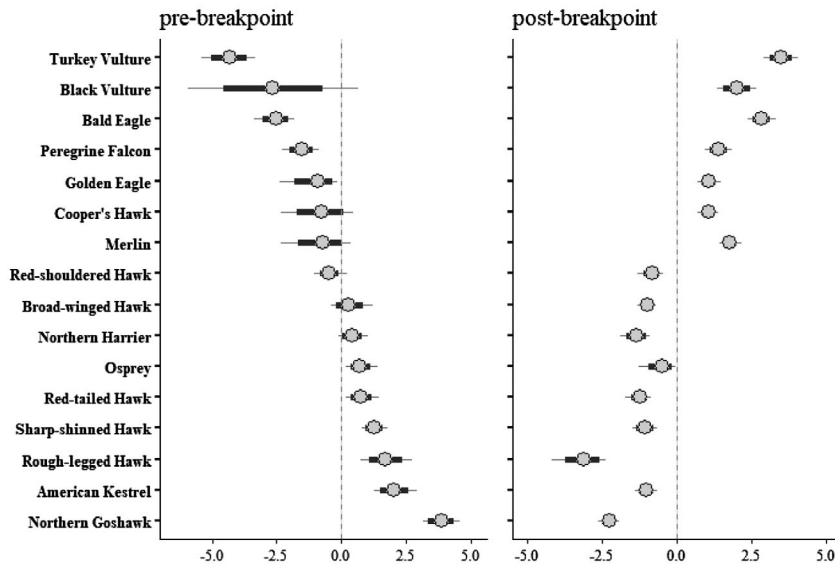
**FIGURE 1** Long-term count trends of representative species recorded at Hawk Mountain Sanctuary from 1946 to 2018. Trends for bald eagle counts are similar to those of the black and turkey vultures, Cooper's hawk, golden eagle, merlin and peregrine falcon. Trends for American kestrel counts are similar to those for the sharp-shinned hawk, northern goshawk, northern harrier, broad-winged, red-tailed, red-shouldered and rough-legged hawks and ospreys. White lines are mean predicted counts, and each grey line is one of the 5,000 draws of the posterior distribution of parameters, accounting for both sampling and parameter uncertainty. The dashed vertical line indicates the median breakpoint year, and the vertical shaded region indicates the 95% credible interval for the estimate of the breakpoint year. Other species are shown in the Supporting Information (Appendix S1; Figure S1)

count trends [ $P(\beta_{1,\text{red-shouldered hawk}} \leq 0) = .94$ ,  $P(\beta_{2,\text{red-shouldered hawk}} \leq 0) = .99$ ]; Figure 2].

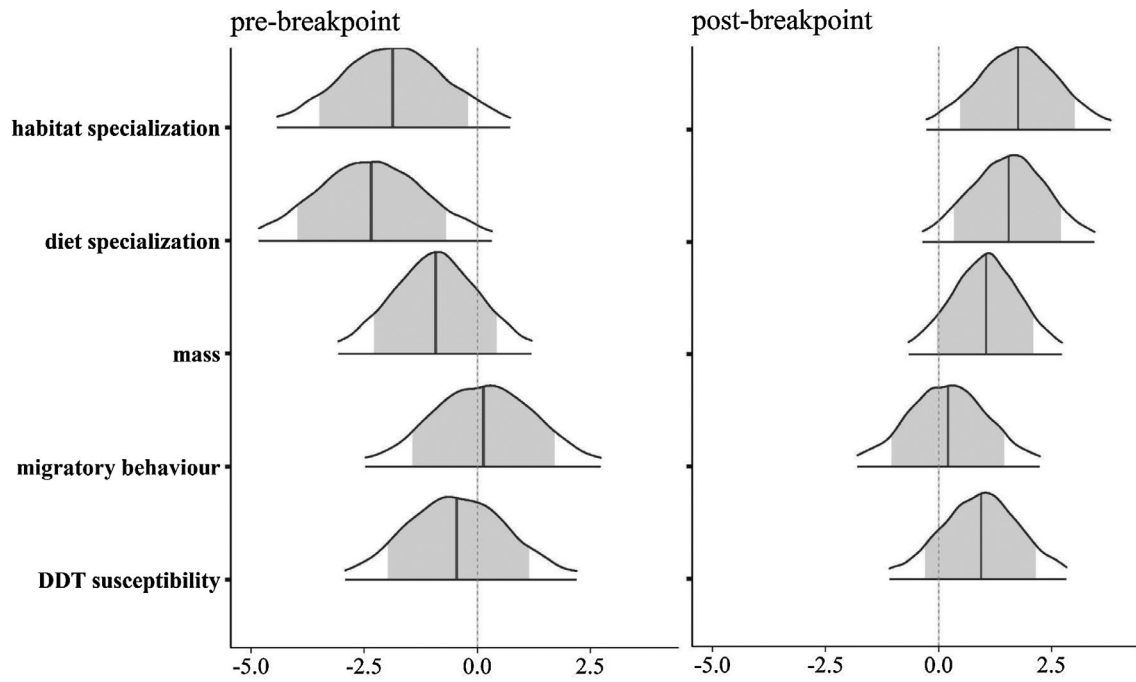
### 3.2 | Effects of traits on counts

Among the traits we evaluated, only degrees of diet and habitat specialization had consistently strong effects on count trends (Figure 3). This was true both before and after the breakpoint.

Before the breakpoint, we estimated with high probability that these two traits were negatively associated with count trends [ $P(\theta_{1,\text{diet specialization}} \leq 0) = .96$ ;  $P(\theta_{1,\text{habitat specialization}} \leq 0) = .92$ ]. This suggests that negative count trends were more likely to occur for species whose diets and habitat associations were diverse (less specialized), whereas positive count trends were more likely for species whose diets and habitat associations were specific (more specialized). During this period, the absolute value of the median effect size for diet was greater than that of any



**FIGURE 2** Estimates of the slopes before (left panel) and after (right panel) an average breakpoint for count trends of 16 species commonly recorded at Hawk Mountain Sanctuary, Pennsylvania. Filled circles indicate the median posterior slope estimate, and thick and thin bands indicate the 80 and 95% credible intervals, respectively



**FIGURE 3** Density plots showing the effects of five traits on the temporal trends of migrating raptors at Hawk Mountain Sanctuary, Pennsylvania, before (left panel) and after (right panel) the breakpoint. Grey lines indicate the median posterior estimate; grey-shaded and unshaded outer regions indicate 80 and 95% probability mass, respectively. Plots for continuous predictors (habitat, diet and mass) are interpreted as a positive or negative relationship between the count trend and the trait. Plots for categorical variables are interpreted as a positive or negative effect relative to the reference categories, which are “complete migrant” and “non-susceptible” to dichlorodiphenyltrichloroethane (DDT). Given that visual interpretations of the 95% credible interval (CI) can be unreliable tests of statistical significance (Makowski et al., 2019; Payton et al., 2003), CIs overlapping zero should be interpreted as indicating a degree of relative uncertainty among parameter estimates. For formal tests that relate to significance, refer to the probability of direction (PD) statistics described in the Results section

other predictor, followed closely by that for habitat specialization (Figure 3).

After the breakpoint, the degree of diet and habitat specialization were also strongly influential on count trends, but the effects were in the opposite direction from the earlier time period. In this

case, we estimated with high probability that these two traits were positively associated with count trends [ $P(\theta_{2,diet\ specialization} \geq 0) = .93$ ;  $P(\theta_{2,habitat\ specialization} \geq 0) = .96$ ]. This suggests that negative count trends were more likely to occur for species whose diets and habitat associations were more specialized, whereas positive



count trends were more likely for species whose diets and habitat associations were diverse. During this period, habitat specialization had a slightly greater median effect than diet specialization (Figure 3).

Susceptibility to DDT, migratory behaviour and body mass were, in both time periods, weakly associated with count trends, and the directions of effects were uncertain. Before the breakpoint, the probabilities of a directional effect of migratory behaviour and DDT susceptibility on count trends were near 50% [ $P(\theta_{1,\text{migratory behaviour}} \geq 0) = .53$ ;  $P(\theta_{1,\text{DDT susceptibility}} \leq 0) = .64$ ]. These estimates indicate uncertainty over whether being either a complete or partial migrant or a DDT-susceptible or non-susceptible species had positive or negative effects on count trends. Before the breakpoint and relative to DDT susceptibility and migratory behaviour, there was a slightly higher probability that body mass was negatively associated with count trends [ $P(\theta_{1,\text{mass}} \leq 0) = .82$ ], suggesting that larger species were slightly more likely to have negative count trends. However, the median effect size of body mass was much less than that of habitat or diet specialization (Figure 3).

After the breakpoint, uncertainty over whether migratory behaviour impacted count trends remained high [ $P(\theta_{2,\text{migratory behaviour}} \geq 0) = .58$ ]. In contrast, the probability that susceptibility to DDT and high body mass had a positive effect on count trends was  $> 80\%$  [ $P(\theta_{2,\text{DDT susceptibility}} \geq 0) = .83$ ;  $P(\theta_{2,\text{mass}} \geq 0) = .89$ ]. In this case, being a non-susceptible species or a species with larger body mass tended to result in positive count trends. However, once again, the relative effect sizes of both traits were smaller than those of diet and habitat specialization (Figure 3).

## 4 | DISCUSSION

### 4.1 | Temporal patterns of a migratory raptor assemblage

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

A prominent hypothesis used to explain changes in raptor abundance globally is the presence of DDT in the environment (Joiris & Delbeke, 1985; Rosenberg et al., 2019). The effects of this toxicant were pervasive and wide ranging, although geographically variable (Kauffman et al., 2003), resulting in the decline of non-target species, such as raptors (Ratcliffe, 1970). Furthermore, it is highly likely that in addition to documented population-level direct effects, the toxicant also had indirect effects on factors such as the diet and habitat of raptors (i.e., DDT influenced their prey and habitat availability). The assemblage-wide shift in count trends that we detected in

the early 1970s is synchronous to the policy change controlling the use of DDT in the USA. This synchrony illustrates the likely importance of the role that DDT played in driving changes in the count trends of some species within the assemblage we studied.

The weak association of count trends with the discontinuation of widespread use of DDT in the USA suggests that it was not the sole factor behind the temporal shifts we observed. Given that the count trends of susceptible species were highly variable after the breakpoint year, this suggests that a suite of additional factors, acting together with release from DDT pressures, affected the recovery of species from pesticide-linked declines. In fact, a suite of other human behavioural changes and environmental policies and regulations were implemented around the same time as the DDT ban. Most notable among these were legal statutes that criminalized the persecution of raptors (Bildstein, 2008). Together, these factors, some associated with DDT and some not, appear to have contributed to the change we observed in count trends across the wider assemblage of species, at HMS and globally.

### 4.2 | 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 that shape them. Thus, there is often more evidence for the drivers of population dynamics of individual species than of communities (Simberloff, 2004). However, it is well established that the responses of species to abiotic pressures can be influenced by their traits (Pacifi et al., 2017) and, as was the case in this study, these responses provide insight into how assemblages might be influenced by large-scale processes.

Among all traits we evaluated, diet and habitat specialization were the most influential on count trends. The negative association between count trends and diet and habitat specialization before the breakpoint seems to indicate a role for human-raptor interactions in driving these observed count trends. Two of these interactions, persecution and habitat alteration, seem particularly relevant to the count trends we document here.

Raptors have a long history of being persecuted. However, in the late 1960s and early 1970s, these species gained a series of legal protections within the USA (Bildstein, 2008). Persecution pressure is likely to impact raptor generalists and specialists differently, and our results provide insight into these differences. Generalist raptor species are those that tend to occupy and forage in areas close to human settlements. As such, at a time of increased persecution pressures and compared with their specialist counterparts, generalists might be relatively more vulnerable to direct assault. Likewise, when direct persecution is no longer a main threat, generalists might be released from this demographic pressure. This is consistent with our results suggesting that habitat and diet generalists tended to do poorly before the breakpoint, a period when persecution was demonstrably higher, and better after the breakpoint, when persecution pressure was reduced (Bildstein, 2008). As such, our finding

adds important nuance to conventional wisdom suggesting that, in the face of anthropogenic stressors, generalist species tend to do better than specialists (McKinney & Lockwood, 1999).

Persecution pressure is likely to act in concert with other stressors, such as anthropogenically driven habitat change, an ongoing process throughout the entire period of data collection for this study. The consequences of habitat alteration are likely to play out differently for specialist and generalist raptor species. In the assemblage we studied, traits that allow for exploitation of more resources in novel environments might have benefitted several species. In particular, after the breakpoint, positive count trends for synanthropic species, such as the peregrine falcon and bald eagle, might be linked to their ability to thrive in heterogeneous environments heavily impacted by humans (e.g., urban and suburban areas, agricultural settings; Kettel et al., 2019; Millsap et al., 2004). Moreover, for scavengers, such as bald eagles and vultures, increases in road density and road kills might also have been beneficial (Avery, 2004). All these benefits to generalist species have increased over time as human populations grow and human-altered environments expand (Seto et al., 2012).

Specialist species, which have narrower niche breadth, are evolutionarily predisposed to thrive in stable environments (Kassen, 2002). The same increased rate of habitat alteration that appears to have benefitted the generalists, is likely to have affected the specialists negatively after the breakpoint. Thus, the reduced availability of intact forests and remote areas is likely to have reduced the quality of the remaining pristine habitats (i.e., shifts in forest age structure and increased use of new toxicants, such as neonicotinoids; de Sy et al., 2015; Li et al., 2020), to the detriment of specialists. Species such as the American kestrel and northern harrier had negative count trends after the breakpoint, and both are potentially impacted negatively by reforestation and loss of open habitats in the eastern USA (McClure et al., 2017). In contrast, the northern goshawk is an old-growth forest specialist that is likely to be affected negatively by the same patterns of increase of second-growth forests and the concomitant increase of loss and disturbance of old-growth forests (Byholm et al., 2020). Given that human population growth and expansion of human-impacted landscapes have increased over time, these specialists would have been less affected by these factors before the breakpoint but more so afterwards.

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

Body mass and migratory behaviour were two traits that might also have influenced count trends for some species. However, these did not appear to be as important in driving assemblage-wide patterns as were diet and habitat specialization. That said, although mass had relatively weak effects during both time periods, the reversal of the directionality of its effects on count trends was consistent with the shifts in the effects exhibited by habitat and diet specialization. Generally, body size is recognized as an important species

trait (Brown et al., 1993), owing to its effect on ecological interactions (i.e., competitive dominance and predator-prey relationships; Blanchard et al., 2011). Likewise, flexibility of migratory behaviour, especially for partial migrants, allows species to shift habits to take advantage of prevailing environmental conditions (Bildstein, 2006). Thus, despite model uncertainty in the assemblage-wide role of body size and migratory behaviour, these traits might be relevant for some of the species we considered.

Factors we did not measure, such as species interactions, might also have important roles in assemblage-wide count trends. For example, measures of regional numbers of ospreys counted at north-eastern USA inland hawk watch sites suggest significantly declining trends (Brandes et al., 2016; Crewe et al., 2016). However, Breeding Bird Survey (BBS) data suggest stable trends across North America (Sauer et al., 2017). These conflicting trend estimates might suggest that inland osprey population levels are regulated by environmental factors that we did not measure (Farmer et al., 2008). In fact, there is good evidence that growing populations of bald eagles can limit recovery of osprey populations (Cruz et al., 2019). In a similar manner, predation by Cooper's hawk might contribute to the decreasing trends in counts of American kestrels (Farmer et al., 2008).

Shifts in breeding range and migratory behaviour could also have contributed to the count trends we observed. For example, the positive change in count trends of both species of vultures after the breakpoint can be attributed, in part, to the northward expansion of their breeding ranges (Avery, 2004). Change in migratory behaviour (Paprocki et al., 2017) might have driven changes in count trends for the red-tailed hawk in this study and at other north-eastern USA hawk watch sites (Brandes et al., 2016; Crewe et al., 2016). This hypothesis is reinforced by the increasing or stable trends for this species in the USA (Link & Sauer, 2002). Given that count trends are declining but population sizes are not, a logical conclusion is that some of these birds are exhibiting migratory short-stopping or altered migration routes, and thus, are counted less at hawk watch sites. In future work with survey data, researchers might wish to explore the role of these and other potential demographic or ecological drivers of count trends.

Finally, we treated DDT susceptibility as a categorical variable. The unevenness in the data on this trait might have resulted in a loss of information, causing us to detect a weak effect of this parameter. In fact, DDT exposure is likely to affect each species differently. One potential way to address this problem in the future would be to use information on biomarkers of contaminant exposure (Fossi, 1998). As we increase our understanding of the sublethal effects of DDT on raptors, these continuous data might become more broadly available and useful in analyses such as ours.

### 4.4 | Conclusions

Ongoing global changes are associated with reorganization of ecological communities and assemblages. Thus, ecologists are challenged to make better predictions of the impacts of interacting



anthropogenic stressors. Trait-based frameworks have shown promise for making generalized assumptions of the trajectories of species abundance amidst global change and have the potential to be used in multispecies conservation planning (McGill et al., 2006). Our results provide a new interpretation of the interacting role of DDT with factors such as dietary and habitat specialization in driving count trends of raptors. As such, they illustrate the utility of evaluating the role of species traits in drawing inference about drivers of synchronous count trends for raptors. Furthermore, the modelling approach we used provides a foundation for testing hypotheses about drivers of assemblage-wide trends. This information is useful in identifying unexpected roles of both natural and anthropogenic stressors that might be relevant components of biodiversity change.

## ACKNOWLEDGMENTS

We thank the volunteer counters, staff and trainees who collected Hawk Mountain's migration count data. Financial support for data analysis was provided to P.K.T.D. by a grant from Hawk Mountain Project Soar and from the Raptor Research Center at Boise State University. Sam Brilleman helped in code development. Jim Belthoff, the Katzner and Caughlin laboratory groups, Catherine Sheard and three anonymous reviewers provided helpful reviews of the manuscript. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is Hawk Mountain contribution to conservation science number 339.

## AUTHOR CONTRIBUTIONS

P.K.T.D., K.L.B. and T.E.K. conceived the study; L.J.G. provided data access; P.K.T.D., A.Z. and T.T.C. analysed the data and interpreted them with assistance from K.L.B., L.J.G. and T.E.K.; P.K.T.D. led manuscript writing, and all authors contributed to revisions.

## DATA AVAILABILITY STATEMENT

Count totals for all species included in the analyses can be accessed through the Hawk Migration Association of North America (HMANA) database available on their webpage: [www.hawkcount.org](http://www.hawkcount.org). The Stan code for the breakpoint model is provided in the Supporting Information (Appendix S1).

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## BIOSKETCH

Patricia Kaye T. Dumandan is a PhD student interested in quantitative and community ecology. Her research focuses on adopting trait-based approaches to understand and predict biodiversity patterns.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Dumandan PKT, Bildstein KL, Goodrich LJ, Zaiats A, Caughlin TT, Katzner TE. Shared functional traits explain synchronous changes in long-term count trends of migratory raptors. *Global Ecol Biogeogr.* 2020;00:1–11. <https://doi.org/10.1111/geb.13242>