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Avian Behavior, Ecology, and Evolution

Community science reveals biennial irruptive migration in the White-breasted Nuthatch (*Sitta carolinensis*)

Ciencia comunitaria revela migración bianual irruptiva en *Sitta calorinensis*

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ABSTRACT. The White-breasted Nuthatch (*Sitta carolinensis*) is usually considered a resident species, despite occasional reports of local movement. We show that the eastern North American population engages in regular, approximately biennial irruptive migration that extends from the northern edge of the range to as far south as the mid-Atlantic states. Both adults and juveniles take part, and neither sex nor age proportions differ between years with or without irruption. The biennial pattern is detectable in daily counts at migration concentration sites and, more subtly, across the landscape as reflected by a variety of broad-scale community science initiatives. Within northeastern North America, indices of irruption from all data sources were negatively correlated with indices of soft mast production by plant species monitored across southern and central Ontario. Perturbation in the biennial pattern of irruption coincided with change in the pattern of plant masting. Size of the breeding population was unrelated to size of irruption in the same fall, unlike the case for the Red-breasted Nuthatch (*S. canadensis*). The geographic scale and regular occurrence of irruption in White-breasted Nuthatch have likely been overlooked because migrants are widely dispersed and remain within the breeding range, where immigrants mix unnoticed with local residents. Community science programs provide opportunities for novel insights into seemingly well-known bird species, and further studies may reveal similar patterns in other temperate species thought to move only sporadically.

RESUMEN. *Sitta carolinensis* es considerado usualmente una especie residente, a pesar de reportes ocasionales de movimientos locales. Mostramos que la población del este de Norte América realiza regularmente, aproximadamente bianualmente, migración irruptiva que se extiende desde el extremo norte de su rango hasta tan al sur como los estados de Atlántico medio. Ambos, adultos y juveniles hacen parte de la migración, y ni sexo o proporciones de edad difieren entre años con o sin irrupción. El patrón bianual es detectable en conteos diarios en los sitios de concentración migratorio, más sutilmente, a través del paisaje como lo es reflejado por una variedad de iniciativas de ciencia comunitaria a gran escala. En el noreste de Norte América, los índices de irrupción a partir de todas las fuentes de datos estuvieron negativamente correlacionados con índices de producción ligera de frutos por especies de plantas monitoreadas a lo largo del sur y el centro de Ontario. Perturbaciones en el patrón bianual de la irrupción coincidió con cambios en el patrón de producción masiva de frutos en las plantas. El tamaño de la población reproductiva no estuvo correlacionado con el tamaño de la irrupción en el mismo otoño, como es el caso de *Sitta canadensis*. La escala geográfica y la ocurrencia regular de la irrupción en *Sitta carolinensis* ha sido probablemente pasada por alto porque los migrantes se dispersan ampliamente y se mantienen en el rango reproductivo, donde los inmigrantes se mezclan inadvertidamente con los residentes locales. Los programas de ciencia comunitaria proveen oportunidades para nuevas miradas a especies que aparentemente son bien conocidas y estudios futuros pueden revelar patrones similares en otras especies de zonas templadas las cuales se piensa que se mueven solo esporádicamente.

Key Words: *irruption; mast; migration; migration ecology; nuthatch; White-breasted Nuthatch*

INTRODUCTION

Irruption in birds is a form of irregular facultative migration that varies widely in magnitude and direction, depending on spatiotemporal variation in food resources or other ecological factors (Newton 2006). A wide variety of bird species irrupt, but the phenomenon has been most studied in boreal songbirds and raptors of north-temperate regions. In North America, irruptive songbirds include many finches (Fringillidae; Bock and Lepthian 1976), as well as Red-breasted Nuthatch (*Sitta canadensis*; Dunn 2019), Bohemian Waxwing (*Bombycilla cedrorum*; Witmer 2020), Varied Thrush (*Ixoreus naevius*; Wells et al. 1996) and others. These species respond to the mast cycles of coniferous and deciduous trees in the boreal forest that govern the annual production of the seeds, nuts, and fruits these birds consume. Continental patterns in temperature and precipitation act to synchronize mast production across large regions, requiring birds to travel long distances when local food resources are low (Koenig and Knops 2001, Newton 2006, Newton 2012, Strong et al. 2015).

Irruption has been less studied for species living in temperate regions, such as the White-breasted Nuthatch (*Sitta carolinensis*), and links to food resources have not been quantified. This nuthatch is usually described as resident but has long been known to appear during winter at localities where it did not breed (Forbush and May 1955), and there are scattered historical reports of migratory behavior. During autumn 1968, for example, nearly

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300 individuals were counted at a lookout in the Appalachian Mountains in Pennsylvania, actively migrating in the company of Red-breasted Nuthatches (Heintzelman and McClay 1971), and Maurice Broun reported more than 100 individuals flying past Hawk Mountain in the fall seasons of 1951, 1953, 1957 and 1959 (Broun, unpublished. data). These and most other reported movements (e.g., Miller 1979, Bradley and Bradley 1983) have generally been interpreted as local and sporadic, perhaps only representing juvenile dispersal (Grubb and Pravosudov 2020). Christmas Bird Count data from southeastern Pennsylvania often showed White-breasted Nuthatch abundance rising one year and falling the next (Bolgiano 2004), but this hint of a more regular irruptive pattern has not been examined further.

In contrast, the congeneric Red-breasted Nuthatch is well-recognized as an irruptive migrant (Dunn 2019, Ghalambor and Martin 2020). Both nuthatches are widespread across North America, although White-breasted has a more southerly range and inhabits deciduous and mixed forest rather than coniferous woodland. Both are insectivorous in summer, and in other seasons they cache seeds for later consumption, including both natural mast and seeds taken from bird feeders (Grubb and Pravosudov 2020, Ghalambor and Martin 2020).

The realization that White-breasted Nuthatch might irrupt regularly arose from community-led discussions within the Morning Flight Facebook group about observation of this species in active migration. This led us to wonder how frequent and widespread such movements might be, and whether they might be linked to variation in food supplies, as had been found for Red-breasted Nuthatch (Koenig and Knops 2011). The few quantitative data available on foods eaten by the White-breasted Nuthatch show that the proportion of seeds in the diet varies seasonally: 29% in fall, 68% in winter, and 48% in spring (Martin et al. 1951). Oak mast is an important dietary component (Williams and Batzli 1979), and patterns of oak masting are known to affect population movements in the Red-headed Woodpecker (*Melanerpes erythrocephalus*; Frei et al. 2020)

Here we investigate movements of the eastern White-breasted Nuthatch, *S. c. carolinensis*; omitting western North America because populations there are complicated by extensive cryptic diversification (Spellman and Klicka 2007, Walstrom et al. 2012), and systematic observations of visible songbird migration in that region are few. We evaluate the spatiotemporal dynamics of irruptive migration in the White-breasted Nuthatch (hereafter 'nuthatch' unless otherwise specified) using four types of community science data: visible migration counts, banding records, window collision monitoring, and several broad-scale multi-species surveys. We then compare detected movements with factors that might be associated with irruption, such as age and sex of emigrants, population levels, and food resources.

METHODS

Detecting irruption

Irruption results in increased annual counts and/or frequency of observation over expected background values, the latter reflecting any long-term population trend. For each data source described below, using the longest available set of data from 1983-2018, we calculated expected background levels by regressing indices of annual abundance or distribution on year (to second order when appropriate). Durbin-Watson tests showed whether annual indices were autocorrelated, indicative of regular alternation of low and high residuals. Residuals from the regressions represent deviations from expected numbers, both positive and negative, which we hereafter refer to as 'irruption indices.'

For migration count sites, we used abundance as the basis for calculation of irruption indices. Daily count effort in most cases was not strictly standardized, but we restricted analyses to dates in which daily effort was comparable in all years. For broad-scale multi-species surveys we examined annual variation in the proportion of seasonal records that reported presence of at least one nuthatch, because that measure varied more widely among years and regions than did mean abundance where the species was present. As our objective was limited to determining whether irruptions detected at migration count sites were also detected across the broader landscape, we used proportions that were unadjusted for observer effort, assuming that parallel fluctuation of irruption indices at local and regional scales could not reasonably be ascribed to simultaneous changes in observation effort among all survey participants.

Migration sites

Long Point Bird Observatory (LPBO)

LPBO has conducted daily migration counts each spring and fall at three locations on the north shore of Lake Erie (42.583, -80.397, Fig. 1), since 1961 and 1962 at its two longest-running sites and since 1983 at the third. From mid-April through early June, and mid-August through early November, daily counts of all birds detected within defined boundaries and hours of the day are determined by amalgamating results from mist-netting, fixed route censuses, and incidental observations (Hussell and Ralph 2005; see Birds Canada 2020 for results and analysis details). Unless otherwise specified, results reported here are limited to 1983-2018, years in which annual abundance figures represent combined data from all three sites.

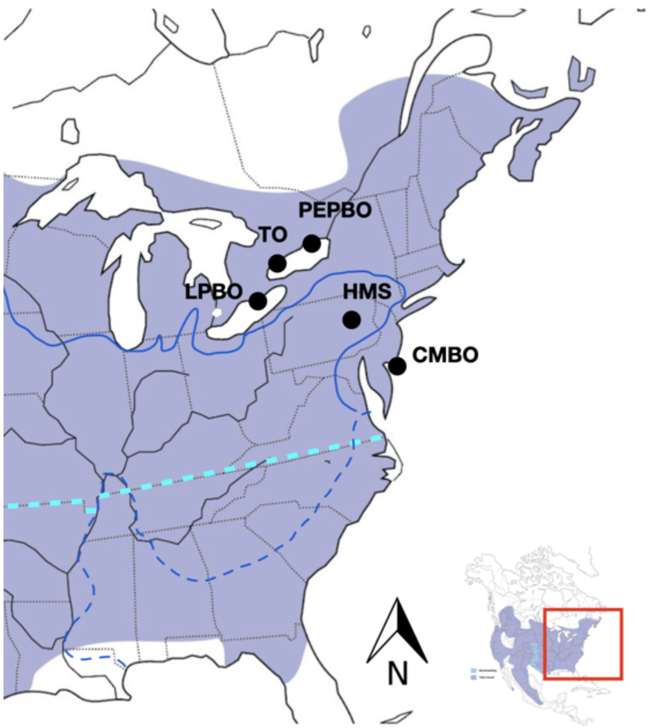
Prince Edward Point Bird Observatory (PEPBO)

PEPBO, on the north shore of Lake Ontario (43.940, -76.861, Fig. 1), employs standardized daily count procedures as described for LPBO. Annual abundance values for this site (2001-2018; Birds Canada 2020) were calculated from daily counts that combined data from standardized mist-netting and a fixed route census.

Fatal Light Awareness Program data from Toronto (TO)

FLAP Canada compiles reports of birds killed or injured by striking windows from across the country. Data are most complete for Toronto, Ontario (43.7, -79.4, Fig. 1), where the project began and many volunteers regularly search for and report casualties. We downloaded records from Bird Safe Canada's Global Bird Collision Mapper (https://birdmapper.org/app/) for all White-breasted Nuthatch found in Toronto between 29 August and 31 October 2000-2018 (n = 222). Irruption indices were based on annual totals. Because the collection comes from a small geographic area, we treated this data set as a migration count site rather than as a broad-scale survey.

Fig. 1 Year-round range of the White-breasted Nuthatch in eastern North America (Grubb and Pravosudov 2020), indicating migration count locations: Long Point Bird Observatory (LPBO), Toronto (TO), Prince Edward Point Bird Observatory (PEPBO), Hawk Mountain Sanctuary (HMS) and Cape May Bird Observatory (CMBO). Analysis regions for broad-scale surveys (see results) are indicated as follows: Northeast and Southeast Project FeederWatch regions are split by the light blue dashed line, while dark blue lines divide North, Central and South regions for eBird.



Hawk Mountain Sanctuary, Pennsylvania (HMS)

HMS (40.634, -75.986, Fig. 1) recorded non-raptor migrants passing over its North Lookout in some autumns since 1934, and in 1990 began doing so on a daily basis. Counts are conducted by one or two observers and begin no later than 08:00 EDT, and usually by 07:00 during peak passerine movement in August and September. During August and December on days with low raptor counts, the count often ends around 16:00 EDT, but during September and October it often extends past 17:00 PM EDT. All passerines are counted if they are actively flying over the mountain past the lookout or are filtering quickly through the trees in a southwesterly direction. Night-migrating passerines are often seen in early morning hours, before 09:00 EDT as they land at the ridge-top lookout and move down-slope into the forest. Peak in-flight migration tends to be observed on mornings with light northerly winds. No count is conducted in heavy rain or snow. We calculated irruption indices for nuthatch based on the annual mean daily abundance from August 15 to November 15, 1990-2018.

New Jersey Audubon's Cape May Bird Observatory (CMBO)

New Jersey Audubon's CMBO (New Jersey) conducts a Morning Flight Songbird Count from a lookout at the Higbee Beach Wildlife Management Area dike (38.966, -74.963, Fig. 1), where reorientation, or "reverse" autumn migration, is frequently observed (Wiedner et al. 1992, Van Doren et al. 2015, Van Doren et al. 2016). Daily counts begin 15 minutes before sunrise and continue until 2-4 hours after sunrise, depending on the extent of morning flight activity observed. On days with extended flights, the count is prolonged until activity tapers off. The count is suspended on days with moderate to heavy precipitation or after 30 minutes without any migratory activity. Annual irruption indices for this site were based on mean daily counts for northbound nuthatches observed from August 15 to October 31 in all years from 2003-2018.

Data from broad scale surveys

eBird

We downloaded eBird checklist data (2005-2017; both 'traveling' and 'stationary' counts) for each Bird Conservation Region (BCR) in eastern North America (eBird 2021; see Sullivan et al. 2009, 2014). We divided eastern North America into three regions (Fig. 1), based on groups of BCRs with similar rates of detection. For each of these regions, we calculated an annual irruption index (see first section of Methods) that represented the proportion of all checklists submitted in October through March that reported at least one nuthatch.

To explore seasonal variation in eBird throughout the year we calculated the annual proportion of submitted checklists that reported at least one nuthatch, for every week of the year in each of the three regions shown in Fig. 1. 'Weeks' were defined as four periods of every month, the first three made up of 7 days each, and the fourth comprised of all remaining days of the month (e.g., January 22-31). Weeks were rearranged into annual periods from July through June of the following year, to encompass the full fall and winter of each irruption event.

Étude des Populations d'oiseaux du Quebec (ÉPOQ)

ÉPOQ (Study of Bird Populations in Quebec) is an antecedent to eBird that began in 1950. Each checklist reports the number of each species detected during a single day at a single locality, an area less than one minute of latitude and longitude (about 3.2 km²; Cyr and Larivée 1993, Dunn et al. 1996). We used data collected from 1983-2018 from the region south of 48° N and west of -70° W (southwestern Quebec, covering most of the White-breasted Nuthatch breeding range in that province; Fig. 1). The irruption index for each year, as for eBird indices, was based on the proportion of checklists submitted from October through March that reported at least one nuthatch. ÉPOQ observations are included also in the eBird dataset, but the latter is limited to 2005-2017 (see above), while the Quebec data alone covers an additional 20 years.

Project FeederWatch (PFW)

Figures for the percent of feeders visited in Northeast and Southeast PFW regions during each winter (November through April) from 1990-91 through 2018-19 were downloaded from https://feederwatch.org/explore/trend-graphs/. The Northeast region includes Canada from Ontario eastward, and U.S. states east of the Mississippi River and south through Kentucky and Virginia

(Fig. 1). The Southeastern region consists of the more southern states in the east, but also extends westward through Oklahoma and Texas. Irruption indices for each region represent the proportion of all participant submissions that reported at least one nuthatch from November through March.

Banding data

The number of White-breasted Nuthatches banded annually from 1983-2019, and encounter details for individuals banded in any year between 1924 and 2020, were obtained from the USGS Bird Banding Laboratory for the portion of North America east of -90° W.

Age analyses used the same criteria for data selection as described below for LPBO, especially important for multi-site comparison because proportion of birds aged annually varied widely within and among locations.

Potential correlates of irruption

Age, sex, and condition

We compiled LPBO banding data from all three of its banding sites from 1961-2018, including mass (gm) and unflattened wing chord (mm). Analysis of fat scores was restricted to data collected from 2005 onward, the date at which LPBO began using the 7-point scale of Ralph et al. (1993). Most captured birds were aged and sexed by plumage, often with skull ossification as an additional aging character (Pyle 1997, Ralph et al. 1993). We restricted calculation of the annual proportion of fall captures that were young of the year to seasons in which > 90% of birds were aged, because ageing in fall is not straightforward (Piranga 2021) and proportions left unclassified could be biased by age class. Similarly, analysis of sex proportions was restricted to seasons in which > 90% of captured individuals were sexed.

Population size

Breeding Bird Survey (BBS) indices of abundance (birds/route) for 1966-2018 were downloaded for each Bird Conservation Region in eastern North America (Sauer et al. 2017).

Food resources

Since 1997, seed and fruit production in a wide variety of wildlife food plants has been recorded annually throughout Ontario by the Ministry of Natural Resources and Forestry. Field staff assess production of 25 plant species using a ranked qualitative scale of 0 to 4, where 0 = none or almost no seed or fruit production, 1 = below average, 2 = average, 3 = above average, and 4 = bumper crop (Potter and Obbard 2017). Annual indices for plants used by small mammals, hereafter referred to as the Ontario Mast Index (OMI), are the average scores across Ministry districts in southern Ontario for a wide range of coniferous and deciduous trees and fruiting shrubs. The survey area is approximately the portion of Ontario south of Lake Superior, which includes most of the nuthatch breeding range in the province (Fig. 1).

Statistical analyses

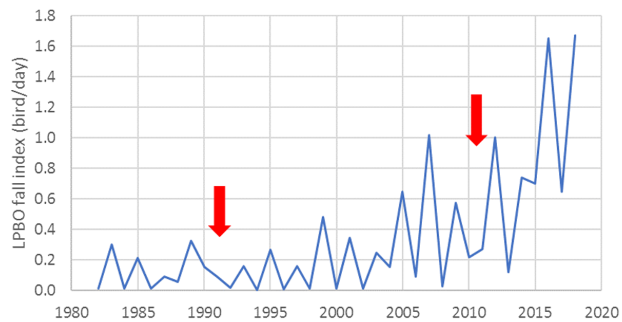
We used Spearman rank correlation for all comparisons. Significance level for results in tables are indicated by symbols: *** = $p < 0.001$., ** = $p < 0.01$, and * = $p < 0.05$. All analyses and statistical tests were done using SigmaStat v4.0.

RESULTS

Migration count sites

Fall irruption of White-breasted Nuthatch was detected regularly at LPBO, usually biennially (Fig. 2). Annual indices were significantly inversely autocorrelated (failed Durbin-Watson test, see Methods), with low years highly likely to be followed by high years and vice versa, despite the occasional disruptions indicated by arrows in Fig. 2. Irruptions generally took place in odd-numbered years, but a second consecutive low year in 2011 heralded a shift of irruption from odd-numbered to even-numbered years.

Fig. 2. Annual fall abundance (birds per day) of White-breasted Nuthatch at Long Point Bird Observatory (not detrended). Red arrows indicate sets of years that deviate from the regular two-year pattern of irruption.



Indices from all other migration count sites were also significantly autocorrelated. With the exception of CMBO, indices at all other count sites were strongly correlated and largely coincident with those at migration count sites in Canada (Table 1, Fig. 3). Large irruptions recorded in Canada were detected at HMS, but some years with modest movement were not. CMBO indices were correlated only with those from HMS, the count site nearest to it geographically, and only began to fluctuate regularly after 2010 (Fig. 3) when there was a sharp increase in numbers observed during irruption years.

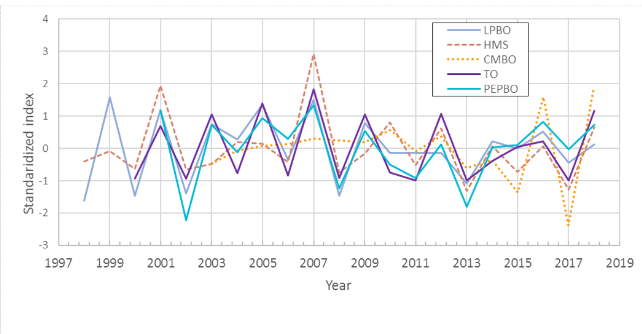
Table 1. Spearman correlation of fall irruption indices among migration count sites, shown as r, significance level (see Methods), and (n of years).

	PEPBO	TO	HMS	CMBO
LPBO	0.85*** (18)	0.79*** (19)	0.50** (29)	0.20 NS (16)
PEPBO		0.84*** (18)	0.61 ** (18)	0.35 NS (16)
TO			0.72*** (19)	0.49^{+} (16)
HMS				0.70** (16)

Long Point Bird Observatory (LPBO), Prince Edward Point Bird Observatory (PEPBO), Fatal Light Awareness Program data from Toronto (TO), Hawk Mountain Sanctuary, Pennsylvania (HMS), New Jersey Audubon's Cape May Bird Observatory (CMBO)

The degree of correlation among count locations allows us to use a single site as a reference point for further analyses because data from correlated locations should show the same patterns. We chose LPBO because irruption years there coincided with those

Fig. 3. Standardized fall irruption indices of White-breasted Nuthatch at migration count sites.
Note: Long Point Bird Observatory (LPBO), Hawk Mountain Sanctuary (HMS), New Jersey Audubon's Cape May Bird Observatory (CMBO), Fatal Light Awareness Program data from Toronto (TO), Prince Edward Point Bird Observatory (PEPBO)



in other Canadian counts, it had banding data relevant to analysis of irruption with respect to age and morphometric factors, and it is the only site with data from both fall and spring.

Irruptive movements might be displayed as movement of large numbers within a few days, as increase in days of occurrence without any rise in daily numbers, or as a combination of both. At LPBO there were increases both in observation days and in the number of birds observed on such days (Table 2), with few days of unusually high counts. Daily totals >10 were observed on 11.6% of days when the species was present (n = 683), with 25 or more seen on only 1.5% of days. Other fall migration count sites typically recorded low daily numbers as well. Daily counts were < 10 on 99% of count days at CMBO on which the species was recorded (n = 864) and on 99.8% of such days at HMS during the study period (n = 1224). Nuthatch casualties for Toronto were not suitable for daily analysis, but the average total recorded during fall migration was ten times higher in years with irruption than in years with no movement (21.1 vs 2.3 per season, respectively).

In years with no movement at Long Point, the few nuthatches observed were most often seen in the latter half of September (Fig. 4). September observations increased during years with at least some movement, but irruption movements were most obvious throughout October. Timing similar to that at LPBO was recorded at other Canadian count sites and at HMS, while at CMBO activity was greatest in the second half of October.

Spring observations fluctuated in parallel with those of the previous fall: low numbers when there had been no fall movement and vice versa (Table 2, Fig. 4). Spring counts were lower than in fall, but fall-spring pairs of irruption indices were strongly correlated (r = 0.87, p < 0.001, n = 35).

Broad-scale surveys

Annual indices for all broad-scale surveys were autocorrelated, as already described for migration count indices. Fall irruption indices from LPBO were significantly positively correlated with indices from the northern regions of Project FeederWatch and eBird but not for indices from more southern areas (Table 3. see Fig. 1 for regional boundaries). Although data from EPOQ for 2005 onward are duplicated in eBird, the correlation for non-overlapping years (1983-2004) is the same as shown in Table 3. Irruptions clearly reach northern portions of the eastern U.S., but may only sporadically extend into the central portion of the eastern U.S. and rarely, if ever, reach the most southern states.

Table 2. Frequency of observation and daily numbers of White-breasted Nuthatch at the tip of Long Point, Ontario 1983-2018 in relation to three levels of Long Point Bird Observatory fall irruption index. Levels = Low (indices < -0.5), Medium (-0.5 to 0.5), and High (indices > 0.5). Spring index levels are those for the preceding fall.

Season	Level of irruption index (n years)	Mean N days recorded	Mean daily count when present	Maximum daily count
Fall	Low (12)	3.4	1.2	3
	Medium (10)	16.6	3.5	30
	High (13)	33.4	5.0	51
Spring	Low (12)	3.0	0.9	2
	Medium (9)	7.7	1.6	6
	High (14)	16.4	2.4	40

Fig. 4. Timing of White-breasted Nuthatch migration at the eastern tip of Long Point, Ontario (1983-2018), expressed as the proportion of years in which the species was detected on a given date, separated by level of irruption index. Levels = Low (indices < -0.5), Medium (-0.5 to 0.5), and High (indices > 0.5). Spring index levels are those for the preceding fall.

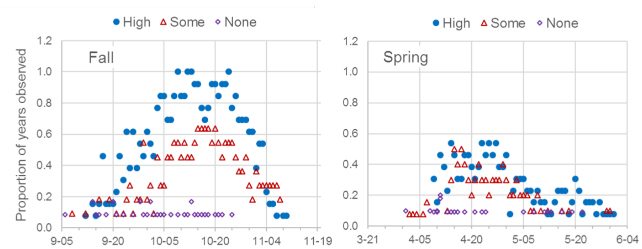


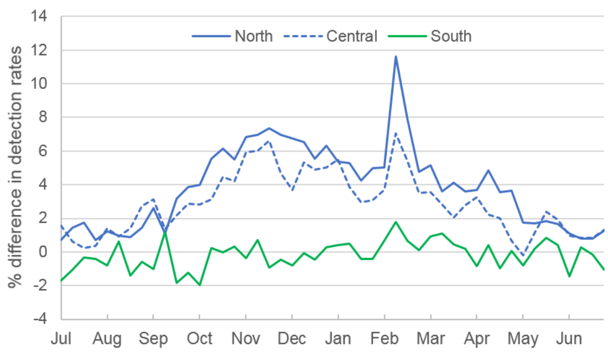
Table 3. Correlation between fall irruption indices at Long Point Bird Observatory and those from broad-scale, multi-species surveys. See Figure 1 for regional boundaries.

Survey and region	r, significance (n years)
ÉPOQ - Quebec	0.62*** (36)
eBird - North	0.73** (13)
eBird - Central	0.39 NS (13)
eBird - South	-0.49 * (13)
PFW - Northeast	0.47 * (29)
PFW - Southeast	-0.02 NS (29)

Étude des Populations d'oiseaux du Quebec (ÉPOQ), Project FeederWatch (PFW)

This conclusion is further bolstered by the weekly eBird data in Fig. 5. In the South eBird region, where White-breasted Nuthatch is reported on about 8% of checklists submitted from October through March, there is no difference in reporting rate between irruption and non-irruption years at LPBO. In the Central and North eBird regions, the species is reported to eBird in non-irruption years on 29% and 39% of checklists, respectively; rates that increase during irruption years by 2-6% in the Central region and slightly more in the North (Fig. 5). Elevated observation rates persist for the entire period between fall irruption and the following spring.

Fig. 5. Difference in the weekly percent of eBird checklists reporting White-breasted Nuthatch between years with positive vs. negative fall irruption indices at Long Point, Ontario (2005-2017). Regions are groups of geographically contiguous Bird Conservation Regions, divided geographically as indicated in Figure 1. (The spike in February reflects the influx of reports from the Great Backyard Bird Count).

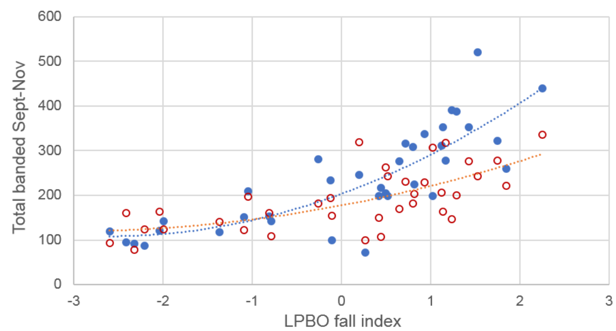


Project FeederWatch data mirror the eBird results. in the Northeast PFW region (Fig. 1), nuthatches were reported on 75% of checklists in years with negative irruption indices at LPBO and on 80.5% of lists from irruption years; a small difference that is nonetheless reflected in significant autocorrelation of PFW indices and positive correlation between PFW and LPBO indices. In the Southeast PFW region, White-breasted Nuthatch was detected at 39% of feeders regardless of irruption level at LPBO.

Banding data provide yet another data source that reflects the extent of irruption. A total of 15,496 nuthatches were banded in 1983-2018 from September through November at all sites in eastern North America combined. Increased numbers were banded in years with positive irruption indices at LPBO (Fig. 6), particularly so in the area north of 42° (the approximate northern border of Pennsylvania, the state in which HMS is located; Fig. 1). In years with negative irruption indices at LPBO, mean numbers banded in the south vs. the north did not differ (135 vs. 134 respectively). In irruption years, numbers banded rose significantly in both regions, and significantly more so in the north than in the south (299 and 226, respectively; (ANOVA $p < 0.001$).

Despite the widespread increase in nuthatch detection during irruption years, it is unclear how far individual birds might move. Of 2904 encounters of birds banded in eastern North America, 35 (1.2%) were encountered more than 100 km from the banding site. However, few of those were encountered in the same fall/winter season as when banded, such that the movements cannot be ascribed to a particular year. The only case of a bird certain to have moved within a single season was an adult banded in Maine in August 1965 (an irruption year at LPBO) and encountered in Connecticut six weeks later, having traveled 525 km (USGS Bird Banding Laboratory).

Fig. 6. Total number of White-breasted Nuthatch banded annually in eastern North America from September through November (1983-2018) in relation to fall irruption indices at Long Point, Ontario. Numbers are divided into those banded north or south of 42°N.



Correlates of irruption

We examined age and sex proportions in the fall sample of all White-breasted Nuthatch banded east of -90° and north 42°N (see Fig. 6), and for birds captured at LPBO alone, in all cases restricting analysis to seasons that qualified for inclusion (see Methods).

For the broad-scale sample, only seven years qualified for analysis of sex proportions. Of the 1225 birds banded in these years 42% were female, a figure that did not differ between years with and without irruption at LPBO (Chi-Square $p > 0.5$, n= 740 and 485, respectively). For birds captured at LPBO alone, females made up 52% of captures in fall (n = 847; 35 qualifying years) and 51% in spring (n = 448; 31 years), also with no difference between seasons or between years with positive of negative fall irruption indices (Chi-Square $p > 0.5$ for all comparisons).

Based on evidence already presented that irruptions vary in southern extent, we limited analysis of age to banding data from north of 42°N to minimize possible bias in age composition by combining years with differing proportions of irruptive vs. local individuals. Only 11 fall seasons from the broad-scale sample qualified for analysis (see Methods). Out of 3024 birds banded, 68% were in their hatch year, and there was no difference in that percentage between years with positive vs. negative irruption indices at LPBO (68 vs. 66%; Chi-Square p = 0.59, = 2533 and 491).

For birds captured in fall at LPBO alone (n = 648 from 26 qualifying seasons), age proportions differed according to irruption size. Hatch year percentage was 69% in irruption years, close to the 68% found in the regional sample. It increased to 89% in years without any movement, largely due to reduced capture of adults (Table 4, Chi-Square $p < 0.001$). Few adults are seen on the Long Point peninsula except during irruption, whereas young of the year are present in all years, perhaps reflecting juvenile dispersal. Whatever the reason, the banding data both from LPBO and from the wider landscape indicate that adults, as well as young of the year, take part in irruptions.

Table 4. Age of White-breasted Nuthatch captured in fall by Long Point Bird Observatory (LPBO) (1983-2018) in years with positive or negative fall irruption indices.

LPBO irruption index	Hatch year n	Adult n	Total aged	Percent HY
Negative	218	27	245	89%
Positive	277	126	403	69%

We found no within-sex differences in wing-length of birds captured at LPBO according to age or season (Table 5; ANOVA pairwise multiple comparison). Mass, an indicator of body condition, also did not differ by sex, age, or season when all samples were combined. However, mean mass in springs that followed fall irruption was significantly elevated relative to years with no fall movement (Table 6, $F_{(1,670)} = 59.4$, $p < 0.001$). Average fat score in fall of years with positive abundance indices was 1.6 on a 7-point scale (n = 430), while birds caught in the following springs had a mean fat score of 2.5 (n = 86), suggesting birds were in good condition after irruption winters. However, there were too few data for springs following years of no irruption to provide a comparison.

Table 5. Mass and wing chord of White-breasted Nuthatch captured at Long Point Bird Observatory, shown as mean + SEM (n). Data from all banding sites, 1983-2018

Season	Sex	Age	Mass (gm)	Wing chord (mm)
Fall	F	AHY	20.2 ± 0.18 (56)	88.1 ± 0.32 (57)
		HY	20.2 ± 0.10 (271)	88.4 ± 0.12 (277)
Fall	M	AHY	21.0 ± 0.22 (101)	89.4 ± 0.32 (103)
		HY	20.5 ± 0.11 (194)	89.7 ± 0.14 (196)
Spring	F	AHY	20.9 ± 0.15 (104)	88.8 ± 0.21 (104)
Spring	M	AHY	21.3 ± 0.14 (117)	89.5 ± 0.22 (119)

Table 6. Mass ± SEM of White-breasted Nuthatch captured at Long Point Bird Observatory (all sites, 1983-2018) in years with positive or negative fall irruption indices. Spring data are grouped by the preceding fall index.

LPBO index	Mass in fall	Mass in following spring
Positive	20.3 ± 0.05 (573)	21.1 ± 0.10 (216)
Negative	20.5 ± 0.12 (93)	20.7 ± 0.31 (35)

LPBO irruption indices for White-breasted Nuthatch were unrelated to detrended Breeding Bird Survey indices for any of the ten Bird Conservation Regions within the eastern North American breeding range (all correlations with p < 0.05, n = 35 years).

Irruption indices from all sources other than Cape May, both site counts and broad-scale surveys, were significantly negatively correlated with Ontario Mast Index production indices (Table 7). The pattern of opposite fluctuation in OMI and irruption indices was particularly consistent among the migration sites in Ontario (Fig. 7). Biennial alternation was perturbed in 2011 when OMI increased for the second year in a row (arrow in Fig. 7). This was simultaneously mirrored by two successive years without irruption at migration count sites, resulting in a shift of irruptions at Canadian count sites from odd-numbered to even-numbered years. HMS indices were also negatively correlated with OMI, but those at CMBO were not (Table 7).

Fig. 7. Patterns of fluctuation in standardized indices from the Ontario Mast Index (OMI) and from migration count sites in Canada. The arrow indicates the year in which the biennial patterns of irruption and mast production simultaneously shifted by a year.
Note: Long Point Bird Observatory (LPBO), Fatal Light Awareness Program data from Toronto (TO), Prince Edward Point Bird Observatory (PEPBO)

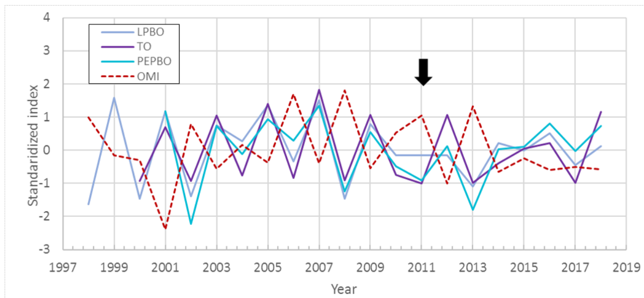


Table 7. Data sets with significant correlation between irruption indices and the Ontario Mast Index.

Data set	r, significance (n years)
LPBO	-0.54 * (21)
TO	-0.63 ** (19)
PEPBO	-0.64 ** (18)
HMS	-0.53 * (21)
ÉPOQ - Quebec	-0.68 ** (21)
eBird North	-0.58 * (13)
PFW Northeast	-0.53 * (21)

Long Point Bird Observatory (LPBO), Fatal Light Awareness Program data from Toronto (TO), Prince Edward Point Bird Observatory (PEPBO), Hawk Mountain Sanctuary (HMS), Étude des Populations d'oiseaux du Quebec (ÉPOQ), Project FeederWatch (PFW)

DISCUSSION

Irruption in the White-breasted Nuthatch is similar to that of the Red-breasted Nuthatch (Dunn 2019) in that LPBO irruption indices for the two species are strongly correlated with each other (r = 0.68, p < 0.001, n = 36 years), timing of movements is similar, adults as well as juveniles take part, and both show evidence of spring return. A major difference, however, is that irruption in the Red-breasted Nuthatch is more likely to occur when the breeding population is high, and irruptions are often followed by a reduction in breeding population (Dunn 2019). We found no support for either of these associations in White-breasted

Nuthatch but did find a strong relationship to an index of mast production by plants in Ontario. Such a link has long been suggested (e.g., Forbush and May 1955), but until now this has not been supported with quantitative data.

The pattern of high OMI in even-numbered years changed in 2011 when there was a second year in a row of high mast production. At the same time, irruption indices at migration count sites were low for two years in succession (Fig. 7). Prior to the start of Ontario's mast surveys there were additional changes in irruption patterns at LPBO, one in 1991 (Fig. 2) and two in the 1960s. Continued data collection is therefore likely to record future perturbations, allowing stronger tests of direct links between food resources and irruption.

Berry and seed crops of wild plants in Ontario are inversely related to production levels in the previous year and independent of weather conditions, suggesting that their approximately biennial alternation of high and low mast years reflects energy budgeting and/or adaptive strategies intrinsic to the plants themselves (Howe et al. 2012). The factors causing two sequential low years in the OMI (Fig. 7) are unknown, but as 25 tree and shrub species were affected simultaneously (Potter and Obbard 2017), the shift probably resulted from an unusual set of environmental conditions affecting a wide area.

The immediate shift in nuthatch irruption patterns to match the new pattern in masting provides strong circumstantial evidence that nuthatch irruption is a response either to plant conditions themselves or to another, closely correlated factor. Facultative migrants are known to make the decision to emigrate well before movements begin (Ramenofsky et al. 2012), such that actual food shortage is not experienced directly, but birds might assess plant condition to predict future food supplies or perhaps respond to changes in insect abundance that are themselves related to plant production (Selås et al. 2001).

OMI and irruption indices from all migration count sites in Ontario were closely linked, but irruption in Ontario was not always detected at migration count sites further south. Birds counted at HMS and CMBO are engaged in morning flight, which is strongly affected by wind conditions (Van Doren et al. 2016). Studies of raptor migration at both these sites have shown that wind effects add considerable variance to annual indices (Farmer et al. 2007), and wind-related variance might underlie some of the misalignments with LPBO indices. Finally, data both from eBird and Project FeederWatch indicate that irruptions do not extend much beyond the mid-Atlantic states, so there is probably annual variation in the proportion of irrupting individuals that move as far south as HMS or CMBO.

It is hardly surprising that the extent and regularity of widespread irruption of this species have previously gone unrecognized. Except at migration count sites where birds are concentrated, nuthatches are dispersed throughout the landscape and small increases at any one location go unnoticed against the backdrop of local residents. Red-breasted Nuthatches are known to migrate both diurnally and nocturnally and the same is believed to be true of White-breasted Nuthatch (Evans and O'Brien 2002). The species is thought to be mostly silent in nocturnal flight, like many other nocturnal migrants, but nocturnal flight calls were recently recorded during a fall irruption (2022 update in Evans and O'Brien 2002). Nocturnal migration might explain the propensity to engage in reoriented migration at Cape May's Higbee Beach count site and also the high frequency of White-breasted Nuthatch window collisions in Toronto. Diurnal migration may also occur, however, and some observers in the interior of the continent have detected birds actively migrating in daylight, sometimes at altitudes at the limits of visibility using binoculars (Evans 2021, PH and LG, Gavin Aquila personal communication).

Our results suggest fruitful areas for additional research. Finer geographic analysis of eBird and Project FeederWatch data and radio-tracking of individuals could help determine whether White-breasted Nuthatch movements are restricted to individuals from northern and high elevation regions, document the directions and distances they travel, and determine the proportion of emigrants that return to their original breeding area. We have no explanation for the significant decline in eBird observation rate in the southernmost U.S. during irruption years (Table 3). In the West, the Pacific and Rocky Mountain subspecies should be examined, especially given their status as potentially distinct species (Spellman and Klicka 2007, Walstrom et al. 2012).

Analyses similar to ours could more thoroughly document the geographic extent and regularity of movement in other species that have been described as irruptive in northern portions of their range, such as Downy Woodpecker (*Dryobates pubescens*; Yunick 2019), Blue Jay (*Cyanocitta cristata*; Smith 1986), and Black-capped Chickadee (*Poecile atricapillus*; Bagg 1969, Hussell 1996, Bolgiano 2004). The link we found between White-breasted Nuthatch irruption and annual indices of mast production in Ontario could be tested for other species as well. Combining community science data from long-term migration counts, banding sites, and broad-scale surveys makes a powerful combination for discovering patterns and testing hypotheses that cannot be addressed using single data sources alone.

Responses to this article can be read online at:
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Author Contributions:

JG, AD, and PH compiled and explored numerous data sources before recruiting additional co-authors. ED finalized analyses and led the writing, which involved all authors in discussion and revision.

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Data Availability:

Data analyzed in this work are from publicly accessible community science sources.

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