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EFFECTS OF GYPSY MOTH OUTBREAKS ON NORTH AMERICAN WOODPECKERS

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Abstract. We examined the effects of the introduced gypsy moth (*Lymantria dispar*) on seven species of North American woodpeckers by matching spatially explicit data on gypsy moth outbreaks with data on breeding and wintering populations. In general, we detected modest effects during outbreaks: during the breeding season one species, the Red-headed Woodpecker (*Melanerpes erythrocephalus*), increased over pre-outbreak levels, while during the winter one species, the Yellow-bellied Sapsucker (*Sphyrapicus varius*), increased and one, the Downy Woodpecker (*Picoides pubescens*), decreased from pre-outbreak levels. Responses following outbreaks were similarly variable, and in general we were unsuccessful at predicting population responses to outbreaks from a priori knowledge of woodpecker ecology and behavior. We did, however, find evidence that the response of at least half of the species changed over the 34-year period covered by the study: except for the Northern Flicker (*Colaptes auratus*), whose response to outbreaks during the winter decreased, populations generally responded more positively to outbreaks with time. This temporal response suggests that North American woodpeckers may be taking greater advantage of the resource pulse and/or habitat changes caused by outbreaks of this exotic pest now than previously, so in the future the effects of gypsy moth outbreaks on these species may increase.

Key words: *cavity-nesting birds, gypsy moths,* Lymantria dispar, *pulsed resources, woodpeckers.*

Efectos de las Erupciones de *Lymantria dispar* sobre Pájaros Carpinteros Norteamericanos

Resumen. Examinamos los efectos de la polilla introducida *Lymantria dispar* sobre siete especies norteamericanas de pájaros carpinteros mediante el cruce de información espacialmente explícita de los eventos de erupción de *L. dispar* con datos de las poblaciones reproductivas e invernales. En general, detectamos efectos modestos durante las erupciones. En la época reproductiva, la población de una especie (*Melanerpes erythrocephalus*) se incrementó por encima de los niveles previos a la erupción, mientras que durante el invierno la población de una especie (*Sphyrapicus varius*) aumentó y la de otra (*Picoides pubescens*) disminuyó en relación con los niveles previos. Las respuestas posteriores a las erupciones fueron igualmente variables y, en general, no tuvimos éxito en predecir las respuestas poblacionales a las erupciones a partir de conocimiento previo sobre la ecología y comportamiento de los carpinteros. Sin embargo, encontramos evidencia de que la respuesta de al menos la mitad de las especies cambió a lo largo de los 34 años abarcados por el estudio. Con excepción de *Colaptes auratus*, cuya respuesta a las erupciones durante el invierno disminuyó, las poblaciones generalmente respondieron de forma más positiva a las erupciones con el paso del tiempo. Esta respuesta temporal sugiere que, actualmente, los carpinteros norteamericanos podrían estar aprovechando mejor que antes los pulsos en los recursos y/o los cambios en el hábitat causados por las erupciones de esta peste exótica. Por esto, los futuros efectos de las erupciones de *L. dispar* sobre estas especies podrían incrementarse.

INTRODUCTION

Hardwood forests, which once dominated eastern North America, have been particularly hard hit by biological invasions as a consequence of European colonization, including both the direct effects of deforestation (Clawson 1979, Lorimer 2001) and fragmentation (Sampson and DeCoster 2000) and the indirect effects of exotic forest diseases such as chestnut blight (*Cryphonectria parasitica*) and Dutch elm disease (*Ophiostoma ulmi*), both of which transformed eastern North American communities in the 20th century by eliminating major components of the native forests (Karnosky 1979, Anagnostakis 1987, McKeen 1995). A second significant indirect effect has been mediated through the introduction of exotic insect pests, of which the gypsy moth (*Lymantria dispar*) has been one of the most ecologically important since its introduction near Boston, Massachusetts, in 1869 (Elkinton and Liebhold 1990). Since then, gypsy moths have invaded over 10^6 km^2

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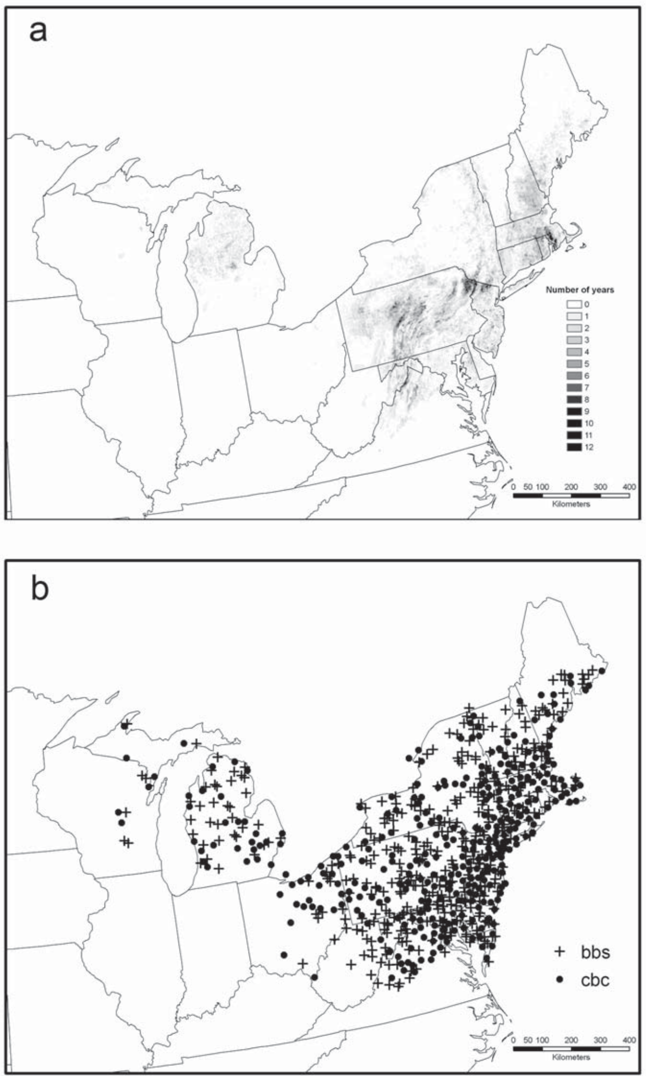

FIGURE 1. (a) Episodes of gypsy moth defoliation in the U.S., 1975–2008. The frequency of episodes is indicated by the shading. (b) Sites of Breeding Bird Surveys (BBS) and Christmas Bird Counts (CBC) used in the analyses.

of forest in the northeastern U.S. (Liebhold et al. 1992) and caused extensive defoliation and considerable tree mortality, prompting expenditures of millions of dollars each year on management and monitoring (Mayo et al. 2003; Fig. 1).

There are a variety of ways that an exotic insect such as the gypsy moth can affect avian communities. Like many invasive species, it may negatively affect native species through competitive interactions (Vilà et al. 2004, Salo et al. 2007). Less commonly, it may facilitate native species through habitat alteration, competitive or predator release, pollination, or "trophic subsidies"—providing a new food resource for predators (Rodriguez 2006). Such trophic subsidies may be particularly relevant to invasive insects that attain high densities, providing a novel prey resource that may increase the fitness of insectivorous birds (Branch and Steffani 2004) and provide a food pulse of a magnitude sufficient to have effects on community structure (Ostfeld and Keesing 2000, Koenig and Liebhold 2005).

Prior studies have yielded mixed results regarding the degree to which gypsy moths are eaten by native animals and in turn how outbreaks influence their predators' populations. Many gypsy moths in North America pupate in tree litter, presumably as an avoidance response to avian predators in their native habitat. In North America, however, the white-footed mouse (*Peromyscus leucopus*) has capitalized on this behavior and depredates the hairy larvae at very high levels (Campbell and Sloan 1976). Birds' predation on egg masses and larvae plays a major role in the regulation of gypsy moth populations in Japan and possibly Europe (Higashiura 1989, Elkinton and Liebhold 1990), suggesting that the moths are having important effects on bird populations as well. These findings, however, contrast with the situation in North America, where most bird species prefer hairless caterpillars (Whelan et al. 1989) and studies have generally failed to find that gypsy moth larvae are a major food item in common birds' diets (Elkinton and Liebhold 1990). Indeed, at least one study in North America has found that gypsy moth outbreaks led to declines of several avian species through increased defoliation and visibility of nests to predators (Thurber et al. 1994).

Consistent with this apparent avoidance of hairy lepidopteran larvae, few positive effects of gypsy moth outbreaks on avian populations in North America have been detected, including in experiments where gypsy moth populations were increased artificially (Gould et al. 1990). Notable exceptions are the two North American species of cuckoos (*Coccyzus erythropthalmus* and *C. americanus*), both of which are attracted to insect outbreaks (Koenig and Liebhold 2005) and are found at significantly higher densities during gypsy moth outbreaks (Barber et al. 2008). Gypsy moth outbreaks cause extensive defoliation, temporarily reducing the abundance of closed-canopy species (Gale et al. 2001) and increasing numbers of birds dependent on more open habitats (Bell and Whitmore 1997). Outbreaks also elevate tree mortality and increase the abundance of snags and so may favor cavity-nesting species. In the only study investigating such indirect effects to date, Showalter and Whitmore (2002) confirmed an increase in snags and cavity-nesting birds for 5 years following a gypsy moth outbreak in West Virginia, after which both the snags and the birds declined.

In summary, the evidence for effects of gypsy moth outbreaks on North American birds is currently relatively modest. However, given that such outbreaks result in both a huge resource pulse and often precipitate major habitat changes, including subsequent increases in wood-boring insects colonizing trees stressed by defoliation (Muzika et al. 2000), we felt that it would be worthwhile to investigate the possibility that more significant effects on bird populations have been overlooked by previous analyses, whose geographic scale has generally been relatively small. Although effects on many bird species are possible, we focused our analyses on North American woodpeckers, both because they are potential predators of gypsy moth larvae and because, as cavity nesters, their populations are often dependent on snags, the abundance of which is affected by gypsy moth outbreaks.

Here we investigate the effects of gypsy moth outbreaks on seven common North American woodpeckers on a temporal and spatial scale much larger than prior studies. Using two continent-wide bird-survey schemes combined with spatial data on gypsy moth outbreaks between 1975 and 2008, we examined the overall effects of outbreaks on populations of woodpeckers and investigated the possibility that their response to outbreaks has changed over the period covered by this study. The woodpecker species chosen occur in sufficient numbers within the current or historical range of gypsy moth outbreaks to allow analysis of each; therefore, we compiled data for all areas experiencing at least one outbreak during the period of the study. We also compiled data for all woodpecker species combined to gain an idea of how this group as a whole was affected by gypsy moth outbreaks.

PREDICTIONS

Prior to conducting these analyses, we predicted the effects of gypsy moth outbreaks on the seven species of woodpeckers both during and after outbreaks (Table 1), as detailed below.

(1) *Hairy Woodpecker* (Picoides villosus)—Despite Forbush and Fernald's (1896) assertion to the contrary, more recent work by Smith (1985), based on 20 birds collected within an outbreak area, suggests that this species does not prey upon gypsy moths. As a result, we did not expect the Hairy Woodpecker to increase during outbreaks even though its numbers increase following outbreaks of bark beetles (*Dendroctonus* spp. and *Scotytus* spp.) (Koplin 1969, Crockett and Hansley 1978, Kroll and Fleet 1979) and it eats codling moth (*Carpocapsa pomonella*) pupae (Neff 1928, MacLellan 1958), cecropia moth (*Hyalophora cecropia*) pupae (Waldbauer et al. 1970), and tent caterpillars (*Malacosoma* spp.; Lawrence 1967).

This species nests primarily in living trunks of trees with fungal heart rot (Conner et al. 1976), so we did not predict a significant increase in numbers following gypsy moth outbreaks as a result of increased snag abundance. No increase following outbreaks was observed in this species by Showalter and Whitmore (2002).

(2) *Downy Woodpecker* (Picoides pubescens)—On the basis of birds collected by Smith (1985), this species rarely eats gypsy moths; only 2 of 26 (8%) contained gypsy moth remains. Consequently, we predicted that there would be little if any increase in this species during outbreaks, although, like the previous species, Downy Woodpeckers feed on both tent caterpillars (Soule 1899) and cecropia moth pupae (Waldbauer et al. 1970). Expectations following outbreaks were less clear. Downy Woodpeckers nest in dead and living trees and thus might be expected to increase following gypsy moth outbreaks even though Showalter and Whitmore (2002) did not find an increase in this species after a gypsy moth outbreak in West Virginia. Thus we tentatively predicted a positive response related to increased snag abundance following outbreaks.

(3) *Yellow-bellied Sapsucker* (Sphyrapicus varius)—Although Beal (1911) found lepidopteran larvae to form a small proportion of its diet, more recent work has found moths to be an important food resource for this species (Lawrence 1967, Gibbon 1970). Thus, although gypsy moths have not been detected in the diet of this species, we predicted that sapsuckers, in contrast to the other woodpecker species, would increase during outbreaks. This species usually nests in live trees (Walters et al. 2002), so we did not predict a numerical response related to increased snag abundance after outbreaks.

(4) *Pileated Woodpecker* (Dryocopus pileatus)—This species primarily eats wood-boring beetle larvae (Hoyt 1957), so we did not predict a response during outbreaks. It nests primarily in snags (Bull and Jackson 1995), so we predicted an increase following outbreaks, as Showalter and Whitmore (2002) found after the gypsy moth outbreak they studied in West Virginia.

(5) *Red-headed Woodpecker* (Melanerpes erythrocephalus)—This species feeds primarily on seeds, nuts, and

TABLE 1. Predicted and observed changes in populations of woodpeckers during and following gypsy moth outbreaks. + = positive; – = negative; o = no difference. In the columns reporting the results observed, + and – specify effects significant at the $P < 0.05$ level.

	During outbreaks			After outbreaks		
		Observed			Observed	
Species	Predicted	BBS	CBC	Predicted	BBS	CBC
Hairy Woodpecker	o	o	o	o	–	o
Downy Woodpecker	o	o	–	+	o	–
Yellow-bellied Sapsucker	+	o	+	o	o	o
Pileated Woodpecker	o	o	o	+	o	o
Red-headed Woodpecker	o	+	o	+	o	o
Red-bellied Woodpecker	o	o	o	+	o	+
Northern Flicker	o	+	o	+	+	o

flying insects and is not known to forage extensively on lepidopterans (Smith et al. 2000). Consequently we did not predict a response during outbreaks. It nests, however, in dead trees or dead portions of live trees (Kilham 1983, Smith et al. 2000), so we predicted it should increase following outbreaks as a result of increased snag abundance.

(6) *Red-bellied Woodpecker* (Melanerpes carolinus)—Red-bellied Woodpeckers are not known to forage extensively on lepidopterans (Beal 1911) but often nest in snags and dead limbs (Short 1982). We thus predicted no increase during outbreaks but an increase following outbreaks related to increased snag abundance.

(7) *Northern Flicker* (Colaptes auratus)—Lepidoptera make up only a small proportion of the diet of this species (Beal 1911), but nest cavities are typically excavated in dead or diseased trees (Wiebe and Moore 2008). Therefore, we did not predict an increase during outbreaks but predicted an increase related to greater snag availability following outbreaks.

METHODS

Relative abundance data for the woodpecker species came from both the National Audubon Society's Christmas Bird Counts (CBC) and the U.S. Geological Survey's (USGS) Breeding Bird Survey (BBS). CBC data are gathered from specific circles 24 km in diameter and take place each year on a day within a 3-week period around Christmas. Because the number of observers and amount of effort they expend is highly variable, we divided the number of birds counted by the number of "party-hours" (Raynor 1975, Bock and Root 1981). BBSs are also performed once per year but during the spring breeding season rather than the winter. Each census consists of a 3-min observation at a series of 50 stops 0.8 km apart along a road transect (Bystrak 1981); data are available from the USGS web site (http://www.mbr-pwrc.usgs.gov/bbs).

For BBSs, we compiled data from 1973 to 2008 (starting 2 years prior to the data on gypsy moth outbreaks). In order to minimize any potential bias due to feeder watchers, which have been included in CBC counts only since 1975 (Dunn 1995), we restricted analysis of CBCs to the years 1975–2008. We then manipulated the data by log-transforming the number of birds counted (birds per party-hour in the case of the CBC data), detrending within each site × year series to eliminate long-term trends, and then standardizing to mean = 0 and standard deviation = 1 so that each survey or route was weighted equally in the analyses. We refer to these values as "mean standardized population size" (MSPS).

Gypsy moth outbreaks occur on approximately 10-year cycles, during which they may defoliate large regions of deciduous hardwood forest (Johnson et al. 2005). Damage was particularly great during the early 1980s, with over 50 000 km^2 affected annually (USDA Forest Service 2008). Every year, forest defoliation caused by the gypsy moths in the United States was determined by aerial sketch-mapping by state and federal agencies. These data were compiled by the USDA Forest Service Northeastern Area Forest Health Protection staff and archived. Sketch-map data from 1974 to 1999 were recorded on paper maps that were scanned and compiled in a GIS format by AML. Defoliations from 2000 to 2008 were recorded and archived directly into a GIS (Liebhold et al. 1997). For each year, we compiled all cases in which gypsy moth defoliation occurred within the range of one or both surveys (estimated to be within 12 km of the center [CBC] or start [BBS] of surveys). For each such case, we then determined the average MSPS of birds counted during the 2 years prior to an outbreak (years –2 and –1); for all years during the outbreak itself (year 0; for the CBC, this was taken to be the winter following the outbreak); and for up to 9 years following outbreaks (years +1 to +9).

Outbreak length was variable, with a mean (± SD) of 2.8 ± 2.5 years (BBS) and 2.5 ± 2.0 years (CBC) and a range from 1 to 16 years. In order to avoid potential problems associated with extraordinarily long outbreaks, we included only outbreaks ≤6 years in length; this excluded 7.4% of the 783 outbreaks occurring within the range of the BBS data and 5.9% of the 731 outbreaks occurring within the range of the CBC data. We included years before and after the event only if another outbreak had not occurred within 12 km of the survey during that event.

We tested for changes in the woodpeckers' MSPS related to gypsy moth outbreaks with repeated-measures general linear models. Year the outbreak started and the length of the outbreak (in years) were included as fixed factors. Statistical significance for MSPS relative to pre-outbreak levels was based on linearly independent pairwise comparisons of each category vs. MSPS during the 2 years prior to outbreaks. We then plotted mean (±2 SE) values for each category relative to gypsy moth outbreaks.

The repeated-measures general linear models indicated that in many of the species there was a significant effect of year; that is, MSPS values for the species changed (usually increased) over the course of the study. Long-term population trends may have contributed to these effects but are unlikely to be the whole story since population estimates for individual routes were detrended and standardized. To investigate the possibility that changes in the response to gypsy moth outbreaks had also taken place, we conducted linear regressions of x on the year an outbreak started, where x was either (1) mean MSPS during an outbreak minus mean MSPS during the 2 years prior to the outbreak, or (2) MSPS averaged over the 9 years following an outbreaks minus the mean MSPS during the 2 years prior to the outbreak. All statistical analyses were performed in R 2.10.0 (R Development Core Team 2009).

RESULTS

We compiled data on 783 outbreaks associated with BBS routes and 731 associated with CBC routes. The number of outbreaks each year varied considerably (Fig. 2). After excluding

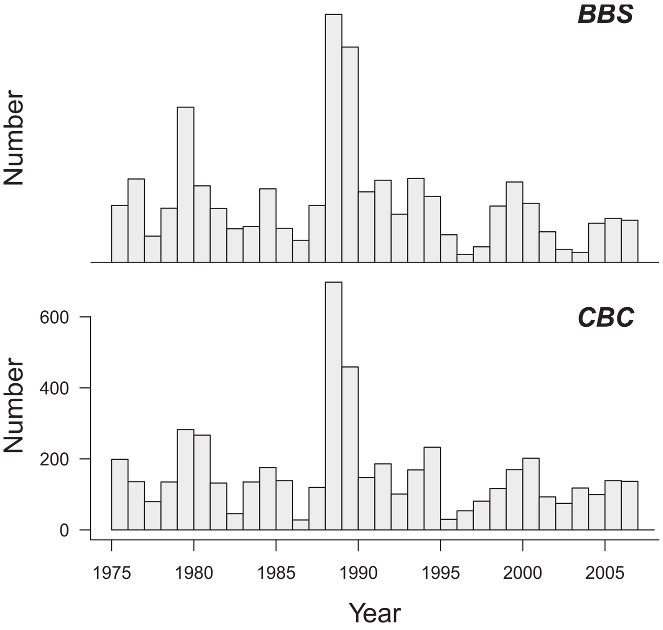

FIGURE 2. Annual variability in the number of gypsy moth outbreaks analyzed as part of the Breeding Bird Survey (BBS) and Christmas Bird Count (CBC) data. Only the first year of multiyear outbreaks is included. Only CBC data from 1977 on were analyzed in order to minimize bias due to the inclusion of feeder watchers starting in 1975 (see text).

outbreaks over 6 years in length, we found no significant effects of outbreak length in any of the analyses and do not discuss this variable further, although it is included in the analyses.

During outbreaks (year 0), we detected increases during the breeding season of the Red-headed Woodpecker and Northern Flicker (Fig. 3) and during the winter of the Yellow-bellied Sapsucker (Fig. 4); we detected lower numbers during the winter of the Downy Woodpecker. In terms of our predictions (Table 1), we successfully predicted the increase in sapsuckers (CBC data) but failed to predict the increases in the Red-headed Woodpecker or Northern Flicker (BBS) or the decrease in the Downy Woodpecker (CBC).

Population responses after outbreaks were equally variable. During the breeding season no species exhibited a significant effect during the first 3 years following an outbreak. After the first 3 years, numbers of the Northern Flicker were elevated during year 4, while numbers of the Hairy Woodpecker and all woodpeckers combined were depressed during either year 8 or 9 (Fig. 3). During the winter, numbers of the Downy Woodpecker and all woodpeckers combined were depressed within 1 to 3 years of an outbreak, while later, from years 6 to 9, numbers of the Yellow-bellied Sapsucker were depressed while those of the Red-bellied Woodpecker and all woodpeckers combined were elevated. Neither analysis found the positive response to outbreaks we predicted for many of the woodpecker species (Table 1).

In contrast to these variable results, we found relatively strong evidence that MSPS values increased through the study for at least four of the seven species ("overall year effect" columns in Table 2). Given that the data were detrended, this pattern suggests temporal changes in how these species responded to gypsy moth outbreaks. To investigate this possibility further we performed regressions of the mean difference between MSPS values during and after outbreaks and those before outbreaks on year the outbreak started. Results from the BBS and/or CBC (Table 2) confirmed a significantly positive temporal effect for the Downy Woodpecker, Yellow-bellied Sapsucker, Red-headed Woodpecker, and Red-bellied Woodpecker, as well as all woodpeckers combined, either during or after outbreaks. Only one species (Northern Flicker) exhibited a decrease with time (CBC, after outbreaks).

We plotted these changes for the Red-bellied Woodpecker, for which temporal effects were particularly strong, by dividing the data for this species into outbreaks prior to 1992 and those from 1992 to 2008. Results indicated that MSPS values were generally depressed during and after outbreaks prior to 1992, particularly in the winter, but also to a somewhat lesser extent during the breeding season. In contrast, MSPS values were significantly enhanced or unaffected during and following outbreaks that started in or after 1992 (Fig. 5).

DISCUSSION

Prior studies have generally found that gypsy moth outbreaks have, at best, modest effects on North American birds (DeGraaf 1987, Gould et al. 1990, Gale et al. 2001) with the apparent exception of the Black-billed and Yellow-billed Cuckoos, both of which are attracted to insect outbreaks and found at significantly higher densities during such events (Barber et al. 2008). Earlier studies, however, detected significant indirect effects of outbreaks related to habitat alteration by gypsy moths, including defoliation opening the canopy and creating a dense shrub layer benefiting Eastern Towhees (*Pipilo erythrophthalmus*) (Bell and Whitmore 1997) and increased tree mortality creating snags that in turn benefited several species of cavity-nesting birds (Showalter and Whitmore 2002).

Our results support the conclusion that the overall direct effects of gypsy moth outbreaks on North American woodpeckers have generally been modest, with three species increasing during outbreaks (Red-headed Woodpecker and Northern Flicker during the breeding season and Yellow-bellied Sapsucker during the winter) and one species decreasing (Downy Woodpecker during the winter). The indirect habitat effects of gypsy moths following outbreaks were similarly undramatic, with only a few statistically significant effects (both positive and negative) scattered among the years following outbreaks, none of which was significant for more than 2 of the 9 years following outbreaks analyzed. Overall, during the breeding season woodpeckers responded negatively in year 8,

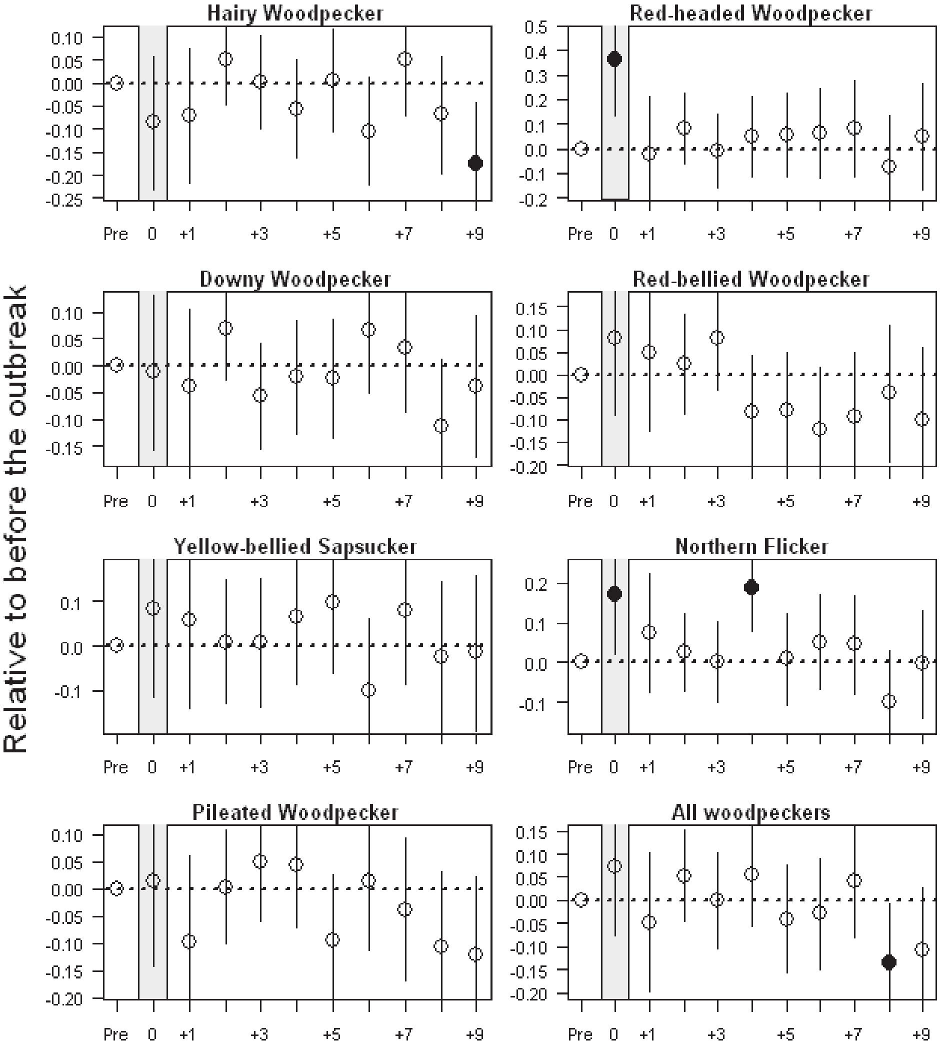

FIGURE 3. Population changes of seven species of woodpeckers and all woodpeckers combined during the breeding season as affected by gypsy moth outbreaks, on the basis of Breeding Bird Survey data. Plotted are mean standardized population sizes (MSPS) during outbreaks (year 0) and for each of the 9 years following outbreaks (years +1 to +9) relative to MSPS for the 2 years prior to outbreaks ("Pre," values of which are set = 0) based on repeated-measures general linear models. Thus values >0 indicate populations more abundant than prior to outbreaks while those <0 indicate populations less abundant. Values greater than or less than "Pre" values at the $P < 0.05$ level are plotted as black circles.

while during the winter their response was initially negative (year 1) but then switched to positive (year 8).

Two earlier studies provide relevant results. Gale et al. (2001) analyzed BBS data before, during, and after six gypsy moth outbreaks in three states and found few effects, and those that they did find were typically short-term and spatially variable. Showalter and Whitmore (2002) examined cavity-nesting species following a gypsy moth outbreak in Virginia and found that species' responses varied widely. In general, they found that woodpeckers and other cavity-nesting species increased immediately after outbreaks and then decreased, whereas we found no decrease following an outbreak (during the breeding season) or an initial decrease followed by an increase (during the winter). Our results also failed to do a particularly good job of matching our a priori predictions, with the possible exception of the CBC data during outbreaks, which correctly identified the Yellow-bellied Sapsucker as being the only species to increase in direct response to gypsy moth outbreaks. Given that this species is migratory, this finding suggests that either some individuals may be remaining closer to their breeding range instead of migrating farther south (Walters et al. 2002) or that some individuals nesting farther north are choosing to overwinter at outbreak sites. In any case, taken together, these results support the conclusion that, except for the cuckoos previously studied by Barber et al. (2008), the response of most North American birds to gypsy moth outbreaks is small and variable.

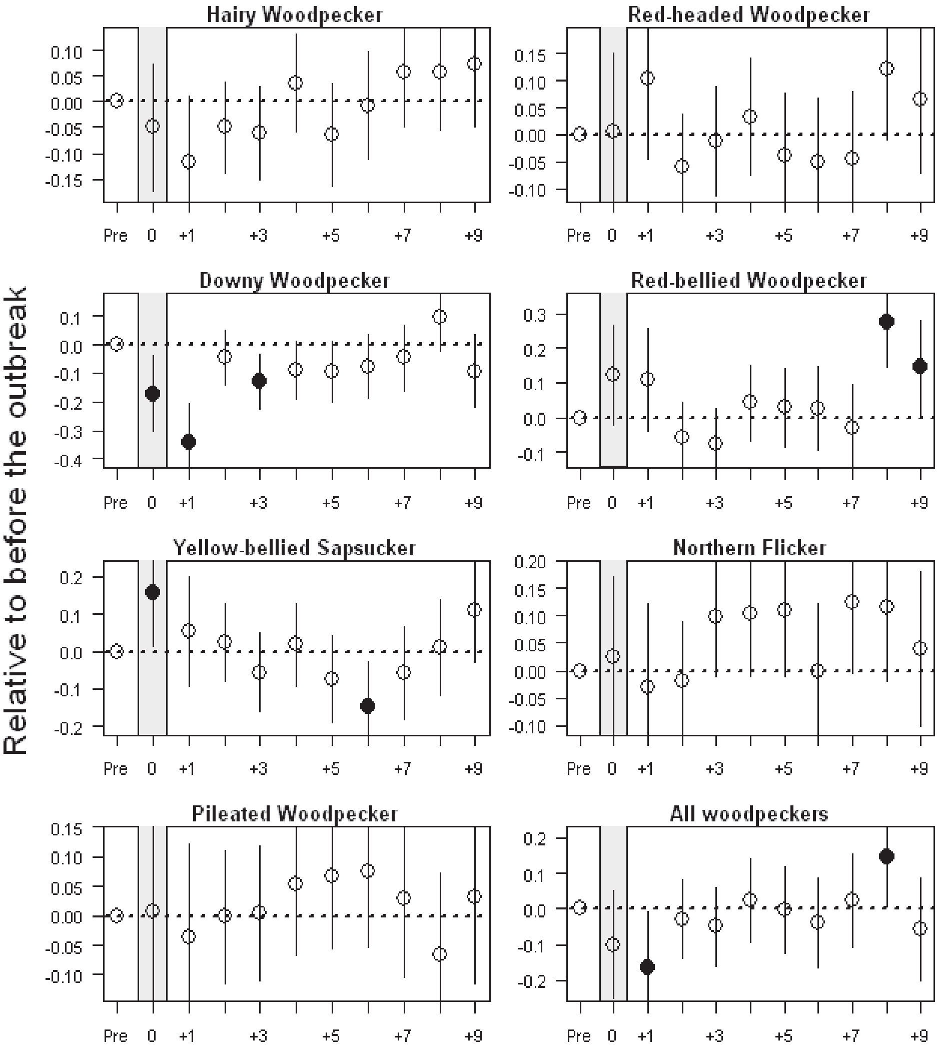

FIGURE 4. Population changes of seven species of woodpeckers and all woodpeckers combined during the winter as affected by gypsy moth outbreaks, on the basis of Christmas Bird Count data. Analyses, categories, and symbols as in Figure 3.

Given the large pulse of food provided by gypsy moth outbreaks and the dramatic consequences such outbreaks have on the trees on which the larvae feed, their relatively small effect on avian communities is surprising. In our case, one possibility for our failure to detect more dramatic effects is that the geographic scale of the bird surveys, which are on the order of 25–50 km, was mismatched to that of the outbreaks themselves, which are in some cases detectably synchronous on the scale of hundreds of kilometers (Peltonen et al. 2002). Such a scale difference might be problematical if effects were primarily at the edges of outbreaks where birds are more likely to be able to move between patches than in the core area of outbreaks. Additional analyses are necessary for all such alternatives to be rejected, however.

Our analyses did, however, suggest the possibility that at least some species of woodpeckers may be responding more favorably to gypsy moth outbreaks now than in the earlier years of the invasion. Overall, we detected positive temporal effects during the winter or the breeding season (or both) in six of the seven species along with woodpeckers as a whole. Such effects may be due in part to the changing face of northeastern North American forests as they recover from the logging and overexploitation of the 19th and first half of the 20th centuries, or possibly to effects related to climate change (Bentz et al. 2010). Analyses, however, looking more specifically at temporal responses to outbreaks indicated that at least some of these effects might be due to birds responding more favorably to outbreaks through time. Moreover, because we observed responses both during and after outbreaks, it seems likely that the differences were not only due to birds eating more gypsy moth eggs or larvae but that birds might also be becoming more adept at dealing with the ecological aftermath of outbreaks. The

TABLE 2. Temporal changes in the mean standardized population size (MSPS) of North American woodpeckers, both overall and as related to gypsy moth outbreaks, 1975–2008, on the basis of the Breeding Bird Survey (BBS), or 1977–2008, on the basis of the Christmas Bird Count (CBC). The "overall year effect" columns are the mean overall effect size of year in the repeated-measures general linear models; values in these columns indicate that there were significant changes in MSPS values over the course of the study. The other columns are the regression coefficients of x on year of outbreak. For the "during outbreaks" columns x is the MSPS during outbreaks minus mean MSPS pre-outbreak; for the "after outbreaks" columns x is the mean MSPS 1–9 years after outbreaks minus mean MSPS pre-outbreak. Only values for which $P < 0.05$ are listed; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Breeding season (BBS)			Winter (CBC)		
Species	Overall year effect	During outbreaks	After outbreaks	Overall year effect	During outbreaks	After outbreaks
Hairy Woodpecker	—	—	—	0.0147***	—	—
Downy Woodpecker	—	—	0.0092*	—	—	—
Yellow-bellied Sapsucker	0.0097**	—	0.0164*	0.0076***	—	—
Pileated Woodpecker	—	—	—	0.0077***	—	—
Red-headed Woodpecker	—	—	—	—	0.0149*	—
Red-bellied Woodpecker	0.0093***	—	0.0195***	0.0328***	0.0148**	0.0258***
Northern Flicker	0.0042*	—	—	–0.0049*	—	–0.0153**
Woodpecker species combined	0.0044*	—	0.0138**	0.0099***	—	—

best illustration of this change was provided by the Red-bellied Woodpecker, which generally appeared to respond negatively to outbreaks during the first half of the period covered by our study but positively during and following outbreaks during the second half, particularly during the winter (Fig. 5). It would clearly be of interest to study the behavior of these birds to see if they are indeed preying upon gypsy moth egg masses and larvae to an increasing extent, as other avian taxa already do in Japan and other areas where gypsy moths are native (Higashiura 1989, Elkinton and Liebhold 1990).

We conclude that the effects of gypsy moth outbreaks on woodpeckers are variable and relatively unpredictable, at least

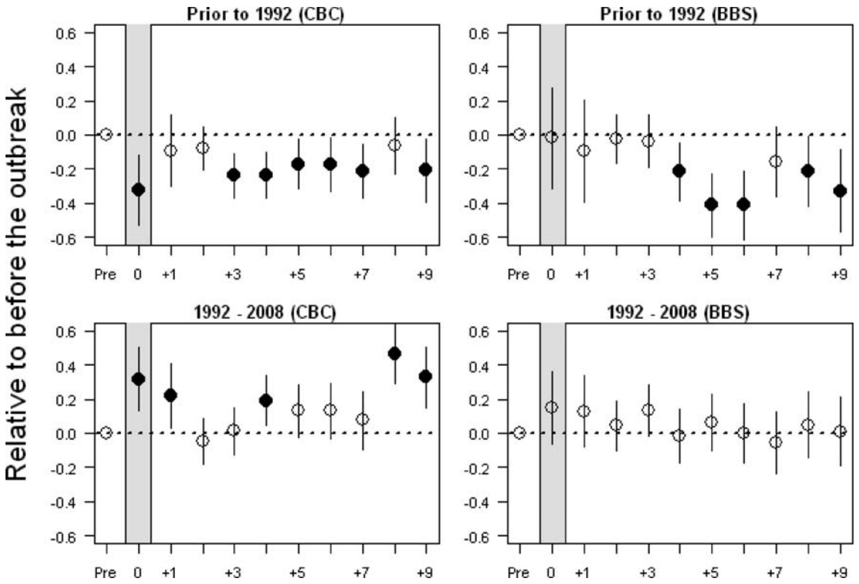

FIGURE 5. Population changes of the Red-bellied Woodpecker vis-à-vis gypsy moth outbreaks during the winter, on the basis of the Christmas Bird Count (CBC, left), and the breeding season, on the basis of the Breeding Bird Survey (BBS, right), as determined by repeated-measures general linear models and divided into outbreaks that started prior to 1992 (top) and those occurring between 1992 and 2008 (lower). Categories and symbols as in Figure 3.

insofar as we attempted to determine a priori how species were likely to respond to outbreaks on the basis of prior understanding of their biology. The fact that our current knowledge of this relatively well-studied group did not allow us to successfully predict how it would respond to a major event such as a gypsy moth outbreak is a sobering reminder that we are still a long way from having the kind of insight about most species that will permit us to accurately predict population changes as a result of even the most dramatic ecological phenomena.

In contrast to the unsatisfyingly variable results we found overall, we detected relatively strong temporal effects, with several woodpecker species responding more positively to gypsy moths later in the study. The Red-bellied Woodpecker exemplified this effect both during and after outbreaks in the CBC data and after outbreaks in the BBS data. This result suggests that at least some North American birds, which have traditionally avoided the hairy, exotic larvae of the gypsy moth, might be changing their behavior in ways that could allow them to exploit this pulsed resource more effectively (Carlsson et al. 2009) and match more closely the behavior of birds in areas where gypsy moths are native and their history of coevolving with birds is longer.

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