

## Budworm-linked warblers as early indicators of defoliation by spruce budworm: A field study



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### ABSTRACT

Outbreaks of eastern spruce budworm (*Choristoneura fumiferana*; hereafter SBW) are a major natural disturbance in coniferous forests of eastern North America. These outbreaks provide a superabundant source of food for insectivorous birds. Three species, referred to as budworm-linked warblers, exhibit strong positive numerical responses to early increases of SBW density: Tennessee Warbler (*Leiothlypis peregrina*), Cape May Warbler (*Setophaga tigrina*), and Bay-breasted Warbler (*S. castanea*). Their abundance increases even before defoliation is visible from aerial surveys. Budworm-linked warblers may detect new epicenters of SBW outbreaks through natal dispersal, as this movement is typically much more extensive than subsequent (breeding dispersal) movements. Our main objectives were, thus, (1) to determine whether sudden increases in the abundance of budworm-linked warblers could be used to detect early stages of SBW outbreaks, and (2) to examine age-specific responses of budworm-linked warblers to local and landscape-level habitat characteristics, in order to investigate the potential role of natal dispersal in the detection of new epicenters. To do so, we estimated the abundance of each species of budworm-linked warbler in 75 study plots sampling a gradient of SBW density and related them to 7 stand variables and landscape metrics with generalized additive mixed models. We also compared the responses of yearling (second-year; SY) and older (after-second-year; ASY) individuals to the density of SBW larvae and habitat variables at different spatial scales. We captured 31 Tennessee Warblers, 27 Cape May Warblers, and 57 Bay-breasted Warblers. The abundance of all three species of budworm-linked warblers increased with SBW larval density, but the numerical response of Bay-breasted Warbler was initiated earlier and it varied with age. SY individuals tended to be associated with stands supporting lower larval densities than ASY individuals and, as suggested by other authors, Bay-breasted Warbler appeared to be more efficient at exploiting SBW larvae at low density. For that reason, this species represents an early indicator of stands undergoing SBW outbreaks and we propose to use its abundance as an indicator to orient labour-intensive ground surveys of SBW larvae.

### 1. Introduction

Among the natural disturbances occurring in the boreal forest, insect outbreaks such as those of eastern spruce budworm (*Choristoneura fumiferana*; hereafter SBW) represent one of the major forces driving forest dynamics (Kneeshaw et al., 2015). SBW is a native defoliating insect that periodically reaches such high densities that it causes extensive mortality to its host tree species, balsam fir (*Abies balsamea*),

white spruce (*Picea glauca*), and to a lesser extent, red spruce (*P. rubens*) and black spruce (*P. mariana*) (Hennigar et al., 2008). Recent research suggests that the progression of SBW outbreaks could be impeded if small populations are controlled before they grow (Régnière et al., 2013, 2014). During endemic periods, populations are so low that a mate-finding Allee effect is thought to maintain SBW densities at a level where larvae populations cannot escape mortality by natural enemies (Régnière et al., 2013). Below a putative “Allee threshold” (i.e. 4 larvae/

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45 cm-long branch, MacLean et al., 2019), males have difficulty locating and mating with females. Hence, an early intervention strategy aiming to maintain budworm densities could help control SBW outbreaks (Régnière et al., 2001; MacLean et al., 2019). In early intervention strategies, spraying must be conducted at very low SBW densities (i.e. less than 4 to 5 larvae per branch) to effective. Although detection of this key transition from low to rising populations at broad spatial scales is challenging with current techniques (Pureswaran et al., 2016; Bouchard et al., 2018), it is essential for successful implementation of an early intervention strategy (MacLean et al., 2019).

Many predators of Lepidoptera benefit from SBW outbreaks (Morris et al., 1958; Venier and Holmes, 2010). For example, 2- to 5-fold increases in densities of forest songbirds have been reported during SBW outbreaks in response to high food availability (Kendeigh, 1947; Sanders, 1970; Holmes et al., 2009). Most studies that have investigated the relationship between birds and SBW suggest that some species respond more consistently and strongly than others to increases in SBW larval densities. Indeed, three species have been labeled “budworm-linked warblers”, namely Tennessee Warbler (*Leiothlypis peregrina*), Cape May Warbler (*Setophaga tigrina*) and Bay-breasted Warbler (*S. castanea*) (Venier and Holmes, 2010). Although all three species show numerical increases when SBW densities are rising, the shape of their responses varies (Holmes et al., 2009; Drever et al., 2018). Bay-breasted Warbler has been reported to respond earlier than the two other budworm warbler species (Holmes et al. 2009; Germain et al., in review), whereas Cape May Warbler and Tennessee Warbler show later, but more rapid increases in their densities (Venier and Holmes, 2010). In spite of these findings, a finer understanding of the numerical responses of budworm-linked warblers to the first stages of SBW outbreaks is necessary before we can use these bird species as early indicators of the progression of an outbreak, both spatially and temporally.

Although the numerical response of budworm-linked warblers to SBW outbreaks may reflect the plasticity in clutch size observed in these species (MacArthur, 1958), local increases in abundance in the early stages of outbreaks are more likely to result from immigration. In most passerine birds, the bulk of dispersal occurs during the first year of life, i.e., through natal dispersal (Greenwood, 1980; Greenwood and Harvey, 1982). Natal dispersal movements allow yearling individuals to prospect for new territories (e.g. Pärt et al., 2011; Ponchon et al., 2017). After their first breeding season, individuals may use personal information (i.e. experience acquired during their previous breeding attempt) to disperse (after reproductive failure) or to return to the vicinity of their previous breeding site (e.g. after successful reproduction; Greenwood and Harvey, 1982; Sedláček et al., 2008; Thériault et al., 2012). Owing to their extensive movements, we would expect natal dispersers to be more likely to detect new epicentres of SBW outbreaks, whereas older birds would be expected to return to their breeding sites, especially if they bred successfully. Thus, older individuals would be expected to dominate populations at higher budworm densities (i.e. stands that have potentially already exceeded the “Allee threshold”), whereas yearlings breeding for the first time would be expected to dominate sites experiencing the early stages of a SBW outbreak.

Previous studies have shown that the abundance of budworm-linked warblers increased at both stand and landscape levels during a SBW outbreak (Holmes et al., 2009; Drever et al., 2018). However, the detailed demographic processes through which budworm-linked warblers respond to spatial variation in the density of SBW larvae have yet to be elucidated. Our first objective was to determine whether budworm-linked warblers could be used as indicators of early stages of SBW outbreaks. We hypothesized that the abundance of budworm-linked warblers would be most strongly associated with local density of SBW larvae, because it will promote larger clutch sizes and, possibly, immigration. Hence, we predicted that the abundance of all three species of budworm-linked warblers would increase during the rising phase of SBW outbreaks (i.e. before reaching the “Allee threshold”), but that the Bay-breasted Warbler would respond earlier than the other two

species, as reported by Holmes et al. (2009) and Germain et al. (in review). Considering the scarcity of information on the relative influence of immigration on variation in local abundance of budworm-linked warblers, our second objective was to investigate age-specific patterns in habitat use to make inferences about dispersal. As yearlings undergo long-distance dispersal and older individuals are relatively faithful to their previous breeding site (Greenwood, 1980; Hallworth et al., 2008), especially when they have bred successfully (Pärt and Gustafsson, 1989; Thériault et al., 2012), we hypothesized that yearlings will be more likely to detect new epicenters of SBW infestation and that previous breeding experience will influence the selection of good quality nest sites. Hence, we predicted that SY individuals will occupy stands with lower SBW larval density than ASY individuals.

## 2. Methods

### 2.1. Study area

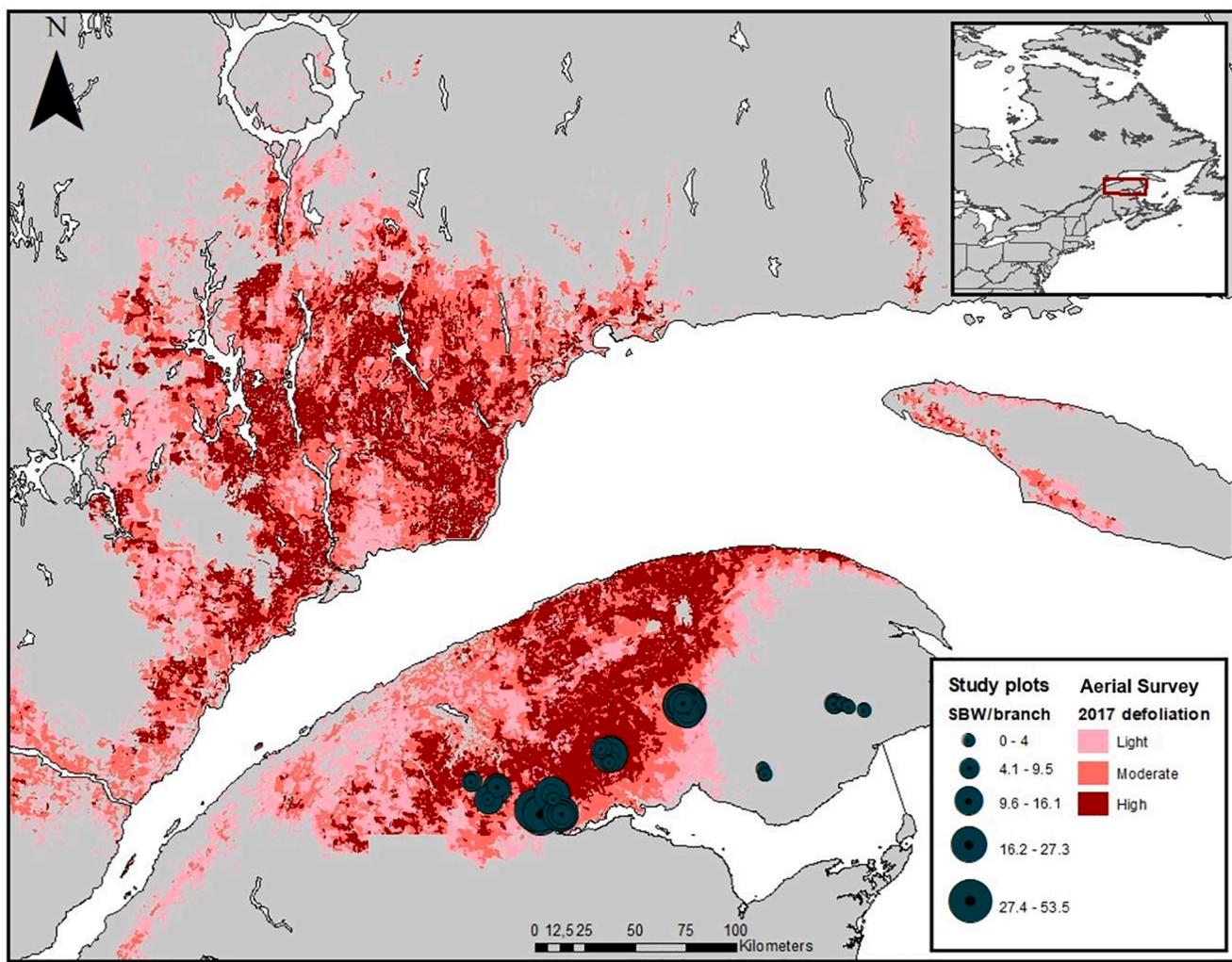
The study was conducted in the Gaspésie and Bas-Saint-Laurent regions of eastern Québec, Canada (Fig. 1). The study area falls within the balsam fir – yellow birch and the balsam fir – white birch forest regions (Robitaille and Saucier, 1998). Forest stands were dominated by balsam fir and white spruce, with white birch (*Betula papyrifera*) or yellow birch (*Betula alleghaniensis*) as subdominant species. The study area is characterized by extensive plateaus with a maximum elevation of 500 m, dissected by broad valleys (Robitaille and Saucier, 1998). Since 2006, populations of eastern spruce budworm have increased steadily in Québec, especially on the north shore of the St. Lawrence River and northeast of the Lac St-Jean region (Fig. 1). This outbreak started unusually far north, reaching the southern shore of the St. Lawrence River in 2010 (MFFP, 2017a).

Because our project mainly focused on the early or rising stages of SBW outbreaks, we surveyed regions where SBW densities were low but still increasing in 2017.

We selected 75 study plots based on the presence of SBW host tree species, and then along a gradient of density of SBW larvae. We used 1:20 000 ecoforest maps published by the *Ministère de la Forêt, de la Faune et des Parcs* (hereafter MFFP), which provide precise information (4 ha resolution) about stand composition and structure, to select plots with a high proportion of SBW host trees. We selected stands whose basal area was dominated by balsam fir, white spruce, and black spruce combined, as indicated on Quebec ecoforest maps. To estimate SBW densities, we used both (1) SBW density estimates derived from fall 2nd-instar-larvae ground surveys conducted by the *Société de protection des forêts contre les insectes et les maladies* (SOPFIM, 2017a, 2017b) and (2) aerial survey data from MFFP (MFFP, 2017b). These data allowed the estimation of SBW density at both local and regional scales and, thus, to select study plots along a gradient of density of SBW larvae, ranging from null to high values. For logistical reasons, study plots were clustered in groups of 3 to 6, but plots within a cluster were separated by a minimum distance of 250 m following Bibby et al. (2000).

### 2.2. Bird surveys

From 7 June to 4 July 2017, we surveyed budworm-linked warblers using the point count method (Bibby et al., 2000). Each of the 75 study plots was sampled once between sunrise and 1000. We performed 10-min counts, split into two 5-min periods (Ralph et al., 1993). Each individual of each focal species (Tennessee Warbler, Cape May Warbler and Bay-breasted Warbler) detected by sight or sound was recorded and its distance from the plot center was estimated using the following distance classes: 0–50 m, 50–75 m, 75–100 m and > 100 m (Thompson et al., 2002). The abundance of each species was then estimated as the maximum number of pair equivalents recorded within 100 m during either of the two 5-min counts (Bibby et al., 2000). Point counts were performed by three experienced observers. To minimize observer



**Fig. 1.** Defoliation map based on aerial survey data (MFFP 2017b) and density of SBW larvae in each study plot.

effects, we calibrated our distance estimates before undertaking the survey (Scott, 1981). All counts were performed under favorable weather conditions (i.e. low wind and no rain).

We attempted to capture at least one individual of each budworm-linked warbler species present in each plot using a 6-m mist net and playbacks of conspecific vocalizations. All individuals were captured between 7 June and 16 July 2017. Capture and manipulation protocols were approved by Université de Moncton's Animal Care Committee (certificate #CPA-17-06). In 12 (i.e. ~15%) of the 75 plots, we captured more than one individual without any extra effort. For each bird captured, we measured wing chord, tarsus length, and body mass, and we photographed one open wing, the open tail and the bird's profile. All individuals were independently aged using photographs by a co-investigator (P. Pyle) who did not participate in field work. Birds were classified according to molt patterns into two age classes: second-year (SY) and after-second-year (ASY) (Pyle, 1997). Age determination of captured landbirds using similar photographic methods resulted in an error rate of 8.1% for 29 boreal species (Pyle et al., 2020).

### 2.3. Explanatory variables

#### 2.3.1. Stand characteristics

We characterized stand composition and structure using estimates of basal area of SBW host tree species (balsam fir, white spruce, and black spruce), percentage of basal area of deciduous trees, and canopy depth (distance between the first branch with foliage and the top of the tree).

The basal area of SBW host trees and the percentage of deciduous trees were measured at four points within a 50-m radius buffer around the plot center; we used the mean of the four points as an estimate of basal area for each study plot. We used the same plots to estimate the percentage of deciduous trees and averaged the values to use the mean values in subsequent analyses. Basal area was estimated with a metric prism and the percentage of deciduous trees was calculated as the proportion of deciduous tree stems included in basal area estimation (Ordre des ingénieurs forestiers du Québec, 2009). Canopy depth (i.e. crown length) was estimated with a clinometer at plot centers for three representative SBW host trees (irrespective of species). To account for the influence of host tree density on SBW abundance (Bognounou et al., 2017), we included the basal area of SBW host trees in each model. Because the basal area of balsam fir was correlated to that of all SBW host trees combined (Pearson correlation coefficient  $r = 0.61$ ,  $P = 0.01$ ), we used the basal area of SBW host trees because it performed best according to Akaike's information Criterion corrected for small samples (hereafter AIC<sub>c</sub>) (Burnham and Anderson, 2002).

#### 2.3.2. Landscape characteristics

We classified forest polygons on 1:20 000 ecoforest maps published by MFFP as "habitat" and "non-habitat" for budworm-linked warblers as a function of habitat descriptions published in Birds of the World species accounts (Baltz and Latta, 2020; Rimmer and McFarland, 2020; Venier et al., 2020). Budworm-linked warblers are associated with stands dominated by balsam fir and spruces with a minimum canopy height of

7 m. In the absence of these stand characteristics, polygons were considered as “non-habitat”. Polygons were then converted into 25 × 25 m pixels to calculate the percentage of habitat within the following radii: 100 m, 250 m, 500 m, 1 km, 2.5 km, 5 km, 8 km, 10 km, 12 km, and 15 km. Following Lesmerises et al. (2018), we used AIC<sub>c</sub> to select the most appropriate buffer size for each dependent variable. The elevation (in m) of each plot was extracted from a digital elevation model. In the statistical analyses, we used mean elevation within a 500-m radius around the study plot.

### 2.3.3. Eastern spruce budworm sampling

In each study plot, we sampled 4th-instar SBW larvae (L4) using extendable pole pruners. We clipped two 45-cm branch tips from the mid-crown of three SBW host trees (i.e. balsam fir or white spruce) following Morris (1955). All branches sampled were bagged and taken to the laboratory, where we counted SBW larvae. Fourth-instar larvae are often reported in the literature as the first larval stage consumed by insectivorous birds (Venier and Holmes, 2010). Sampling L4 is also a standardized approach in entomological research (Morris, 1955). Hence, we used the software BioSIM 11 to predict the dates at which larvae would reach the L4 stage (Réginière et al., 2017). Budworms were sampled between 14 and 28 June 2017.

The branches sampled were also used to estimate cumulative defoliation. For each shoot, we estimated the percentage of needles removed by SBW using Fette's defoliation categories (Fette, 1950). As SBW defoliates almost exclusively the current year's growth, defoliation estimates can be made for current and preceding years based on the number of internodes from the current year. Percent defoliation was determined by averaging the midpoint of defoliation categories for each shoot of a given year on a given branch (Dorais and Hardy, 1976). Because it reflects canopy openness and probability of tree survival, we estimated percent cumulative defoliation by summing percentages of defoliation of the three previous years (2016–2015–2014). Therefore, estimates ranged from a minimum of 0% to a maximum of 300%.

## 2.4. Statistical analyses

### 2.4.1. Numerical response of budworm-linked warblers

To determine whether the abundance of budworm-linked warblers was a reliable indicator of early-stage SBW outbreaks, we combined explanatory variables (see Table 1 and the section above for a description) into candidate models (Table 2). The set of candidate models was built hierarchically, i.e., most models included the same SBW-related variables but stand and landscape variables differed. Because relationships between dependent variables and predictors could be nonlinear, we used generalized additive mixed models (GAMMs) (*gam* function in R form *mgcv* package) (Wood, 2016, 2017) to model the abundance of each warbler species. In a GAMM framework, the relationship is modeled as the sum of smoother functions of covariates, allowing the relationship to follow any smooth curve rather than being constrained to a parametric curve (Wood, 2017). However, parametric relationships (such as linear relationships) can also be modeled using GAMMs. Smoothing parameter estimations were performed using the residual maximum marginal likelihood (REML) method (Wood, 2011). The GAMM structure allowed us to account for observer effects, as well as count date and hour, which were included as random factors. The abundance of each species of budworm-linked warbler was modeled as a Poisson-distributed response variable. In all cases, we tested for spatial autocorrelation in response variables using Moran's I (Moran, 1948). Because some spatial autocorrelation was detected, we used principal coordinates of neighbour matrices (PCNM) to account for the observed spatial structure (Dray et al., 2006). When PCNMs had a significant independent effect on dependent variables, they were forced into all subsequent candidate models following Leblond et al. (2015). Models were ranked using AIC<sub>c</sub> to identify the most parsimonious model (Burnham and Anderson, 2002) (Appendix A).

**Table 1**

Description and descriptive statistics for independent variables included in candidate models.

Variables	Descriptions	Mean ± SD	Min-max
Abundance of each species of budworm-linked warbler	Abundance of species estimates with point counts		
	Abundance of BAY-BREASTED WARBLER	1.8 ± 1.53	0–6
	Abundance of CAPE MAY WARBLER	1.01 ± 1.13	0–4
	Abundance of TENNESSEE WARBLER	0.38 ± 0.61	0–2
Basal area of SBW host tree	Plot level basal area of SBW host trees (m <sup>2</sup> /ha)	39.71 ± 9.59	17–59
Canopy depth	Distance between the first branch with foliage and the top of the tree (m)	9.44 ± 2.33	4.9–16.3
Cumulative % defoliation	Cumulative % defoliation of the past three years	83.07 ± 97.07	17.09–211.01
Elevation	Mean elevation within a 500 m radius (m)	399.89 ± 97.07	230.70–566.69
Proportion of deciduous trees	Proportion of basal area in deciduous trees	0.12 ± 0.12	0–0.44
Proportion of habitat	Proportion of habitat within different radii		
	Radius of 100 m	0.83 ± 0.25	0.11–1
	Radius of 250 m	0.77 ± 0.21	0.28–1
	Radius of 500 m	0.70 ± 0.19	0.32–1
	Radius of 1 km	0.64 ± 0.18	0.33–0.95
	Radius of 2.5 km	0.57 ± 0.17	0.26–0.84
	Radius of 5 km	0.51 ± 0.15	0.22–0.76
	Radius of 9 km	0.50 ± 0.13	0.23–0.73
	Radius of 12 km	0.49 ± 0.12	0.26–0.69
	Radius of 15 km	0.48 ± 0.10	0.29–0.65
SBW	Log (budworm larvae/branch tip + 1)	1.88 ± 1.13	0–3.99

### 2.4.2. Age-specific patterns in occurrence of budworm-linked warblers

To determine whether study plots with high SBW larval density were dominated by ASY individuals (Table 3), we used the same approach as in 2.4.1. We developed a set of candidate models using combinations of explanatory variables (see Table 1). We then compared the set of candidate models for each age class of each species and ranked them using AIC<sub>c</sub> to identify the most parsimonious model (Burnham and Anderson, 2002). We used binomial GAMMs with logit-link functions to model the probability of occurrence of an ASY or a SY individual by contrasting study plots where an ASY (or SY) was captured (presence, coded 1) with those where none were captured (absence, coded 0). Because the inclusion of multiple capture events at a single study plot had no qualitative influence on the results, all captured individuals were included in the analysis. Again, we entered significant PCNMs into all subsequent models to account for spatial autocorrelation. There was no evidence for multicollinearity among independent variables (variance inflation factor < 3.5; Graham, 2003). All statistical analyses were performed with R 3.5.1 (R Core Team, 2019).

## 3. Results

Bay-breasted Warbler was the most abundant species in our study area, with an average of 1.8 individuals per plot (range: 0 to 6; absent from 15 plots). It was followed by Cape May Warbler (mean: 1.0; range:

**Table 2**

Candidate models used to assess the effects of habitat/landscape characteristics on the abundances of Bay-breasted Warbler, Cape May Warbler, and Tennessee Warbler. Independent variables are described in Appendix B. The “+” symbol represents the addition of a variable into the model while the “\*\*” symbol represents an interaction between variables.

Model ID	Hypothesis family	Model structure
M1	SBW	SBW + Basal area of SBW host trees
M2		SBW + cumulative % defoliation + Basal area of SBW host trees
M3		SBW * cumulative % defoliation + Basal area of SBW host trees
M4	SBW, stand structure and composition	M1 + canopy depth + % deciduous trees
M5		M2 + canopy depth + % deciduous trees
M6		M3 + canopy depth + % deciduous trees
M7	SBW, stand structure and composition and landscape	M4 + % habitat + elevation
M8		M5 + % habitat + elevation
M9	structure	M6 + % habitat + elevation
M10		SBW * % habitat + elevation + canopy depth + % of deciduous trees
M11	SBW and landscape structure	M1 + % habitat + elevation
M12		M2 + % habitat + elevation
M13		M3 + % habitat + elevation
M14		SBW * % habitat + basal area of SBW host trees + elevation
M15	No SBW influence	Canopy depth + basal area of SBW host trees + % deciduous trees
M16		% habitat + elevation
M17		M15 + % habitat + elevation

**Table 3**

Candidate models used to assess the effects of habitat/landscape characteristics on the probability of occurrence of an ASY or SY bird of each budworm-linked warbler species. Independent variables are described in Appendix B. The “+” symbol represents the addition of a variable in the model while the “\*\*” symbol represents an interaction between variables.

Model ID	Hypothesis family	Model structure
M1	SBW	SBW + Basal area of SBW host trees
M2		SBW + % cumulative defoliation + Basal area of SBW host trees
M3		SBW * % cumulative defoliation + Basal area of SBW host trees
M4	SBW, stand structure and composition	M1 + canopy depth + % deciduous trees
M5		M2 + canopy depth + % deciduous trees
M6		M3 + canopy depth + % deciduous trees
M7	SBW, stand structure and composition and landscape	M4 + % habitat + elevation
M8		M5 + % habitat + elevation
M9	structure	M6 + % habitat + elevation
M10		SBW * % habitat + elevation + canopy depth + % of deciduous trees
M11	SBW and landscape structure	M1 + % habitat + elevation
M12		M2 + % habitat + elevation
M13		M3 + % habitat + elevation
M14		SBW * % habitat + basal area of SBW host trees + elevation
M15	SBW and conspecific attraction	M1 + abundance of the species
M16		M2 + abundance of the species
M17		M3 + abundance of the species
M18	No SBW influence	Canopy depth + basal area of SBW host trees + % deciduous trees
M19		% habitat + elevation
M20		M15 + % habitat + elevation

0 to 4; absent from 31 plots), and Tennessee Warbler (mean: 0.4; range: 0 to 2; absent from 53 plots) (Table 1). Bay-breasted Warbler was also the most frequently captured species (49 males and 5 females). Of these, 25 were classified as ASY and 29 as SY. Tennessee Warbler was second (30 males and 1 female), including 15 ASY and 16 SY. Cape May Warbler ranked third (26 males, 1 female), including 12 ASY and 15 SY. It should be noted that we could not always capture all budworm-linked warblers present in a given study plot because some individuals were not attracted to the broadcasts.

As expected, there was large variation in the density of SBW larvae and cumulative percent defoliation among study plots. SBW density varied from 0 to 53.5 larvae per 45-cm branch (0 – 3.99 log (budworm/branch + 1)) and 3-year cumulative defoliation varied from 17.1% to 211.0% (Table 1). Even though cumulative defoliation is directly caused by SBW, the current-year's larval density and cumulative defoliation were not significantly correlated (Pearson correlation coefficient  $r = 0.36$ ,  $p = 0.23$ ).

### 3.1. Numerical response of budworm-linked warblers

As predicted, the density of SBW larvae had a significant effect on the abundance of the three warbler species in each of the most parsimonious models (Table 4 and Fig. 2). Model ranking showed little difference in AIC<sub>c</sub> between some of the candidate models. For each species, ~ 6 models had a delta AIC<sub>c</sub> < 2 (Appendix A). Nevertheless, we always selected the model with the lowest AIC<sub>c</sub> value as the most parsimonious and we did not conduct model averaging because the set of candidate models was built hierarchically (Arnold, 2010). Thus, little difference

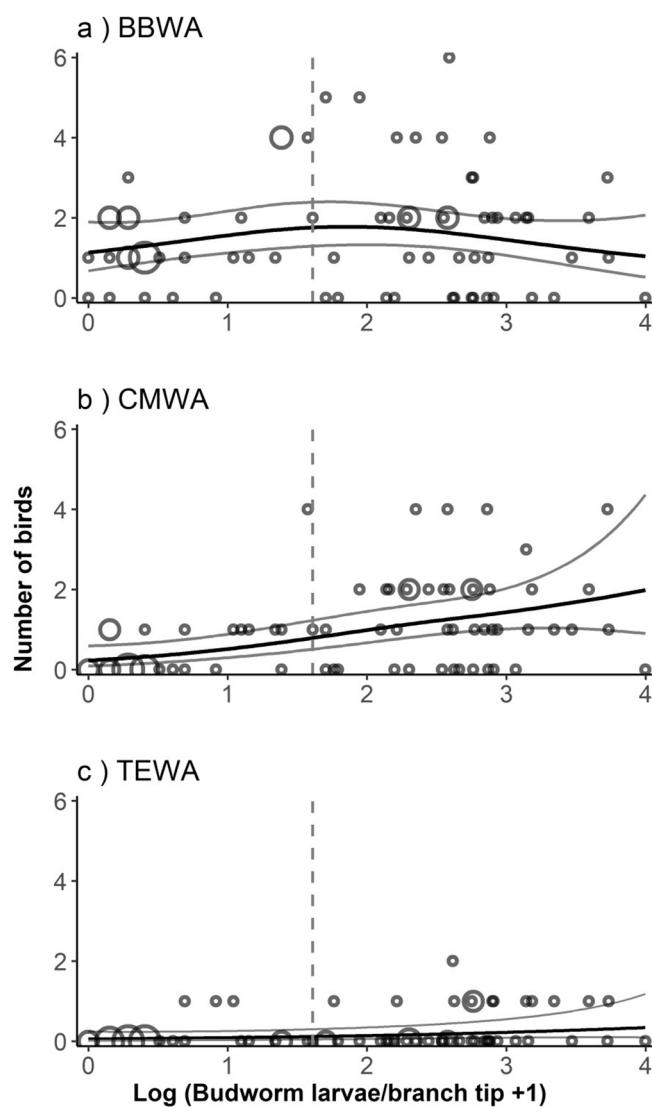
**Table 4**

Summary of the most parsimonious GAMM models predicting the abundance of each species of budworm-linked warbler: Bay-breasted Warbler, Cape May Warbler, and Tennessee Warbler. Significant effects are shown in bold.

Species	Variables	Effective degrees of freedom	X <sup>2</sup>	P-value
BAY-BREASTED WARBLER	<b>Log SBW</b>	<b>2.045</b>	<b>7.453</b>	<b>0.025*</b>
	Basal area of SBW host trees	4.488e <sup>-04</sup>	0.000	0.354
	Cumulative % defoliation	3.187e <sup>-05</sup>	0.000	0.999
	Canopy depth	2.104e <sup>-05</sup>	0.000	0.999
	% deciduous trees	1.429	4.668	0.076
	PCNM X2	1.121e <sup>-05</sup>	0.000	0.849
	<i>Random effects</i>			
	<b>Observers</b>	<b>1.654</b>	<b>8.738</b>	<b>&lt;0.001***</b>
	Date	6.402e <sup>-06</sup>	0.000	0.349
	Hour	0.792	3.947	0.065
CAPE MAY WARBLER	<b>Log SBW</b>	<b>1.644</b>	<b>15.082</b>	<b>&lt;0.001***</b>
	Basal area of SBW host trees	6.599e <sup>-05</sup>	0.000	0.700
	% habitat <sup>a</sup>	<b>1.310</b>	<b>5.533</b>	<b>0.008**</b>
	Elevation	5.570	1.057	0.129
	PCNM X3	8.190e <sup>-05</sup>	2.804	0.051
	<i>Random effects</i>			
	<b>Observers</b>	<b>1.463</b>	<b>4.971</b>	<b>0.033*</b>
	Date	0.372	0.602	0.195
	Hour	7.933e <sup>-06</sup>	0.000	0.753
	<b>TENNESSEE WARBLER</b>	<b>0.964</b>	<b>3.829</b>	<b>0.027*</b>
	Basal area of SBW host trees	0.469	0.882	0.162
	% habitat <sup>b</sup>	2.283e <sup>-04</sup>	0.000	0.885
	Elevation	1.660	3.440	0.103
	PCNM X1	8.241	2.379	0.071
	<i>Random effect</i>			
	<b>Observers</b>	<b>1.609e<sup>-06</sup></b>	<b>0.000</b>	<b>0.942</b>
	Date	2.282e <sup>-07</sup>	0.000	0.613
	Hour	3.628e <sup>-07</sup>	0.000	0.720

<sup>a</sup> within a 2.5 km radius.

<sup>b</sup> within a 500 m radius.



**Fig. 2.** Relationships (solid black lines) between SBW larvae density and abundance of a) Bay-breasted Warbler, b) Cape May Warbler and c) Tennessee Warbler as per the most parsimonious model for each species (Table 4). Gray lines represent 95% confidence intervals. Dots represent data points ( $n = 75$ ), with dot size proportional to the number of observations for each species. The vertical dashed line represents the “Allee threshold” of budworm populations, as suggested by Régnière et al., (2013) and MacLean et al., (2019).

was expected among those models, especially when density of SBW larvae had a significant effect. However, as predicted, the magnitude of budworm-linked warbler responses to the density of SBW larvae varied among species (Fig. 2).

Bay-breasted Warbler abundance varied with the density of SBW larvae in a nonlinear, non-monotonic fashion (Fig. 2a). At relatively low densities of SBW larvae, Bay-breasted Warbler abundance increased slightly, then it started to decline with further increases in the density of SBW larvae (Fig. 2a). The most parsimonious model explained 39.4% of the deviance and the density of SBW larvae appeared to explain an important proportion, although there was also a significant observer effect (Table 4). The abundance of Cape May Warbler also increased slightly with the density of SBW larvae (Fig. 2b). In contrast with Bay-breasted Warbler, Cape May Warbler abundance continued to increase as the density of SBW larvae reached high or very high levels (Fig. 2b). For Cape May Warbler, the most parsimonious model explained 40.2% of the deviance, with density of SBW larvae and landscape structure (Table 4) explaining most of the deviance (29.7%). Although variation

in Tennessee Warbler abundance was low, it increased slightly but consistently with the density of SBW larvae (Fig. 2c). The most parsimonious model explained 25.2% of the deviance. Bay-breasted Warbler thus appeared to respond slightly earlier to an increase in the density of SBW larvae than either Cape May Warbler or Tennessee Warbler.

### 3.2. Age-specific patterns in occurrence of budworm-linked warblers

The probability of occurrence of SY Bay-breasted Warblers was negatively related to the density of SBW larvae (Table 5, Fig. 3a). These individuals also appeared to settle in study plots with a lower proportion of habitat within a 250-m radius (Table 5). However, the most parsimonious model explaining variation in the probability of occurrence of SY individuals received moderate support (deviance explained: 17.9%).

For ASY Bay-breasted Warblers, the most parsimonious model included an interaction between density of SBW larvae and cumulative defoliation (Table 5, Fig. 3b). The probability of occurrence of ASY was positively related to the density of SBW when cumulative defoliation was low or moderate, whereas the same relationship became negative when cumulative defoliation was high (Fig. 3b). The most parsimonious model for ASY Bay-breasted Warblers performed well, explaining 33.2% of the deviance.

Density of SBW larvae was not included in the most parsimonious models explaining variations in the probability of occurrence of ASY or SY Cape May Warblers. In fact, only elevation had a significant effect on the occurrence of SY Cape May Warblers (Table 4). With respect to SYs, the most parsimonious model explained 19.6% of the deviance, whereas

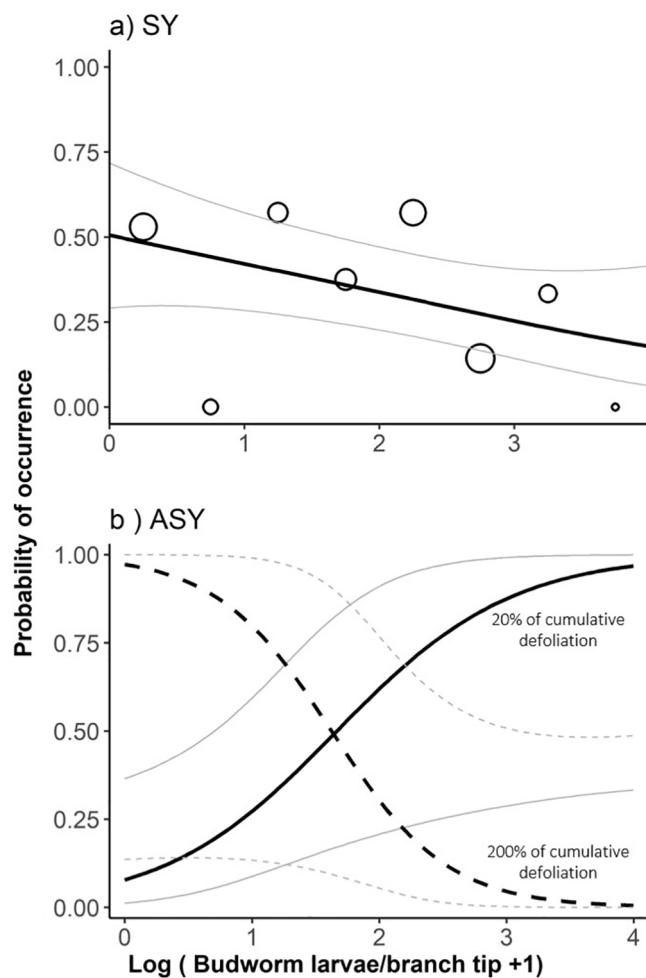
**Table 5**

Summary of the most parsimonious GAMM models predicting the probability of occurrence of budworm-linked warblers of a given age class (SY: second-year; ASY: after-second-year). Significant effects are shown in bold.

Species-age classes	Variables	Effective degrees of freedom	$\chi^2$	P-value
BAY-BREASTED WARBLER-SY	<b>Log SBW</b>	<b>0.943</b>	<b>3.731</b>	<b>0.033*</b>
	Basal area of SBW host trees	1.982e <sup>-05</sup>	0.000	0.858
	% habitat <sup>a</sup>	<b>0.832</b>	<b>3.196</b>	<b>0.041*</b>
	Elevation	2.660e <sup>-05</sup>	0.000	0.834
	<b>Log SBW * cumulative % defoliation</b>	<b>4.727</b>	<b>11.445</b>	<b>0.055**</b>
	Basal area of SBW host trees	2.131e <sup>-05</sup>	0.000	0.739
BAY-BREASTED WARBLER-ASY	Canopy depth	0.147	0.169	0.272
	% deciduous trees	<b>1.244</b>	3.408	0.059.
	% habitat <sup>b</sup>	1.116e <sup>-05</sup>	0.000	0.611
	<b>Elevation</b>	<b>1.901</b>	<b>9.000</b>	<0.001**
	% habitat <sup>a</sup>	9.483e <sup>-05</sup>	0.000	0.423
	<b>Elevation</b>	<b>4.006</b>	<b>10.260</b>	<b>0.025*</b>
CAPE MAY WARBLER-SY	% habitat <sup>b</sup>	0.713	1.932	0.091.
	Elevation	2.793e <sup>-05</sup>	0.000	0.808
	<b>Log SBW * % cumulative defoliation</b>	<b>0.755</b>	<b>10.562</b>	0.253
	Basal area of SBW host trees	1.261e <sup>-05</sup>	0.000	0.792
	Canopy depth	0.923	3.051	0.050
	% deciduous trees	0.874	2.133	0.092
CAPE MAY WARBLER-ASY	<b>PCNM X1</b>	<b>1.171</b>	<b>7.384</b>	<b>0.002*</b>
	<b>Log SBW</b>	<b>4.686e<sup>-05</sup></b>	<b>0.000</b>	<b>0.573</b>
	<b>Cumulative % defoliation</b>	<b>0.965</b>	<b>3.285</b>	<b>0.041*</b>
	Basal area of SBW host trees	0.643	1.062	0.183
	% habitat <sup>b</sup>	<b>2.572</b>	<b>11.363</b>	<b>0.002**</b>
	Elevation	9.473e <sup>-06</sup>	0.000	0.632
TENNESSEE WARBLER-ASY	PCNM X4	0.661	1.342	0.131

<sup>a</sup> within a 2.5 km radius.

<sup>b</sup> within a 500 m radius.



**Fig. 3.** Probability of occurrence of second-year (SY) (a) and after-second-year (ASY) (b) Bay-breasted Warblers as a function of density of SBW larvae, as per the most parsimonious models (see Table 5 for details). Panel b also shows the influence of percent cumulative defoliation on the probability of occurrence of ASYs. Bold, black lines show the relationship for different values of cumulative percent defoliation. The solid line shows the 5th quantile (20% of cumulative defoliation) and the dashed line shows the 95th quantile (200% of cumulative defoliation). Gray lines represent the lower and upper bounds of the 95% confidence intervals for the predicted data. Dots in panel a) represent data points, dot size being proportional to the number of observations.

this proportion was only 4.2% for the most parsimonious model explaining the probability of occurrence of ASY birds.

The probability of occurrence of SY Tennessee Warblers was not related to any of the variables included in candidate models, but this response variable was spatially autocorrelated. For ASYs, the most parsimonious model included only cumulative percent defoliation; as cumulative defoliation increased, so did the probability of occurrence of an ASY Tennessee Warbler (Table 5). Deviance explained by the most parsimonious model reached 32.4%. Thus, Bay-breasted Warbler was the only species for which there was a clear response to the density of SBW larvae, although this response varied with the age of individuals. Density of budworm larvae had no effect on the probability of occurrence of either Cape May or Tennessee Warbler, irrespective of the age of individuals.

#### 4. Discussion

Our study confirms the positive effects of SBW outbreaks on the abundance of budworm-linked warblers and highlights the fact that Bay-

breasted Warbler is the most efficient of our three study species at exploiting SBW larvae at low densities, as suggested by MacArthur (1958). We also found evidence for age-specific differences in the response of this species to the density of SBW larvae.

##### 4.1. Numerical response of budworm-linked warblers

Budworm-linked warblers showed numerical responses to the density of SBW larvae, but those responses were not as strong as predicted. Our most parsimonious models only explained a part of the deviance. However, these weaker responses might reflect geographical variation in the propagation dynamics of SBW outbreaks. Budworm outbreaks occur over very large spatial scales, with large variations in frequency, extent, duration, and amplitude (Candau et al., 1998; Robert et al., 2012, 2018). Both stand structure and landscape configuration vary geographically within regions undergoing SBW outbreaks, as well as forest management intensity and the overall intensity of outbreaks (Blais, 1968; Sturtevant et al., 2015). Indeed, Drever et al. (2018) observed differences in budworm-linked warbler responses to the degree of defoliation among geographic regions. In the Gaspésie region (i.e. our study area), warbler responses to defoliation were poor or null at both regional and local scales (see stratum Quebec-14 in Drever et al., 2018), while responses observed in Ontario were much stronger (see stratum Ontario-12 in Drever et al., 2018). At large spatial and temporal scales, budworm defoliation can be used as a proxy for SBW density. However, at finer temporal and spatial scales, SBW density may differ from the degree of defoliation. In our study area, we suspect that some plots not yet heavily defoliated were highly infested by SBW due to moth dispersal movements. A major moth dispersal event estimated to comprise trillions of individuals was observed by radar in 2016, resulting in a large immigration of SBW across most of our study area (Canadian Forest Service, 2018). The low correlation between SBW density and cumulative defoliation observed in our study area could reflect the influence of this event. Moth dispersal can generate large changes in the density of SBW larvae in a stand (i.e. from null to high in a single year) (Greenback et al., 1980), which might result in a time-lagged response by budworm-linked warblers. Thus, the low response to budworm density by budworm-linked warblers that we observed could reflect geographical variations, but also particular patterns in the propagation and dispersal of this SBW outbreak in the Gaspésie region.

We hypothesized that the numerical response of budworm-linked warblers to the SBW outbreak would be species-specific. However, responses were weaker than expected and, therefore, interspecific differences in response patterns were also more subtle than expected. Bay-breasted Warbler reached higher abundances than either Cape May Warbler or Tennessee Warbler. A slower response by Cape May Warbler and Tennessee Warbler to increases in the density of SBW larvae was also observed by Holmes et al. (2009) and Venier and Holmes (2010). The latter authors showed that Bay-breasted Warbler abundance increased three years before those of Cape May Warbler and Tennessee Warbler. The late response of Cape May Warbler and the lack of response by Tennessee Warbler suggest that these species might not be as efficient at exploiting SBW larvae at low densities, making them less attractive as indicators of early stages of SBW outbreaks.

Although Bay-breasted Warbler's numerical response to the density of budworm larvae was not as strong as predicted, our results are consistent with the hypothesis that this species is most strongly associated with the early stages of SBW outbreaks. Its ability to exploit budworm at low densities can be explained by its foraging behaviour, which MacArthur (1958) qualified as "deliberate": the Bay-breasted Warbler spends more time feeding on a specific branch and moves more slowly while foraging than other budworm-linked warbler species. Hence, Bay-breasted Warbler might be a more efficient forager when larvae are at low densities. Its broader foraging zone (MacArthur, 1958) might also favor Bay-breasted Warbler. While Cape May Warbler forages mostly on the upper and outer branches of spruces and firs (Baltz and Latta, 2020)

and Tennessee Warbler gleans insects from the outer foliage of trees and shrubs (Rimmer and McFarland, 2020), Bay-breasted Warbler forages over a broader range of heights with less restriction on tree and branch sections (MacArthur, 1958; Venier et al., 2020). The broader foraging zones combined with the “deliberate” searching method might allow Bay-breasted Warbler to perform better at lower budworm densities. Holmes et al. (2009) observed a similar response, with an increase in Bay-breasted Warbler density when budworm density was still low. Germain et al. (in review) also reported a similar pattern: the probability of occurrence of Bay-breasted Warbler increased by an order of magnitude 4 years before major defoliation could be detected through aerial surveys.

Thus, even though model performances were not as strong as expected, the influence of SBW was clear and consistent. Admittedly, our model only explained a part of the deviance in Bay-breasted Warbler abundance and some of that deviance was attributable to an observer effect. Such effects could be avoided by using autonomous recording units, or ARUs. With the development of open-source acoustic hardware (Hill et al., 2019), ARUs are becoming increasingly affordable, but they still generate vast amounts of data for analysis. Protocols for automated acoustic detection of specific vocalizations are also being rapidly developed with the use of machine learning (e.g. Stowell et al., 2018; Knight et al., 2020) and it is now possible to process large data sets more quickly by reducing the proportion of false positives.

Nonetheless, our results still highlight the specific response of Bay-breasted Warbler to SBW. Other factors might also influence the abundance of the species, but our results consistently indicated that SBW density was an important driver of that abundance. Hence, Bay-breasted Warbler abundance could be a useful indicator to apply early intervention strategies to control SBW outbreaks. To be successful, an early intervention strategy to control spruce budworm requires suppressing populations at very low densities, which thus requires detection at these low densities (MacLean et al., 2019). Current evaluations of SBW abundance are based on ground surveys of overwintering larvae concentrated in buffer areas around defoliated forest stands or where pheromone-trap catches of male moths are high. These techniques have proven to be effective in northern New Brunswick (MacLean et al., 2019) as the advancing outbreak coming from Québec (to the north) is known, but to develop an early intervention strategy that could be used across the range of SBW would require an early indicator to direct the location of labour-intensive (both in the field and subsequently in the laboratory) sampling of overwintering larvae. Detection of areas where the abundance of Bay-breasted Warbler increases suddenly could be used as an early indicator to orient direct ground sampling of SBW larvae and to guide early intervention.

#### 4.2. Age-specific patterns in the occurrence of budworm-linked warblers

The increase we observed in Bay-breasted Warbler abundance in response to a local increase in the density of SBW larvae could be interpreted as a function of dispersal patterns. As predicted, and as reported in other bird species (Holmes et al., 1996; Siegel et al., 2016; Pyle et al., 2020), yearlings (SYs) occupied either lower-quality territories (i.e. with low densities of SBW larvae) or territories relatively isolated from nearby habitat, whereas older (ASY) individuals were captured in territories hosting higher densities of SBW larvae and those territories were characterized by low cumulative defoliation. As predicted, these results suggest that yearlings were more likely to detect and colonize plots at early stages of SBW infestation and that older individuals dominated higher-quality habitat, either as a result of breeding site fidelity by older birds, despotic behaviour by older birds over yearlings (Holmes et al., 1996; Rohwer, 2004; Pyle et al. 2020), or a combination thereof. The fact that breeding adults of these budworm-linked warblers showed low site fidelity relative to other species of wood warblers (Moisan Perrier et al., in review) suggests that older birds track high-density patches of SBW larvae, resulting in relatively extensive

breeding dispersal movements.

During SBW outbreaks, areas supporting lower densities of larvae represent suboptimal habitat for budworm-linked warblers, but study plots showing high cumulative defoliation are also suboptimal for more complex reasons. Although the highest cumulative defoliation that we observed was not sufficient to lead to tree mortality (that normally occurs after 4 or 5 years of severe defoliation; MacLean, 1980), it appeared to influence the perception of habitat quality by ASY Bay-breasted Warblers. Other authors have also observed an influence of habitat change on budworm-linked warblers. For example, Holmes et al. (2009), found that habitat change caused by defoliation led to a decline in the abundance of budworm-linked warblers. In our study area, cumulative defoliation did not lead to major habitat change nor did it influence Bay-breasted Warbler abundances. However, the negative effect of SBW density on the probability of occurrence of ASY Bay-breasted Warblers when cumulative defoliation was high suggests that experienced individuals tended to disperse under those conditions.

There was no evidence for age-specific responses of Cape May Warbler or Tennessee Warbler to SBW larval density or other habitat variables. This suggests that intraspecific despotic behaviour might not be an important driver of age structure in these species. It may also explain the low numerical responses of Cape May Warbler and Tennessee Warbler to increases in SBW larval density.

#### 5. Conclusion

Our results highlight that outbreak dispersal and differences in outbreak magnitude among regions might influence budworm-linked warbler responses. Along with those of other studies (e.g. Germain et al., in review), our results also suggest that Bay-breasted Warbler represents an efficient indicator or sentinel species to identify early rising SBW populations. Incipient SBW outbreaks are exceedingly difficult to locate with aerial or ground surveys, and the response of Bay-breasted Warbler could provide an effective early-warning system to trigger intervention before massive defoliation occurs. The abundance of this bird species could be monitored using autonomous recording units (ARUs) in areas deemed most vulnerable to SBW. By moving ARUs through the peak of the breeding season, it should be possible to detect areas where Bay-breasted Warblers are increasing before the SBW exceeds the Allee threshold beyond which control is no longer effective.

#### CRediT authorship contribution statement

**Jeanne Moisan Perrier:** Methodology, Writing - original draft.  
**Daniel Kneeshaw:** Conceptualization, Methodology, Funding acquisition, Writing - review and editing. **Martin-Hugues St-Laurent:** Conceptualization, Writing - Review and editing, Supervision. **Peter Pyle:** Methodology, Writing - review and editing. **Marc-André Villard:** Conceptualization, Methodology, Funding acquisition, Writing - review and editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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