
THE RESPONSE OF AVIAN PREDATOR POPULATIONS TO FOREST TENT
CATERPILLAR (*Malacosoma disstria*; Lepidoptera: Lasiocampidae)
OUTBREAKS IN ONTARIO, CANADA.

by

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ABSTRACT

Outbreaks of insect defoliators have broad ecological effects on forested ecosystems because they can cause extensive mortality in host tree populations. They also represent peaks in the density of food for specialist and generalist predators, and some species of insectivorous birds show strong responses to outbreaks of defoliators. Using over 50 years of bird counts and defoliation data, I examined the response of four species with a range of foraging specializations to outbreaks of the forest tent caterpillar, a major defoliator of deciduous trees in eastern North America. The specialist black-billed cuckoo (*Coccyzus erythrophthalmus*) showed strong aggregative and numerical responses to the outbreaks of forest tent caterpillar at local and regional spatial scales, respectively. In contrast, species with a lower degree of foraging specialization, the least flycatcher (*Empidonax minimus*), the yellow warbler (*Setophaga petechia*), and the black-capped chickadee (*Poecile atricapillus*) showed weak or null aggregational and numerical responses to the outbreaks, suggesting that they forage opportunistically on forest tent caterpillars and that this does not result in increased reproductive output. The results of this study are consistent with the idea that only species with a high degree of foraging specialization can take advantage of a food resource that fluctuates in a predictable manner, and highlights the need to consider the predator-prey dynamics when managing population outbreaks of insect defoliators.

Keywords: Aggregative response, numerical response, defoliator outbreaks, forest tent caterpillar, specialist predators, generalist predators.

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INTRODUCTION

In contrast to abiotic disturbances in forest ecosystems, forest insect defoliator outbreaks result in ecological effects that are synchronized over large areas; they are periodic and selective, unlike those caused by fire, windstorms or flooding (Cooke et al. 2007). In Canada, outbreaks of at least 106 species of Lepidoptera, Hymenoptera, and Coleoptera not only cause widespread damage to their host tree species, but also represent a pulse in the availability of food for insectivorous birds (Johns et al. 2016). For example, outbreaks of spruce budworm (*Choristoneura fumiferana*; Zach and Falls 1975, Patten and Burger 1998, Venier and Holmes 2010, Drever et al. 2018), gypsy moth (*Lymantria dispar*; Gale et al. 2001, Koenig et al. 2011), and mountain pine beetle (*Dendroctonus ponderosae*; Drever et al. 2009, Edworthy et al. 2011, Cockle and Martin 2015) are followed by increases in some of their avian predators.

Predators respond to changes in the density of their prey with processes operating at both individual and population levels. The first is the functional response, described by Holling's disc equation as the change in rates at which an individual predator captures, consumes and digests its prey, as a function of prey density (Solomon 1949, Holling 1959, Hassel 1978, Holt and Kimbrell 2007). The second is a numerical response normally described by changes in reproduction and mortality at the population level, modelled as the shape of the curve of increasing density of predators with increases in its prey's density (Solomon 1949, Holling 1959, Turchin 2003). For predators that reproduce once

yearly, an increase in prey density may occur after the breeding period, and the numerical response will also be temporally lagged. The third is an aggregative response should individual predators respond to increases in prey density by moving to areas where their prey is more abundant, resulting in local increases in their density. It is a spatially explicit process not usually considered in predator-prey theory and treated by many authors as part of the numerical response (Turchin 2003). However, unlike the numerical response, aggregation of predators occurs at a fast time scale and does not involve changes to birth and death rates. Together, these three responses link foraging decisions to the dynamic of predator populations in response to changes in prey density.

At least 60 species of birds forage on the forest tent caterpillar (*Malacosoma disstria*), a major defoliator of deciduous trees in eastern North America (Witter and Kulman 1972). Periodic outbreaks of the forest tent caterpillar occur every 9 to 14 years in Quebec (Cooke and Lorenzetti 2006), and every 13.0 ± 0.95 years in Ontario (Fleming et al. 2000). Peaks in defoliation between 1947 and 2018 are on the order of tens of millions of hectares, a magnitude comparable to that of spruce budworm outbreaks, the main insect defoliator of coniferous trees in eastern North America. However, unlike the spruce budworm, outbreaks of the forest tent caterpillar in Ontario are remarkably regular in their periodicity and this makes them suitable to test hypothesis about the strong specialization of their predators (Figure 1). Defoliation by forest tent caterpillar begins in spring when larvae emerge from their eggs to feed on the foliage of poplars (*Populus* spp.), birches (*Betula* spp.),

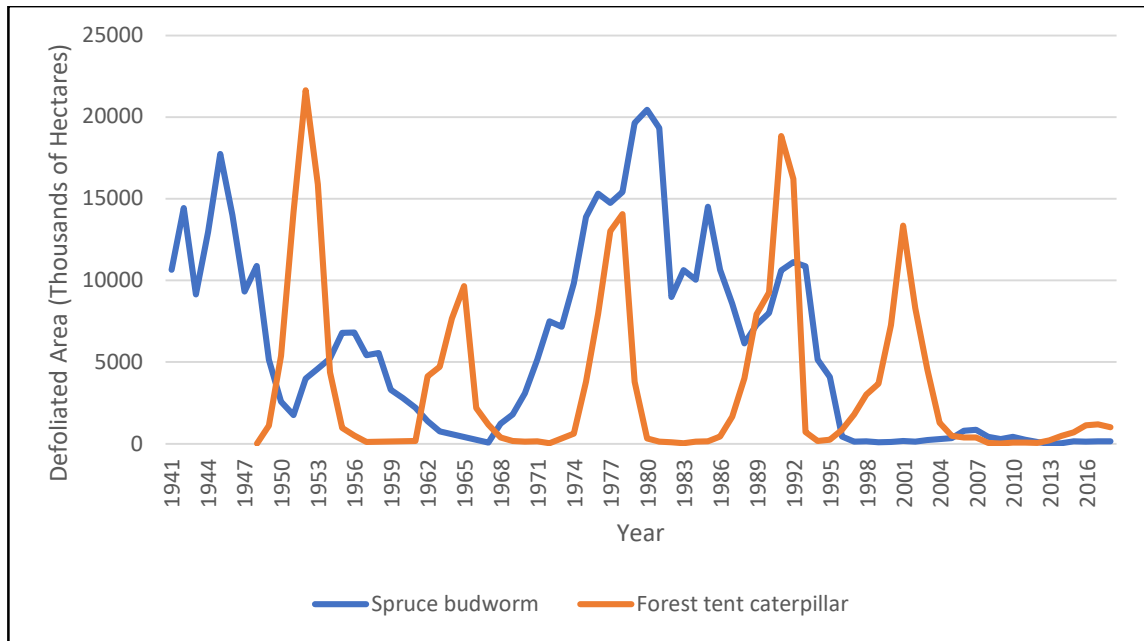


Figure 1. Temporal patterns of the extent of spruce budworm (1941 – 2018) and forest tent caterpillar (1948 – 2018) outbreaks in Ontario, Canada, based on defoliation data obtained from Natural Resources Canada. Until the early 2000s, outbreaks of forest tent caterpillar showed a remarkable regularity, unlike spruce budworm.

maples (*Acer* spp.), oaks (*Quercus* spp.) and other hardwoods. In laboratory conditions, larvae feed and undergo 5 – 8 instars over 4 to 7 weeks, before wandering to seek pupation sites (Schowalter 2017). Repeated defoliation can lead to reduced tree growth and cause dieback in twigs, branches, roots and stems, as the photosynthetic capacity of a tree is reduced (Kulman 1971; Cooke et al. 2007). Increased tree mortality follows consecutive years of defoliation in trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*; Ghent 1958, Churchill et al. 1964, Candau et al. 2002, Man and Rice 2010), and allows the release of coniferous trees from the understory of mixedwood stands (Fitzgerald 1995, Chen and Popadiuk 2002). Thus, forest tent caterpillar

outbreaks can influence its predators both directly by increasing the availability of a food resource and indirectly by changing the structure and composition of forested ecosystems.

The strength of the aggregative and numerical responses of insectivorous birds to outbreaks of forest tent caterpillar can be influenced by their physiology, the availability of alternate prey, and the defense mechanisms of the forest tent caterpillar (Buckner 1966). Forest birds consume more than 300 million metric tons of insects, representing 70% of their total consumption per year globally (Nyffeler et al. 2018). Thus, insectivorous birds have the physiological potential to respond strongly to insect outbreaks, especially during the breeding season when energy demands are the highest. However, if the species has a generalist diet, their aggregative and numerical responses to the outbreaks may be dampened by the presence of alternate prey, if the birds choose to forage on the latter (Buckner 1966). This means that increases in the abundance of alternate prey can reduce the numerical response and the impact of generalist insectivorous birds on the outbreak species. In contrast, the response of specialist bird species may not be limited by the availability of alternate prey.

The larvae of Lepidoptera have several mechanisms to defend themselves from predators, including the presence of urticant hairs, warning colorations, and “jerking” behaviors that persuade predators to avoid their consumption (Greeney et al. 2012). The body of forest tent caterpillars is hirsute and, contrary to palatable species of Lepidoptera, forest tent caterpillars spend most of their time on the dorsal surfaces of leaves, petioles and branches, often

exposed to direct sunlight (Heinrich 1979). Hairy caterpillars like the forest tent caterpillar are thus less attractive to insectivorous birds than glabrous caterpillars, and birds choose the latter when both types of prey are available (Whelan et al. 1989). However, some birds have evolved morphological, behavioral, or physiological adaptations to consume hairy caterpillars and may be able to take advantage of the food pulses during their outbreaks.

Foraging theory predicts that temporal variation in resource availability favours dietary generalization within habitats (Stephens and Krebs 1986, Ruel and Ayres 1999, Holt and Krimbell 2007). However, if resources fluctuate in a predictable manner, as defoliators with periodic outbreaks do, then selection should favour the evolution of adaptations that promote dietary specialization and allow foragers to respond to pulsed resources (Holt and Krimbell 2007). Adaptations to foraging on hairy caterpillars range from low to a high degree of specialization. Some forest passerines, such as the black-capped chickadee (*Poecile atricapillus*), show a low level of specialization, and switch to foraging on non-urticating stages of the forest tent caterpillar, i.e., moths, eggs and early-instar larvae (Barbaro and Battisti 2011). Species with moderate degrees of specialization include the least flycatcher (*Empidonax minimus*) and the yellow warbler (*Setophaga petechia*), which crush forest tent caterpillars to expose and eat their viscera, and discard the integuments. Finally, the highest degree of specialization is shown by species of cuckoos, such as the black-billed cuckoo (*Coccyzus erythrophthalmus*), which possess a soft gizzard wall structure that allow them to regurgitate the consumed hair and setae (Meise and Schifter

1972, Gill 1980, Payne 1997). Here, I compare the aggregational and numerical responses of the black-capped chickadee, least flycatcher, yellow warbler, and black-billed cuckoo to test the hypothesis that the strength of their responses is related to their degree of foraging specialization. To test this hypothesis, I use long-term forest tent caterpillar defoliation and bird count data for two ecologically distinct Bird Conservation Regions in Ontario, Canada, that cover the geographic extent of forest tent caterpillar outbreaks in Ontario.

METHODS

STUDY SPECIES

The black-billed cuckoo is a notorious consumer of outbreak species, including the eastern tent caterpillar (*Malacosoma americanum*), fall webworm (*Hyphantria cunea*), and larvae of the gypsy moth (*Lymantria dispar*; Hughes 2020). In eastern Canada and the northeastern U.S., the black-billed cuckoo is usually found in edges and clearings of young deciduous and mixed deciduous-coniferous woods, abandoned farmland with trembling aspen, other poplars, and birches. Black-billed cuckoos have a high degree of specialization in the consumption of hairy caterpillars, and have developed behavioral and morphological adaptations to allow their consumption. For instance, black-billed cuckoos shake and hammer caterpillars on branches before swallowing them, crushing them to consume only their guts (Forbush 1907). If the black-billed

cuckoo swallows whole caterpillars, their hairs and spines pierce the gizzard lining and remain there until the whole lining is regurgitated (Beal 1897, McAtee 1917). This highly specialized adaptation suggests that black-billed cuckoos may show strong aggregative responses to outbreaks. In addition, because the onset of nesting in the black-billed cuckoo may be synchronized with insect outbreaks, and localized food abundance has been linked to numerical responses (Hughes 2020), they may also show strong numerical responses to outbreaks of forest tent caterpillar.

The least flycatcher and the yellow warbler are predators of the forest tent caterpillar with a moderate degree of specialization (Barbaro and Battisti 2011). The least flycatcher is one of the smallest species of *Empidonax* and it breeds in deciduous and mixed forests in most of eastern, central and western Canada, and the northern United States (Tarof and Briskie, 2020). In summer, it feeds almost exclusively on arthropods (Tarof and Ratcliffe 2004), and larvae of Lepidoptera make up a large proportion of the food delivered to the nestlings (Darveau et al. 1993). The yellow warbler is found throughout most of North America in wet, deciduous thickets (Lowther et al. 2020). The diet composition of yellow warblers during the breeding season is variable and they forage on prey items in proportion to their abundance (Busby and Sealy 1979). Least flycatchers and yellow warblers use a foraging adaptation to consume hairy *Malacosoma* caterpillars, by which they bang large caterpillars on branches to rupture them, eating their viscera and discarding the head and integuments (McAtee 1926, Grant 1959, Root, 1966, Parry et al. 1997). Least flycatchers and

yellow warblers are expected to respond to forest tent caterpillar outbreaks with moderate aggregations and weak or no numerical responses.

The black-capped chickadee is a generalist predator with a low degree of foraging specialization (Barbaro and Battisti 2011). It is a non-migratory species that occurs in much of Canada and the northern U.S. (Foote et al. 2020). As a habitat generalist, it occupies deciduous and mixed woodlands, urban parks and disturbed areas. During the breeding season, caterpillars are a major component of the diet of black-capped chickadees (Heinrich and Collins 1983), especially early instar larvae of gypsy moth and eastern tent caterpillars (Pelech and Hannon 1995). But, the low degree of specialization, suggests that black-capped chickadees may only show weak to moderate aggregative responses to outbreaks of forest tent caterpillar. On the other hand, the reproductive success of black-capped chickadees may not be positively influenced by outbreaks of eastern tent caterpillar and, on the contrary, it has been proposed that heavy defoliation may be associated with breeding failure (Pelech and Hannon 1995). The interaction between the positive effect of a food pulse and the negative influence of heavy defoliation in the breeding success suggests that the numerical response of black-capped chickadees to outbreaks of forest tent caterpillar is weak and variable.

STUDY AREA

This study is spatially structured to match data from the North American Breeding Bird Survey, following Smith et al. (2014). The study area is divided into Bird Conservation Regions (BCRs) 8 and 12, within the province of Ontario, Canada, where reporting of the forest tent caterpillar was consistent over xxx years (Figure reference if you do put it back). BCRs 8 and 10 also represent most of the area affected by forest tent caterpillar outbreaks in Ontario (Figure 2). The Boreal Softwood Shield region (BCR 8, hereafter Boreal region) spans northern Ontario, between the north shore of Lake Superior and the Hudson Bay Lowlands, covering nearly 490,000 km² (Environment Canada 2014a). The Boreal Hardwood Transition region (BCR 12, hereafter Hardwood Transition region) is separated into two disjunct areas east and west of the north shore of Lake Superior, covering a total area of 170,000 km² (Environment Canada 2014b). There is a large contrast in the vegetation of the two regions. The Boreal region is dominated by coniferous forest (41%), with mixed (~18%) and deciduous forest occupying minor proportions (~5%), and the Hardwood Transition region is dominated by mixed forest (45%) with smaller proportions of deciduous and coniferous forest (~15%). The remaining portions of each region include shrub and early successional forest, wetlands, waterbodies, cultivated land, and urban areas.

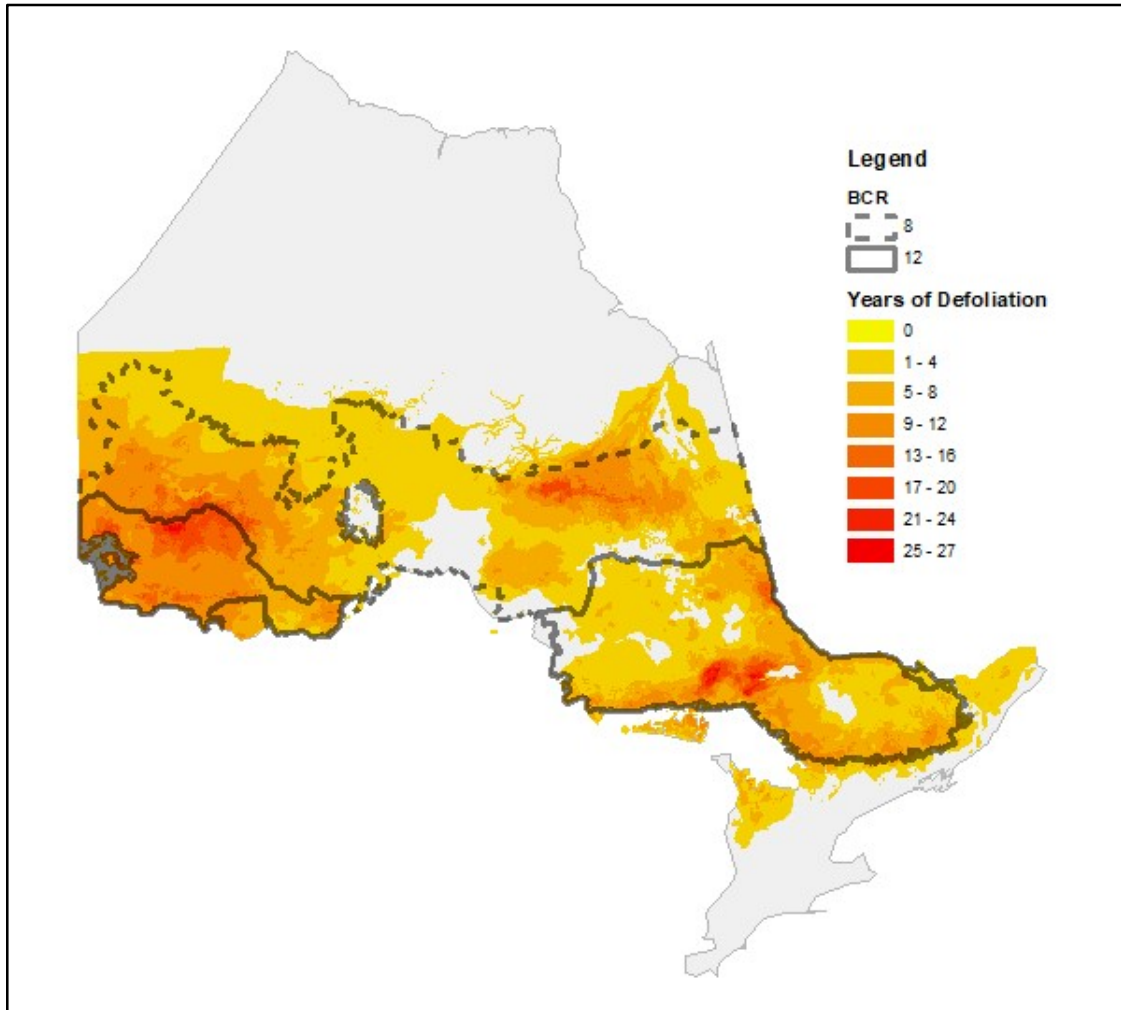


Figure 2. Map of Ontario, Canada, showing the extent of forest tent caterpillar outbreaks in bird conservation regions (BCRs) 8 and 12. The colour gradient showing extent corresponds to the cumulative number of years of moderate to severe defoliation since 1996.

BREEDING BIRD SURVEY DATA

I obtained bird count data from the North American Breeding Bird Survey (BBS; <ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/>), a volunteer-based survey that has been conducted annually since 1966. During surveys, observers count the songs or sightings of birds at 50 point stops along a fixed-length route.

Until 1997, observations were combined into a single count by species per route. Currently, BBS stop-level data is available for the period since 1997. However, during this period a single peak in defoliation of the forest tent caterpillar has occurred in Ontario (in 2001), and outbreak occurrences have remained at low levels since 2001 (Figure 1). Thus, the finest scale at which the BBS data analysis is currently possible for this study is the route level. For each species, I included only routes that met the weather quality conditions (i.e. low wind), as indicated by a quality index of 1 in the BBS dataset.

Since 1966, 78 routes in the Boreal and 120 routes in Hardwood Transition regions have been surveyed in Ontario as part of the North American BBS (Figure 3), and the number of years each route was surveyed has ranged from 1 to 36 (mode = 5)

INSECT OUTBREAK DATA

Defoliation data for forest tent caterpillar outbreaks was obtained in the form of geospatial layers (Natural Resources Canada 2019). In Ontario, areas defoliated by forest tent caterpillar outbreaks are recorded via aerial survey conducted each year following the completion of caterpillar feeding, when the extent of the damage is maximum and distinguishable from the air. Defoliation data derived from aerial surveys are a good proxy of caterpillar density because the forest tent caterpillar is an efficient forager that consumes most tree foliage and thus the extent of defoliation is easily delineated from the air (Cooke and

Lorenzetti 2006). Outbreak areas are delineated on topographic maps and the severity of the damage is classified as light (11%-30%), moderate (31%-70%), severe (70%-100%) and nil (0%-10%).

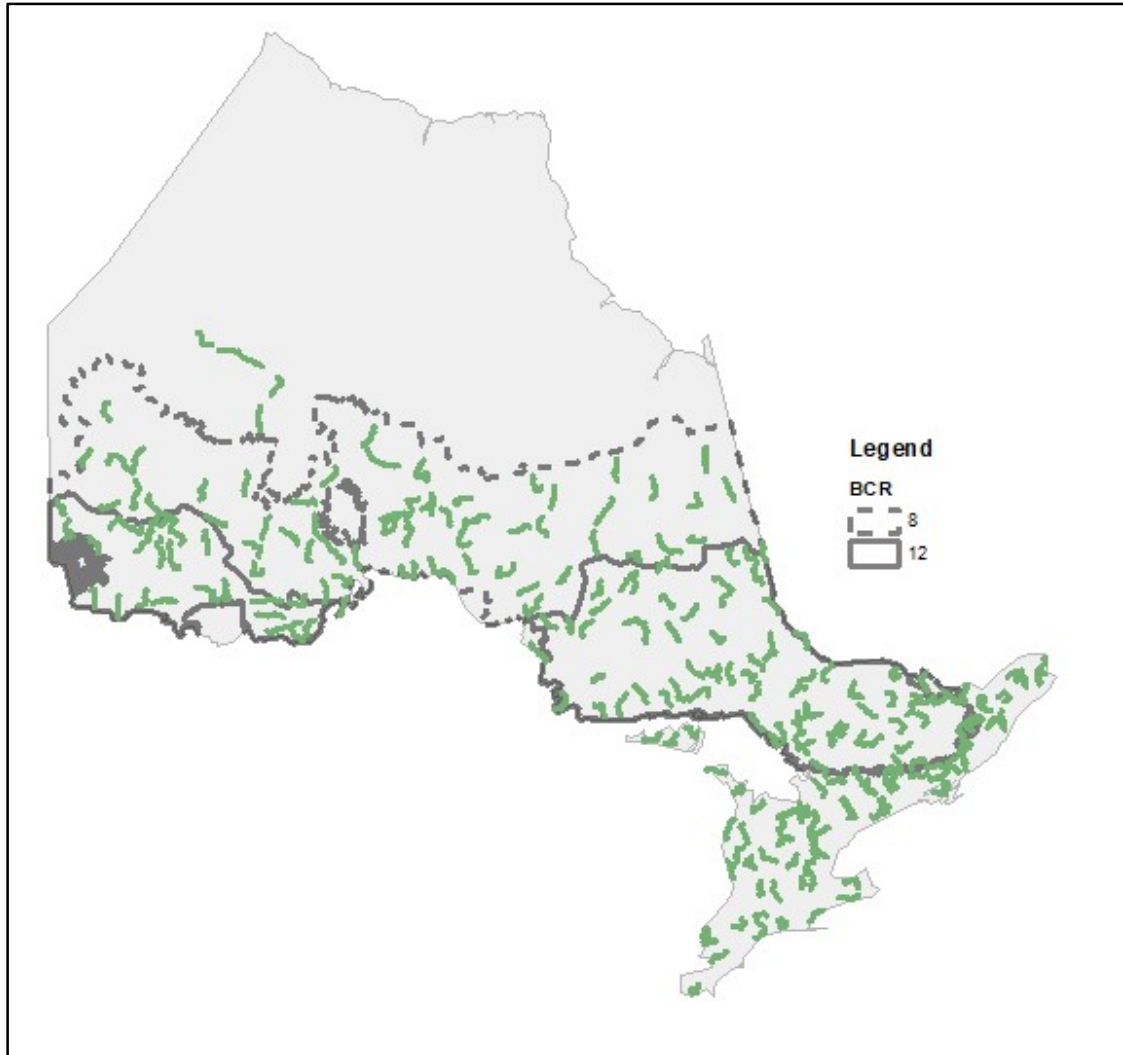


Figure 3. Distribution of breeding bird survey routes in the Boreal region (BCR 8) and Hardwood Transition region (BCR12) in Ontario. Routes outside the boundaries of the regions (i.e. north and south of the delineated areas) were excluded from this study.

I calculated defoliation covariates for each combination of bird species, route and year using ArcGIS 10.4 (ESRI Corporation, California, USA) at two spatial scales (local and regional), based on areas with moderate to severe damage, corresponding to a high density of caterpillars, and following Drever et al. (2018). At the route-level (local scale), I calculated a defoliation covariate as the proportion of area within a 5-km buffer of each BBS route- j in stratum- i (region) that was affected by defoliation in each year- t . I used a local scale covariate to test the hypothesis that increased density of forest tent caterpillar at local scale results in an aggregative response from the four avian predators included. A 5-km buffer is an arbitrary choice that is broad enough to compensate for spatial errors in the datasets and discrepancies due to their resolution, again following Drever et al. (2018). At the BCR-level (regional scale), I calculated a defoliation covariate for each year t as the average proportion of each region defoliated during the previous four years. I used this covariate to test a lagged response to forest tent caterpillar outbreaks, representing a numerical, reproductive response from the four avian predators.

STATISTICAL MODELING

I modeled the counts of birds of each of the four bird species in the BBS routes as coming from an overdispersed Poisson distribution. While a Poisson distribution assumes that the variance in counts is equal to the mean, the variance of bird count data usually exceeds the mean (Ver Hoef and Boveng

2007), and overdispersed Poisson models, such as those developed to analyze BBS trends, can account for the additional variation (Link and Sauer 2016). For each bird species, I fit a hierarchical Bayesian model using a Markov Chain Monte Carlo (MCMC) algorithm in JAGS (Lunn et al. 2009), implemented through R, using the package `runjags` 2.0.4-2 (Denwood 2016). In contrast to traditional frequentist approaches, hierarchical Bayesian methods have the advantage of directly estimating the parameters of interest and appropriately incorporating uncertainty into the estimates (Fordyce et al. 2011). In addition, a hierarchical model accounts for relationships between response and covariates at different scales, as well as for interdependencies of the data.

The hierarchical model I used is an extension of the model for the effects of outbreaks of a single defoliator on bird species counts developed by Drever et al. (2018), which is itself an extension of a model utilized in the analysis of BBS data (Link and Sauer 2016). In this model, the count of birds of each species $C_{i,j,t}$ in each BCR i , in each route j , and each year t , is a random Poisson variable with mean $\lambda_{i,j,t}$.

$$C_{i,j,t} = \text{Poisson}(\lambda_{i,j,t})$$

The means of the Poisson distribution are functions of: a year effect ($\gamma_{i,t}$); a combined observer-route effect (ω_j); the effect of an observer's first year on a route ($\zeta I_2(j, t)$); an observation-level random effect that accounts for overdispersion $\varepsilon_{i,j,t}$; the local scale forest tent caterpillar (β_{1_j}) defoliation covariate; and a regional scale forest tent caterpillar (β_{2_i}) defoliation covariate.

$$\log(\lambda_{i,j,t}) = \gamma_{i,t} + \beta_{1j} \times b_{1i,j,t} + \beta_{2i} \times b_{2i,t} + \omega_j + \zeta I_2(j, t) + \varepsilon_{i,j,t}$$

I treated all parameters β_n for defoliation as random effects drawn from normal distributions:

$$\beta_n \sim \text{Normal}(B_n, \sigma^2_{B_n})$$

I estimated median values for the coefficients via MCMC in JAGS along with 95% credible intervals derived from the posterior distributions. For counts of each species, I initiated three MCMC chains and ran 110,000 iterations, with a 100,000 burn-in period and a thinning factor of four because test runs showed that those parameters were sufficient to achieve convergence. I assessed mixing and convergence of the MCMC chains visually, using diagnostic tools included in the package DBDA2E-utilities (Kruschke 2015).

RESULTS

At the local-scale in the Boreal region, the black-billed cuckoo had a very strong response to forest tent caterpillar defoliation, with a median increase in the counts of birds to roughly eight times baseline density when defoliation was total (Figure 4). The 95% credible intervals were broad, but did not overlap zero. In contrast, the remaining three species responded only weakly to defoliation. The median response of the least flycatcher was nearly zero, the response of the yellow warbler was slightly negative, and credible intervals around the median estimates for both species overlapped zero. The black-capped chickadee had a slightly positive response to defoliation, but with credible

intervals overlapping zero. Responses at the local scale in the Hardwood Transition region were similar but less variable around the median estimates, i.e., with narrower credible intervals (Figure 5). The response of the black-billed cuckoo in the Hardwood Transition region was much weaker compared to the Boreal region, but counts increased by more than 200% when defoliation was total. The credible interval around the median estimate of the response for black-billed cuckoo did not overlap zero. The least flycatcher and the yellow warbler had slightly positive and negative responses respectively, and although credible intervals were comparatively narrower than in the Boreal region, both overlapped zero. The response of the black-capped chickadee was moderate, with increases in the of nearly 140% when defoliation was total and credible intervals that did not overlap zero.

At the regional level, lagged responses to cumulative defoliation were generally weaker than at the local scale, with broad credible intervals around median estimates. In the Boreal region, the response of the black-billed cuckoo was positive but weak: counts increased by roughly 180% in response to total defoliation, but the credible intervals were broad and overlapped zero (Figure 6). The responses of the other three species were neutral with credible intervals overlapping zero. Similarly, the regional-scale response of the black-billed cuckoo in the Hardwood Transition region was moderate, with increases in the counts of birds of roughly 160% in response to total defoliation and credible intervals overlapping zero (Figure 7). The response of the yellow warbler was roughly neutral, while that of the least flycatcher was slightly negative, and

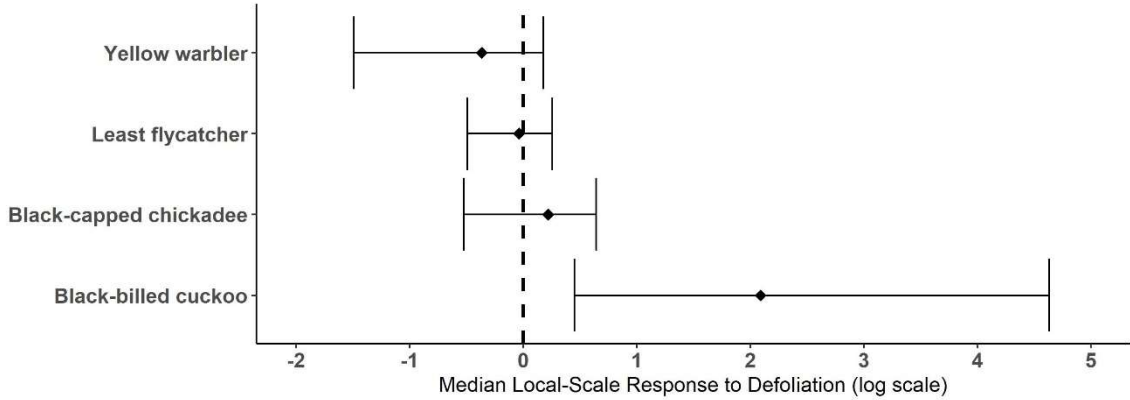


Figure 4. Median responses to forest tent caterpillar defoliation at the local scale in the Boreal region. Bars represent 95% credible intervals around Bayesian estimates of the median.

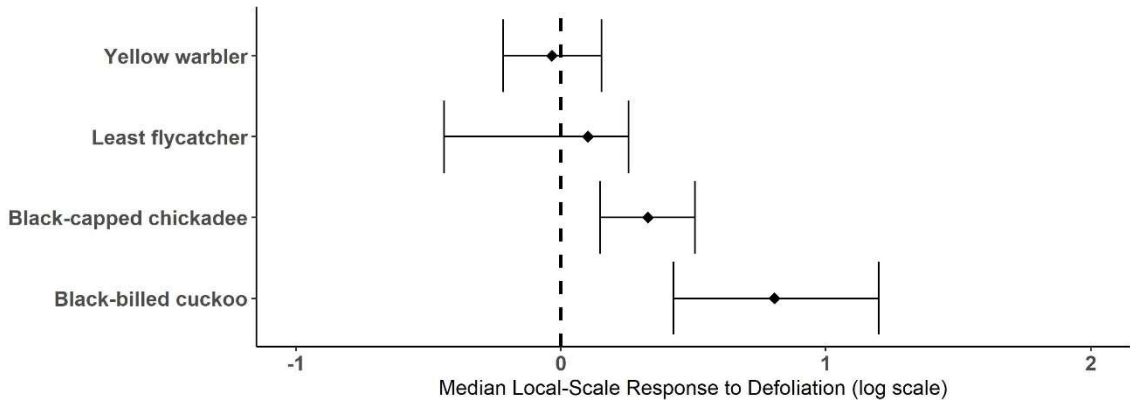


Figure 5. Median responses to forest tent caterpillar defoliation at the local scale in the Hardwood Transition region. Bars represent 95% credible intervals around Bayesian estimates of the median.

confidence intervals for both species overlapped zero. The black-capped chickadee had slight increases of roughly 100% with total defoliation, but with credible intervals broadly distributed and overlapping zero.

In summary, a general correspondence between peaks in defoliation and counts of black-billed cuckoos occurred (Appendix 1). However, a major peak in

defoliation reached in 2001 does not appear to be associated with increases in the counts of black-billed cuckoos in the Boreal region. In contrast, the least flycatcher, yellow warbler, and black-capped chickadee were responding less to peaks in the forest tent caterpillar defoliation (Appendices 2 to 4).

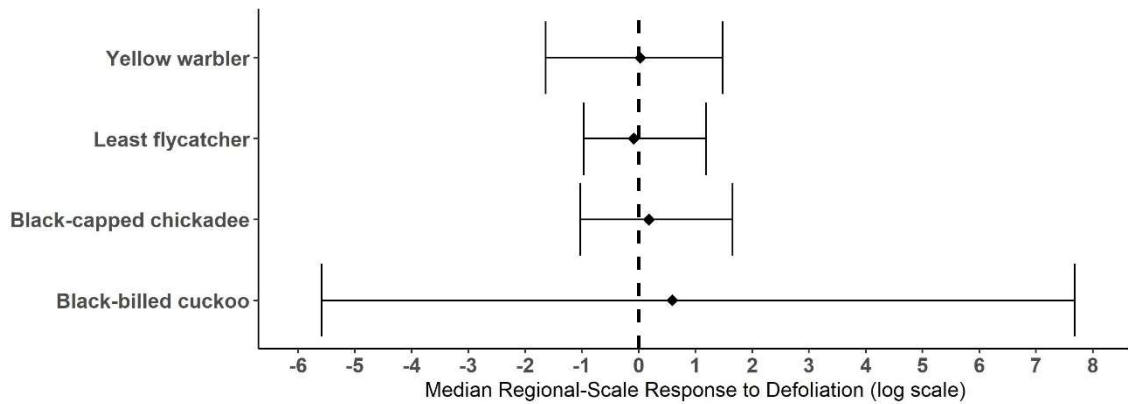


Figure 6. Median responses to forest tent caterpillar defoliation at the regional scale in the Boreal region. Bars represent 95% credible intervals around Bayesian estimates of the median.

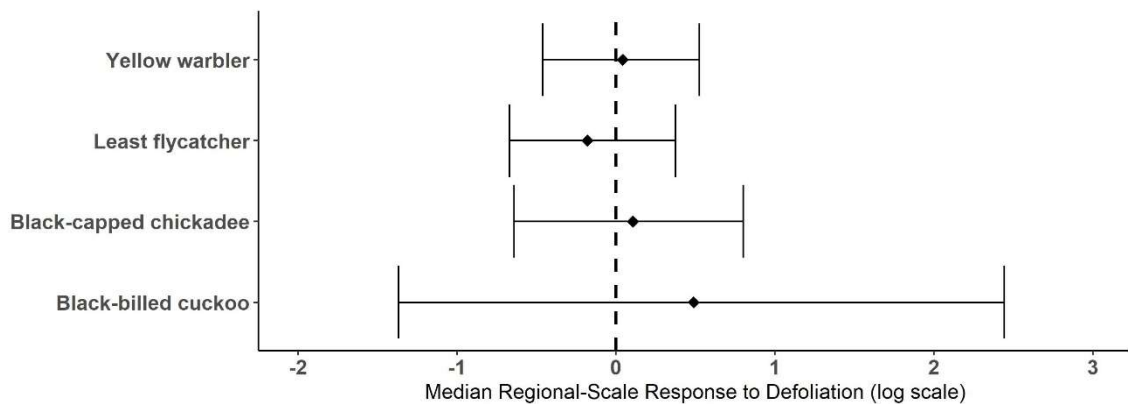


Figure 7. Median responses to forest tent caterpillar defoliation at the regional scale in the Hardwood Transition region. Bars represent 95% credible intervals around Bayesian estimates of the median.

DISCUSSION

Comparing the inference that specialist warblers have an aggregative response to outbreaks of the spruce budworm in the Boreal region, made by previous authors with the same approach to the data used here, I suggest that black-billed cuckoos have a stronger aggregative response to increased density of forest tent caterpillars. In eastern Canada, counts of Tennessee and Cape May warblers increase by about 200% when budworm defoliation in 5-km buffered BBS routes is complete, and bay-breasted warbler counts increase by about 115% (Drever et al. 2018). The increases of about 800% in the Boreal region and 200% in the Hardwood Transition region for black-billed cuckoos suggest a response similar to what is observed with outbreaks of gypsy moths, to which cuckoos disperse in a post-migration nomadic phase (Barber et al. 2008). The response is aggregative as it does not involve a time lag, and it is likely influenced by the highly specialized digestive adaptations of cuckoos. Cuckoos of at least four genera (*Cuculus*, *Chrysococcyx*, *Clamator*, and *Coccyzus*; Meise and Schifter 1972) share the adapted digestive system that suggests a long history of ecological interactions with caterpillar outbreaks.

At the local scale, the median responses of the least flycatcher and the yellow warbler in both regions provided no evidence that a presumed moderate degree of specialization in the consumption of hairy caterpillars results in any significant aggregative response to increases in forest tent caterpillars. These two species may only opportunistically consume forest tent caterpillars. The

black-capped chickadee, on the other hand, increased modestly with caterpillar outbreaks in the Hardwood Transition region, compatible with the idea of a generalist predator with a low degree of specialization responding with aggregative behaviour. However, no increase in this species was observed in the Boreal region. One possible explanation lies in the behavior of the chickadees and the ecological differences between regions. Black-capped chickadees are highly philopatric (Ratcliffe et al. 2007) and their capacity to mobilize to areas with high density of caterpillars may depend on the proximity of the outbreaks. Southern areas in the Hardwood Transition region are dominated by deciduous and mixedwood forests, and the proportion of coniferous trees increases northwards into the Boreal region (Rowe 1972). Thus, defoliation by forest tent caterpillar is generally more extensive in the Hardwood Transition region, while cumulative defoliation in the Boreal region is lower and the spatial extent, defoliation damage, and cumulative years of defoliation may be more variable. The combined effect of the philopatry of the black-capped chickadee and the ecology of the Boreal region means that outbreaks of forest tent caterpillar in this region may be less accessible, thus reducing any aggregative response of the predator.

Other mechanisms may contribute to dampen the aggregative responses of some birds with caterpillar outbreaks. First, the loss of foliage due to the increased density of forest tent caterpillar may lead, in turn, to decreases in the densities of more palatable caterpillars and insects. Thus, the availability of food for some generalists could be locally reduced during the outbreaks. Second, the

increased density of specialists in response to outbreaks of forest tent caterpillar may increase competitive interactions between them. Such a response has been observed in the magnolia warbler (*Setophaga magnolia*), whose numbers are negatively correlated with the abundance of spruce budworm specialists during outbreaks of this caterpillar (Patten and Burger 1998). Third, if forest tent caterpillar were the only, yet superabundant, prey available, generalist passerines could benefit from feeding on them at the expense of additional handling time. However, the advantage of a superabundant prey disappears if alternative, easier to handle prey is also available. Although this and other studies have not examined the effect of alternative prey on the response to an outbreak species, the preference of birds for glabrous over hairy caterpillars is consistent with this putative effect (Whelan et al. 1989). Future studies may be able to disentangle this relationship by incorporating covariates representing the availability of alternative prey on models of breeding bird counts. Finally, the Breeding Bird Survey may not properly represent the abundance of birds that feed on early instars of the forest tent caterpillar. For instance, analyses of the stomach contents of yellow warblers in Manitoba following an outbreak of the forest tent caterpillar showed only very early instars were consumed (Busby and Sealy 1978). The Breeding Bird Survey is conducted between late May and late June, a period that spans roughly the last two thirds of the development of the forest tent caterpillar. Thus, if least flycatchers, yellow warblers, and black-capped chickadees forage on very early instars and then disperse, the counts of the survey would not reflect the aggregative response.

The regional-level responses of the black-billed cuckoo suggest a numerical response to the outbreaks of forest tent caterpillar in both Boreal and Hardwood Transition regions. However, because of large variation around the median estimates, it is difficult to make a consistent association of the numerical responses and the extent of the outbreaks. This is, perhaps, because of a complex interaction between increases in insect density and tree mortality. Repeated defoliation by the caterpillar, in combination with periods of drought, can result in extensive mortality in poplar stands in Ontario (Candau et al. 2002), accelerating forest succession towards coniferous dominated stands (Man and Rice 2010). Thus, while high densities of the forest tent caterpillar may cause a numerical response in some predators, higher tree mortality can have an opposite effect by reducing the quantity and quality of habitat available for the birds that occupy deciduous and mixedwood forests. Overall, for the black-billed cuckoo this may mean that strong local responses only partially translate to increased reproductive output following cumulative years of defoliation. Because climate change is expected to influence the timing and extent of outbreaks of defoliating insects (Pureswaran et al. 2015), it is important to understand the whole breadth of ecological effects of such disturbances. Other factors, including forest management and pest control policies, may influence the periodicity and spatial scale of the outbreaks, and understanding how they interact with climate change may contribute to the management of outbreak species and the populations of their avian predators.

The weak regional-level responses of the least flycatcher, yellow warbler, and black-capped chickadee to outbreaks of the forest tent caterpillar suggest that these species do not respond numerically. Considering their moderate to low levels of forage specialization, I suggest that these species may forage opportunistically on forest tent caterpillars, but that the increased availability of prey does not translate in increased reproductive output. This conclusion agrees with observations of lack of breeding synchronization and increased reproductive failure in the black-capped chickadee in association with forest tent caterpillar outbreaks, likely due to lower availability of palatable prey in periods of heavy defoliation (Pelech and Hannon 1995). Similar studies are lacking for the least flycatcher and the yellow warbler, and they would provide key information on the relevance of forest tent caterpillar outbreaks to their populations.

This study demonstrates that outbreaks of hairy caterpillars can have an important influence in the dynamics of the populations of specialized predators, such as the black-billed cuckoos. Because outbreaks of defoliating insects can have important economic consequences for the forest industry, the insects are considered a problem to be avoided. However, the results shown here and by other studies should encourage forest managers to consider the broad effects that the suppression of outbreaks of defoliating insects could have on their specialist avian predators and on the efforts required to dampen future outbreaks in the absence of these forest birds.

LITERATURE CITED

- Barbaro, L., and A. Battisti. 2011. Birds as predators of the pine processionary moth (Lepidoptera: Notodontidae). *Biological Control*, 56, 107-114.
- Barber, N. A., R. J. Marquis, and W. P. Tori. 2008. Invasive prey impacts the abundance and distribution of native predators. *Ecology*, 89(10), 2678-2683.
- Beal, F.E.L. 1897. Some common birds in their relation to agriculture. US Department of Agriculture Farmers' Bulletin, 54.
- Buckner, C. H. 1966. The role of vertebrate predators in the biological control of forest insects. *Annual Review of Entomology*, 11(1), 449-470.
- Buckner, C. H. 1967. Avian and mammalian predators of forest insects. *Entomophaga*, 12, 491-501.
- Busby, D. G., and S. G. Sealy. 1979. Feeding ecology of a population of nesting Yellow Warblers. *Canadian Journal of Zoology*, 57, 1670-1681.
- Candau, J. N., V. Abt, and L. Keatley. 2002. Bioclimatic analysis of declining aspen stands in Northeastern Ontario. Ontario Ministry of Natural Resources, Ontario Forest Research Institute, Sault Ste. Marie, Ontario, Canada. Forest Research Report No. 154.
- Chen, H. Y. H., and R. V. Popadiouk. 2002. Dynamics of North American boreal mixedwoods. *Environmental Reviews* 10, 137-166.

- Churchill, G. B., H. H. John, D. P. Duncan, and A. C. Hodson. 1964. Long-term effects of defoliation of aspen by the forest tent caterpillar. *Ecology*, 45, 630-636.
- Cockle, K. L., and K. Martin. 2015. Temporal dynamics of a commensal network of cavity-nesting vertebrates: Increased diversity during an insect outbreak. *Ecology*, 96, 1093-1104.
- Cooke, B. J., and F. Lorenzetti. 2006. The dynamics of forest tent caterpillar outbreaks in Quebec, Canada. *Forest Ecology and Management*, 226, 110-121.
- Cooke, B. J., V. G. Nealis, and J. Régnière. 2007. Insect defoliators as periodic disturbances in northern forest ecosystems. Pages 487-525 *in* E. Johnson, and K. Miyanishi, editors. *Plant Disturbance Ecology: The Process and the Response*. Academic Press, Cambridge, MA, USA.
- Darveau, M., G. Gauthier, J. L. DesGranges, and Y. Mauffette. 1993. Nesting success, nest sites, and parental care of the Least Flycatcher in declining maple forests. *Canadian Journal of Zoology*, 71, 1592-1601.
- Denwood, M. 2016. Package 'runjags'.
- Drever, M. C., J. R. Goheen, and K. Martin. 2009. Species – energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. *Ecology* 90, 1095-1105.
- Drever, M. C., D. A. Maclean, A. C. Smith, L. A. Venier, and D. J. H. Sleep. 2018. Cross-scale effects of spruce budworm outbreaks on boreal warblers

in eastern Canada. *Ecology and Evolution*, 8, 7334-7345.

Edworthy, A. B., M. C. Drever, and K. Martin. 2011. Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles. *Forest Ecology and Management*, 261, 203-210.

Environment Canada. 2014a. Bird Conservation Strategy for Bird Conservation Region 8 in Ontario Region: Boreal Softwood Shield. Accessed 27 April 2020. https://www.canada.ca/en/environment-climate-change/services/migratory-bird-conservation/publications/strategy-region-8-boreal-softwood.html#_ack.

Environment Canada. 2014b. Bird Conservation Strategy for Bird Conservation Region 12 in Ontario and Manitoba: Boreal Hardwood Transition. Accessed 27 April 2020. <https://www.canada.ca/en/environment-climate-change/services/migratory-bird-conservation/publications/strategy-region-12-ontario-manitoba.html>.

Fitzgerald, T. D. 1995. *The Tent Caterpillars*. Cornell Series in Arthropod Biology. Cornell University Press, Ithaca, New York, NY, USA. 303 pages.

Fleming, R. A., A. A. Hopkin, and J. N. Candau. 2000. Insect and disease disturbance regimes in Ontario's forests. Pages 141-162 *in* I. D. Thompson, A. Perera, and D. Euler, editors. *Ecology of a managed terrestrial landscape: patterns and processes of forest landscapes in Ontario*. UBC Press, Vancouver, BC, Canada.

Foote, J. R., D. J. Mennill, L. M. Ratcliffe, and S. M. Smith. 2020. Black-capped

- Chickadee (*Poecile atricapillus*), version 1.0. in A. F. Poole, editor. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA.
- Forbush, E. H. 1907. Useful Birds and their Protection. Boston: Massachusetts State Board of Agriculture. Creative Media Partners, Sacramento, CA, USA.
- Fordyce, J. A., Z. Gompert, M. L. Forister, and C. C. Nice. 2011. A hierarchical bayesian approach to ecological count data : A flexible tool for ecologists. Plos One, 6, 1-7.
- Frye, R. D., and D. A. Ramse. 1975. Natural control agents in forest tent caterpillar populations. North Dakota Farm Research, 32, 14-19.
- Gale, G. A., J. A. Dececco, M. R. Marshall, W. R. McClain, and R. J. Cooper. 2001. Effects of gypsy moth defoliation on forest birds: An assessment using breeding bird census data. Journal of Field Ornithology, 72, 291-304.
- Gill, B. J. 1980. Foods of the Shining Cuckoo (*Chrysococcyx lucidus*, Aves: Cuculidae) in New Zealand. New Zealand Journal of Ecology, 3, 138-140.
- Ghent, A. W. 1958. Mortality of overstory trembling aspen in relation to outbreaks of the forest tent caterpillar and the spruce budworm. Ecology, 39, 222-232.
- De Graaf, R. M., N. G. Tilghman, and S. H. Anderson. 1985. Foraging guilds of North American birds. Environmental Management, 9, 493-536.
- Grant, J. 1959. Pine siskins killing forest tent caterpillars (*Malacosoma disstria* Hbn.). Proceedings of the Entomological Society of British Columbia, 56,

20. November 4, 1959, University of British Columbia, Vancouver, BC, Canada.

Greeney, H. F., L. A. Dyer, and A. M. Smilanich. 2012. Feeding by Lepidopteran larvae is dangerous: A review of caterpillars' chemical, physiological, morphological, and behavioral defenses against natural enemies. *Invertebrate Survival Journal*, 9(1), 7-34.

Halperin, J. 1990. Natural enemies of *Thaumetopoea* spp. (Lepidoptera: Thaumetopoeidae) in *Israeli Journal of Applied Entomology*, 109, 425-435.

Hassell, M. P. 1978. *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, Princeton, NJ, USA.

Heinrich, B. 1979. Foraging strategies of caterpillars. *Oecologia*, 42(3), 325-337.

Heinrich, B., and S. L. Collins. 1983. Caterpillar leaf damage and the game of hide-and-seek with birds. *Ecology*, 64, 592-602.

Ver Hoef, J. M., and P. L. Boveng. 2007. Quasi-Poisson vs. negative binomial regression: How should we model overdispersed count data? *Ecology*, 88, 2766-2772.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist*, 91(5), 293-320.

Holmes, R. T., and J. C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Canadian Journal of*

Zoology, 66, 720-728.

Holt, R. D., and T. Kimbrell. 2007. Foraging and population dynamics. Chapter 11, pages 365-396 in D. W. Stephens, J. S. Brown, and R. C. Ydenberg, editors. Foraging: Behavior and Ecology, University of Chicago Press, Chicago, IL, USA.

Hughes, J. M. 2020. Black-billed Cuckoo (*Coccyzus erythrophthalmus*), version 1.0. in P. G. Rodewald, editor. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Johns, R. C., L. Flaherty, D. Carleton, S. Edwards, A. Morrison, and E. Owens. 2016. Population studies of tree-defoliating insects in Canada: A century in review. Canadian Entomologist, 148, S58-S81.

Keast, A., and S. Saunders. 1991. Ecomorphology of the North American Ruby-crowned (*Regulus calendula*) and Golden-crowned (*R. satrapa*) Kinglets. The Auk, 108(4), 880-888.

Koenig, W.D., E. L. Walters, and A. M. Liebhold. 2011. Effects of gypsy moth outbreaks on North American woodpeckers. The Condor, 11, 352-361.

Kruschke, J. K. 2015. Doing Bayesian Data Analysis. A Tutorial with R, JAGS, and Stan. Academic Press, Cambridge, MA, USA.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Annual Reviews of Entomology, 16, 289-324.

Link, W. A., and J. R. Sauer. 2016. Bayesian cross-validation for model

evaluation and selection, with application to the North American Breeding Bird Survey. *Ecology*, 97, 1746-1758.

Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector.

2020. Yellow Warbler (*Setophaga petechia*), Version 1.0. *in* F. Poole, and F. B. Gill, editors. *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Lunn, D., Spiegelhalter, D., Thomas, A., and N. Best. 2009. The BUGS project: Evolution, critique and future directions. *Statistics in Medicine*, 28(25), 3049-3067.

McAtee, W. L. 1917. The shedding of the stomach lining by birds, particularly as exemplified by the Anatidae. *The Auk*, 34(4), 415-421.

McAtee, W.L. 1926. The relation of birds to woodlots in New York State. *Roosevelt Wildlife Bulletin*, 4, 1-152.

Man, R., and J. A. Rice. 2010. Response of aspen stands to forest tent caterpillar defoliation and subsequent overstory mortality in northeastern Ontario, Canada. *Forest Ecology and Management*, 260, 1853-1860.

Meise, W., and H. Schifter. 1972. The cuckoos and their relatives. Pages 625-652 *in* B. Grzimek, editor. *Grzimek's Animal Life Encyclopedia*, vol. 8. Van Nostrand Reinhold, New York, NY, USA.

Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology*, 39, 487-494.

- Morse, D. H. 1971. The insectivorous bird as an adaptive strategy. *Annual Review of Ecology and Systematics*, 2, 177-200.
- Morse, D. H. 1978. Populations of bay-breasted and Cape May warblers during an outbreak of the spruce budworm. *Wilson Bulletin*, 90, 404-413.
- Nyffeler, M., Şekercioğlu, Ç. H., and C. J. Whelan. 2018. Insectivorous birds consume an estimated 400–500 million tons of prey annually. *Science of Nature*, 105(7-8), 47.
- Parry, D., J. R. Spence, and W. J. A. Volney. 1997. Responses of natural enemies to experimentally increased populations of the forest tent caterpillar, *Malacosoma disstria*. *Ecological Entomology*, 22, 97-108.
- Patten, M. A., and J. C. Burger. 1998. Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. *Canadian Journal of Zoology*, 76, 433-439.
- Payne, R.B. 1997. Family Cuculidae (Cuckoos). Pages 508-607 in J. del Hoyo, A. Elliott, and J. Sargatal, J., editors. *Handbook of the Birds of the World: Sandgrouses to Cuckoos*, vol. 4. Lynx Edicions, Barcelona, Spain.
- Pelech, S., and S. J. Hannon. 1995. Impact of tent caterpillar defoliation on the reproductive success of Black-capped Chickadees. *Condor*, 97(4), 1071-1074.
- Pureswaren, D. P., L. De Grandpre, D. Pare, A. Taylor, M. Barrette, H. Morin, J. Regniere, and J. J. Kneeshaw. 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. *Ecology*,

96, 1480-1491.

Ratcliffe, L., D. J. Mennill, and K. A. Schubert, K.A. 2007. Social dominance and fitness in black-capped chickadees. Pages 131-147 *in* K. A. Otter, editor. Ecology and Behavior of Chickadees and Titmice: An Integrated Approach. Oxford University Press, Oxford, UK.

Robichaud, I., and M. A. Villard. 1999. Do Black-throated Green Warblers prefer conifers? Meso-and microhabitat use in a mixedwood forest. The Condor, *101*(2), 262-271.

Root, R. B. 1966. Avian response to a population outbreak of tent caterpillar *Malacosoma constrictum* (Stretch). Pan-Pacific Entomologist, *42*(1), 48.

Rowe, J. S. 1972. Forest regions of Canada. Canadian Forestry Service, Ottawa. 165 p.

Ruel, J. J., and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. Trends in Ecology and Evolution, *14*, 361-366.

Schowalter, T. D. 2017. Biology and management of the forest tent caterpillar (Lepidoptera: Lasiocampidae). Journal of Integrated Pest Management, *8*, 24.

Sealy, S.G. 1978. Possible influence of food on egg-laying and clutch size in the Black-billed Cuckoo. The Condor, *80*(1), 103-104.

Smith, A. C., M.-A. R. Hudson, C. Downes, and C. M. Francis. 2014. Estimating breeding bird survey trends and annual indices for Canada: How do the

new hierarchical Bayesian estimates differ from previous estimates?

Canadian Field-Naturalist, 128, 119-134.

Solomon, M. E. 1949. The natural control of animal populations. *Journal of Animal Ecology*, 18, 1-35.

Stephens, D. W., and J. R. Krebs. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ, USA.

Tarof, S., and J. V. Briskie. 2020. Least Flycatcher (*Empidonax minimus*), version 1.0. *in* A. F. Poole, editor. *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Tarof, S. A., and L. M. Ratcliffe. 2004. Habitat characteristics and nest predation do not explain clustered breeding in least flycatchers (*Empidonax minimus*). *Auk*, 121(3), 877-893.

Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, NJ, USA.

Venier, L. A., and S. B. Holmes. 2010. A review of the interaction between forest birds and eastern spruce budworm. *Environmental Reviews*, 18, 191-207.

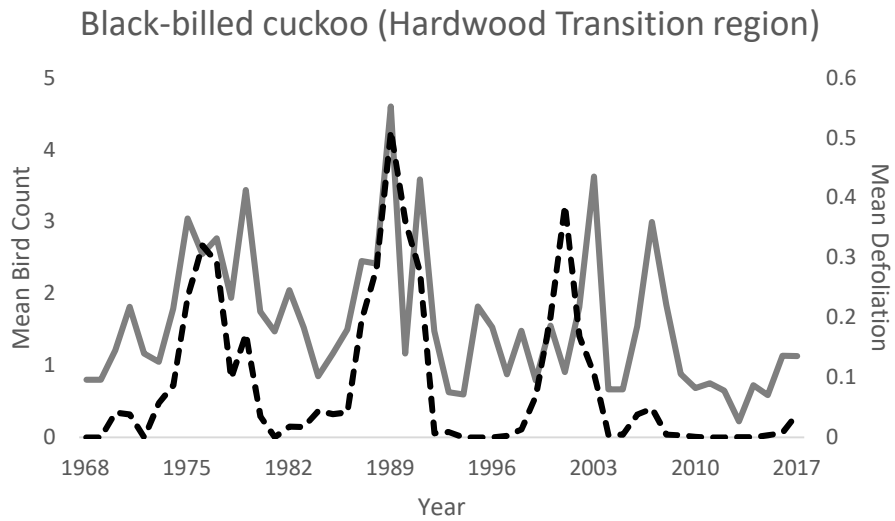
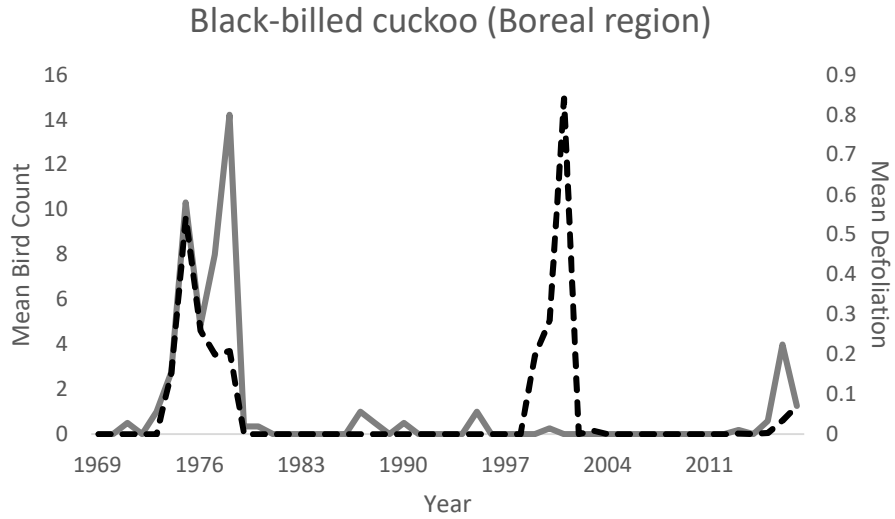
Whelan, C. J., R. T. Holmes, and H. R. Smith. 1989. Bird predation on gypsy moth (Lepidoptera: Lymantriidae) larvae: An aviary study. *Environmental Entomology*, 18, 43-45.

Witter, J. A., and H. M. Kulman. 1972. A review of the parasites and predators of tent caterpillars (*Malacosoma* spp.) in North America. *Newsletter of the*

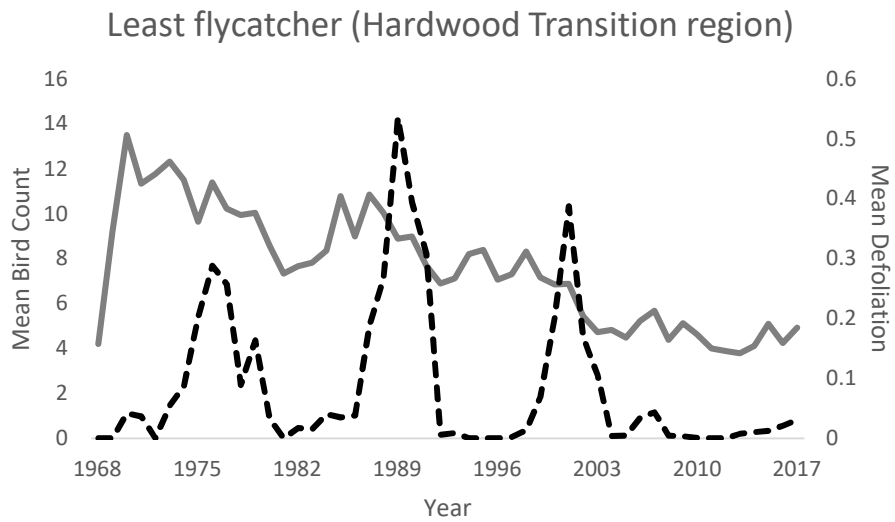
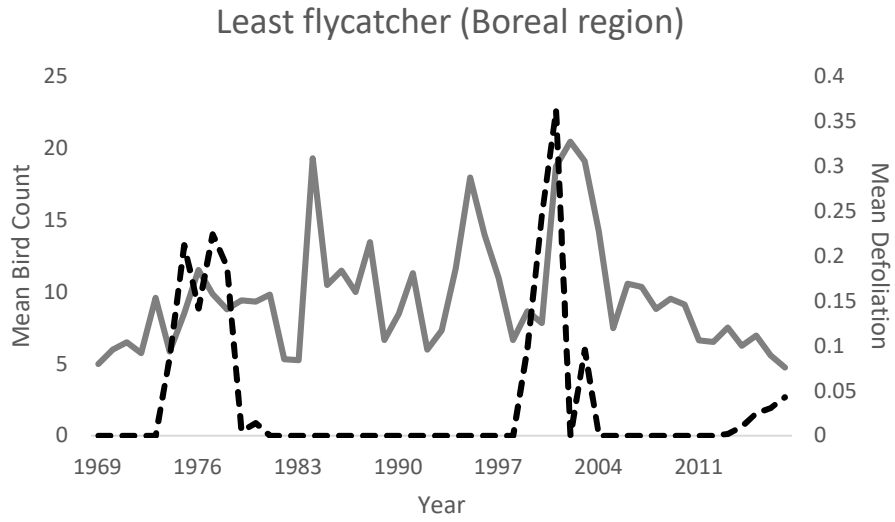
Agricultural Experiment Station, University of Minnesota, 289, 1-48.

Zach, R., and J. B. Falls. 1975. Response of the ovenbird (Aves: Parulidae) to an outbreak of the spruce budworm. *Canadian Journal of Zoology*, 53, 1669-1672.

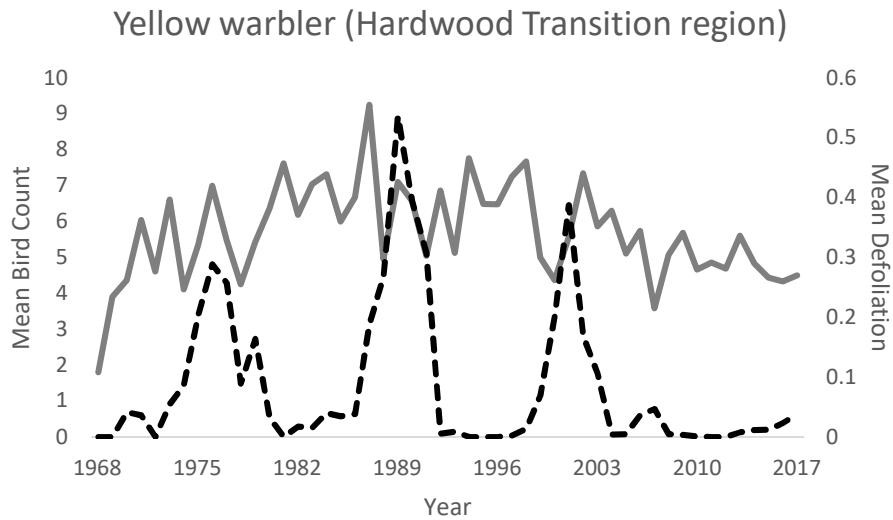
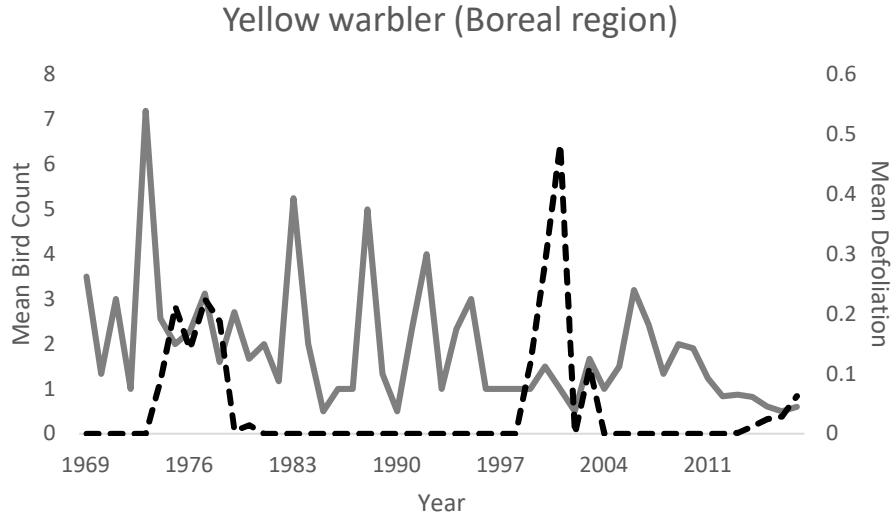
APPENDICES



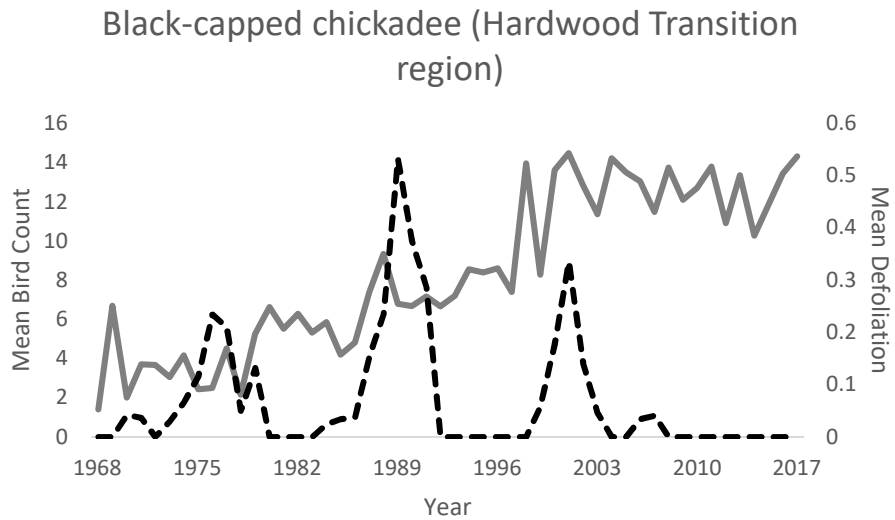
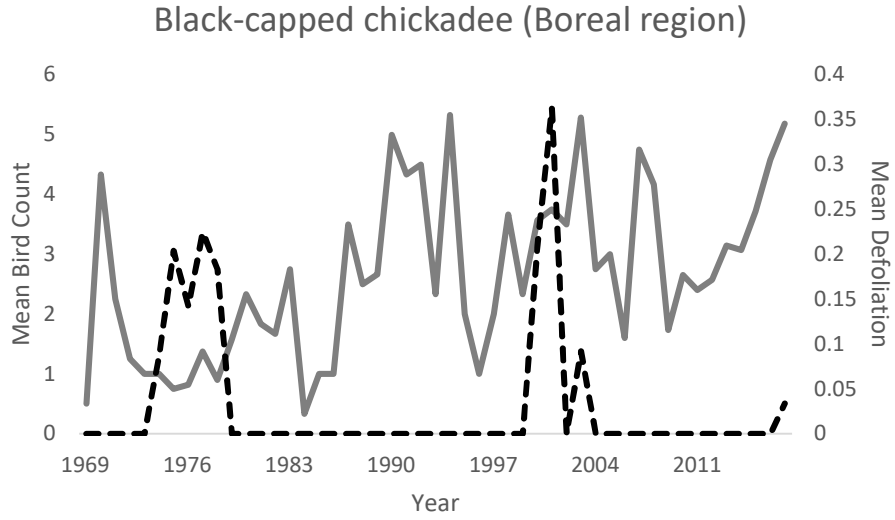
Appendix 1. Time series of mean annual counts of the black-billed cuckoo (solid grey line) and mean annual defoliation by the forest tent caterpillar (black dashed line) in the Boreal and Hardwood Transition regions.



Appendix 2. Time series of mean annual counts of the least flycatcher (solid grey line) and mean annual defoliation by the forest tent caterpillar (black dashed line) in the Boreal and Hardwood Transition regions.



Appendix 3. Time series of mean annual counts of the yellow warbler (solid grey line) and mean annual defoliation by the forest tent caterpillar (black dashed line) in the Boreal and Hardwood Transition regions.



Appendix 4. Time series of mean annual counts of the black-capped chickadee (solid grey line) and mean annual defoliation by the forest tent caterpillar (black dashed line) in the Boreal and Hardwood Transition regions.