RESEARCH ARTICLE

A half-century of changes in migratory landbird numbers along coastal Massachusetts

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Abstract

We analyzed data from across five decades of passerine bird banding at Manomet in Plymouth, Massachusetts, USA. This included 172,609 captures during spring migration and 253,265 during fall migration, from 1969 to 2015. Migration counts are prone to large inter-annual variation and trends are often difficult to interpret, but have the advantage of sampling many breeding populations in a single locale. We employed a Bayesian state-space modeling approach to estimate patterns in abundance over time while accounting for observation error, and a hierarchical clustering method to identify species groups with similar trends over time. Although continent-wide there has been an overall decrease in landbird populations over the past 40 years, we found a variety of patterns in abundance over time. Consistent with other studies, we found an overall decline in numbers of birds in the aggregate, with most species showing significant net declines in migratory cohort size in spring, fall, or both (49/73 species evaluated). Other species, however, exhibited different patterns, including abundance increases (10 species). Even among increasing and declining species, the specific trends varied in shape over time, forming seven distinct clusters in fall and ten in spring. The remaining species followed largely independent and irregular pathways. Overall, life-history traits (dependence on open habitat, nesting on or near the ground, migratory strategy, human commensal, spruce budworm specialists) did a poor job of predicting species groupings of abundance patterns in both spring and fall, but median date of passage was a good predictor of abundance trends during spring (but not fall) migration. This suggests that some species with very similar patterns of abundance were unlikely to be responding to the same environmental forces. Changes in abundance at this banding station were generally consistent with BBS trend data for the same geographic region.

Introduction

Long-term data sets in ecology lead to discoveries often missed in shorter-term studies [1,2], and they are critical for establishing baselines and tracking changes in the natural world [3]. Because birds are widely surveyed by professional and amateur observers alike, and their

natural histories are often well-understood, wild bird populations can be useful sentinels of environmental change and ecosystem condition [4,5] For example, during the 1980s and 1990s, wide-spread surveys were used to identify large-scale declines of birds across the continental U.S. and Canada [6–8]. Contemporary interests include documenting species' range shifts due to climate change [9–11], and modeling the spread of exotic, invasive species like Eurasian Collared-Doves *Streptopelia decaocto* [12]. Prominent long-term bird monitoring data in North America are available for breeding birds in the USGS Breeding Bird Survey (BBS) [13] and the Christmas Bird Count (CBC) [14]. These surveys amass a wealth of valuable data on bird abundance, but there are biases and gaps in survey coverage that necessitate the integration of other data sources. For example, BBS data are biased in space because they are roadside surveys [15,16], and by being of short count duration [17,18]. Survey gaps can be temporal (e.g., during migration) or spatial (e.g., off-shore rocky islands), which in turn makes certain taxa much less likely to be detected. These gaps are filled by other monitoring programs. For example, eBird is allowing large-scale identification of migratory stopover and wintering areas [19], as are targeted taxon surveys such as the International Shorebird Survey (ISS) [20] and various hawk migration watches [21].

Migratory bird banding operations represent an underutilized source of data about the stages of avian life that connect breeding and wintering: migration [22]. These sites often have long-term datasets collected by highly-trained observers, coupled with detailed data on capture effort and local conditions. Although migratory bird data from a single banding station should be interpreted with care because of yearly stochasticity introduced by fluctuations in weather conditions [23,24], banding stations identified the previously-unknown breeding grounds of wintering sparrows in California [25], and demonstrated differences in stopover energetics between hatch-year and adult birds in southern Canada [26]. In addition to answering basic questions of natural history, banding station data have recently been used to describe and assess the way migrating birds are responding to climate change, both in Europe [27] and the Americas [28]. Because banding stations are typically situated in areas such as mountain gaps, desert oases, and coastal points where birds from many breeding populations naturally aggregate during migration, they can evaluate changes in population size across a much larger region from a typical single point in space [22].

Our goal was to analyze fall and spring migration banding data for >50 species of landbirds across almost half a century from Manomet, a banding station in eastern North America, along the Atlantic Flyway. There has been a series of important studies looking at population changes of breeding and migrating birds in this region of North America, mostly focusing on population declines and changing migration phenology associated with global climate change, including extensive work at Manomet [6,7, 29–32]. Often ignored, however, is the presence of stable and increasing species (e.g., Blue-headed Vireo *Vireo solitarius*, Carolina Wren *Thryothorus ludovicianus*) [13,33], perhaps because the stories are less dramatic. Previous analyses of Manomet migration data have focused on attempting to identify common trends among Neotropical migrant species [30,31]. We aim to take these analyses a step further, first by expanding the database with over a decade of new data, and then by examining the ways in which migratory bird abundances cluster over time. We then attempt to quantitatively evaluate what life-history factors best predict these groupings. By using a Bayesian state-space approach to analyzing migration count data, we use more accurate estimates of real trends in migratory cohort size to reduce the uncertainty in identifying species clusters. Generalizations are often made about the particular population vulnerability of, for example, birds of grassland and agricultural habitats [34] or birds that winter in the Neotropics [6]. If these life-history traits and their associated risks are driving the declines of avian guilds, then the shapes of population trends within that guild should be generally similar. This approach allows us to examine

whether life-history traits predict observed trends in migratory cohort size, and to better iden-tify species that are doing especially well or especially poorly along with mechanisms for the different patterns of change.

Methods

Manomet's banding lab has operated mist nets at their coastal site in Plymouth, Massachusetts, USA (41˚ 50' N, 70˚ 30' W) every spring and fall since 1966. The site is dominated by second-growth hardwoods, but also borders swampy areas, old cleared fields, and a seaside coastal bluff. Migrating birds were captured using a system of 45–50 (depending on year) nylon mist nets (12 m long, 2.6 m high, 36 mm extended mesh) set at fixed spots along a series of trails covering part of the Manomet property. Opening and closing times for all nets were recorded and used to create a standard effort measure of net-hours. Nets were typically open from a half-hour before sunrise to a half-hour after sunset, 5–7 days per week depending on weather, in spring (15 April– 15 June) and fall (15 August– 15 November). Nets were occasionally closed due to weather conditions that might endanger birds; all such closures were recorded and factored into effort calculations.

All banding activity at Manomet was performed by trained personnel under the supervision of a master bander with an active Federal Bird Banding and Marking Permit from the USGS Bird Banding Lab, and MassWildlife bird banding and salvage permits from the Massachusetts Division of Fisheries and Wildlife. Lloyd-Evans is also a bird banding trainer certified by the North American Banding Council (1998).

Four-letter abbreviation codes and scientific names for all species analyzed appear in Table 1. Relevant wing formula data for the separation of Alder Flycatcher and Willow Fly-catcher were not collected for more than half the study period, thus we have adopted the parsi-monious strategy of not separating these two species trends and both are presented as "Traill's Flycatcher.".. Subspecies of Palm Warbler were recorded as Yellow Palm Warblers (*Setophaga palmarum hypochrysea*) and Western Palm Warbler (*S. p. palmarum*). Hybrid Blue-winged x Golden-winged Warblers were recorded as Blue-winged Warblers. For a handful of species frequently caught in ground traps (White-throated Sparrow, Red-winged Blackbird, and Brown-headed Cowbird), we included hours of ground trap deployment in calculations of total effort-hours.

Data processing

Records used in this analysis were from 1969–2015, and excluded repeat captures within the same season as well as local breeders (distinguished by physiological signs of breeding readi-ness, or local fledgling birds caught during spring migration). Although Manomet personnel banded birds from over 150 species during the target years, many of these occurred only a handful of times. Within fall and spring data, we removed from analysis all species not caught in at least 15 different years, and then examined the total birds caught for each of the remain-ing species. For the 108 remaining species, we removed those that had insufficient data to determine a significant trend, which we defined as a capture rate <5 individuals/year. This left us with 62 species with sufficient data to be analyzed for fall migration trends, and 52 species for spring migration.

Because sampling effort varies through time, and different species have their migratory peaks at different parts of each season, we calculated a peak migration window for each species according to the methods used in Lloyd-Evans and Atwood [31]. Briefly, we identified the dates that accounted for 98% of all captures—thereby excluding the first and last 1% of cap-tures—for each species across all years, and excluded sampling effort outside this period when

Table 1. Complete summary of all species analyzed.

Species	Code	Cluster+		Number Caught		Overall Trends		BBS Trends+		
		Fall	Spr	Fall	Spr	Fall	Spr	NEMA	ANF	BSS
Ruby-throated Hummingbird (*Archilochus colubris*)	RTHU	–	–	–	837	NA	Increase	Increase	Increase	–
Downy Woodpecker (*Dryobates pubescens*)	DOWO	–	–	844	–	Stable	NA	Increase	Increase	Stable
Northern (Yellow-shafted) Flicker (*Colaptes a. auratus*)	YSFL	–	–	607	–	Decline	Decline	Decline	Decline	Decline
Eastern Wood-Pewee (*Contopus virens*)	EAWP	–	6	129	264	NA	Decline	Stable	Decline	–
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	YBFL	1	–	261	526	Decline	Decline	–	Stable	Increase
Alder & Willow (Traill's) Flycatcher (*E. alnorum & traillii*)	TRFL	–	1	445	1442	Decline	Decline	Increase	Stable	Stable
Least Flycatcher (*E. minimus*)	LEFL	–	2	395	419	Decline	Decline	Decline	Decline	Decline
Eastern Phoebe (*Sayornis phoebe*)	EAPH	4	–	735	217	Increase	Stable	Stable	Decline	Stable
Great Crested Flycatcher (*Myiarchus crinitus*)	GCFL	–	–	–	422	NA	Increase	Increase	Decline	–
Blue-headed Vireo (*Vireo solitarius*)	BHVI	4	–	484	–	Increase	NA	Stable	Increase	Increase
Philadelphia Vireo (*V. philadelphicus*)	PHVI	–	–	244	–	Stable	NA	–	Increase	Increase
Red-eyed Vireo (*V. olivaceus*)	REVI	5	–	3627	464	Decline	Decline	Decline	Increase	Increase
Blue Jay (*Cyanocitta cristata*)	BLJA	6	10	2352	3211	Decline	Decline	Decline	Increase	Increase
Black-capped Chickadee (*Poecile atricapillus*)	BCCH	2		29064	1255	Decline	Decline	Stable	Increase	Increase
Tufted Titmouse (*Baeolophus bicolor*)	TUTI	–	5	5814	399	Increase	Increase	Increase	Increase	–
Red-breasted Nuthatch (*Sitta canadensis*)	RBNU	3	–	230	–	Decline	NA	Stable	Increase	Stable
White-breasted Nuthatch (*S. carolinensis*)	WBNU	–	–	292	–	Increase	NA	Increase	Increase	–
Brown Creeper (*Certhia americana*)	BRCR	1	6	1677	192	Decline	Decline	Stable	Increase	Increase
Carolina Wren (*Thryothorus ludovicianus*)	CARW	–	–	599	–	Increase	NA	Increase	–	–
Winter Wren (*Troglodytes hiemalis*)	WIWR	1	–	206	–	Decline	NA	–	Stable	Stable
Golden-crowned Kinglet (*Regulus satrapa*)	GCKI	1	–	3090	–	Decline	NA	–	Increase	Stable
Ruby-crowned Kinglet (*R. calendula*)	RCKI	5	9	1921	1245	Decline	Decline	–	Decline	Stable
Blue-gray Gnatcatcher (*Polioptila caerulea*)	BGGN	7	–	341	–	Stable	NA	Increase	–	–
Veery (*Catharus fuscescens*)	VEER	–	–	561	612	Decline	Stable	Decline	Decline	Increase
Swainson's Thrush (*C. ustulatus*)	SWTH	–	–	1255	1517	Stable	Decline	–	Decline	Stable
Hermit Thrush (*C. guttatus*)	HETH	–	–	2009	1553	Stable	Stable	Decline	Stable	Stable
Wood Thrush (*Hylocichla mustelina*)	WOTH	–	10	207	385	Decline	Decline	Decline	Decline	–
American Robin (*Turdus migratorius*)	AMRO	–	–	7262	1179	Decline	Decline	Decline	Decline	Stable
Gray Catbird (*Dumetella carolinensis*)	GRCA	–	1	22923	17533	Stable	Decline	Increase	Decline	–
Northern Mockingbird (*Mimus polyglottos*)	NOMO	–	–	512	–	Decline	NA	Decline	–	–
Brown Thrasher (*Toxostoma rufum*)	BRTH	1	–	313	429	Decline	Decline	Decline	Decline	–
Cedar Waxwing (*Bombycilla cedrorum*)	CEDW	–	–	507	471	Decline	Decline	Increase	Stable	Stable
Blue-winged Warbler (*Vermivora cyanoptera*)	BWWA	–	–	218	–	Decline	NA	Decline	–	–
Tennessee Warbler (*Oreothlypis peregrina*)	TEWA	–	–	214	125	Decline	Decline	–	Decline	Stable
Nashville Warbler (*Oreothlypis ruficapillus*)	NAWA	–	–	665	–	Stable	NA	Decline	Decline	Stable
Northern Parula (*Setophaga americana*)	NOPA	–	4	–	366	NA	Stable	Increase	Increase	Increase
Yellow Warbler (*S. petechia*)	YEWA	2	–	250	874	Decline	Stable	Stable	Decline	Decline
Magnolia Warbler (*S. magnolia*)	MAWA	5	–	814	3380	Decline	Increase	–	Stable	Increase
Cape May Warbler (*S. tigrine*)	CMWA	–	–	469	–	Decline	NA	–	Decline	Decline
Black-throated Blue Warbler (*S. caerulescens*)	BTBW	–	–	684	567	Stable	Stable	Stable	Increase	Increase
Yellow-rumped (Myrtle) Warbler (*S. coronata coronate*)	MYWA	1	–	21014	754	Decline	Stable	Stable	Stable	Stable
Black-throated Green Warbler (*S. virens*)	BTNW	–	4	353	219	Stable	Stable	Stable	Stable	Stable
Prairie Warbler (*S. discolor*)	PRAW	–	–	–	142	NA	Decline	Decline	–	–
Yellow Palm Warbler (*S. palmarum hypochrysea*)	YPWA	–	4	–	342	NA	Increase	–	Increase	Stable
Western Palm Warbler (*S. palmarum palmarum*)	WPWA	2	–	286	–	Decline	NA	–	–	–
Bay-breasted Warbler (*S. castanea*)	BBWA	–	–	726	–	Decline	NA	–	Decline	Stable

(Continued)

Table 1. (Continued)

Species	Code	Cluster⁺		Number Caught		Overall Trends		BBS Trends⁺		
		Fall	Spr	Fall	Spr	Fall	Spr	NEMA	ANF	BSS
Blackpoll Warbler (*S. striata*)	BLPW	1	3	7718	1113	Decline	Decline	–	Decline	–
Black-and-white Warbler (*Mniotilta varia*)	BAWW	–	1	1129	2442	Decline	Decline	Decline	Decline	Stable
American Redstart (*S. ruticilla*)	AMRE	–	–	3943	2965	Decline	Decline	Stable	Decline	Stable
Ovenbird (*Seiurus aurocapilla*)	OVEN	7	–	700	1512	Stable	Stable	Decline	Increase	Stable
Northern Waterthrush (*Parkesia noveboracensis*)	NOWA	–	3	922	1330	Decline	Decline	Stable	Decline	Increase
Mourning Warbler (*Geothlypis philadelphia*)	MOWA	5	2	366	535	Stable	Decline	–	Decline	Stable
Common Yellowthroat (*G. trichas*)	COYE	1	1	2125	4658	Decline	Decline	Decline	Decline	Decline
Wilson's Warbler (*Cardellina pusilla*)	WIWA	6	–	880	822	Decline	Decline	–	Decline	Stable
Canada Warbler (*C. canadensis*)	CAWA	6	–	496	1466	Decline	Decline	Decline	Decline	Stable
Yellow-breasted Chat (*Icteria virens*)	YBCH	6	–	1121	–	Decline	NA	Decline	–	–
Eastern Towhee (*Pipilo erythrophthalmus*)	EATO	2	6	893	1525	Decline	Decline	Decline	Decline	–
Field Sparrow (*Spizella pusilla*)	FISP	2	–	275	–	Decline	NA	Decline	Decline	–
Song Sparrow (*Melospiza melodia*)	SOSP	5	7	3107	877	Decline	Stable	Decline	Decline	Decline
Lincoln's Sparrow (*M. lincolnii*)	LISP	3	–	216	324	Decline	Stable	–	Decline	Stable
Swamp Sparrow (*M. georgiana*)	SWSP	–	7	1160	1341	Stable	Stable	Decline	Increase	Stable
White-throated Sparrow (*Zonotrichia albicollis*)	WTSP	–	1	8563	7038	Decline	Decline	Decline	Decline	Decline
Dark-eyed (Slate-colored) Junco (*Junco hyemalis hyemalis*)	SCJU	1	8	2237	241	Decline	Stable	Stable	Decline	Stable
Northern Cardinal (*Cardinalis cardinalis*)	NOCA	–	5	1892	747	Increase	Increase	Increase	Increase	–
Red-winged Blackbird (*Agelaius phoeniceus*)	RWBL	–	–	–	818	NA	Decline	Decline	Decline	Decline
Common Grackle (*Quiscalus quiscula*)	COGR	–	–	–	1543	NA	Stable	Decline	Decline	Stable
Brown-headed Cowbird (*Molothrus ater*)	BHCO	–	8	–	393	NA	Decline	Stable	Decline	Decline
Baltimore Oriole (*Icterus galbula*)	BAOR	2	6	774	1033	Stable	Decline	Decline	Decline	–
American Goldfinch (*Spinus tristis*)	AMGO	–	–	455	848	Stable	Decline	Increase	Stable	Stable
Scarlet Tanager (*Piranga olivacea*)	SCTA	–	–	231	–	Stable	NA	Decline	Decline	Stable
Purple Finch (*Haemorhous purpureus*)	PUFI	2	–	718	–	Decline	NA	Decline	Decline	Stable

⁺Cluster indicates which abundance trend cluster the species was sorted into by hierarchical clustering, if any. BBS Trends include the trend from three Breeding Bird Survey Regions: New England / Mid-Atlantic (NEMA), Atlantic Northern Forests (ANF), and Boreal Softwood Shield (BSS) for all birds with medium or high survey confidence in the region in question.

calculating effort-hours for a given species. For example, 98% of all spring Ovenbird captures across all years occurred between May 1 and June 5; therefore, all sampling efforts from outside this period were excluded when calculating the total spring effort-hours for Ovenbirds.

Once we had calculated the effort windows for each species, we converted the number of individuals caught in each year to the number of individuals caught / 10,000 effort-hours, in order to control for differing numbers of net-hours across years.

State-space modeling

Because migration counts from a single site only sample a small portion of the population, and such counts are susceptible to the effects of weather [35], we used a state-space modeling approach to estimate the underlying trends in the actual size of each species' migratory cohort at Manomet. A state-space modeling approach allows us to separate the process variation (differing numbers of birds migrating through each year) from the observation variation (different proportions of those birds being caught each year) [36]. Our model was adapted from the one used by Kéry and Schaub [37], with the effort-adjusted number of birds caught in the first year

of reliable survey data (1969 for fall, 1970 for spring) as the prior for initial size of the migratory cohort. All models were run 200,000 times, with the first 100,000 runs discarded as a burn-in, using WinBUGS through R and the R2WinBUGS package [38, 39].

Once the models were complete, we made a coarse assessment of each species' net change in migratory cohort size across the study period by comparing the bird's estimated abundance in 2015 with the 95% confidence interval around its abundance in the first year of data (1969 for fall, 1970 for spring). Birds whose 2015 abundance exceeded the first year's upper 95% CI were classified as having significantly increased since the first year, while birds whose 2015 abundance was less than the first year's lower 95% CI were classified as having significantly declined. We then compared these qualitative trends to the trend estimates provided by the USGS Breeding Bird Survey for the New England Mid-Atlantic Region (BCR 30), the Atlantic Northern Forests Region (BCR 14), and the Boreal Softwood Shield Region (BCR 8) [40], since these regions are the likeliest breeding grounds of birds caught at Manomet. We only used BBS trend estimates for species that had Medium or High Regional Credibility in a given region.

Cluster analysis of population patterns

With state-space model patterns in migratory cohort size over time already calculated, we were interested to determine if species could be grouped by their patterns of abundance over time. Accordingly, we standardized each species' time series to its own maximum value, thus preserving the shape of the overall trend and allowing us to compare species on the basis of trend shape alone. We clustered our species within each season (fall and spring) using the hierarchical Ward's method [41] as implemented in the R package pvclust [42]. Each point in a species' standardized time series was compared against equivalent points in each of the other time series, and the algorithm minimizes the Euclidean distances between time series to form clusters of similar trends. The pvclust packages identifies clusters that are statistically supported at the $p < 0.05$ level and creates a dendrogram.

In order to determine whether these clusters aligned with life-history traits among species, we classified all species according to several life-history traits that are frequently cited as being of conservation relevance [34,43]: dependence on open habitats (e.g., grassland and shrubland), nesting on or very near the ground, human commensals (frequently visit bird feeders and/or especially thrive in human-altered habitats), and being a spruce budworm (*Choristoneura* sp.) specialist. We also included different migratory strategies, since several studies have suggested that birds with longer migrations may be adjusting their migratory behavior less, and may fare especially poorly in response to climate change [44, 45]. Migratory strategies included: Resident (non-migratory), Facultative migrant (individuals within the same population may or may not migrate), and likely predominant wintering location: Southeastern United States, Caribbean, Central America, and South America. Many species belonged to more than one category of migratory strategy, but species were assigned to categories judged to be most representative of the migratory behavior of birds caught at Manomet. For a complete list of species life-history traits by species, see the Supplemental Material (S1 Table). We also calculated the median date of passage for each species in each season, with the assumption that migration timing might be a surrogate for a suite of possible ecological factors not covered by the other traits (e.g., distance migrated, which might be associated with the potential for phenological disruption [46–48]).

We then used these life-history traits in a k-modes clustering approach to sort all species into an equal number of clusters as in the time-series analysis (seven clusters for fall, ten clusters for spring). If membership in a particular time-series cluster is driven primarily by life-history traits, then we would expect the life-history clusters and time-series clusters to show high

concordance. For example, we might expect to see high concordance between a cluster of steadily declining time-series trends and a life-history cluster of open habitat specialists who migrate to South America. Concordance was assessed using multinomial logistic regression, with membership in a life-history cluster as a predictor variable and membership in a time-series cluster as a response variable. These results were compared to a null model (time-series cluster membership is random) and a model using median date of passage as a predictor variable.

Results

In total, we analyzed information from 253,265 birds caught across 1,487,999 net hours during fall migration, and 172,609 birds captured across 925,327.5 net hours during spring migration (Table 1). The average 98% migration window was longer in the fall (65.6 days, ± 16.8) than in the spring (40.5 days, ± 13.2) (Table 1), as might be expected based on selective pressures for early arrival for breeding [49,50]. For the 43 species in our samples that appeared in both the fall and spring counts, the differences in migration windows are likely driven by the larger sample size and longer banding season in the fall.

Each of the season-specific state-space model graphs for every species is found in the Supplemental Materials. State-space model trends removed much of the interannual variation of raw time-series data (see example in Fig 1), but trends over time were often nonlinear and occasionally complex, defying easy categorization. Of the 62 fall species evaluated, 30 sorted into seven statistically significant clusters based on their time-series trends (Fig 2, Table 1). Group sizes ranged from 2 to 9 species. Cluster significance was determined by an approximately unbiased (AU) p-value < 0.05 from multiscale bootstrap resampling [42]. The clusters show that some species declined sharply in the late 1970s and then persisted at lower abundance (such as Eastern Towhee, Field Sparrow, Purple Finch, and Baltimore Oriole in cluster 2) while others have declined steadily over time (e.g., Magnolia Warbler, Mourning Warbler, Red-eyed Vireo and Song Sparrow in cluster 6). Others have increased overall, such as Blue-headed Vireo and Eastern Phoebe in cluster 4. (Fig 3; S1 Table). Some species showed a fair amount of interannual variation, but overall had no distinct net change over time (e.g., Blue-gray Gnatcatcher and Ovenbird in cluster 7).

Of the 52 spring species evaluated, 26 sorted into ten statistically significant clusters based on their time-series trends, with 2–5 species within each cluster (Fig 4). As with the fall clusters, different clusters of declining species exhibit distinct timing in the onset of decline. Birds in cluster 2 (Mourning Warbler and Least Flycatcher) showed a steep crash in spring captures in the late 1990s, while spring cluster 7 (Song Sparrow and Swamp Sparrow) had their greatest declines before 1980, and have since been stable or even recovering (Fig 5). Spring cluster 4 (Black-throated Green Warbler, Northern Parula, and Yellow Palm Warbler) are primarily united by an incredibly high rate of spring captures in 2010. Concordance in cluster membership between spring and fall clusters was remarkably low (Table 1).

For fall trends, 41 species (66%) showed significant declines in migratory cohort size between 1969 and 2015 (Table 1). Six species (10%) showed significant increases in migratory cohort size, and 15 species did not have a significantly different abundance in 2015 than in 1969. For spring migrants, 32 species (62%) showed a decline in abundance at Manomet since 1970, while six species (12%) increased significantly, and 14 species (27%) neither increased nor declined overall from 1970 to 2015. Several species demonstrated notable peaks and dips in abundance during the intervening years (see fall cluster 7 in Fig 4 for an example of this).

The group (cluster) affiliations of species based on life-history characteristics showed no concordance with cluster affiliations based on patterns of population size over time (Table 2).
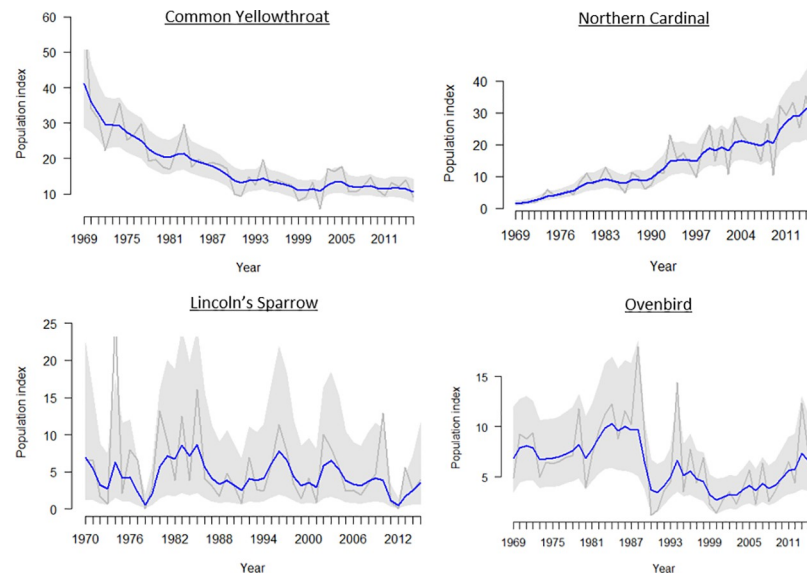
Fig 1. Example time-series graphs of bird captures at Manomet for four different species from four different trend clusters. Grey lines indicate raw capture data, blue lines indicate state-space estimates of actual migratory cohort size, and the shaded area is the 95% confidence interval around the state-space model estimate. Some species are unambiguously increasing or declining, while others show more complicated patterns. Lincoln's Sparrow data is from spring migration, all others are from fall.

This was true for both fall and spring, where their models never had support over the null model. The same is true for median passage date for fall birds, but not for spring birds. In spring, median date of passage was the best-supported model (Table 2), explaining a moderate amount of the variation in species membership between the two cluster types (maximum likelihood pseudo-r^2 = 0.56).

Our clustering analyses that evaluated species similarities in population size change over time left 47 fall species and 47 spring species not affiliated with any cluster. Of these, 27 species were found unclustered in both seasons.

Discussion

In general, the patterns of abundance observed at Manomet signal that many of our landbird species are in trouble. With more than 60% of all species in both fall and spring showing significant declining trends, and fewer than 15% apparently increasing, our data support the widespread conservation concern that has hovered around North American migratory songbirds for decades [7,51]. That said, the lack of association between our trend clusters and life history traits suggests that simple narratives about the species most vulnerable to decline might not suffice.

For example, aerial insectivores are frequently cited as an avian group particularly at risk for decline [52,53]. Indeed, our data and the Breeding Bird Survey agree that Least Flycatchers and Eastern Wood-Pewees are probably declining in northeastern North America, yet the signals for Yellow-bellied Flycatchers are decidedly mixed, and Eastern Phoebes and Great Crested Flycatchers appear to be stable or increasing. Eastern Phoebes are short-distance migrants, but Great Crested and Yellow-bellied Flycatchers are Neotropical wintering birds just as Least Flycatcher is, and all use a wide variety of forested and second-growth habitats on their shared Central American wintering grounds [54–56]. Least Flycatchers are certainly declining in the eastern portion of their range, but the performance of other flycatchers
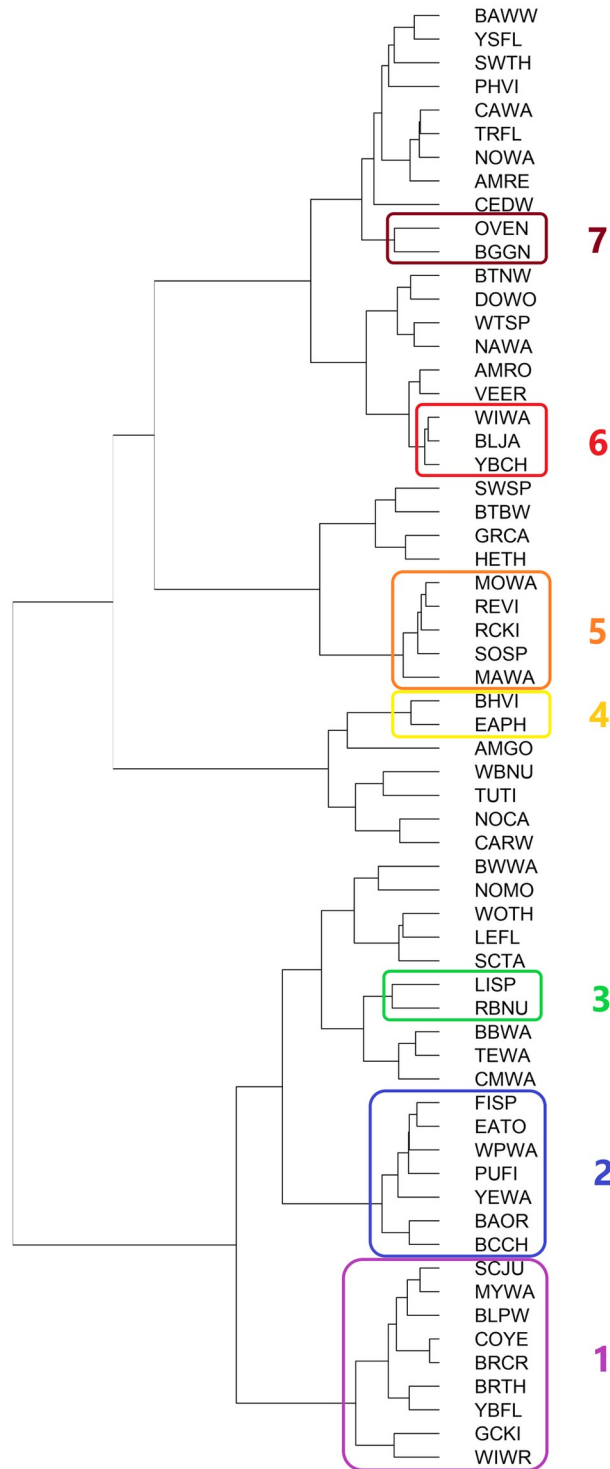
Fig 2. Dendrogram of fall bird species, clustered via Ward's hierarchical clustering with a Euclidean distance method based on time series trend shape. Colored rectangles enclose clusters significant at the approximately unbiased (AU) $p < 0.05$ level. 4-letter species codes and cluster numbers at the right of the figure match those in Table 1.
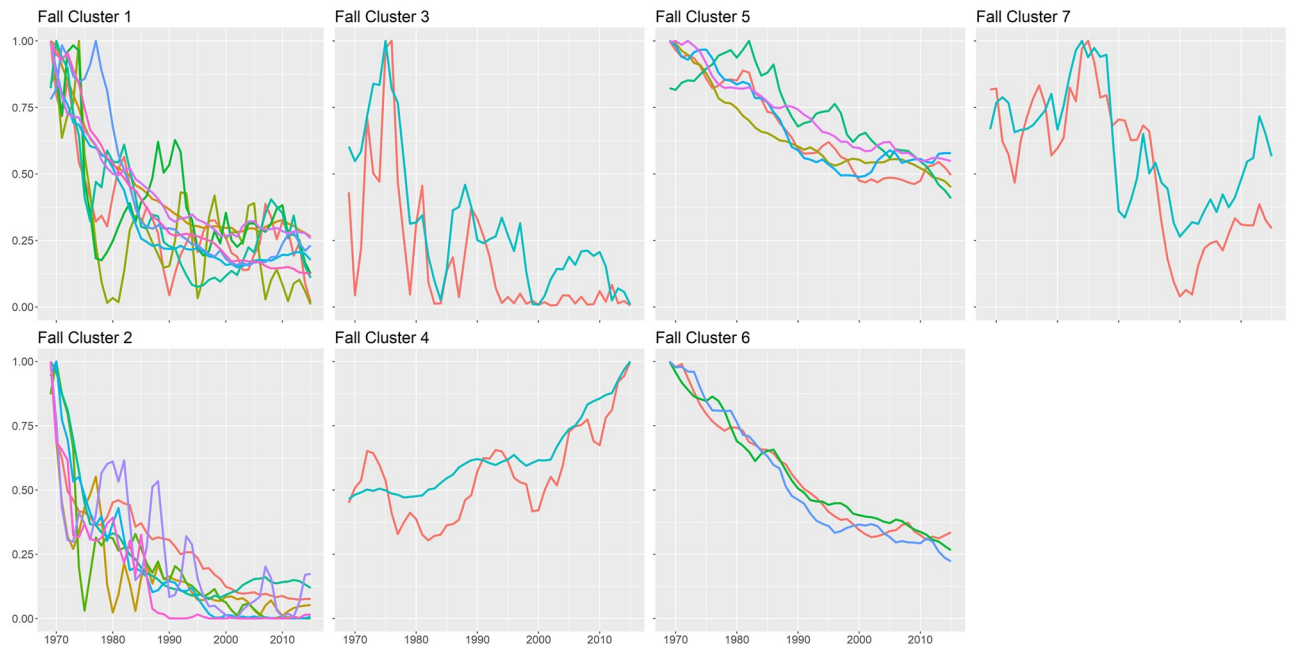
https://doi.org/10.1371/journal.pone.0222232.g002

Fig 3. Graphs of abundance trends over time of each significant fall species cluster. Each colored line is a different species.

suggests that the explanation cannot be as simple as "loss of aerial insect food" or "loss of habitat in the Neotropics."

Magnolia Warbler is another interesting case. Declining at Manomet in the fall but increasing in the spring, the Breeding Bird Survey indicates that breeding populations north of Massachusetts are stable or increasing. It may be the case that Magnolia Warblers coming north in the spring represent a mixture of many breeding populations that separate somewhere north of Manomet. Fall birds may be primarily hatch-year birds from the breeding populations northeast of Manomet in New Brunswick and Nova Scotia, which are locally declining according to the Breeding Bird Survey. Magnolia Warblers are known to take more eastern routes in fall than in spring [57], and this serves as a good example of how migration capture data can supplement breeding-season surveys to complete an otherwise puzzling narrative. Such "loop migration" has also been demonstrated in Blackpoll Warblers. Via stable isotope analysis, northward spring migrant Blackpolls at Manomet have been linked to breeding populations east of Hudson Bay, while fall migrant Blackpolls that congregate at Manomet before crossing the Atlantic appear to be from western breeding populations [58].

Similarly, birds exhibiting similar trends over time are not necessarily responding to the same threats. Blue Jay and Wood Thrush, for example, show remarkably similar declines in spring abundance in cluster 10 (Fig 5). Aside from being broadly associated with "forests," however, these birds have almost nothing in common. They have different diets, different migration routes, different wintering grounds, and different nesting habits [59,60]. Yet, both are significantly declining in the New England region in both Manomet captures and Breeding Bird Survey abundance (Table 1). Vulnerability to cowbird parasitism, complex edge dynamics, and loss of Neotropical wintering habitat have all been implicated in Wood Thrush declines [59], but these seem unlikely to be major factors in the decline of Blue Jays [61]. Finally, discrepancies between patterns of abundance at Manomet and apparent trends in the Breeding Bird Survey underscore the complexity of avian population dynamics. Black-capped
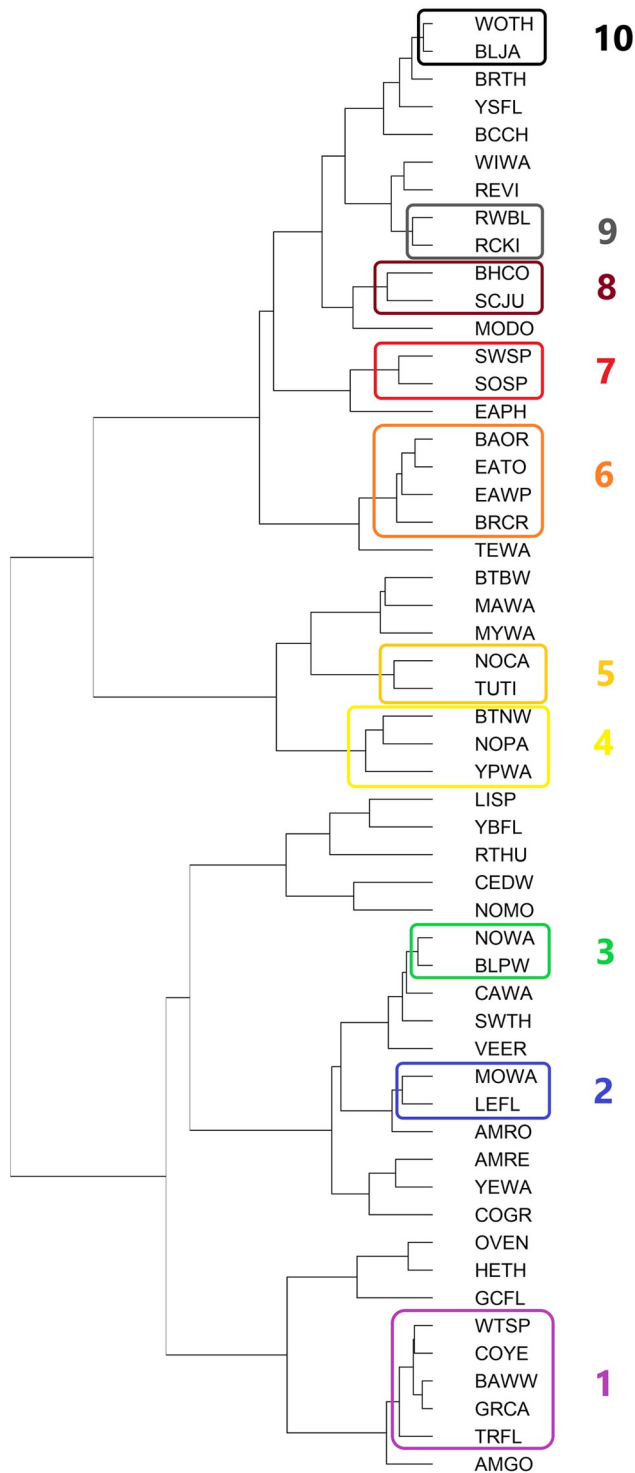
Fig 4. Dendrogram of spring bird species, clustered via Ward's hierarchical clustering with a Euclidean distance method based on time series trend shape. Colored rectangles enclose clusters significant at the approximately unbiased (AU) $p < 0.05$ level. 4-letter species codes and cluster numbers on the right of the figure match those in Table 1.
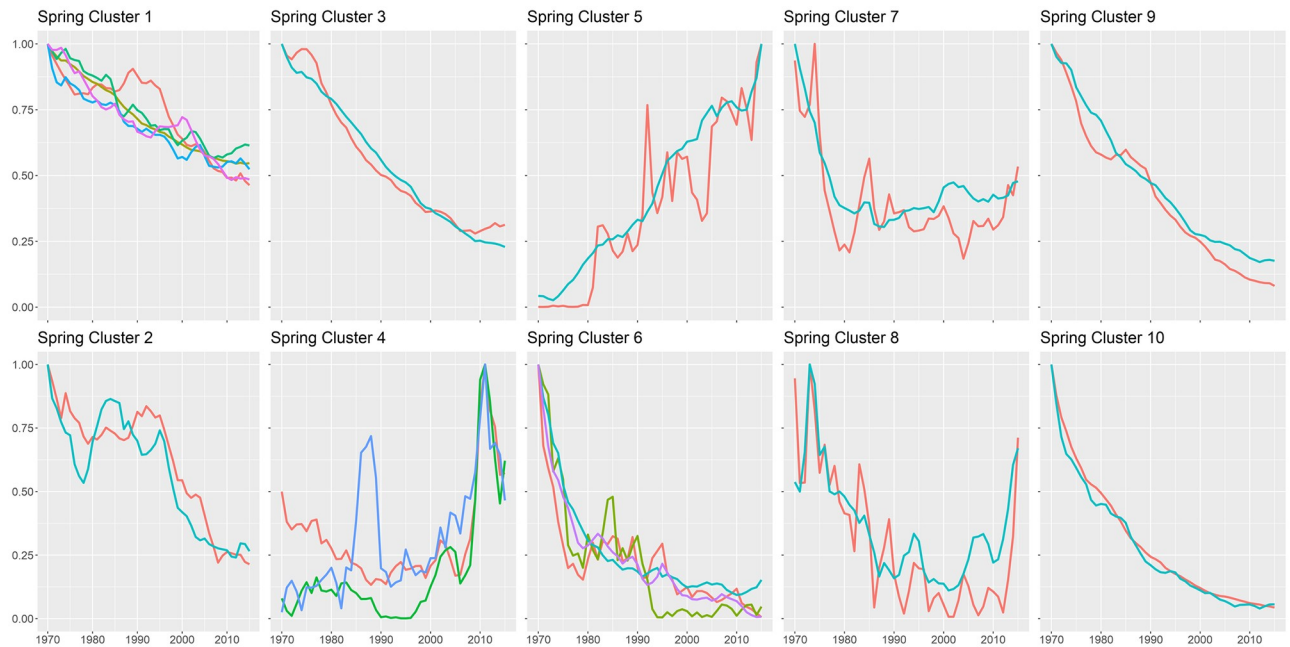
https://doi.org/10.1371/journal.pone.0222232.g004

Fig 5. Graphs of abundance trends over time of each significant spring species cluster. Each colored line is a different species.

Chickadees are non-migratory and one of the most frequently caught birds at Manomet. In both fall and spring, chickadee captures have declined considerably since banding started at Manomet. The Breeding Bird Survey, by contrast, shows chickadee populations are stable or increasing in all regions nearby. Closer examination of the Black-capped Chickadee fall trends (S2 Table) shows that the apparent decline is driven by several "spikes" in fall captures during 1971 and the 1980s. Breeding seasons with high fledging success followed by a poor autumn seed crop have been shown to lead to these irruptive movements in an otherwise non-migratory species [62]. An increase in winter bird feeding by humans and milder winters as a result of climate change may have resulted in fewer large-scale autumn movements of Black-capped Chickadees, but determining the true population trend of northeastern chickadees from these data is not a straightforward enterprise. Apparent fall declines at Manomet in other species with short or facultative migration, such as Yellow-rumped Warbler, may similarly reflect changes in migratory behavior rather than actual population declines [63], but more complex dynamics may also be at play.

Table 2. Multinomial modeling results.

Model (fall)	k	ΔAICc	ω	Model (spring)	k	ΔAICc	ω
Null model	6	0.0	0.946	Median arrival date	18	0.0	0.70
Median arrival date	12	5.9	0.048	Null model	9	3.3	0.13
Life history	12	10.3	0.006	Life history + median arrival	27	3.4	0.13
Life history + median arrival	18	17.0	<0.001	Life history	18	5.6	0.04

Results of multinomial models relating species affiliations with clusters based on patterns of change with the same number of clusters based on life-history characteristics (dependence on open habitats, nesting on or very near the ground, human commensals, and whether or not the species was a spruce budworm specialist). Degrees of freedom (k), differences in Akaike Information Criterion corrected for small sample size (ΔAICc), and model weights (ω) are reported.

Even so, for many species, trends at Manomet and those reported by the Breeding Bird Survey are in agreement, and the overall picture is a troubling one. Our findings on the prevalence of landbird declines are consistent with those of earlier analyses of Manomet data [31] as well as data from other northeastern migration sites [64,65]. Many migrant songbirds are showing significant long-term declines in migratory cohort size. This phenomenon is evident in Neotropical migrants, but also in many common and familiar species that migrate only short distances, such as American Robin and Blue Jay. Many of the species that show significant increasing trends in Manomet capture rates are resident human commensal species, such as Tufted Titmouse, Northern Cardinal, and White-breasted Nuthatch. Other increasing birds like Yellow Palm Warbler and Blue-headed Vireo are likely individuals wintering in the Gulf states of the USA rather than in the Neotropics.

Generally speaking, of the 28 species that did not fall into any significant clusters in either season, many had nearly horizontal abundance trendlines over time, either broadly stable (e.g., Hermit Thrush, S1 Table) or slowly declining (e.g., American Robin, Canada Warbler, S1 Table). Many were species that Manomet catches in relatively small numbers (e.g., Ruby-throated Hummingbird, Yellow-bellied Sapsucker, Great Crested Flycatcher). There were no obvious life history traits in common among these species, although smaller groups of birds with commonalities do exist within the group. A few (Bay-breasted Warbler, Cape May Warbler, and Tennessee Warbler) showed trends clearly driven by spruce budworm outbreaks in the 1970s [66], and a few exhibited strange patterns that defy easy description but may be related to unpredictable captures of wandering foraging flocks in late fall (e.g., American Goldfinch, Cedar Waxwing; see S1 Table).

Interestingly, the large proportion of bird trend clusters defy simple mechanistic categorization. Some life-history traits were consistent with time-series groupings; for example, the spring significant trend cluster of Northern Cardinal and Tufted Titmouse accurately reflects the similar life histories of these resident seed-eating backyard birds. However, there are no apparent connections between species in many of the other clusters. The poor ability of life-history traits to predict time-series trend cluster membership strongly suggests that there are many "paths" to the same apparent abundance trajectory, as shown by the example of Blue Jay and Wood Thrush, above.

Even the largest clusters of species show few (or no) commonalities in life history. Fall cluster 1 (Yellow-bellied Flycatcher, Brown Creeper, Winter Wren, Golden-crowned Kinglet, Brown Thrasher, "Myrtle" Warbler, Blackpoll Warbler, Common Yellowthroat, and Dark-eyed Junco) are united by the fact that they all declined sharply in abundance at Manomet through the mid-1980s, and then leveled off to slower declines or near-stability. The closest apparent unifying life-history trait among them is association with mature conifer-dominated forests for breeding. However, two of these species (Brown Thrasher and Common Yellowthroat) do not use mature conifer woods at all, instead preferring disturbed areas of brushy shrubland for breeding, and other species that are strongly associated with breeding in conifer woodlands (such as Blue-headed Vireo and Black-throated Green Warbler) did not associate with this cluster.

The predictive utility of median date of migration in predicting spring trends underscores a point made by previous researchers about the importance of weather in the movements of migrating birds [30,67]. Large movements can occur with little warning as conditions change, and birds with similar migratory timing may be caught in large numbers or missed altogether depending on whether nets are open during a major migratory fallout [68]. Spring migration, especially, is a time when migrating birds are attempting to return to the breeding grounds as quickly as possible in order to secure high-quality territories and mates [69]. For example, as previously mentioned, spring trends for Blue Jay and Wood Thrush align very neatly and

clustered significantly in the hierarchical analysis (Fig 5), but in terms of life history, these two birds share very little ecologically beyond being "forest birds" in the broadest possible sense. However, their peak spring migration dates are the same, and so their annual spring capture rates were likely strongly influenced by weather during peak migration. That both birds are declining is supported by their Manomet abundance trends and by the Breeding Bird Survey [13], but again, it is likely that they are declining for different reasons.

As with any migration study based on data from a single site, even if that site is drawing birds from larger breeding and wintering ranges, these results should be interpreted with care. Birds captured at Manomet do not compose a random sample of any species' populations, but in many cases they integrate data from several breeding populations, as well as from birds whose breeding grounds are too remote for effective surveys by other methods [30]. Recent work from Long Point Bird Observatory and Powdermill Avian Research Center has confirmed that banding stations tend to capture fall juvenile birds out of proportion with their abundance in the population [70]. Manomet's coastal location probably amplifies this effect, especially in the fall [23], since younger inexperienced birds are more likely to become disoriented or exhausted at coastal sites and land there [71]. Where fall and spring apparent trends differed, as in 13 of 73 (18%) of the species analyzed here, such differences are likely attributable to 1) differences in fecundity (fall) and overwinter survival (spring), 2) differences in the breeding populations being sampled in each season, as for Magnolia Warbler or Blackpoll Warbler, 3) species taking different migratory routes in each season, and 4) differences in age structure of migratory populations sampled at coastal sites. In this way, as long as the data are interpreted with a careful understanding of their limitations, insights can be drawn from migratory data that breeding and wintering surveys alone cannot provide.

In an era of rapid global change, studies using migration data can detect potential behavioral shifts such as those of Black-capped Chickadees and Yellow-rumped Warblers, above. Such population-wide changes in migratory behavior in wild birds have already been observed [72,73]. As winters in northern North America grow milder and storms become more unpredictable, it seems likely that short-distance and facultative migrant species will overwinter farther north than in the past, or in some cases, not migrate at all.

Supporting information

S1 Table. This table indicates which life history traits were assigned to each species, which cluster that species was sorted into in fall and spring based on life history traits (lifehist. num.f and lifehist.num.s), which statistically significant cluster that species was sorted into in fall and spring (trend.f and trend.s), the start date, end date, and length (in days) of each species' window of passage in fall and spring, median date of passage (in ordinal day of year) in fall and spring, and an estimate of the species' apparent trend in fall and spring abundance at Manomet over the full study period.
(XLSX)

S2 Table. The number of new fall captures of each species by Institute for Bird Populations (IBP) four-letter code for each year from 1969–2015. NET.HOURS indicates the total number of effort-hours for that season.
(CSV)

S3 Table. The number of new spring captures of each species by Institute for Bird Populations (IBP) four-letter code for each year from 1970–2015. NET.HOURS indicates the total number of effort-hours for that season.
(CSV)

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Author Contributions

References

1. Willis KJ, Araújo MB, Bennett KD, Figueroa-Rangel B, Froyd CA, Myers N. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. Philosophical Transactions of the Royal Society B: Biological Sciences. 2007 Feb 28; 362:175

2. Lindenmayer DB, Likens GE, Andersen A, Bowman D, Bull CM, Burns E, et al. Value of long-term ecological studies: Value of long-term ecological studies. Austral Ecology. 2012 Nov; 37(7):745–57.

3. Magurran AE, Baillie SR, Buckland ST, Dick JMcP, Elston DA, Scott EM, et al. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends in Ecology & Evolution. 2010 Oct; 25(10):574–82.

4. Furness RW, Greenwood JJD (eds). Birds as Monitors of Environmental Change. London, Chapman & Hall; 1993.

5. Piersma T, Lindström Å. Migrating shorebirds as integrative sentinels of global environmental change. Ibis. 2004 Sep 23; 146:61–9.

6. Robbins CS, Sauer JR, Greenberg RS, Droege S. Population declines in North American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences. 1989 Oct 1; 86(19):7658–62.

7. Terborgh JW. Where Have All the Birds Gone? Princeton, Princeton University Press; 1989.

8. Rappole JH, McDonald MV. Cause and effect in population declines of migratory birds. The Auk. 1994; 111(3): 652–660.

9. Tingley MW, Monahan WB, Beissinger SR, Moritz C. Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences. 2009 Nov 17; 106(Supplement_2):19637–43.

10. Gillings S, Balmer DE, Fuller RJ. Directionality of recent bird distribution shifts and climate change in Great Britain. Global Change Biology. 2015 Jun; 21(6):2155–68. https://doi.org/10.1111/gcb.12823 PMID: 25482202

11. Socolar JB, Epanchin PN, Beissinger SR, Tingley MW. Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. Proceedings of the National Academy of Sciences. 2017 Dec 5; 114(49):12976–81.

12. Bled F, Royle JA, Cam E. Hierarchical modeling of an invasive spread: the Eurasian Collared-Dove *Streptopelia decaocto* in the United States. Ecological Applications. 2011 Jan; 21(1):290–302. PMID: 21516906

13. Sauer JR, Niven DK, Hines JE, Ziolkowski Jr. DJ, Pardieck KL, Fallon JE, Link WA. The North American Breeding Bird Survey, Results and Analysis 1966–2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, MD

14. National Audubon Society. The Christmas Bird Count Historical Results. [Internet][cited 2019 May 28].]. http://www.christmasbirdcount.org

15. Temple SA, Wiens JA. Bird populations and environmental changes: can birds be bio-indicators? American Birds. 1989; 43: 260–270.

16. Keller CME, Fuller MR. Comparison of birds detected from roadside and off-road point counts in the Shenandoah National Park. USA Forest Service General Technical Report. 1995.

17. Welsh DA. An overview of the forest bird monitoring program in Ontario, Canada. USDA Forest Service General Technical Report. 1995.

18. Jobin B, DesGranges J-L, Boutin C. Population trends in selected species of farmland birds in relation to recent developments in agriculture in the St. Lawrence Valley. Agriculture, Ecosystems & Environment. 1996; 57: 103–116.

19. Laughlin AJ, Taylor CM, Bradley DW, LeClair D, Clark RG, Dawson RD, et al. Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. The Auk. 2013 Apr; 130(2):230–9.

20. Howe MA, Geissler PH, Harrington BA. Population trends of North American shorebirds based on the International Shorebird Survey. Biological Conservation. 1989; 49(3):185–99.

21. Bildstein KL. Long-term counts of migrating raptors: a role for volunteers in wildlife research. The Journal of Wildlife Management. 1998 Apr; 62(2):435.

22. Dunn EH. Bird observatories: an underutilized resource for migration study. The Wilson Journal of Ornithology. 2016 Dec; 128(4):691–703.

23. Ralph CJ. Age ratios and their possible use in determining autumn routes of passerine migrants. Wilson Bull. 1981; 93(2):164–88.

24. Dunn EH, Hussell DJT. Using migration counts to monitor landbird populations: review and evaluation of current status. In: Power D.M,. editor.(eds) Current Ornithology. Current Ornithology, vol 12. Boston, Springer; 1990.

25. Seavy NE, Humple DL, Cormier RL, Gardali T. Establishing the breeding provenance of a temperate-wintering north american passerine, the Ggolden-crowned Ssparrow, using light-level geolocation. Votier S, editor. PLoS ONE. 2012 Apr 10; 7(4).

26. Jones J, Francis CM, Drew M, Fuller S, Ng MWS. Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. The Condor. 2002; 104(1):49.

27. Stervander M, Lindström Å, Jonzén N, Andersson A. Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. Journal of Avian Biology. 2005 May; 36(3):210–21.

28. Mills AM. Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming: Passerine migration and global warming. Ibis. 2005 Mar 1; 147 (2):259–69.

29. Askins RA, Lynch JF, and Greenberg R. Population declines in migratory birds in eastern North America. pPp. 1–57. In: Power DM Power D.M., editor (Ed.). Current Ornithology. Vol. 7. New York, Plenum Publishing; 1990. pp. 402.

30. Hagan JM III, Lloyd-Evans TL, Atwood JL, Wood DS. Long-term changes in migratory landbirds in the northeastern Uunited Sstates: evidence from migration capture data. In: Hagan JM III, and Johnston DW, editors. (eds) Ecology and Conservation of Neotropical Migrant Landbirds. Washington, DC, Smithsonian Institution Press; 1992.

31. Lloyd-Evans TL, Atwood JL. 32 years of changes in passerine numbers during spring and fall migrations in coastal Massachusetts. The Wilson Bulletin. 2004 Mar; 116(1):1–16.

32. Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Satzinger P. Bird migration times, climate change, and changing population sizes. Global Change Biology. 2008 Sep; 14(9):1959–72.

33. Kamm, MD, Walsh J, Galluzzo J, Petersen W. Iin: Walsh, J and Petersen W, editors (eds.) Massachusetts Breeding Bird Atlas 2. New York, Mass Audubon and Scott & Nix; 2013.

34. Brennan LA, Kuvlesky WP. Invited paper: Nnorth Aamerican grassland birds: an unfolding conservation crisis? Morrison, editor. Journal of Wildlife Management. 2005 Jan; 69(1):1–13.

35. Alerstam T. Analysis and a theory of visible bird migration. Oikos. 1978; 30(2):273–349.

36. de Valpine P, Hastings A. Fitting population models incorporating process noise and observation error. Ecological Monographs 2002: 21.

37. Kéry M., Schaub M. State-space models for population counts. In Bayesian population analysis using WinBUGS/OpenBUGS—a hierarchical perspective. Academic Press; 2012.

38. Lunn DJ, Thomas A, Best N, Spiegelhalter D. WinBUGS—A Bayesian modelling framework: Concepts, structure, and extensibility. Statistics and Computing. 2000: 13.

39. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2019. URL https://www.R-project.org/.

40. NABCI. BCR Map. 2016. [Internet][cited 2019 May 28]. http://nabci-us.org/resources/bird-conservation-regions-map/

41. Ward JH. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association. 1963 Mar; 58(301):236–44.

42. Suzuki R, Shimodaira H. Pvclust: an R package for assessing the uncertainty in hierarchical clustering. Bioinformatics. 2006 Jun 15; 22(12):1540–2. https://doi.org/10.1093/bioinformatics/btl117 PMID: 16595560

43. Brown JA, Lockwood JL, Avery JD, Curtis Burkhalter J, Aagaard K, Fenn KH. Evaluating the long-term effectiveness of terrestrial protected areas: a 40-year look at forest bird diversity. Biodiversity and Conservation. 2019 Mar; 28(4):811–26.

44. Butler CJ. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. In: Ibis [Internet]. 1 Jul 2003 [cited 12 Aug 2019]. https://doi.org/10.1046/j.1474-919X.2003.00193.x

45. Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society B: Biological Sciences. 2010 Apr 22; 277(1685):1259–66. https://doi.org/10.1098/rspb.2009.1525 PMID: 20018784

46. Jones T, Cresswell W. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? Journal of Animal Ecology. 2010 Jan 1; 79(1):98–108. https://doi.org/10.1111/j.1365-2656.2009.01610.x PMID: 19694874

47. Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Huppop K, et al. Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society B: Biological Sciences. 2011 Mar 22; 278(1707):835–42. https://doi.org/10.1098/rspb.2010.1778 PMID: 20861045

48. Gardali T, Seavy NE, DiGaudio RT, Comrack LA. A climate change vulnerability assessment of Ccalifornia's at-risk birds. Hyrenbach D, editor. PLoS ONE. 2012 Mar 2; 7(3):e29507. https://doi.org/10.1371/journal.pone.0029507 PMID: 22396726

49. McNamara JM, Welham RK, Houston AI. The timing of migration within the context of an annual routine. Journal of Avian Biology. 1998 Dec; 29(4):416.

50. Kokko H. Competition for early arrival in migratory birds. J Anim Ecology. 1999 Sep; 68(5):940–50.

51. Ward MP, Benson TJ, Deppe J, Zenzal TJ, Diehl RH, Celis-Murillo A, et al. Estimating apparent survival of songbirds crossing the Gulf of Mexico during autumn migration. Proceedings of the Royal Society B: Biological Sciences. 2018 Oct 24; 285(1889):20181747. https://doi.org/10.1098/rspb.2018.1747 PMID: 30355710

52. Böhning-Gaese K., Taper ML, Brown JH. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biology 1993; 7:76–86.

53. Nebel S, Mills A, McCracken JD, Taylor PD. Declines of aerial insectivores in north america follow a geographic gradient. Avian Conservation and Ecology [Internet]. 2010 [cited 2019 Mar 28]; 5(2). Available from: http://www.ace-eco.org/vol5/iss2/art1/

54. Gross DA, Lowther PE. Yellow-bellied Flycatcher (*Empidonax flaviventris*), version 2.0. In: Poole AF, editor. The Birds of North America (Poole A. F., Editor). Ithaca, Cornell Lab of Ornithology, 2011.

55. Tarof S, Briskie JV. Least Flycatcher (*Empidonax minimus*), version 2.0. In: Poole AF, editor. The Birds of North America (Poole A. F., Editor). Ithaca, Cornell Lab of Ornithology; 200

56. Miller K. E. and Lanyon W. E. Great Crested Flycatcher (*Myiarchus crinitus*), version 2.0. In: Poole AF, editor. The Birds of North America. (Poole A. F., Editor). Ithaca, Cornell Lab of Ornithology; 2014.

57. Dunn EH, Hall GA. Magnolia Warbler (*Setophaga magnolia*), version 2.0. In: Poole AF, editor. The Birds of North America (Poole A. F., Editor). Ithaca, Cornell Lab of Ornithology; 2010.

58. Holberton RL, Wilgenburg SLV, Leppold AJ, Hobson KA. Isotopic (δ2Hf) evidence of "loop migration" and use of the Gulf of Maine Flyway by both western and eastern breeding populations of Blackpoll Warblers. Journal of Field Ornithology. 2015 Sep 1; 86(3):213–28.

59. Evans M, Gow E, Roth RR, Johnson MS, Underwood TJ. Wood Thrush (*Hylocichla mustelina*), version 2.0. In: Poole AF, editor. The Birds of North America (Poole A. F., Editor). Ithaca, Cornell Lab of Ornithology; 2011.

60. Smith KG, Tarvin KA, Woolfenden GE. Blue Jay (Cyanocitta cristata), version 2.0. In: Poole AF, editor. The Birds of North America (Poole A. F., Editor). Ithaca, Cornell Lab of Ornithology; 2013.

61. Rothstein SI. An experimental and teleonomic investigation of avian brood parasitism. The Condor. 1975 Oct; 77(3):250–71.

62. Foote JR, Mennill DJ, Ratcliffe LM, Smith SM. Black-capped Chickadee (*Poecile atricapillus*), version 2.0. In: Poole AF, editor. The Birds of North America (Poole A. F., Editor). Ithaca, Cornell Lab of Ornithology, 2010.

63. Terrill SB, Ohmart RD. Facultative extension of fall migration by yellow-rumped warblers (*Dendroica coronata*). The Auk. 1984 July; 101(3):427–438.

64. Blancher PJ, Phoenix RD, Badzinski DS, Cadman MD, Crewe TL, Downes CM, et al. Population trend status of Ontario's forest birds. The Forestry Chronicle. 2009 Mar; 85(2):184–201.

65. Osenkowski JE, Paton PWC, and Kraus D. Using long-term constant-effort banding data to monitor population trends of migratory birds: a 33-year assessment of adjacent coastal stations. The Condor. 2012 Aug; 114(3):470–81.

66. Bolgiano NC. Changes in boreal bird irruptions in eastern Nnorth Aamerica relative to the 1970s spruce budworm infestation. The 104th Christmas Bird Count, National Audubon Society:8.

67. Dossman BC, Mitchell GW, Norris DR, Taylor PD, Guglielmo CG, Matthews SN, et al. The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology. 2016; 27(2):567–74.

68. Richardson WJ. Timing and amount of bird migration in relation to weather: a review. Oikos. 1978; 30 (2):224.

69. McKellar AE, Marra PP, Ratcliffe LM. Starting over: experimental effects of breeding delay on reproductive success in early-arriving male American redstarts. Journal of Avian Biology. 2013; 44(5):495–503.

70. Mills AM. Banding data reveal bias in age-class sampling of songbirds during spring migration. Journal of Field Ornithology. 2016 Sep; 87(3):323–36.

71. Ehnbom S, Karlsson L, Ylvén R, Åkesson S. A comparison of autumn migration strategies in robins *Erithacus rubecula* at a coastal and an inland site in southern Sweden. Ringing & Migration. 1993 Aug; 14(2):84–93.

72. Austin GE, Rehfisch MM. Shifting nonbreeding distributions of migratory fauna in relation to climatic change. Global Change Biology. 2005; 11(1):31–8.

73. Pulido F, Berthold P. Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. Proceedings of the National Academy of Sciences. 2010 Apr 20; 107 (16):7341–6.