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Demographic trends for the Boreal Owl, *Aegolius funereus*, using standardized migration monitoring data in eastern North America

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ABSTRACT

Many boreal species have declined during recent decades in North America. Various indexes suggest that populations of the Boreal Owl *Aegolius funereus* are declining across North America, but very few long-term, standardized monitoring schemes allow for reliable assessment. We combined various datasets monitoring Boreal Owls in eastern North America to assess its population trend. Using autumn migration monitoring from 1996 to 2023 at Tadoussac (Québec, Canada) and Whitefish Point (Michigan, USA), we assessed population trends with Bayesian hierarchical generalized linear models. We also analyzed the trends in the proportion of juveniles and body condition over time. We correlated migration monitoring with participatory science observations recorded throughout the year to assess Boreal Owl population trends in eastern North America. We observed a dynamic of four-year cycles and a longer-term decline in relative abundance for both the total number of captured individuals and the number of juveniles alone. The proportion of juveniles and mean body condition both varied annually but showed stable trends over time. However, we detected a reduction in the recorded fat score over time, suggesting that conditions encountered in the boreal forest could be deteriorating. This study provides population trends for the Boreal Owl, an important bioindicator of the boreal ecosystem, and could ultimately support and orient the development of future monitoring projects during the breeding period.

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Aegolius funereus; dynamique des populations cycliques; indice de condition corporelle; indice de succès reproducteur; Nyctale de Tengmalm

Tendances démographiques pour la Nyctale de Tengmalm, *Aegolius funereus*, à partir de données normalisées de surveillance des migrations dans l'est de l'Amérique du Nord

RÉSUMÉ

De nombreuses espèces boréales ont connu un déclin au cours des dernières décennies en Amérique du Nord. Différentes études suggèrent que les populations de nyctales de Tengmalm (*Aegolius funereus*) sont en déclin en Amérique du Nord, mais très peu de programmes de suivi normalisés et à long terme permettent une évaluation fiable. Nous avons combiné divers ensembles de données de suivi des nyctales de Tengmalm dans l'est de l'Amérique du Nord afin d'évaluer la tendance de sa population. Grâce au suivi des migrations automnales de 1996 à 2023 à Tadoussac (Québec, Canada) et à Whitefish Point (Michigan, États-Unis), nous avons évalué les tendances démographiques avec des modèles linéaires généralisés hiérarchiques bayésiens. Nous avons aussi étudié la proportion de juvéniles et de la condition corporelle au cours des dernières décennies. Nous avons corrélé le suivi des migrations avec les observations de science participative enregistrées tout au long de l'année afin d'évaluer la tendance de la population de nyctales de Tengmalm dans l'est de l'Amérique du Nord. Nous avons observé une dynamique cyclique de quatre ans et un déclin à plus long terme de l'abondance relative, tant pour le nombre total d'individus capturés que pour le nombre de juvéniles. La proportion de juvéniles et l'indice moyen de condition corporelle variaient tous deux annuellement, mais présentaient des tendances stables au fil du temps. Cependant, nous avons détecté une diminution du taux de gras enregistré au fil du temps, ce qui suggère que les conditions rencontrées dans la forêt boréale pourraient se détériorer. Cette étude fournit des tendances démographiques pour la nyctale de Tengmalm, un bioindicateur important de l'écosystème boréal, et pourrait à terme appuyer le développement de futurs projets de surveillance pendant la période de reproduction.

The diverse suite of bird species inhabiting the boreal forest can be sentinels of this fragile ecosystem and many avian populations have undergone declines in abundance over the last decades in North America (Sauer et al. 2013, 2020; Rosenberg et al. 2019). Some key species of the boreal forest are showing alarming trends in recent years (Niven et al. 2004; Rosenberg et al. 2019; Virkkala et al. 2023). The causes of these declines remain largely unknown and global environmental changes (e.g., increases in temperature, precipitation, and extreme climatic events such as forest fires) are likely to affect birds throughout their life cycle (Stralberg et al. 2015; Cadieux et al. 2020). In addition, abiotic and biotic factors (e.g., wildfires, spruce budworm infestations) can affect the entire food web (Weed et al. 2013) and could exacerbate the threats birds face (Venier and Holmes 2010; Drever et al. 2018; Žmihorski et al. 2019). In particular, human influence such as intensive forestry and global climate change seem very harmful to some species (Korpimäki and Hakkarainen 2012; Brambilla et al. 2020; Virkkala et al. 2023). However, precise and reliable information is sometimes lacking, which limits our ability to address the threats boreal species face

(Stralberg et al. 2015). It is therefore important to assess demographic trends of boreal forest species.

The Boreal Owl, *Aegolius funereus*, is a small, nocturnal, cavity-nesting bird of prey, inhabiting the boreal forest across North America and Eurasia (Hayward and Hayward 2020). The species is known to exhibit winter irruptions, where several individuals move south of their boreal forest range during the non-breeding season (Hayward and Hayward 2020). This phenomenon is most likely linked to fluctuating food availability on their boreal forest breeding grounds (Newton 2006). Throughout the year, its diet is largely composed of small mammals and it is therefore sensitive to annual variations in rodent abundance (Cheveau et al. 2004; Côte et al. 2007). Classified as “Least Concern” by the International Union for Conservation of Nature, the Boreal Owl is a sensitive species and an important bioindicator of boreal forest health (Hayward et al. 1993). In North America, the Boreal Owl has exhibited an alarming decline of 10% per year between 1993 and 2015, according to the Breeding Bird Surveys (Sauer et al. 2017), although this monitoring program alone might not capture the population trend precisely in this species. Life history traits and population trends are well documented in Fennoscandia (e.g., Korpimäki and Hakkarainen 2012), but limited information exists about population status for the species across North America (Hayward and Hayward 2020).

Several sources of information could provide insights into vital rates and population trends of North American birds (Meehan et al. 2022). Banding stations using standardized protocols during migration provide relative abundance, proportion of age classes (which can serve as an index of breeding success), and individual body condition indexes annually (e.g., Wall et al. 2020; Van Brempt et al. 2023). By combining this information with participatory science observations throughout the year such as eBird (Sullivan et al. 2014), Breeding Bird Surveys (BBS) (Sauer et al. 2017), and Christmas Birds Counts (CBC) (Niven et al. 2004), scientists can draw a global understanding of population trends, age structure and body condition (Meehan et al. 2022). Here we aim to assess trends in relative abundance, proportion of juveniles, and body condition for the Boreal Owl using all available sources of information across eastern North America.

Methods

The long-term autumn migration monitoring banding stations of Tadoussac Bird Observatory (hereafter Tadoussac), located in Tadoussac, Québec, Canada (48°9'27"N 69°39'52"W), and Whitefish Point Bird Observatory (hereafter Whitefish), located at Whitefish Point, Michigan, USA (46°13'14"N 84°57'26"W) provided data from 1996 to 2023 and 1995 to 2022, respectively. Both sites are located at the southern edge of the boreal forest and the Boreal Owl breeding range (Hayward and Hayward 2020). Boreal Owls are not present at either site during the breeding season. At both sites, Boreal Owls were captured, banded with aluminum bands (Bird Banding Lab), and measured (mass, wing length) using a standardized protocol. Boreal Owls are one of the most dimorphic owls, with females being larger than males (Hayward and Hayward 1991). However, there is currently no reliable sexing protocol for this species (Hipkiss 2002, 2007), and in the absence of genetic analysis, we couldn't calculate the sex ratio.

Capture sessions occurred annually from 1 September to 30 October at Tadoussac and 14 September to 30 October in Whitefish, using an array of mist-nets and an audio lure. In

Tadoussac, activities began 1 h after sunset and continued for a period of 7 h after nets were opened, unless weather conditions did not allow it. Individuals were identified either as juveniles (no molt; hatch-year: HY) or adults (molted flight feathers; all other age classes) using molt pattern described in Korpimäki and Hakkarainen (2012). Details on net arrangement and banding protocols are described further in Côte et al. (2007). At Whitefish, activities began 30 min after sunset and concluded 30 min prior to sunrise, unless inclement weather conditions prevented nets from being opened.

Population trends from captures

We assessed inter-annual relative abundance of Boreal Owls as the number of individuals captured during autumn migration per unit effort (500 mist-net hours). We used Bayesian hierarchical generalized linear models to estimate population trends and population cycles of Boreal Owl separately at the two sites. We created a null model that included an offset to account for sampling effort (*EFFORT*). Including an offset is mathematically equivalent to dividing the response variable by the offset, thereby correcting relative abundance for survey effort. Model predictions of relative abundance of Boreal Owls represented the number of owls captured per 500 mist-net hours.

We used posterior predictive checks to evaluate which statistical distribution provided the best goodness-of-fit to the data including Poisson, negative binomial, and zero-inflated Poisson distributions with the global models (described below). We assumed the distribution with a Bayesian *P*-value (hereafter BP) closest to 0.50 provided the best model fit. We favor parsimony and preferred simpler distributions with fewer parameters when no difference in fit was observed. The Poisson distribution provided the best goodness-of-fit ($BP_{Tadoussac} = 0.57$, $BP_{Tadoussac \text{ juveniles}} = 0.46$, and $BP_{Whitefish} = 0.76$), whereas negative binomial ($BP_{Tadoussac} = 0.57$, $BP_{Tadoussac \text{ juveniles}} = 0.60$, and $BP_{Whitefish} = 0.82$) and zero-inflated Poisson ($BP_{Tadoussac} = 0.66$, $BP_{Tadoussac \text{ juveniles}} = 0.57$, and $BP_{Whitefish} = 0.78$) provided poorer fit. Therefore, we retained the Poisson distribution for further analysis modeling the capture data (y) as $y_t \sim Poisson(\gamma_t)$ where y are the data and γ is the mean estimated count during each time step (t).

We observed temporal cycles in the data and autocorrelation plots suggested a period of about 4 years at both sites (Fig. 1). We created an explanatory variable named CYCLE to model cyclic data and estimate population cycles having a four-year periodicity to avoid confounding population trends. CYCLE is scaled so that every 4 years is equal to one unit of CYCLE (e.g., 8 years = $8/4 = 2$ CYCLE units). This allowed the modeling of cyclical data using standard regression methods (Crawley 2012). To estimate these cycles, we began with a null model that included four year cycles as:

$$\log y_t = \delta_0 + \log(EFFORT_t) + \delta_1 \cos(2\pi CYCLE_t) + \delta_2 \sin(2\pi CYCLE_t).$$

Here, δ is a vector of model estimated coefficients where δ_1 and δ_2 influence the amplitude and phase shift of cycles and $\log(EFFORT)$ is the offset term.

We expanded the null model to create a global model that included all covariates. We included population cycles with 4-year periodicity, quadratic polynomial of year to estimate long-term trends (*YEAR* and $YEAR^2$), and interactions between cycles and long-term trends as:

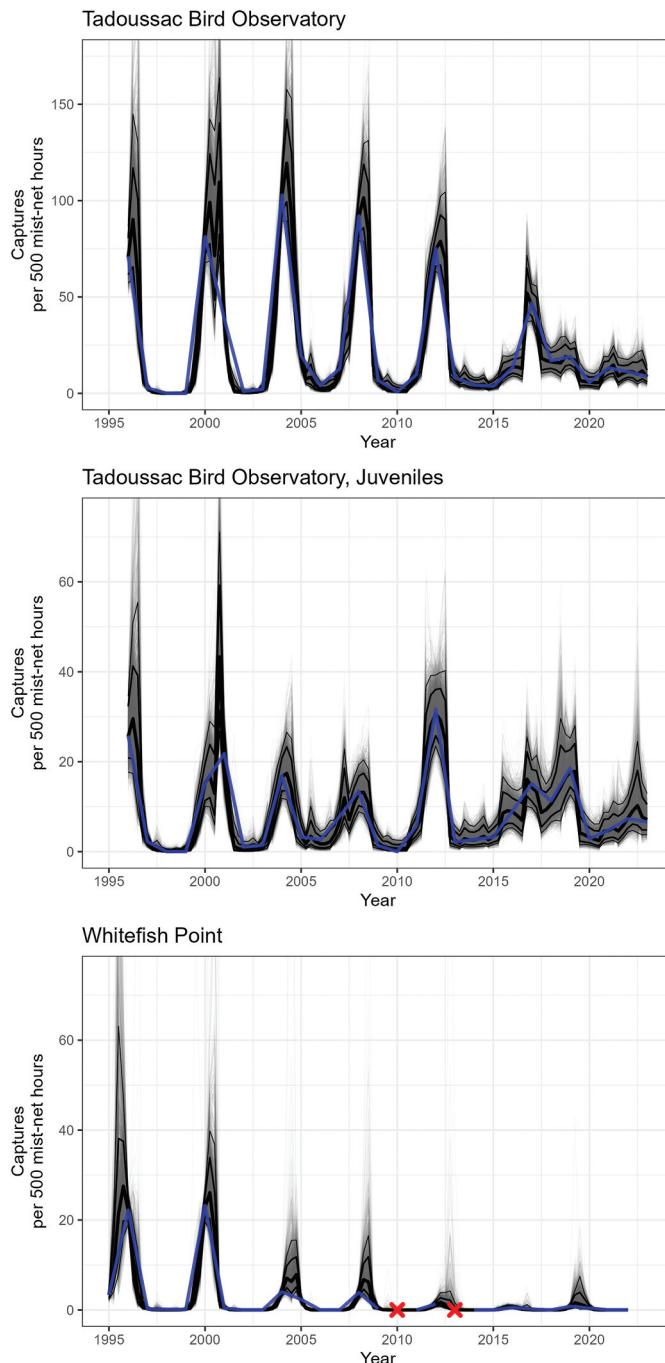


Figure 1. Abundance of Boreal Owls (number captured per 500 mist-net hours) during autumn migration from 1996 to 2023 at Tadoussac Bird Observatory (QC, Canada) for all captured birds and juveniles only and from 1995 to 2022 at Whitefish Point (MI, USA) and predictions from model (Table 1). Blue lines depict data of Boreal Owl captures divided by effort. Black lines depict predictions from the model including medians (thickest), 80% (medium), and 95% (thinnest) highest posterior density intervals. Transparent gray lines depict the 4,000 posterior draws from the model. Red points in the shape of an "x" depict years without capture effort. A random effect of year was included in model predictions by rounding to the nearest predicted year for years without capture effort.

$$\begin{aligned}
 \log(y_t) = & \delta_0 + \log(EFFORT_t) + \delta_1 \cos(2\pi CYCLE_t) + \delta_2 \sin(2\pi CYCLE_t) + \delta_3 YEAR_t \\
 & + \delta_4 YEAR_t^2 + \delta_5 \cos(2\pi CYCLE_t) YEAR_t + \delta_6 \sin(2\pi CYCLE_t) YEAR_t \\
 & + \delta_7 \cos(2\pi CYCLE_t) YEAR_t^2 + \delta_8 \sin(2\pi CYCLE_t) YEAR_t^2 \\
 & + \varepsilon_t \text{ and } \varepsilon_t \sim normal(0, \sigma)
 \end{aligned}$$

We calculated the probability of direction for each covariate from global models that included all covariates for each site. The probability of direction tests for the existence of an effect and tends to be correlated with frequentist *p*-values (Makowski et al. 2019). We assigned covariates as having an existing effect when the probability of direction was ≥ 0.975 . We retained covariates when an effect existed, and we retained highest order polynomials having an effect along with all corresponding lesser order polynomials (Zar 1999) for further inference.

We implemented models using Bayesian methods in NIMBLE v1.0.1 (de Valpine et al. 2017) with R version 3.6.1 (R Core Team 2023) as an interface. We implemented each model using four chains with each having $\geq 10,000$ burn-in and $\geq 20,000$ posterior iterations. We thinned posterior iterations from each chain by retaining one of ≥ 10 iterations totaling 4,000 draws for each posterior distribution. Thinning this way avoided autocorrelation between posterior draws and increased effective sample sizes from the posterior. For final model runs and to achieve convergence for more complex models (i.e., zero-inflated Poisson), we increased the number of iterations as needed for burn-in, posterior draws, and thinning. We assessed convergence of posterior chains using traceplots, density plots, and Gelman-Rubin diagnostic (\hat{R} , Gelman and Rubin 1992), and we assigned adequate convergence when traceplots of parameters did not visually appear to drift and $\hat{R} \geq 1.1$. We used vague prior distributions for model-estimated probabilities of $\sim \text{beta}(1, 1)$; weakly informative prior distributions for standard deviations associated with random effects as $\sim \text{uniform}(0, 10)$; and weakly informative prior distributions for regression coefficients as $\sim \text{normal}(\text{mean} = 0, \text{SD} = 10)$. Code for implementation and postprocessing of Bayesian models is archived online (<https://github.com/The-Peregrine-Fund/Boreal-Owl-Population-Trends>).

Proportion of juveniles

We assessed the annual proportion of juveniles (all things being equal, this serves as an annual index of reproductive success; e.g., Santonja et al. 2018) using the age-class ratio of captured individuals at Tadoussac. We calculated the proportion of juveniles as the number of first-year individuals divided by the total birds captured.

Body condition

We used the “scaled mass index” (Peig and Green 2010) to assess yearly mean body condition of birds captured at Tadoussac. This index is particularly recommended when considering individuals belonging to different age classes (Peig and Green 2010). Sexual dimorphism does not affect the index value. The scaled mass index, \hat{M}_i , standardizes body mass (± 0.01 g) at a fixed value of a linear body measurement based on the scaling relationship between mass and length, according to the equation:

$$\hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$$

where M_i and L_i are the body mass and linear body measurement of individual i, respectively; b_{SMA} is the scaling exponent estimated by the standardized major axis (SMA) regression of $\ln M$ on $\ln L$; L_0 is an arbitrary value of L (e.g., the arithmetic mean value for the study population); and \hat{M}_i is the predicted body mass for individual i when the linear body measure is standardized to L_0 . The scaled mass index was calculated for the population using wing chord as a linear measure of size positively related to body mass (Spearman correlation coefficient: $r = 0.705$, $p < 0.001$). We computed an index of body condition for every individual and took the mean of the values annually. Data met the assumptions of linearity, homoscedasticity, and normality of residuals. Linear regression of body condition against year used annual means weighted by the annual sample size. Because of the low abundance of captured individuals in 1998, 1999, and 2010, we excluded these years from the analysis. After the year 2000, we scored body fat (index ranging from 1-thin to 3-fat; Labocha and Hayes 2012) for each captured individual. Linear regression of scored body fat was weighted by the annual sample size to account for the annual difference in individuals sampled. We took the mean of these values annually and correlated them with the scaled-mass index. Again, data met the assumptions of linearity, homoscedasticity, and normality of residuals.

Participatory science

We used participatory science observations of Boreal Owls collated in eBird across Eastern North America (longitude: -97.8 to -57 , latitude: 29 to 62 ; eBird Basic Dataset, Version: ebd_relSep-2024. Cornell Lab of Ornithology, Ithaca, New York; Fink et al. 2020) and Christmas Bird Counts (National Audubon Society 2020) throughout their annual cycle from 1996 to 2023 to correlate with relative abundances measured during migration over time. Across the study period, we analyzed a total of 53,867,588 eBird checklists and only retained the ones which contained observations of Boreal Owls. We separated observations according to three seasons as follows: winter (January to April), breeding (May to July), and autumn migration (August to December). To account for variation in sampling effort over time, we first estimated relative abundance as the ratio of observed counts to checklist effort (count per checklist). However, Boreal Owl is a rare species, meaning that increased sampling effort does not always translate into higher counts, as the probability of observation remains low. Conversely, Boreal Owl is also a sought-after species so any individual could also translate into several observations by various observers during the same season. In early years, sampling effort was minimal, likely resulting in many missed observations. More recent data reflect increased checklist effort, but also a shift in observer expertise and checklist consistency (Fink et al. 2020). In the face of these challenges and to avoid misinterpreting trends, we limited our analysis to a visual comparison of the peaks and lows on the resulting graph of a Generalized Additive Model (GAM), which we created using the *mgcv* package in R (Wood 2023), incorporating the total number of lists, year, and season as predictors of Boreal Owl relative abundance (see Online Supplementary Material). The model was not designed to assess trends over time *per se* but rather to adjust seasonal abundance annually according to effort so that we could visually compare patterns of

estimated abundance to those obtained from banding. The model included a smoothing term for year within each season ($s(\text{year}, \text{by} = \text{season}, k = 25)$) and an effort adjustment term for the logarithm of total checklists ($s(\log(\text{total_lists}))$). This GAM approach allowed us to adjust relative abundance for variations in checklist effort over time.

Results

Population trends from captures

From 1996 to 2023, we captured 1638 Boreal Owls (532 juveniles, 1064 adults, and 42 of unknown age) during migration at Tadoussac and a total of 478 at Whitefish from 1995 to 2022. Relative abundance at both sites decreased over time, and cyclical peaks diminished over time. During migration at Tadoussac, relative abundance of Boreal Owls was best described by a four-year population cycle (CYCLE; **Table 1**). Relative abundance had a quadratic relationship with YEAR. Population cycles interacted with a linear coefficient of year of study (YEAR). Peaks in relative abundance included the years 1996, 2000, 2004, 2008, 2012, 2016, and 2022 (**Fig. 1**) with peaks diminishing during recent years. The year 2020 was not a peak as expected with a four-year cycle because of the interaction with year of study. Plotting isolated trends over time (i.e., effects of YEAR) became impossible because of an interaction between population cycles and long-term population trends; therefore, we describe trends during peak years of catches. Boreal Owl relative abundance had a moderate peak in 1996 (median = 70.7, 95% HDIs = [57.3, 86.7]), followed by

Table 1. Parameter estimates from models retaining covariates with effects on population trends of Boreal Owls in eastern North America at two sites, Tadoussac (1996–2023) and Whitefish (1995–2022), including median, lower 95% highest posterior density interval (HPDI) and higher 95% HPDI. An effect was assigned as existing when the probability of direction (PD) was ≥ 0.975 and when a higher order polynomial had an effect.

Site	Parameter	Covariate	Median	Lower 95% HPDI	Higher 95% HPDI	PD
Tadoussac (all birds)	μ	Intercept	2.55	2.05	3.06	NA
	$\delta[1]$	YEAR	0.90	0.25	1.53	1.00
	$\delta[2]$	YEAR2	-1.54	-2.70	-0.33	0.99
	$\delta[3]$	CYCLE	-0.61	-1.14	-0.13	0.99
	$\delta[4]$	CYCLE	1.59	1.07	2.14	1.00
	$\delta[5]$	CYCLE:YEAR	0.75	-0.07	1.62	0.96
	$\delta[6]$	CYCLE:YEAR	-2.40	-3.33	-1.44	1.00
	Σ	Random effect of year	0.81	0.54	1.17	NA
Tadoussac (juveniles)	μ	Intercept	1.34	0.90	1.76	NA
	$\delta[1]$	YEAR	0.80	0.16	1.57	0.99
	$\delta[3]$	CYCLE	-0.22	-0.75	0.34	0.80
	$\delta[4]$	CYCLE	1.14	0.55	1.68	1.00
	$\delta[5]$	CYCLE:YEAR	0.74	-0.16	1.70	0.96
	$\delta[6]$	CYCLE:YEAR	-1.57	-2.54	-0.62	1.00
	Σ	Random effect of year	0.90	0.56	1.30	NA
	μ	Intercept	-2.74	-4.15	-1.59	NA
Whitefish	$\delta[1]$	YEAR	-1.33	-2.79	-0.26	0.99
	$\delta[2]$	YEAR2	1.05	-1.02	3.50	0.83
	$\delta[3]$	CYCLE	-3.66	-5.31	-2.21	1.00
	$\delta[4]$	CYCLE	-2.37	-3.86	-1.06	1.00
	$\delta[5]$	CYCLE:YEAR	1.01	-0.77	2.31	0.88
	$\delta[6]$	CYCLE:YEAR	1.55	0.05	3.05	0.98
	$\delta[7]$	CYCLE:YEAR2	0.95	-1.71	3.72	0.78
	$\delta[8]$	CYCLE:YEAR2	5.72	2.98	8.40	1.00
	Σ	Random effect of year	0.72	0.26	1.45	NA

a maximum peak during 2004 (median = 102.9, 95% HDIs = [89.3, 117.2]), and gradually decreased thereafter having the last cyclical peak in 2022 (median = 11.3, 95% HDIs = [7.4, 17.5]). The analysis on juveniles alone at Tadoussac provided similar trends over time as for total abundance, except that the quadratic effect of year (YEAR2) was not significant (Table 1).

Similarly, during migration at Whitefish, relative abundance of Boreal Owls was best described by a four-year population cycle (CYCLE; Table 1). Population cycles interacted significantly with a quadratic coefficient of year of study (YEAR²); therefore, the global model was used for inference (Table 1). Generally, the first few years of the present study (late 1990s into early 2000s) had greater relative abundances of Boreal Owls that decreased over time and cycles diminished. A maximum peak occurred in 1996 (median = 22.2, 95% HDIs = [19.2, 25.7]), gradually decreasing thereafter through 2022 (median = 0.01, 95% HDIs = [0.004, 0.277]). After 2014 (median = 0.002, 95% HDIs = [0.000, 0.030]), peaks were very diminished.

Age structure and body condition during autumn migration

High relative abundance years were typically represented by a low proportion of juveniles (< 35%; Fig. 2b) suggesting winter irruptions are mainly composed of adults following poor breeding success (Newton 2006; Minton et al. 2012). Years with a high proportion of juveniles (>50%) typically occurred one 1 to two 2 years after the observed peaks in relative abundance (Fig. 2a,b).

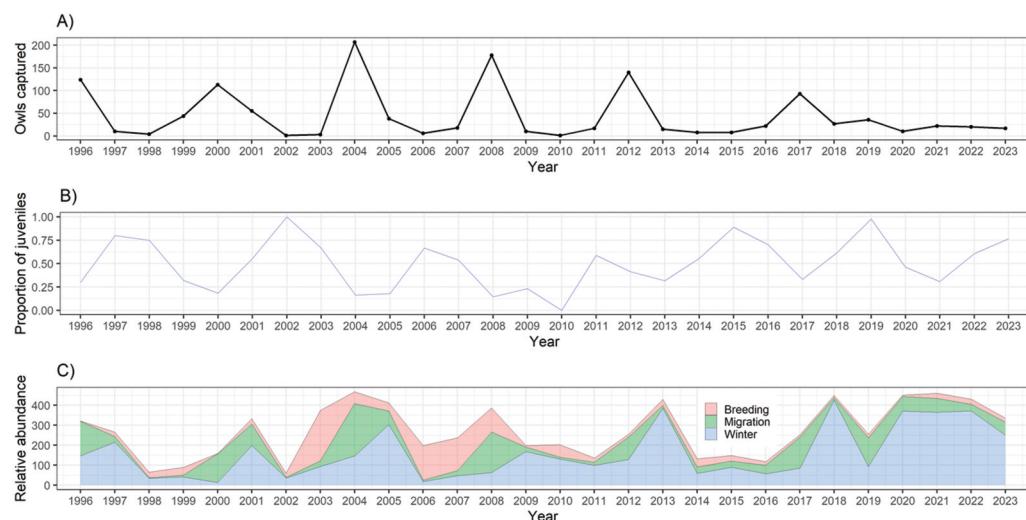


Figure 2. (A) Number of Boreal Owls captured annually during autumn migration at Tadoussac Bird Observatory (QC, Canada). (B) Proportion of juveniles among Boreal Owls captured annually during autumn migration at Tadoussac Bird Observatory (QC, Canada). (C) Relative abundance (estimated by GAM, see Online Supplementary Material) of Boreal Owls observed via participatory science by seasons (red: breeding, May–July; Green: autumn migration, August–December; Blue: winter, January–April) from 1996 to 2023.

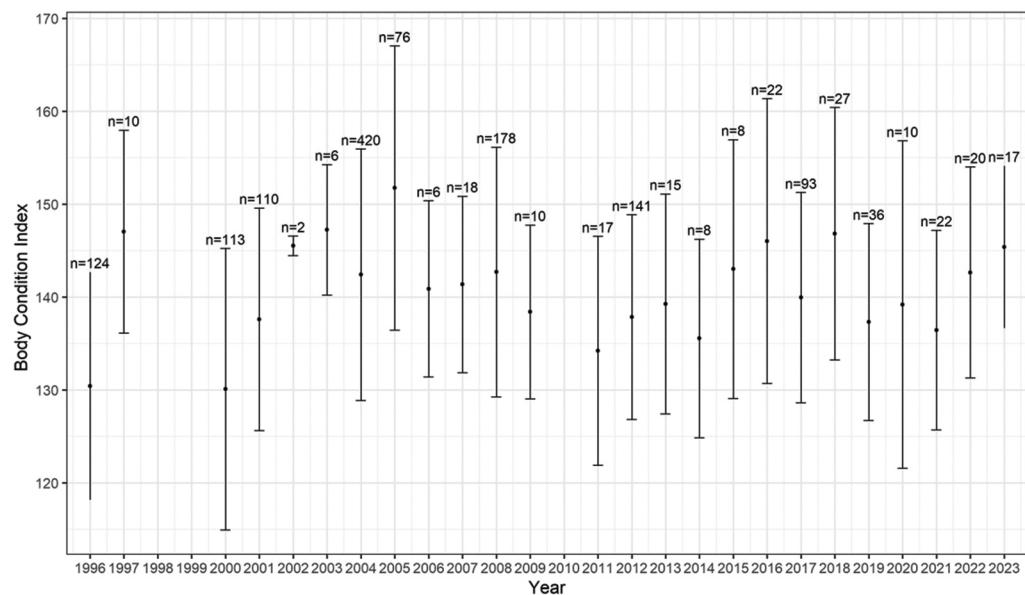


Figure 3. Annual body condition index (mean \pm standard deviation) for Boreal Owls captured during autumn migration at Tadoussac Bird Observatory (QC, Canada) from 1996 to 2023. Data points were averaged annually and presented here only for graphical purposes.

Measured values for the body condition index ranged between 101.2 and 219.7 (mean \pm SD = 139.9 ± 13.9 g) and reflected the size of individuals represented by their wing chord (173.7 ± 6.3 mm) and body mass (140.0 ± 17.2 g; Fig. 3). We did not detect any temporal trends in mean body mass ($r = 0.16$, $F = 2.52$, $df = 26$, $p = 0.12$) or wing chord ($r = 0.02$, $F = 0.26$, $df = 24$, $p = 0.62$) over the study period. The measured body condition index showed large annual variations but no consistent trend over time ($r = 0.11$, $F = 2.82$, $df = 23$, $p = 0.11$; Fig. 3). In general, adult individuals (2.04 ± 0.62) had a greater fat score than juveniles (1.79 ± 0.66 ; Wilcoxon test; $W = 162905$, $p < 0.001$). The measured fat score was not correlated with the calculated body condition index ($r = 0.002$, $df = 1366$, $p = 0.06$; Fig. 3). We detected a decline in the mean annual fat score over time ($r = -0.053$, $F = 57.13$, $df = 22$, $p < 0.001$; Fig. 4).

Population trends from eBird data

We obtained 5,715 participatory science observations from eBird across Eastern North America (4006 in winter, 511 during breeding, and 1198 during autumn migration). Boreal Owls exhibited annual variation in relative abundance with peaks occurring approximately every four years during autumn migration (Fig. 2c). Despite a general increase in Boreal Owl observations in recent years due to a growing contribution in participatory science programs (Sullivan et al. 2014), observations from participatory science in North America during breeding and winter seasons exhibited large annual variations (Fig. 2c) that mostly occurred synchronously with the highs and lows measured from captured individuals at

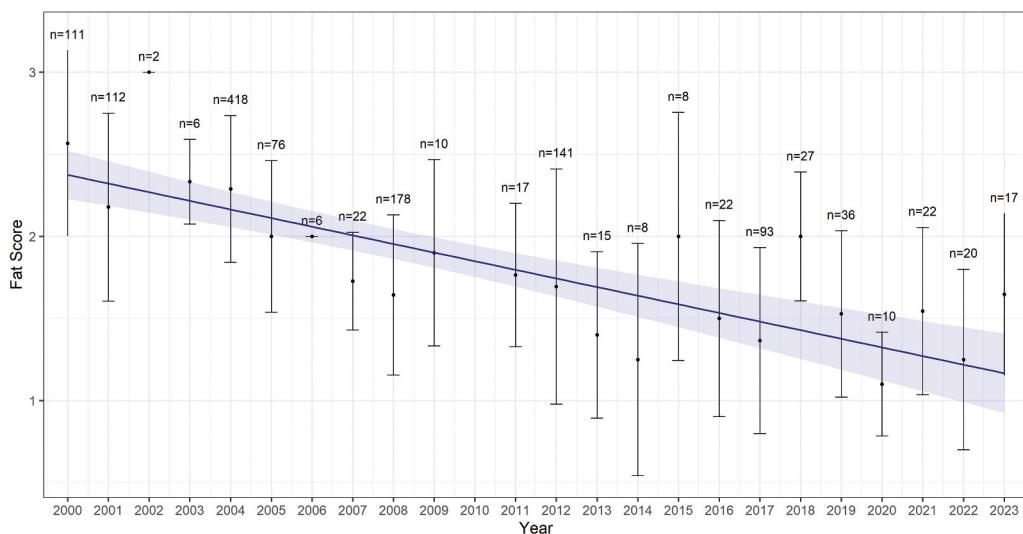


Figure 4. Fat score (mean \pm standard deviation) for Boreal Owls captured during autumn migration at Tadoussac Bird Observatory (QC, Canada) from 1996 to 2023. Linear regression of the fat score against year is shown as a blue line with 95% confidence interval. Data points were averaged annually and presented here only for graphical purposes.

banding stations during autumn migration (Pearson correlation; $r = 0.811$, 95% CI [0.623; 0.911], $t = 6.938$, $df = 25$, $p < 0.001$).

Discussion

The Boreal Owl exhibits large annual variations in abundance, making it a challenging task to estimate absolute numbers, population trends, and life history traits. We were nonetheless able to evaluate population trends as well as annual juvenile-to-adult ratio and body condition from individuals captured at two banding stations located along major flyways of eastern North America and using standardized protocols during migration. We noted a decrease in relative abundance over time for Boreal Owls in eastern North America. Additionally, the decline over time observed in the fat score measured during autumn migration could indicate that habitat conditions across the boreal forest from September to October are declining. We therefore recommend careful monitoring of annual abundance, growth, reproduction, and survival rates.

As observed in Boreal Owls from Fennoscandia (e.g., Korpimäki and Hakkilainen 2012) as well as in many other owl species (e.g., Snowy Owl *Bubo scandiacus*), Boreal Owl populations in North America undergo important annual fluctuations in abundance, most likely linked with the variation in abundance of their prey (Newton 2006; Therrien et al. 2021). Indeed, Boreal Owl abundance has been documented to be affected by their main prey on the breeding grounds, the red-backed vole (*Clethrionomys gapperi*) (Hayward et al. 1993; Cheveau et al. 2004; Côte et al. 2007). In northwestern Quebec, vole density has been shown to fluctuate (up to 41-fold) with a cyclical pattern and four-year periods (Fauteux et al. 2015). In this time series, vole population crashes in the boreal forest in 2004 and 2008 are well synchronized with irruption years documented here during

migration at Tadoussac for Boreal Owls. Moreover, it has been suggested that periodic, large amplitude fluctuation in abundance of small mammals could be dampening (e.g., Ecke et al. 2017), which could affect body condition of individuals, winter irruptions, and population dynamics of predators such as the Boreal Owl. From the present results, we can't exclude the possibility that Boreal Owls could simply be migrating less in recent years and overwintering in the boreal forest if food availability allows it, instead of migrating south in autumn, a phenomenon seen in other raptor species (Paprocki et al. 2014). Nevertheless, the observed decline in fat score combined with the observed decline in abundance over time remain causes of concern for North American population of Boreal Owls.

Despite large annual variations, the relatively stable proportion of juveniles in the population over time that we observed in the present study suggests that reproductive success of Boreal Owls has not dramatically decreased in recent decades. Mature boreal spruce forest, however, has severely declined in area covered over recent years following northward expansion of logging activities (Gauthier et al. 2015), which is likely to reduce available habitat for Boreal Owls and the number of owls potentially moving during future irruptive years. In addition, a low proportion of juveniles during the year of owl irruption and years after a crash of voles suggest that juveniles are the first to migrate from the boreal forest when adults, and particularly adult males, stay close to their territory in winter when food is available (Korpimäki et al. 1987).

Following recent analyses reporting on overall biodiversity loss in North America (Rosenberg et al. 2019), it is of utmost importance to understand the demography of sensitive and indicative species, such as the Boreal Owl. Future research should investigate life history traits such as breeding success using nest monitoring and survival rate according to age and sex classes. Long-term monitoring schemes should be developed in North America, similar to those already established in Fennoscandia (Saurola 2009). It would be beneficial to combine traditional methods, such as band recoveries to assess movements and survival (Kaschube et al. 2022), with newer genetic tools to assess changes in the effective population size over time (e.g., Gousy-Leblanc et al. 2023). Additionally, despite the increasing coverage of participatory science databases (Sullivan et al. 2014), special attention should be given to rarer species such as the Boreal Owl because very limited information can currently be gleaned out of these platforms. In the present study, participatory science observations were successfully correlated with annual peaks in relative abundance measured at migration monitoring stations, but overall abundance remained challenging to compare using the two monitoring schemes. Detection rates did not increase in a simple, proportional manner with effort: at low checklist numbers, each additional list substantially improved detection, whereas at higher levels of effort, the marginal increase in observed abundance diminished (see Online Supplementary Material). Indeed, in rare and charismatic species such as the Boreal Owl, it appears very challenging to take observation effort into account using participatory science databases because the species could potentially be sought after and single individuals reported multiple times, therefore boosting the counts. However, an increase in observation effort might not translate proportionally to an increase in numbers in inconspicuous species (such as owls), suggesting population declines only because more people are submitting checklists. Statistical tools are currently being developed to account for these factors (Fink et al. 2020). Moreover, the recent establishment of long-term, standardized audio surveys during the breeding season (e.g., Ethier



et al. 2025) is another step toward a thorough understanding of population trends in owls.

Boreal Owls are indicators of environmental health and ecosystem integrity of the boreal forest. Landscape composition and reduction of forest cover have been shown to affect male survival and reproductive success in the species (Hayward et al. 1993; Laaksonen et al. 2004; Korpimäki and Hakkilainen 2012). An important tool for conservation strategies of North American owls could include the development of nest box monitoring programs which would provide crucial information on reproductive parameters, since the proportion of age classes recorded during migration remains an indirect metric. We recommend that interactions between environmental conditions (forest structure, foraging habitat conditions, prey abundance, predators, competitors, etc.) and demographic parameters should be studied and understood to develop comprehensive management plans for Boreal Owls and other boreal species.

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Research ethics declarations

The authors did not use Generative AI in the production of this manuscript.

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