

Alteration of a temperate forest invertebrate community by invasive Japanese barberry (*Berberis thunbergii*) has limited influence on the diet composition of territorial ovenbirds (*Seiurus aurocapilla*)

Wales A. Carter  and Chad L. Seewagen

Great Hollow Nature Preserve and Ecological Research Center, 225 State Route 37, New Fairfield, CT 06812, USA

Corresponding author: Wales A. Carter (email: wales_carter@uri.edu)

Abstract

Invasive species are widely implicated in the decline of songbird populations, potentially via indirect effects such as the restructuring of ecological communities by non-native plants. We used stable isotope analysis to investigate whether ground-foraging, generalist insectivore ovenbirds (*Seiurus aurocapilla* (Linnaeus, 1766)) shifted diets following invasion by a non-native shrub, Japanese barberry (*Berberis thunbergii* DC.), in a temperate woodland system in New York, USA where barberry was previously linked to trophic downgrading in the leaf litter arthropod community. Assimilated ovenbird diets were primarily composed of predatory invertebrates followed by sucking herbivores, chewing herbivores, and detritivores. The only notable changes in assimilated ovenbird diets were a modest 14.7% decrease in chewing herbivore contributions and a minor 7.0% increase in sucking herbivore contributions in forest patches with high barberry densities. Our results indicate that the effects of non-native plants on connections between higher trophic levels are context-dependent, and comparisons with other studies suggest that community complexity and time since introduction are key contextual differences that affect the outcome of an invasion. Our results may reflect compensatory shifts in individual foraging effort by ovenbirds, but, in combination with our previous research, provide little evidence that barberry affects ovenbird condition and therefore downstream outcomes.

Key words: non-native plant, stable isotope mixing model, *Berberis thunbergii* DC., *Seiurus aurocapilla* (Linnaeus, 1766), Japanese barberry, ovenbirds

Introduction

Global avifauna have experienced dramatic population declines throughout the 20th and 21st centuries (Kirby et al. 2008; Rushing et al. 2016; Rosenberg et al. 2019). Multiple mechanisms have been linked to these trends, including habitat loss (Donovan and Flather 2002; Norris et al. 2004), phenotypic mismatches due to climate change (Both et al. 2006; Arlt and Pärt 2017), collisions with artificial structures (Loss et al. 2015), and environmental pollution (Hallmann et al. 2014; Put et al. 2021). Another potentially important driver of these declines is the introduction of non-native species, which are widely recognized as one of the most pressing issues in biodiversity conservation (Bellard et al. 2016; Blackburn et al. 2019). The most striking impacts of non-native species on birds have typically been associated with the introductions of novel predators, such as domesticated cats, which have been estimated to depredate billions of songbirds per year in the US alone (Loss et al. 2013), and particularly when predators are introduced to island systems (Townsend et al. 2009; O'Donnell et al. 2017). In contrast to these direct interactions between birds and novel threats,

the indirect effects of non-native species are more subtle and relatively understudied, despite their potential importance. Plant introductions can be particularly consequential (Pyšek et al. 2012), due to their capacity for altering nutrient cycling and other basic ecosystem functions (Kourtev et al. 2002; Gaertner et al. 2014) and the structure of ecological communities (de Groot et al. 2007; Pyšek et al. 2012). Such impacts are often greatest among arthropod herbivores and the food webs they support, with nearly two-thirds of studies finding decreases in total arthropod abundance following non-native plant introductions (Litt et al. 2014). Thus, evaluating the indirect effects of plant invasions is an important step for understanding threats to bird populations.

Among all birds, songbirds make particularly heavy use of the invertebrate communities that directly interact with plants at the base of food webs (Nyffeler et al. 2018). Insectivory is important for songbirds during the key life history stages of egg laying and nest provisioning, when an adequately large supply of nutrients and energy is necessary to fuel the growth and development of nestlings (Schwagmeyer and Mock 2008; Senécal et al. 2021). Failure to provide suffi-

cient resources can result in both low survival and adverse effects on fitness, such as impaired immune function and altered behavior (Birkhead et al. 1999; Arnold et al. 2007; Hegemann et al. 2013). As predicted, given the tight connections between invasive plant species and invertebrate communities, and invertebrate communities and songbird populations, several studies have found negative associations between invasive plants and songbirds (George et al. 2013; Nelson et al. 2017; Narango et al. 2018; Riedl et al. 2018; Grzędzicka and Reif 2021). For example, Narango et al. (2018) found that as the proportion of non-native plants in suburban habitats in the Washington, DC, USA area increased, the abundance of insects decreased and the recruitment of Carolina chickadees (*Poecile carolinensis* (Audubon, 1834)) declined below replacement. Similarly, a study of non-native Sosnowsky's hogweed (*Heracleum sosnowskyi* Manden) in Poland found that invasion was associated with decreased populations of all songbird foraging guilds studied and that bush and tree insectivores were particularly impacted (Grzędzicka and Reif 2021). These and similar findings strongly suggest that the impact of invasive plants on songbirds is mediated by diet, but few studies have directly addressed this question with detailed estimates of diet composition (as opposed to trophic level; Narango et al. 2018) in invaded and uninvaded areas. Accordingly, dietary insights into the mechanisms by which plant invasions influence songbird success could have substantial value (Nelson et al. 2017), especially in areas like the temperate forests of eastern North America, which have declining songbird populations, albeit few immediately imperiled (McNulty et al. 2008; Sauer and Link 2011; Rosenberg et al. 2019).

Japanese barberry (*Berberis thunbergii* DC., hereafter “barberry”) is a woody understory (<2 m in height) shrub native to eastern Asia that was introduced to North America in the late 1800s (Ehrenfeld 1997). Nurseries sold barberry as an ornamental throughout the 20th century, which facilitated its progression to being one of the most pervasive alien plant species in the northeastern USA (Silander and Klepeis 1999; Lubell et al. 2008). Moreover, barberry is largely unpalatable to white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), one of the main browsing species in the region, thus allowing it to form dense, extensive patches throughout its invasive range, and at times, exclude native understory plants that are subjected to heavy deer herbivory (Silander and Klepeis 1999; Kourtev et al. 2002; Averill et al. 2016). The intensity of this invasion, coupled with its proximity to large human population centers, has periodically attracted scientific interest (e.g., Kourtev et al. 2002; Maerz et al. 2009; Linske et al. 2018), but relatively little of that work has involved songbirds. Clark and Seewagen (2019) found that the taxonomic composition of leaf litter and shrub-dwelling arthropod communities differed between areas of a forest in eastern New York that were heavily or sparsely invaded by barberry. Although total arthropod biomass was unaffected, high densities of barberry were associated with pronounced taxonomic shifts away from predatory arthropods and towards lower trophic level taxa. This alteration of the arthropod community was subsequently found to have no effect on the physiological condition (body mass, blood metabolites, and

hematology) of a ground-foraging, insectivorous songbird, the ovenbird (*Seiurus aurocapilla* (Linnaeus, 1766); Seewagen et al. 2020). However, the extent to which barberry-driven shifts in arthropod communities constrain the diets of ovenbirds and other insectivores remains unclear.

Here, we investigated the radiating influence of barberry across a temperate forest food web by comparing ovenbird diets between forest patches with differing levels of invasion intensity and previously described differences in arthropod community composition (Clark and Seewagen 2019). Given the generalist diet tendencies of adult ovenbirds (Stenger 1958; Zach and Falls 1979; Holmes and Robinson 1988; Strong 2000), we expected ovenbirds maintaining breeding territories in barberry-invaded areas of forest to shift their consumption of arthropods in general accordance with the altered relative abundance of arthropod taxa, resulting in lower contributions of predators such as spiders and ants. Alternately, it is possible that certain arthropod taxa are nutritionally superior or otherwise preferred, and therefore birds adjusted their foraging behavior to find and consume those diet items in equal proportions between invaded and uninvaded areas of forest, regardless of differing availability.

Materials and methods

Ethics approval

The methods for this study were approved by the Rochester Institute of Technology's Institutional Animal Care and Use Committee (proposals 2011-6 and 2019-1).

Study species and site

The ovenbird is a ground-foraging, insectivorous warbler that breeds in mature hardwood and mixed forests throughout the northern USA and Canada and has been used as a model species in numerous studies of the impacts of various anthropogenic disturbances on forest songbird habitat quality (Porneluzi et al. 2020). Ovenbird breeding habitat quality, territory selection and size, and pairing success are strongly influenced by leaf litter prey availability (Smith and Shugart 1987; Burke and Nol 1998). Adult ovenbirds forage 88%–95% of the time on the forest floor (Holmes and Robinson 1988; Strong 2000), feeding on a wide taxonomic range of leaf litter invertebrates (Stenger 1958; Holmes and Robinson 1988; Strong 2000; Ruhl et al. 2020). A similarly wide range of invertebrate taxa are used to provision nestlings during the breeding season (Streby et al. 2013), meaning that shifts in diet driven by non-native plants could impact both adult and nestling success.

We conducted our study between 2017 and 2019 at the Pawling Nature Reserve in the towns of Pawling and Dover, NY (41.6167°N, 73.5633°W). The reserve is approximately 430 contiguous ha of predominantly second-growth, mixed hardwood forest. The site and much of the surrounding region was historically used for agriculture, including both arable and pasture lands. Range expansion of barberry in this local area has largely occurred within the past 40 years (Silander and Klepeis 1999) and resulted in the presence of “invasion

fronts” in many forests (Kourtev et al. 2002; Maerz et al. 2009), including Pawling Nature Reserve. Barberry invasion fronts are characterized by high-density clusters of barberry within a forest that radiate out from the place of initial colonization to a point at which barberry is only sparse or still absent despite other major forest characteristics being the same (Kourtev et al. 2002; Maerz et al. 2009). High variation in barberry density within a forest, including Pawling Nature Reserve, is also often delineated by historical stone walls that formerly separated small areas of differing agricultural activity (e.g., crops versus pasture; Degasperis and Motzkin 2007). The patchy distribution of barberry but otherwise similar habitat features throughout our study site thus allowed us to investigate the influence of barberry invasion on the diets of ovenbirds while other major habitat characteristics remained constant (Maerz et al. 2009; Nuzzo et al. 2009; Clark and Seewagen 2019; Seewagen et al. 2020).

Bird capture and sample collection

We scouted the forest in early to mid-May of each year to locate any males consistently singing in areas that we initially visually estimated to have uniformly high (>25% ground cover) or uniformly low (<10% ground cover) barberry density over, at a minimum, the surrounding 2 ha (visualized as a circle with a radius of approximately 80 m) and at least 50 m from any forest edge (Seewagen et al. 2020). This was to ensure relatively consistent barberry influence across the majority of an ovenbird’s territory, which typically ranges 0.5–1.5 ha, depending on food abundance (Stenger 1958; Smith and Shugart 1987; Perneluzi et al. 2020). We subsequently captured the birds between 06:30 and 11:30 EST, 16–26 May (the peak period of ovenbird territory defense and largely prior to incubation in this region; CLS, pers. obs.) using 6 m mist nets and playback of conspecific recording broadcast through a wireless speaker. Target birds exhibited a largely binary response to playback, either singing from a distance and avoiding capture or aggressively pursuing calls, which led to their prompt capture. This behavioral trait of sampled birds, combined with a minimum distance of 100 m between sampled territories provided confidence that birds were captured within their respective territories and that barberry densities and invertebrates sampled in the surrounding area (see below) were representative of the resources available to them. Within 5 min of capture, we took an ~150 µL blood sample from the brachial vein using a 26-gauge needle to puncture the vein and a heparinized capillary tube to collect the bead of pooled blood. Following blood sampling and before release, we fitted each bird with an aluminum US Geological Survey leg band, weighed it to the nearest 0.1 g on a digital balance, measured its unflattened wing chord to the nearest mm, and when possible, aged it as second-year or after-second-year based on rectrix shape and other plumage criteria (Donovan and Stanley 1995; Pyle 1997). Blood samples were kept in a cooler on ice until they were transported to the lab at the end of each field day, where they were separated into plasma and red blood cell fractions by centrifugation at 3000 rpm for 10 min. Separated fractions were transferred to cryogenic tubes and stored at –80 °C until analysis. In total,

we collected samples from 10 individuals in 2017, 13 individuals in 2018, and 39 individuals in 2019.

Vegetation sampling and invertebrate collection

We surveyed vegetation in a 0.02 ha circular plot centered at the midpoint of the mist net in which a given bird was captured and then walked perpendicular north–south and east–west transects through the center of the plot, identifying and counting each individual understory shrub (defined as woody plants less than 7.6 cm in diameter) within ~1 m on either side of the transect and between ~0.5 and ~1.5 m above the ground (James and Shugart 1970; Clark and Seewagen 2019; Seewagen et al. 2020). Shrub counts were conducted in duplicate by two observers. To estimate ground cover, we viewed the ground through an ocular tube at 10 evenly spaced points along each transect (James and Shugart 1970) and scored each location as either barberry, other non-native shrub, native shrub, herbaceous vegetation, or no vegetation.

Coincident with the bird capture period in 2019, we collected leaf litter invertebrates from each bird’s territory to characterize the stable isotope values of potential diet items. We collected 0.04 m² of leaf litter from three locations per territory immediately after release of the bird: one at the midpoint of the mist net, one 10 m east of that point, and one 10 m west of that point (Clark and Seewagen 2019; Seewagen et al. 2020). The 0.12 m² total samples were stored in the field in plastic bags inflated with air and then returned to the lab within 6 h. There, we extracted invertebrates from the leaf litter using Berlese funnels operated for 12–18 h with a 40 W incandescent lightbulb and stored them at –80 °C until identification. Extracted invertebrates were identified to order under a dissecting scope, with the exception of several insect specimens that we were able to identify to family, and worms, centipedes, millipedes, and slugs, which we identified to class.

Sample processing and stable isotope analysis

We pooled all invertebrate samples into single-taxon vials for each bird territory to have enough mass for stable isotope analysis and dried the pooled samples in a 60 °C oven for 48 h. We then homogenized the dried invertebrate samples and weighed and crimped ~1 mg of material into tin capsules. To prepare plasma samples, we defrosted and pipetted 10 µL of each sample into a tin capsule, which we then dried for 24 h in a 60 °C oven and crimped to seal.

Stable isotope analyses were carried out by the Cornell University Stable Isotope Laboratory in Ithaca, NY. The carbon and nitrogen stable isotope enrichment of samples were analyzed with an EA Instruments NC2500 elemental analyzer interfaced with a Thermo Delta V isotope ratio mass spectrometer. Every 10th sample was interspersed with two regularly validated in-house standards (“corn” and “trout”), used in a two-point normalization of carbon and nitrogen isotope values to International Atomic Energy Association reference materials. Stable isotope values are presented in per mil delta notation, calculated as: $\delta \text{‰} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is the ratio of heavy:light isotopes of the sample or standard and the standard is Vienna Pee Dee Belemnite for

carbon and atmospheric air for nitrogen. The analytical precision of the instruments used in this analysis, estimated as the within-run standard deviation (SD) of a third internal standard (“deer”), was 0.04 ‰ for both carbon and nitrogen.

Evaluating dietary endpoints

Stable isotope mixing models require isotopically distinct dietary endpoints to accurately resolve contributions to consumer tissues (Phillips et al. 2014). Because of considerable overlap in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among our dietary sources, we aggregated invertebrate taxa a priori into four functional groups based on primary feeding mode: detritivores (Annelida, Diplopoda, Collembola, Isoptera, Orthoptera-Gryllidae, and Isopoda), chewing herbivores (Gastropoda and Lepidoptera), sucking herbivores (Hemiptera), and predators (Araneae, Acari, Pseudoscorpiones, Chilopoda, and Dermaptera). Coleoptera and Diptera are large, functionally diverse insect clades that exhibited wide ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and so we used k-nearest neighbor classification to assign specimens of those taxa to one of our four functional groups. Such a priori aggregation inevitably produces coarser estimates of diet than other methods such as fecal and stomach content analysis (Mudrzynski and Norment 2013; Carter et al. 2021) or metabarcoding (Génier et al. 2021; Hoening et al. 2022), although at the expense of tradeoffs, including bias towards hard-bodied, less digestible insect taxa for fecal analysis and difficulty estimating relative abundances for metabarcoding. Nevertheless, stable isotope analysis has been precise enough to detect plant-driven changes to songbird diets in previous studies (Narango et al. 2018; Riedl et al. 2018), and particularly changes related to trophic level such as we expected based on Clark and Seewagen (2019). The resulting sample sizes for diet sources were as follows: detritivores, $N = 69$; chewing herbivores, $N = 10$; sucking herbivores, $N = 4$; and predators, $N = 94$. We confirmed that functional groups were isotopically distinct using k-nearest neighbors randomization tests with Bonferroni corrections for multiple tests ($P < 0.05$ for all pairs; Fig. 1; Rosing et al. 1998). Functional group mean isotopic values did not differ between high- and low-density barberry areas ($P > 0.26$ for all groups). Although ovenbirds may take some diet items from foliage, ovenbird plasma samples fell within the range of leaf litter invertebrate isotope values (Fig. 1), and there is little evidence to suggest that including foliage invertebrates would change the relative positions of functional groups in isotope space.

Mixing model analyses

We assessed the contributions of invertebrate functional groups to ovenbird tissues with a series of Bayesian mixing models using the package *MixSIAR* version 3.1.12 (Stock et al. 2018) in the R statistical computing environment (version 3.6.2; R Core Team, Vienna, Austria). These models evaluate the proportional contribution of each source through repeated draws from the posterior distributions via Markov chain Monte Carlo sampling (Moore and Semmens 2008). Each model included a multiplicative error term (Stock and Semmens 2016) and was “fully Bayesian”, incorporating both

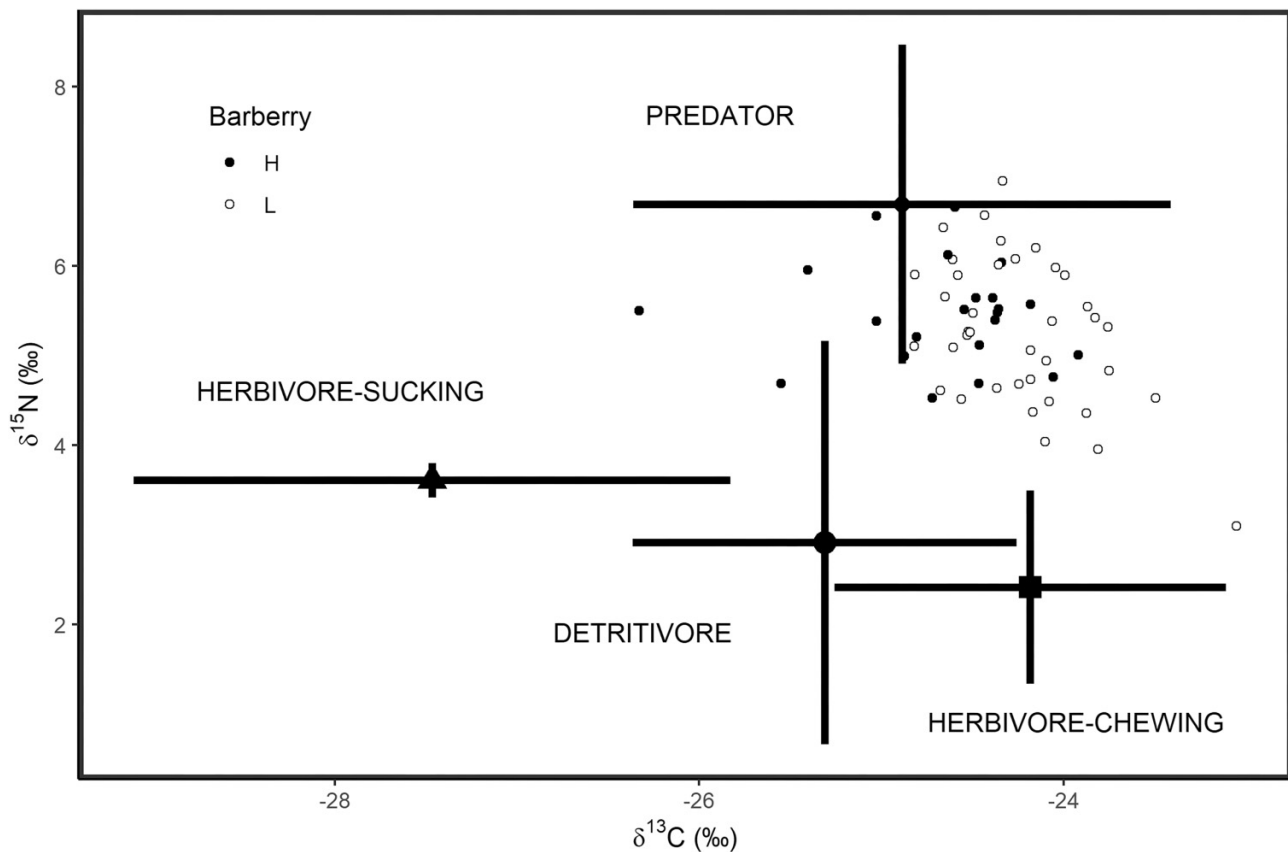
raw values of source items (Ward et al. 2010) and corrections (weights) for carbon and nitrogen concentrations in source items (Phillips and Koch 2002). We used published discrimination factors for songbirds (Hobson and Bairlein 2003; Pearson et al. 2003; Evans Ogden et al. 2004) previously used to estimate ovenbird diets by Ruhl et al. (2020): 0.50 ± 0.28 ‰ for carbon and 3.00 ± 0.85 ‰ for nitrogen. Each model was run in three parallel chains with 50 000 burn-in iterations and 100 000 recorded iterations, which were subsequently thinned by 50 (*MixSIAR* “normal” settings). We used uninformative (generalist Dirichlet) priors to reflect our initial presumption that all combinations of source items were equally likely and we confirmed adequate model convergence using Gelman–Rubin and Geweke diagnostics (Gelman and Rubin 1992).

As in Seewagen et al. (2020), we categorized ovenbird territories as having high barberry density if they contained >4200 barberry shrubs per ha ($N = 20$) and low barberry density if they contained <2720 barberry shrubs per ha ($N = 38$). Five territories had barberry densities between these values, which we excluded from subsequent analyses. To evaluate the influence of barberry density and other covariates on invertebrate functional group contributions to ovenbird diets, we fit each of the following models to our diet: (1) a null model estimating the overall diet of all ovenbirds with no covariates, (2) a model with a fixed effect of barberry density (high versus low), (3) a model with a fixed effect of barberry density and a random effect of sample year, (4) a model with a continuous effect of wing chord as a proxy for body size (and therefore constraints on prey size) and a random effect of year, and (5) a model with a fixed effect of barberry density, a continuous effect of wing chord, and a random effect of year. We then compared model fit with a leave-one-out cross-validation information criterion (LOOIC) analogous to the Akaike information criterion (Vehtari et al. 2017). Finally, we assessed the influence of barberry on the contribution of each functional group in the best-supported model by calculating the proportion of iterations in which the contribution in high-density barberry areas exceeded the contribution in low-density areas (Carter et al. 2021). Contributions were considered to be significantly different if the proportion was either less than 0.05 or greater than 0.95. Data used in mixing model analyses are available as online Supplementary material (Tables S1–S3).

Results

Barberry densities in the territories of our study animals ranged from 0 to 26 182 plants/ha, with an average density of 316 ± 602 plants/ha (mean \pm SD) in territories categorized as low-barberry and an average of $11\,535 \pm 6799$ plants/ha in territories categorized as high-barberry. In total, we collected 404 invertebrate specimens that we pooled into 177 single-territory, single-taxon samples spread across 17 identifiable taxa as follows: Annelida ($N = 18$), Acari ($N = 11$), Araneae ($N = 20$), Pseudoscorpiones ($N = 2$), Chilopoda ($N = 7$), Diplopoda ($N = 13$), Collembola ($N = 21$), Gastropoda ($N = 6$), Coleoptera ($N = 19$), Dermaptera ($N = 6$), Diptera ($N = 17$), Hemiptera ($N = 3$), Hymenoptera ($N = 23$), Isoptera ($N = 1$),

Fig. 1. Carbon and nitrogen isotope values of ovenbird (*Seiurus aurocapilla*) plasma and potential diet items. Small points depict individual ovenbird samples and large symbols with error bars depict means and standard deviations for different invertebrate functional groups (diamond = predators, square = chewing herbivores, triangle = sucking herbivores, and large circle = detritivores). Isotope values of invertebrate functional groups have been corrected with discrimination factors to facilitate visual comparison with ovenbird samples.



Lepidoptera ($N = 3$), Orthoptera-Gryllidae ($N = 1$), and Isopoda ($N = 6$). Mean and SD $\delta^{13}\text{C}$ values were -25.8 ± 1.0 for detritivores, -24.6 ± 1.1 for chewing herbivores, -28.4 ± 1.7 for sucking herbivores, and -25.4 ± 0.9 for predators (Fig. 1). Mean and SD $\delta^{15}\text{N}$ values were -0.3 ± 1.9 for detritivores, -0.6 ± 1.1 for chewing herbivores, 0.5 ± 0.1 for sucking herbivores, and 3.4 ± 1.5 for predators (Fig. 1).

Carbon and nitrogen stable isotope values of ovenbird plasma had means \pm SD of -24.4 ± 0.5 and 5.3 ± 0.7 , respectively, with a range of -26.3 – -23.1 for carbon and 3.1 – 7.0 for nitrogen (Fig. 1). Among invertebrate functional groups, predators had distinctly higher nitrogen values than the other groups, while detritivores, chewing herbivores, and sucking herbivores were mainly distinguished by their carbon values (Fig. 1). Based on LOOIC values, the best-supported model included a fixed effect of barberry density and a random effect of year, with a weight of 0.93 (Table 1). Within the best-supported model, predators made the greatest contribution of any invertebrate functional group, followed by chewing herbivores, and with both sucking herbivores and detritivores making relatively minor contributions (Fig. 2). Contributions of different functional groups were relatively consistent regardless of barberry density (Fig. 3). The probability that proportions in high-density areas exceeded those

in low-density areas was nonsignificant for predators (0.653) and detritivores (0.870), but significant for both chewing herbivores (0.009) and sucking herbivores (0.953). The estimated contribution of chewing herbivores to ovenbird diets was $42.4 \pm 14.7\%$ (mean \pm SD) in low-density areas and $27.7 \pm 12.13\%$ in high-density areas, whereas the contribution of sucking herbivores was $2.3 \pm 3.7\%$ in low-density areas and $9.3 \pm 8.8\%$ in high-density areas (Fig. 3).

Discussion

Although invasive alien plants have well-documented impacts on species with which they directly interact, they are also expected to have indirect effects that radiate throughout local food webs, including to songbirds (Pyšek et al. 2012; Gaertner et al. 2014). One likely mechanism for such influence is the alteration of trophic interactions between herbivores and consumers following changes to herbivore communities driven by both direct and indirect interactions with the non-native plants (de Groot et al. 2007; Thiele et al. 2010; Nelson et al. 2017; Blackburn et al. 2019; Grzędzicka and Reif 2021). However, despite the simplicity and clear predictions of this model, surprisingly few studies have tested it by comparing consumer diets between invaded and uninvaded com-

Table 1. Comparison of mixing model fit by leave-one-out cross-validation information criterion (LOOIC).

Model	LOOIC	SE LOOIC	Δ LOOIC	Weight	ϵ_C	ϵ_N
Barberry density + year	41.6	22.8	0.0	0.93	0.169	0.251
Barberry density + wing + year	46.8	22.9	5.2	0.07	0.156	0.248
Wing + year	56.7	24.4	15.1	0	0.210	0.249
Barberry density	57.2	22.4	15.9	0	0.205	0.313
Null	64.5	23.8	22.9	0	0.229	0.325

Note: Barberry (*Berberis thunbergii*) density (high and low) is a categorical fixed effect, whereas wing length is a continuous effect and year is a categorical random effect. Also presented are the standard errors in LOOIC values (SE LOOIC), the difference in LOOIC between each model and the best-supported model (Δ LOOIC), model weight, and the multiplicative error terms estimated in each model for carbon (ϵ_C) and nitrogen (ϵ_N). As indicated by Δ LOOIC and weight, the model including barberry density and year was the best-supported model.

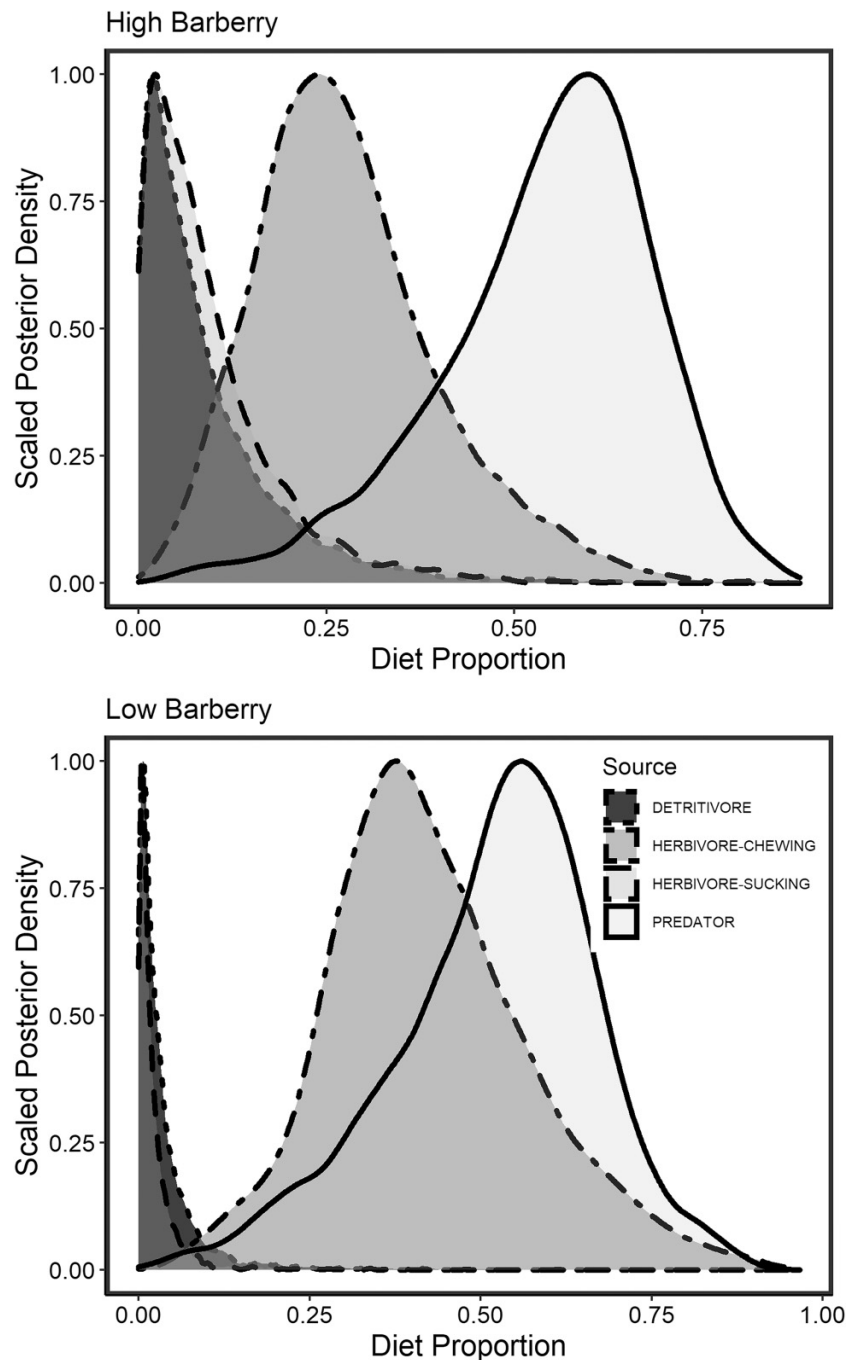
munities. Here, we found the diet composition of an insectivorous songbird to be relatively stable despite changes in arthropod community structure associated with non-native plant invasion in a northeastern USA forest. Ovenbird diets in our study area were mostly composed of predatory invertebrates, followed by chewing herbivores, sucking herbivores, and detritivores, regardless of the density of barberry in their breeding territory. Although our estimates of diet may have missed subtle changes detectable by other methods, such as fecal or stomach content analyses, our finding differs from studies of songbirds that used similar methods and found substantial impacts of non-native plants (Kennedy et al. 2009; Narango et al. 2018; Riedl et al. 2018). These differences suggest that the influence of non-native plants on insectivore diets may often be species- and (or) system-dependent, and not always negative. Consequently, invasive plant management strategies for songbirds (e.g., the complete removal of non-native plant biomass) may be misguided when they involve negative side effects such as disruption of foraging or disturbance of nesting sites (Klaus et al. 2005; Villard et al. 2012).

In one study of the impact of non-native plants on consumer diets, Kennedy et al. (2009) found that invasions of non-native grasses shifted songbird diets away from Coleoptera and towards Orthoptera for four species of ground-nesting birds in the high prairie of western Oregon, USA. Similarly, a study on the invasion of New Mexico locust (*Robinia neomexicana* A. Gray) in riparian areas of northwestern Colorado, USA found a shift by Virginia's warblers (*Leiothlypis virginiae* (S.F. Baird, 1860)) and warbling vireos (*Vireo gilvus* (Vieillot, 1808)) towards consuming and assimilating more aquatic resources in invaded areas (Riedl et al. 2018), while a study in the suburbs of Washington, DC, USA found that invasive plants were associated with foraging at higher trophic levels (e.g., spiders) by Carolina chickadees (Narango et al. 2018). Our work joins this handful of studies in quantifying the diet of a songbird consumer and its response to changes in the local arthropod community driven by the invasion of a non-native plant. However, whereas previous studies found relatively large shifts in consumer diets with non-native plant invasion, we found only a modest shift in the contribution of one invertebrate functional group (chewing herbivores) and a minor shift in the contribution of a second group (sucking herbivores), which, even together, were too small to change the order of contributions to ovenbird diets. This lack of re-

sponse is particularly notable because barberry was associated with a greater than 30% change in the abundance of springtails (Collembola) and greater than 100% changes in the abundance of spiders (Araneae), beetles (Coleoptera), and ants (Hymenoptera: Formicidae), some of the most common leaf litter taxa in our study site (Clark and Seewagen 2019). These changes in the invertebrate community were similar in magnitude to those observed in other studies that also quantified changes in herbivore abundance in response to non-native plant invasion (Laffaille et al. 2005; Kennedy et al. 2009; Narango et al. 2018; Carniatto et al. 2020), providing little evidence to expect greater shifts with further increases in barberry density. Meanwhile, although the direction of change in the contribution of sucking herbivores matched the higher hemipteran abundance in high barberry density areas, the contributions of chewing herbivores shifted in the opposite direction from the ~30% increase in lepidopterans in high-barberry areas, likely due to reduced constraints following declines in generalist predators (Clark and Seewagen 2019). Contrary to expectations, it therefore appears that the influence of large-scale invasions by non-native plants is at least somewhat context-dependent and does not necessarily cascade through the broader community.

One potentially important difference in context between previous studies and ours is that our study took place in a temperate forest as opposed to grassland, suburban, or aquatic ecosystems. Forests tend to have higher levels of productivity than both grasslands and developed areas in temperate regions (Field et al. 1998; Milesi et al. 2003; Turner et al. 2006), which in turn is often related to higher levels of complexity in food webs (Neutel et al. 2007; Armitage and Fourqurean 2009; Arim and Jaksic 2011). Because complexity tends to promote the stability of food webs (Neutel et al. 2007; Stouffer and Bascompte 2011; Plietzko et al. 2012), a higher baseline level of complexity in our system could have allowed for the preservation of a more stable overall community structure despite the trophic downgrading associated with barberry (Clark and Seewagen 2019) and other non-native plant invasions (Estes et al. 2011). A related difference in context that may have contributed to the difference between other studies and ours is the invasion history of our study system. Although our specific study plots included areas in which barberry has only recently arrived and occurs at low densities, barberry has occurred throughout the re-

Fig. 2. Scaled posterior densities of invertebrate functional group contributions to ovenbird (*Seiurus aurocapilla*) plasma in high-density barberry (*Berberis thunbergii*) (top panel) and low-density barberry (bottom panel) areas estimated with stable isotope mixing models. Predators consistently made the greatest estimated contribution, followed by chewing herbivores, sucking herbivores, and detritivores.

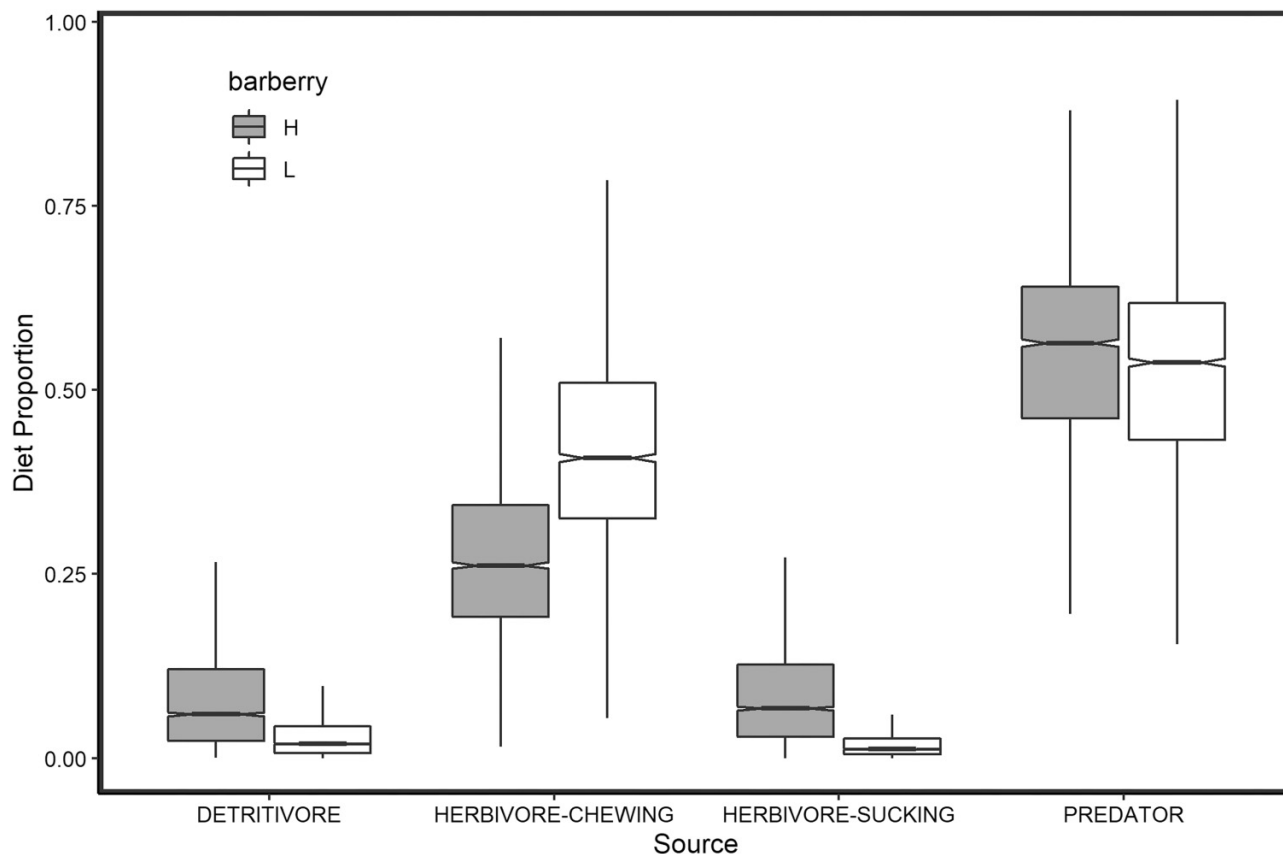


gion for more than 100 years (Ehrenfeld 1997; Silander and Klepeis 1999), thus providing a considerable amount of time for the development of novel links between barberry, herbivores, and consumers. By contrast, several of the previous studies investigating non-native plant effects on consumer diets focused on invasions that were only several decades old (Laffaille et al. 2005; Carniatto et al. 2020). Meanwhile, in one of the longer-term invasions studied, several bird species, including the ground-foraging green-tailed towhee (*Pipilo chloru-*

rus (Audubon, 1839)), showed no shift in diet in response to the presence of the introduced New Mexico locust (Riedl et al. 2018). Moreover, it is plausible that the length of the post-invasion period could interact with ecosystem-type to influence the development of new trophic links between non-native plants and further contribute to the homogeneity of herbivore–consumer interactions in our study system.

At the individual level, our finding of only minor shifts in diet despite major barberry-driven changes in invertebrate

Fig. 3. Boxplots of estimated contributions to ovenbird (*Seiurus aurocapilla*) diets in high- (H) and low-density (L) barberry (*Berberis thunbergii*) areas. Boxes depict median, first and third quartile estimates, and whiskers depict the range encompassed by 1.5 times the interquartile range. Contributions were largely consistent across barberry densities, with only chewing herbivores making a modestly greater contribution in low-density areas and sucking herbivores making a slightly larger contribution in high-density areas.



community composition at our study site can be interpreted in several ways. For one, as the availability of certain dietary resources decreases, it is possible to maintain a consistent diet composition by reducing overall intake such that the resulting absolute rates of consumption are aligned with the availability of the most limited dietary resource. A second option would be to maintain a consistent intake of each dietary resource by increasing foraging effort, such as by expanding foraging area or time (Ferretti et al. 2019). These interpretations suggest the imposition of additional energetic constraints on ovenbirds, either through a reduced budget in the former case or increased costs in the latter case. Increased effort could also produce time constraints and limit other important activities such as territory defense and maintenance. However, both interpretations are inconsistent with our previous finding that ovenbirds breeding in areas with high and low densities of barberry did not differ in physiological condition, including body mass and hematological indices of energy intake and chronic stress (Seewagen et al. 2020). However, increased foraging effort is not always linked to reduced condition in birds (Lamb et al. 2017), and so the costs of adjusting foraging behavior to maintain a consistent diet may be more marginal for ovenbirds than expected and help ex-

plain our results while allowing for no detectable impact on condition.

A third possibility is that ovenbird diet selection shifts based on threshold values of availability, and invertebrate resources remained abundant enough in high-density barberry areas to avoid crossing those thresholds. The role of availability thresholds in determining dietary choices has not been extensively studied in songbirds, but there is some evidence that these thresholds can be quite low. For example, a study on Sardinian warblers (*Currucula melanocephala* (J.F. Gmelin, 1789)) found a distinct shift to frugivory when fruit abundances were still ~ 80 times lower than subsequent peak levels (González-Varo et al. 2022). Similarly, studies on marsh tits (*Poecile palustris* (Linnaeus, 1758)) and European nuthatches (*Sitta europaea* Linnaeus 1758) found consistently high use of caterpillars for nest provisioning over more than a six-fold range in caterpillar abundance, with a clear drop in use below $0.1 \text{ g} \cdot 0.25 \text{ sq. m}^{-1} \cdot \text{d}^{-1}$ frass fall (Wesołowski and Neubauer 2017; Wesołowski et al. 2019). Compared to the scale of these changes, the one- to two-fold changes in abundance observed in our study site (Clark and Seewagen 2019) are relatively minor and could simply be too small to prompt extensive changes in ovenbird diets. This explanation joins the pre-

vious two in suggesting limited impacts of barberry-driven changes to invertebrate communities on ovenbird condition and possibly fitness in invaded areas. Other studies in the northeastern U.S. have shown songbirds to exhibit a preference for nesting in barberry and experience similar or better nesting success compared to native shrubs (Schmidt et al. 2005; Schlossberg and King 2010; Meyer et al. 2015). Taken together, management actions to remove barberry may be unlikely to have substantial benefits to generalist songbirds and may even prove negative, depending on the degree to which they disrupt ecological communities in managed areas.

A final interpretation for our finding of largely consistent ovenbird diets despite varying barberry density is that our selection of territorial males as study animals limited our ability to detect shifts in other age or sex classes. Thus, while breeding males appear to be relatively unaffected by barberry invasion, it may be the case that subdominant individuals, often females in non-breeding warblers (Akresh et al. 2019; Cooper et al. 2021), are disproportionately impacted by barberry invasion. This result would be rather unexpected, because intrapair or intergenerational competition are much more likely to negatively impact reproductive success and consequent fitness than male condition (Schwagmeyer and Mock 2008; Senécal et al. 2021). Meanwhile, the impacts on females trading off foraging time and incubation time or fledglings that are still relatively inefficient at foraging could be much greater in scope. Both of these possibilities highlight the potential value in investigating the impact of barberry invasion on songbirds across ages and sexes, including their parental behavior. It is important to note, though, that none of the mechanisms discussed here are mutually exclusive, and so future studies will have to carefully consider how best to parse their relative importance.

While our results did not show the anticipated barberry-driven variation in ovenbird diets, our estimates of ovenbird diet composition were largely consistent with previous descriptions based on other methods of diet analysis. In particular, the largest contribution of any functional group in our estimates was predators, which aligns with the results of other studies (Strong 2000; Streby et al. 2013; Ruhl et al. 2020). Preliminary analyses, which considered the contributions of specific taxa, suggested that much of the consumption of predatory invertebrates could be attributed to ants (Formicidae), which is interesting as it would most closely match estimates from ovenbirds on their wintering grounds in Jamaica (Strong 2000). This result suggests that there is likely to be a broader shift in diet over the course of the breeding season, as productivity and insect abundance change from the late spring to early summer. Such a shift could also explain the somewhat smaller contributions of chewing herbivores, including Lepidoptera, to ovenbird diets, which were predominant in some previous estimates (Stenger 1958; Streby et al. 2013). Although caterpillars can reach high abundances early in the season (Lany et al. 2016; Shutt et al. 2019), we collected plasma samples for diet reconstruction slightly before average peak abundance in our study area, potentially explaining this small estimate. Alternately, ground-foraging ovenbirds may still source some caterpillars from foliage, potentially resulting in underestimates if the isotopic composition

of foliage-dwelling Lepidoptera was not precisely captured by our sample. Overall, however, our results strongly align with previous characterizations of the ovenbird as a dietary generalist (Stenger 1958; Zach and Falls 1979; Holmes and Robinson 1988; Strong 2000; Ruhl et al. 2020).

Conclusions

In our test case of the indirect influence of a non-native plant on a ground-foraging songbird, we found only weak evidence that this invasion results in altered trophic interactions with the invertebrate community. At the individual level, consistent trophic interactions could be maintained by shifts in foraging effort or may reflect a general abundance of resources that decouples diet selection from the relative proportions of available items. At the community level, the relatively stable position of ovenbirds within the food web of a northeastern USA forest may differ from patterns in other invaded systems due to contextual differences such as the pre-existing community complexity of our temperate forest system or the timing of the invasion. Both observations suggest valuable directions for future studies. On the one hand, the role of availability thresholds in diet selection remains largely unknown for songbirds and could help inform a more mechanistic understanding of their dietary behavior. On the other hand, the impact of broader context on the restructuring of communities by non-native species is currently unclear and large-scale comparative studies across ecosystems may improve our ability to predict the consequences of future plant invasions for songbirds. Ultimately, our study supports the position that the impacts of non-native plants are not universally negative for songbirds (Schlaepfer et al. 2011; Nelson et al. 2017), and so careful consideration of management options is likely necessary, as efforts to remove barberry and other invasive plants could cause more harm than benefit for some species.

Acknowledgements

John Correia, Brittany Harry, Clare Quinlan, Evalyn Machia, Hannah Miller, and Heidi Faulkner provided invaluable assistance in collecting the blood samples and invertebrates used in this study and surveying vegetation. We thank Sarah Deckel for helping to prepare samples for stable isotope analysis and thank the New York Chapter of The Nature Conservancy for permission to work at Pawling Nature Reserve. This study was funded by Great Hollow Nature Preserve & Ecological Research Center, with additional support from a mini-grant to CLS from the Connecticut Ornithological Association.

Article information

History dates

Received: 21 March 2023

Accepted: 7 July 2023

Accepted manuscript online: 31 July 2023

Version of record online: 30 October 2023

Copyright

© 2023 The Author(s). Permission for reuse (free in most cases) can be obtained from [creativecommons.org](https://creativecommons.org/licenses/by/4.0/).

Data availability

Data used in this publication are available as online Supplementary material.

Author information

Author ORCIDs

Wales A. Carter <https://orcid.org/0000-0001-5933-6439>

Author contributions

Conceptualization: CLS

Data curation: WAC

Formal analysis: WAC

Funding acquisition: CLS

Investigation: CLS

Methodology: WAC, CLS

Project administration: CLS

Resources: CLS

Supervision: CLS

Visualization: WAC

Writing – original draft: WAC

Writing – review & editing: WAC, CLS

Competing interests

The authors declare no conflicts of interest.

Funding information

External funding for this project was provided by the Connecticut Ornithological Association.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjz-2023-0058>.

References

Akresh, M.E., King, D.I., and Marra, P.P. 2019. Rainfall and habitat interact to affect the condition of a wintering migratory songbird in The Bahamas. *Ecol. Evol.* **9**(14): 8042–8061. doi:10.1002/ece3.5359. PMID: 31380070.

Arim, M., and Jaksic, F.M. 2011. Productivity and food web structure: association between productivity and link richness among top predators. *J. Anim. Ecol.* **74**(1): 31–40. doi:10.1111/j.1365-2656.2004.00894.x.

Arlt, D., and Pärt, T. 2017. Marked reduction in demographic rates and reduced fitness advantage for early breeding is not linked to reduced thermal matching of breeding time. *Ecol. Evol.* **7**(24): 1–15. doi:10.1002/ece3.3603.

Armitage, A.R., and Fourqurean, J.W. 2009. Stable isotopes reveal complex changes in trophic relationships following nutrient addition in a coastal marine ecosystem. *Estuaries Coasts*, **32**(6): 1152–1164. doi:10.1007/s12237-009-9219-z.

Arnold, K.E., Ramsay, S.L., Donaldson, C., and Adam, A. 2007. Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. *Proc. R. Soc. B Biol. Sci.* **274**(1625): 2563–2569. doi:10.1098/rspb.2007.0687.

Averill, K.M., Mortensen, D.A., Smithwick, E.A.H., and Post, E. 2016. Deer feeding selectivity for invasive plants. *Biol. Invasions*, **18**(5): 1247–1263. doi:10.1007/s10530-016-1063-z.

Bellard, C., Cassey, P., and Blackburn, T.M. 2016. Alien species as a driver of recent extinctions. *Biol. Lett.* **12**(4): doi:10.1098/rsbl.2015.0623. PMID: 26888913.

Birkhead, T.R., Fletcher, F., and Pellatt, E.J. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proc. R. Soc. B Biol. Sci.* **266**(1417): 385–390. doi:10.1098/rspb.1999.0649.

Blackburn, T.M., Bellard, C., and Ricciardi, A. 2019. Alien versus native species as drivers of recent extinctions. *Front. Ecol. Environ.* **17**(4): 203–207. doi:10.1002/fee.2020.

Both, C., Bouwhuis, S., Lessells, C.M., and Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature*, **441**(1): 81–83. doi:10.1038/nature04539. PMID: 16672969.

Burke, D.M., and Nol, E. 1998. Influence of food abundance, nest site habitat, and forest fragmentation on breeding ovenbirds. *Auk*, **115**(1): 96–104. doi:10.2307/4089115.

Carniatto, N., Cunha, E.R., Thomaz, S.M., Quirino, B.A., and Fugi, R. 2020. Feeding of fish inhabiting native and non-native macrophyte stands in a neotropical reservoir. *Hydrobiologia*, **847**(6): 1553–1563. doi:10.1007/s10750-020-04212-2.

Carter, W.A., Pearson, S.F., Smith, A.D., McWilliams, S.R., and Levey, D.J. 2021. Seasonal and interspecific variation in frugivory by a mixed resident-migrant overwintering songbird community. *Diversity*, **13**(7): 314. doi:10.3390/d13070314.

Clark, R.E., and Seewagen, C.L. 2019. Invasive Japanese barberry, *Berberis thunbergii* (Ranunculales: Berberidaceae) is associated with simplified branch-dwelling and leaf-litter arthropod communities in a New York forest. *Environ. Entomol.* **48**(5): 1071–1078. doi:10.1093/ee/nvz095. PMID: 31504361.

Cooper, N.W., Thomas, M.A., and Marra, P.P. 2021. Vertical sexual habitat segregation in a wintering migratory songbird. *Auk*, **138**: 1–11. doi:10.1093/ornithology/ukaa080.

Degasperis, B.G., and Motzkin, G. 2007. Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. *Ecology*, **88**(12): 3115–3125. doi:10.1890/06-2014.1. PMID: 18229845.

de Groot, M., Kleijn, D., and Jogan, N. 2007. Species groups occupying different trophic levels respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*. *Biol. Conserv.* **136**(4): 612–617. doi:10.1016/j.biocon.2007.01.005.

Donovan, T.M., and Stanley, C.M. 1995. A new method of determining ovenbird age on basis of rectrix shape. *J. Field Ornithol.* **66**(2): 247–252.

Donovan, T.M., and Flather, C.H. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecol. Appl.* **12**(2): 364–374.

Ehrenfeld, J.G. 1997. Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC.). *J. Torrey Bot. Soc.* **124**(2): 210–215. doi:10.2307/2996586.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., et al. 2011. Trophic downgrading of planet earth. *Science*, **333**(6040): 301–306. doi:10.1126/science.1205106.

Evans Ogden, L.J., Hobson, K.A., and Lank, D.B. 2004. Blood isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) turnover and diet-tissue fractionation factors in captive dunlin (*Calidris alpina pacifica*). *Auk*, **121**(1): 170–177. doi:10.1093/auk/121.1.170.

Ferretti, A., Maggini, I., Lupi, S., Cardinale, M., and Fusani, L. 2019. The amount of available food affects diurnal locomotor activity in migratory songbirds during stopover. *Sci. Rep.* **9**(1): 1–9. doi:10.1038/s41598-019-55404-3. PMID: 30626917.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., and Falkowski, P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, **281**(5374): 237–240. doi:10.1126/science.281.5374.237.

Gaertner, M., Biggs, R., Te Beest, M., Hui, C., Molofsky, J., and Richardson, D.M. 2014. Invasive plants as drivers of regime shifts: identifying high priority invaders that alter feedback relationships. *Divers. Distrib.* **20**: 733–744. doi:10.1111/ddi.12182.

Gelman, A., and Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**(4): 457–511. doi:10.1214/ss/1177011136.

- Génier, C.S.V., Guglielmo, C.G., Mitchell, G.W., Falconer, M., and Hobson, K.A. 2021. Nutritional consequences of breeding away from riparian habitats in bank swallows: new evidence from multiple endogenous markers. *Conserv. Physiol.* **9**(1): 1–12. doi:10.1093/conphys/coaa140.
- George, A.D., O'Connell, T.J., Hickman, K.R., and Leslie, D.M. 2013. Food availability in exotic grasslands: a potential mechanism for depauperate breeding assemblages. *Wilson J. Ornithol.* **125**(3): 526–533. doi:10.1676/13-003.1.
- González-Varo, J.P., Onrubia, A., Pérez-Méndez, N., Tarifa, R., and Illera, J.C. 2022. Fruit abundance and trait matching determine diet type and body condition across frugivorous bird populations. *Oikos*, **2022**(2): doi:10.1111/oik.08106. PMID: 36644620.
- Grzędzicka, E., and Reif, J. 2021. The impact of sosnowsky's hogweed on feeding guilds of birds. *J. Ornithol.* **162**(4): 1115–1128. doi:10.1007/s10336-021-01898-6.
- Hallmann, C.A., Foppen, R.P.B., Van Turnhout, C.A.M., De Kroon, H., and Jongejans, E. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature*, **511**(7509): 341–343. doi:10.1038/nature13531. PMID: 25030173.
- Hegemann, A., Matson, K.D., Flinks, H., and Tieleman, B.I. 2013. Offspring pay sooner, parents pay later: experimental manipulation of body mass reveals trade-offs between immune function, reproduction and survival. *Front. Zool.* **10**(77): 1–11. PMID: 23356547.
- Hobson, K.A., and Bairlein, F. 2003. Isotopic fractionation and turnover in captive garden warblers (*Sylvia borin*): implications for delineating dietary and migratory associations in wild passerines. *Can. J. Zool.* **81**(9): 1630–1635. doi:10.1139/z03-140.
- Hoening, B.D., Treveline, B.K., Kautz, A., Latta, S.C., and Porter, B.A. 2022. Two is better than one: coupling DNA metabarcoding and stable isotope analysis improves dietary characterizations for a riparian-obligate, migratory songbird. *Mol. Ecol.*(December 2021): 1–14. doi:10.1111/mec.16688. PMID: 34957606.
- Holmes, R.T., and Robinson, S.K. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. *Wilson Bull.* **100**(3): 377–394.
- James, F.C.F.C., and Shugart, H.H.J. 1970. A quantitative method of habitat description.
- Kennedy, P.L., DeBano, S.J., Bartuszevige, A.M., and Lueders, A.S. 2009. Effects of native and non-native grassland plant communities on breeding passerine birds: implications for restoration of northwest bunchgrass prairie. *Restor. Ecol.* **17**(4): 515–525. doi:10.1111/j.1526-100X.2008.00402.x.
- Kirby, J.S., Stattersfield, A.J., Butchart, S.H.M., Evans, M.I., Grimmett, R.F.A., Jones, V.R., et al. 2008. Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conserv. Int.* **18**: S49–S73. doi:10.1017/S0959270908000439.
- Klaus, N.A., Buehler, D.A., and Saxton, A.M. 2005. Forest management alternatives and songbird breeding habitat on the Cherokee National Forest, Tennessee. *J. Wildl. Manag.* **69**(1): 222–234. doi:10.2193/0022-541x(2005)069(0222:fmaasb)2.0.co;2.
- Kourtev, P.S., Ehrenfeld, J.G., and Haggblom, M. 2002. Exotic plant species alter the microbial community structure and function in the soil. *Ecology*, **83**(11): 3152. doi:10.2307/3071850.
- Laffaille, P., Pétilion, J., Parlier, E., Valéry, L., Ysnel, F., Radureau, A., et al. 2005. Does the invasive plant *Elymus athericus* modify fish diet in tidal salt marshes? *Estuar. Coast. Shelf Sci.* **65**(4): 739–746. doi:10.1016/j.ecss.2005.07.023.
- Lamb, J.S., Satgé, Y.G., and Jodice, P.G.R. 2017. Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. *Ecol. Evol.*(June): 1–13. doi:10.1002/ece3.3216.
- Lany, N.K., Ayres, M.P., Stange, E.E., Sillett, T.S., Rodenhouse, N.L., and Holmes, R.T. 2016. Breeding timed to maximize reproductive success for a migratory songbird: the importance of phenological asynchrony. *Oikos*, **125**(5): 656–666. doi:10.1111/oik.02412.
- Linske, M.A., Williams, S.C., Ward, J.S., and Stafford, K.C. 2018. Indirect effects of Japanese barberry infestations on white-footed mice exposure to *Borrelia burgdorferi*. *Environ. Entomol.* **47**(4): 795–802. doi:10.1093/ee/nvy079. PMID: 29850912.
- Litt, A.R., Cord, E.E., Fulbright, T.E., and Schuster, G.L. 2014. Effects of invasive plants on arthropods. *Conserv. Biol.* **28**(6): 1532–1549. doi:10.1111/cobi.12350. PMID: 25065640.
- Loss, S.R., Will, T., and Marra, P.P. 2013. The impact of free-ranging domestic cats on wildlife of the United States. *Nat. Commun.* **4**. doi:10.1038/ncomms2380. PMID: 23360987.
- Loss, S.R., Will, T., and Marra, P.P. 2015. Direct mortality of birds from anthropogenic causes. *Annu. Rev. Ecol. Syst.* **46**: 99–120. doi:10.1146/annurev-ecolsys-112414-054133.
- Lubell, J.D., Brand, M.H., Lehrer, J.M., and Holsinger, K.E. 2008. Detecting the influence of ornamental *Berberis thunbergii* var. *Atropurpurea* in invasive populations of *Berberis thunbergii* (Berberidaceae) using AFLP. *Am. J. Bot.* **95**(6): 700–705. doi:10.3732/ajb.2007336. PMID: 21632395.
- Maerz, J.C., Nuzzo, V.A., and Blossey, B. 2009. Declines in woodland salamander abundance associated with non-native earthworm and plant invasions. *Conserv. Biol.* **23**(4): 975–981. doi:10.1111/j.1523-1739.2009.01167.x. PMID: 19236449.
- McNulty, S.A., Droege, S., and Masters, R.D. 2008. Long-term trends in breeding birds in an old-growth Adirondack forest and the surrounding region. *Wilson J. Ornithol.* **120**(1): 153–158. doi:10.1676/07-032.1.
- Meyer, L.M., Schmidt, K.A., and Robertson, B.A. 2015. Evaluating exotic plants as evolutionary traps for nesting veeries. *Condor*, **117**(3): 320–327. doi:10.1650/CONDOR-14-101.1.
- Milesi, C., Elvidge, C.D., Nemani, R.R., and Running, S.W. 2003. Assessing the impact of urban land development on net primary productivity in the southeastern United States. *Remote Sens. Environ.* **86**(3): 401–410. doi:10.1016/S0034-4257(03)00081-6.
- Moore, J.W., and Semmens, B.X. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. *Ecol. Lett.* **11**(5): 470–480. doi:10.1111/j.1461-0248.2008.01163.x. PMID: 18294213.
- Mudrzyński, B.M., and Norment, C.J. 2013. Influence of habitat structure and fruit availability on use of a northeastern stopover site by fall songbirds. *Wilson J. Ornithol.* **125**(4): 744–754. doi:10.1676/13-060.1.
- Narango, D.L., Tallamy, D.W., and Marra, P.P. 2018. Nonnative plants reduce population growth of an insectivorous bird. *Proc. Natl. Acad. Sci. U.S.A.* **115**(45): 11549–11554. doi:10.1073/pnas.1809259115. PMID: 30348792.
- Nelson, S.B., Coon, J.J., Duchardt, C.J., Fischer, J.D., Halsey, S.J., Kranz, A.J., et al. 2017. Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. *Biol. Invasions*, **19**(5): 1547–1563. doi:10.1007/s10530-017-1377-5.
- Neutel, A.M., Heesterbeek, J.A.P., Van De Koppel, J., Hoenderboom, G., Vos, A., Kaldewey, C., et al. 2007. Reconciling complexity with stability in naturally assembling food webs. *Nature*, **449**(7162): 599–602. doi:10.1038/nature06154. PMID: 17914396.
- Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W., and Ratcliffe, L.M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc. R. Soc. B Biol. Sci.* **271**(1534): 59–64. doi:10.1098/rspb.2003.2569.
- Nuzzo, V.A., Maerz, J.C., and Blossey, B. 2009. Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. *Conserv. Biol.* **23**(4): 966–974. doi:10.1111/j.1523-1739.2009.01168.x. PMID: 19236448.
- Nyffeler, M., Şekerciöğlü, Ç.H., and Whelan, C.J. 2018. Insectivorous birds consume an estimated 400–500 million tons of prey annually. *Sci. Nat.* **105**(7–8). doi:10.1007/s00114-018-1571-z.
- O'Donnell, C.F.J., Weston, K.A., and Monks, J.M. 2017. Impacts of introduced mammalian predators on New Zealand's alpine fauna. *N. Z. J. Ecol.* **41**(1): 1–22. doi:10.20417/nzjecol.41.18.
- Pearson, S.F., Levey, D.J., Greenberg, C.H., and Martínez del Rio, C. 2003. Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Oecologia*, **135**(4): 516–523. doi:10.1007/s00442-003-1221-8. PMID: 16228250.
- Phillips, D.L., and Koch, P.L. 2002. Incorporating concentration dependence in stable isotope mixing models. *Oecologia*, **130**(1): 114–125. doi:10.1007/s004420100786. PMID: 28547016.
- Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., et al. 2014. Best practices for use of stable isotope mixing models in food-web studies. *Can. J. Zool.* **835**(August): 823–835. doi:10.1139/cjz-2014-0127.
- Piltzko, S.J., Drossel, B., and Guill, C. 2012. Complexity-stability relations in generalized food-web models with realistic parameters. *J. Theor. Biol.* **306**: 7–14. doi:10.1016/j.jtbi.2012.04.008. PMID: 22575485.

- Porneluzi, P., Van Horn, M.A., and Donovan, T.M. 2020. Ovenbird (*Seiurus aurocapilla*). In *Birds of the world*. Edited by A.F. Poole. Cornell Lab of Ornithology. doi:10.2173/bow.ovenbi1.01.
- Put, J.E., Mitchell, G.W., Mahony, N.A., Costa, J., Imlay, T.L., Bossuyt, S., et al. 2021. Regional variability in trajectories of barn swallow populations across Canada are not predicted by breeding performance. *Avian Conserv. Ecol.* **16**(2): 10. doi:10.5751/ace-01933-160210.
- Pyle, P. 1997. Identification guide to North American birds part I: Columbidae to Ploceidae. 1st ed. Slate Creek Press, Bolinas, CA.
- Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U., and Vilà, M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob. Chang. Biol.* **18**(5): 1725–1737. doi:10.1111/j.1365-2486.2011.02636.x.
- Riedl, H.L., Stinson, L., Pejchar, L., and Clements, W.H. 2018. An introduced plant affects aquatic-derived carbon in the diets of riparian birds. *PLoS ONE*, **13**(11): 3–5. doi:10.1371/journal.pone.0207389.
- Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., et al. 2019. Decline of the North American avifauna. *Science*, **366**(6461): 120–124. doi:10.1126/science.aaw1313.
- Rosing, M.N., Ben-David, M., and Barry, R.P. 1998. Analysis of stable isotope data: a k nearest-neighbors randomization test. *J. Wildl. Manag.* **62**(1): 380–388. doi:10.2307/3802302.
- Ruhl, P.J., Flaherty, E.A., and Dunning, J.B. 2020. Using stable isotopes of plasma, red blood cells, feces, and feathers to assess mature-forest bird diet during the post-fledging period. *Can. J. Zool.* **98**(1): 39–46. doi:10.1139/cjz-2019-0109.
- Rushing, C.S., Ryder, T.B., and Marra, P.P. 2016. Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proc. R. Soc. B Biol. Sci.* **283**(1823): doi:10.1098/rspb.2015.2846.
- Sauer, J.R., and Link, W.A. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. *Auk*, **128**(1): 87–98. doi:10.1525/auk.2010.09220.
- Schlaepfer, M.A., Sax, D.F., and Olden, J.D. 2011. The potential conservation value of non-native species. *Conserv. Biol.* **25**(3): 428–437. doi:10.1111/j.1523-1739.2010.01646.x. PMID: 21342267.
- Schlossberg, S., and King, D.I. 2010. Effects of invasive woody plants on avian nest site selection and nesting success in shrublands. *Anim. Conserv.* **13**(3): 286–293. doi:10.1111/j.1469-1795.2009.00338.x.
- Schmidt, K.A., Nelis, L.C., Briggs, N., and Ostfeld, R.S. 2005. Invasive shrubs and songbird nesting success: effects of climate variability and predator abundance. *Ecol. Appl.* **15**(1): 258–265. doi:10.1890/03-5325.
- Schwagmeyer, P.L., and Mock, D.W. 2008. Parental provisioning and offspring fitness: size matters. *Anim. Behav.* **75**(1): 291–298. doi:10.1016/j.anbehav.2007.05.023.
- Seewagen, C.L., Slayton, E.J., and Smith Pagano, S. 2020. Physiological indicators of habitat quality for a migratory songbird breeding in a forest invaded by non-native Japanese barberry (*Berberis thunbergii*). *Conserv. Physiol.* **8**(1): 1–12. doi:10.1093/conphys/coaa037.
- Senécal, S., Riva, J.-C., O'Connor, R.S., Hallot, F., Nozais, C., and Vézina, F. 2021. Poor prey quality is compensated by higher provisioning effort in passerine birds. *Sci. Rep.* **11**(1): 1–11. doi:10.1038/s41598-021-90658-w. PMID: 33414495.
- Shutt, J.D., Burgess, M.D., and Phillimore, A.B. 2019. A spatial perspective on the phenological distribution of the spring woodland caterpillar peak. *Am. Nat.* **194**(5): E109–E121. doi:10.1086/705241. PMID: 31613670.
- Silander, J.A., and Klepeis, D.M. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. *Biol. Invasions*, **1**(2–3): 189–201. doi:10.1023/a:1010024202294.
- Smith, T.M., and Shugart, H.H.J. 1987. Territory size variation in the ovenbird: the role of habitat structure. *Ecology*, **68**(3): 695–704. doi:10.2307/1938475.
- Stenger, J. 1958. Food habits and available food of ovenbirds in relation to territory size. *Auk*, **75**(3): 335–346. doi:10.2307/4081979.
- Stock, B.C., and Semmens, B.X. 2016. Unifying error structures in commonly used biotracer mixing models. *Ecology*, **97**(10): 2562–2569. doi:10.1002/ecy.1517. PMID: 27859126.
- Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., and Semmens, B.X. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, **2018**(6): 1–27. doi:10.7717/peerj.5096.
- Stouffer, D.B., and Bascompte, J. 2011. Compartmentalization increases food-web persistence. *Proc. Natl. Acad. Sci. U.S.A.* **108**(9): 3648–3652. doi:10.1073/pnas.1014353108. PMID: 21307311.
- Streby, H.M., Peterson, S.M., Scholtens, B., Monroe, A.P., and Andersen, D.E. 2013. The ovenbird (*Seiurus aurocapilla*) as a model for testing food-value theory. *Am. Midl. Nat.* **169**(1): 214–220. doi:10.1674/0003-0031-169.1.214.
- Strong, A.M. 2000. Divergent foraging strategies of two neotropical migrant warblers: implications for winter habitat use. *Auk*, **117**(2): 381–392. doi:10.2307/4089720.
- Thiele, J., Isermann, M., Otte, A., and Kollmann, J. 2010. Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. *J. Veg. Sci.* **21**(2): 213–220. doi:10.1111/j.1654-1103.2009.01139.x.
- Townsend, J.M., Rimmer, C.C., Brocca, J., McFarland, K.P., and Townsend, A.K. 2009. Predation of a wintering migratory songbird by introduced rats: can nocturnal roosting behavior serve as predator avoidance? *Condor*, **111**(3): 565–569. doi:10.1525/cond.2009.090062.
- Turner, D.P., Ritts, W.D., Cohen, W.B., Gower, S.T., Running, S.W., Zhao, M., et al. 2006. Evaluation of MODIS NPP and GPP products across multiple biomes. *Remote Sens. Environ.* **102**(3–4): 282–292. doi:10.1016/j.rse.2006.02.017.
- Vehtari, A., Gelman, A., and Gabry, J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**(5): 1413–1432. doi:10.1007/s11222-016-9696-4.
- Villard, M.A., D'Astous, É., Haché, S., Poulin, J.F., and Thériault, S. 2012. Do we create ecological traps when trying to emulate natural disturbances? A test on songbirds of the northern hardwood forest. *Can. J. For. Res.* **42**(7): 1213–1219. doi:10.1139/X2012-047.
- Ward, E.J., Semmens, B.X., and Schindler, D.E. 2010. Including source uncertainty and prior information in the analysis of stable isotope mixing models. *Environ. Sci. Technol.* **44**(12): 4645–4650. doi:10.1021/es100053v. PMID: 20496928.
- Wesołowski, T., and Neubauer, G. 2017. Diet of marsh tit *Poecile palustris* nestlings in a primeval forest in relation to food supply and age of young. *Acta Ornithol.* **52**(1): 105–118. doi:10.3161/00016454AO2017.52.1.010.
- Wesołowski, T., Rowiński, P., and Neubauer, G. 2019. Food of nuthatch sitta europaea young in a primeval forest: effects of varying food supply and age of nestlings. *Acta Ornithol.* **54**(1): 85–104. doi:10.3161/00016454AO2019.54.1.008.
- Zach, R., and Falls, J.B. 1979. Foraging and territoriality of male ovenbirds (Aves: Parulidae) in a heterogeneous habitat. *J. Anim. Ecol.* **48**(1): 33–52. doi:10.2307/4098.