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Spatial Variability in Generalist Predation on the Douglas-fir Tussock Moth

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Abstract

The Douglas-fir tussock moth (DFTM) is a forest defoliating insect that is subject to periodic population outbreaks. These outbreaks are sometimes spatially synchronized across hundreds of kilometers. The DFTM's complex population dynamics are thought to result primarily from two regimes of population control: at outbreak-level population densities, DFTM populations are subject to control by viral infection, whereas endemic-level insect densities are maintained by generalist predators. Generalist predation delays the onset of insect outbreaks. In this paper, we show that variation in generalist predation can be modeled as a result of variability between locations and that predation is reduced when the accessibility of larvae to flying predators is restricted. However, protecting larvae from flying predators did not increase larval survival by the same amount from site to site. Thus, local effects of predation show considerable spatial variation, even within a 10-km area. The effects of this variability on the spatial synchrony of population outbreaks remain unclear.

Keywords: Population outbreaks, predation, Douglas-fir tussock moth.

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Introduction

Understanding the dynamics between forest pests and the natural biological controls on their populations may be facilitated with models from ecological theory. The natural enemies of a focal species, including predators, parasites, or pathogens, are linked by cycles of population growth and decline in proportion to the relative species density of each (Gotelli 2008). Simpler models describe two-species interactions in which a predator, parasite, or pathogen is a specialist on the target species and depends exclusively on attacks on that species for survival (Anderson and May 1980, Gotelli 2008). When the target species is limited by a combination of natural enemies, generalist predator models (e.g., Ludwig et al. 1978) predict that the population will persist at either an upper equilibrium, where the population is controlled by resource limitation, or a lower equilibrium maintained by predation. These models assume strong limitation by predators. Consequently, stochastic perturbations that reduce the predator population also allow the prey populations to increase from the lower equilibrium toward the higher equilibrium.

Some outbreaking lepidopteran defoliators are regulated by combinations of generalist predators and specialist pathogens, combined with stochastic fluctuations in their own density. For such cases, Dwyer et al. (2004) showed that insect density is controlled by the pathogen at outbreak densities, and by generalist predation at endemic densities of prey insects. The low-density, predator-maintained equilibrium is only locally stable, and thus the inclusion of stochastic fluctuations in prey density (demographic stochasticity) can induce complex behavior, particularly large-amplitude outbreak cycles with highly irregular periods (Dwyer et al. 2004). In turn, those irregular periods should result in variation in the timing at which populations reach outbreak levels when observed at landscape or regional scales.

Understanding how forest insect outbreaks vary across space may be important not only to their management, but to assessments of the overall vulnerability of

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forests to insect outbreaks and the associated secondary effects at the landscape and regional scales. Synchrony of forest insect outbreaks has been observed over hundreds of kilometers (Peltonen et al. 2002), with implications for the management of forests on public lands or with commercial value. At the regional scale, synchrony of population dynamics is predicted if (1) multiple subpopulations in a region have identical density-dependent population structures (i.e., birth and death rates) (Ranta et al. 1997) and (2) if density-independent factors (most often weather) are shared across the region (Hudson and Cattadori 1999). Thus, regional environmental stochasticity can drive synchrony in population dynamics, a process known as the Moran Effect (Royama 1992). However, this synchrony has been shown to decay more rapidly with distance than would be expected if the underlying population dynamics were truly identical across space as predicted by the Moran Effect (Peltonen et al. 2002). Therefore, it is important to understand the mechanisms that affect outbreak periodicity.

Because the ability of predators to maintain insect populations at an equilibrium density is only locally stable, outbreaks may be triggered by the failure of generalist predators to regulate growth in density of prey insects (Dwyer et al. 2004, Mason et al. 1983). An alternate hypothesis holds that predator/prey population cycles themselves drive spatial synchrony by generating phase-locked oscillations during which periodic high density in some areas creates an opportunity for dispersal to areas of lower density (Vasseur and Fox 2009). Indeed, dispersal of the focal species may restore synchrony in cases where variation in predator activity affects outbreak periodicity (Abbott and Dwyer 2009, Bjørnstad et al. 2010), but Haynes et al. 2012 found that an environmental driver, i.e., precipitation, was a strong explanatory variable for synchrony. Regardless, spatial variation in the activity of generalist predators should have important implications for the occurrence and spatial distribution of forest insect outbreaks. The objective of this study is to examine spatial variability in the intensity of generalist predation on a population of forest insects, the Douglas-fir tussock moth (DFTM) (*Orgyia pseudotsugata*).

The DFTM is a pest of Western U.S. forests as its larvae consume foliage of its primary host trees Douglas-fir, grand fir, and white fir. Its populations show outbreak cycles that occur, on average, every 7 to 10 years, affecting forests at the landscape or even regional scale (Mason, 1996). The larvae are also a nuisance to recreation areas, not only due to the aesthetic impact of defoliation, but through direct contact with humans, causing an allergic response known as tussockosis (Perlman et al. 1976). As a result, DFTM populations are managed by forest health management programs and widely monitored through trapping, ground surveying,

and aerial detection of defoliation (Eidson et al. 2017). Outbreak-level DFTM populations are reduced by some combination of generalist predators, parasitoids, and a species-specific baculovirus similar to the system described in Dwyer et al. (2004). The baculovirus leads to epizootics that may or may not terminate outbreaks (Mihaljevic et al. 2020). The most common parasitoids of the DFTM are ichneumonid and braconid wasps and tachinid flies (Dahlsten et al. 1977). DFTM eggs, larvae, and pupae can all fall victim to parasitoids. Generalist predators that prey on DFTM larvae include coccinellid and pentatomid larvae, as well as birds, ants, and web-spinning and free-living spiders (Dahlsten et al. 1977, Mason and Paul 1988, Mason and Torgersen 1983, Torgersen et al. 1990).

In our study, we used a field experiment to test the hypothesis that there is small-scale spatial variation in predation on DFTM larvae and that flying and branch-dwelling predators have different effects. We showed that predation by generalist (avian) predators varied by site on a scale of ~10 km, which may have implications for the spatial synchrony of outbreaks. Nevertheless, the concurrent DFTM outbreak following our experiments was synchronized at our study sites, and across the larger region in which the sites were located. Therefore, understanding DFTM outbreaks likely requires further insight into the interaction between all of the natural enemies of the DFTM (predators, parasitoids, and the moth's species-specific pathogen).

Methods

Study Sites

We selected three sites in the Boise National Forest, in the vicinity of the Sage Hen Reservoir (elevation ~1500 m) (fig. 1). Two were relatively close to the reservoir shoreline: Sage Hen Down (SHD) is a campground on the shoreline and Sage Hen Upper (SHU) is upslope on the hillside about 500 m from SHD. The third site, Tamarack Flats (TAM) was about 6 km to the northwest of the reservoir. The forest at each site consists of a mixture of Douglas-fir (*Pseudotsuga menziesii (Mirb.) Franco*) and grand fir (*Abies grandis (Douglas ex D. Don) Lindl.*), although TAM has a higher abundance of grand fir, relative to the other two sites. In the summer of 2017, all sites were surveyed and found to have sub-outbreak populations of DFTM larvae. Because sub-outbreak populations are less likely to crash from baculovirus epizootics, this system was ideal for the study of the effects of predators on spatially separated populations. Douglas-fir trees in this area typically contain known invertebrate predators of DFTM larvae, including spiders and ants. Birds of several species in the area, including the Western tanager (*Piranga ludoviciana*), are also predators of DFTM larvae (Brookes et al., 1978). The DFTM populations

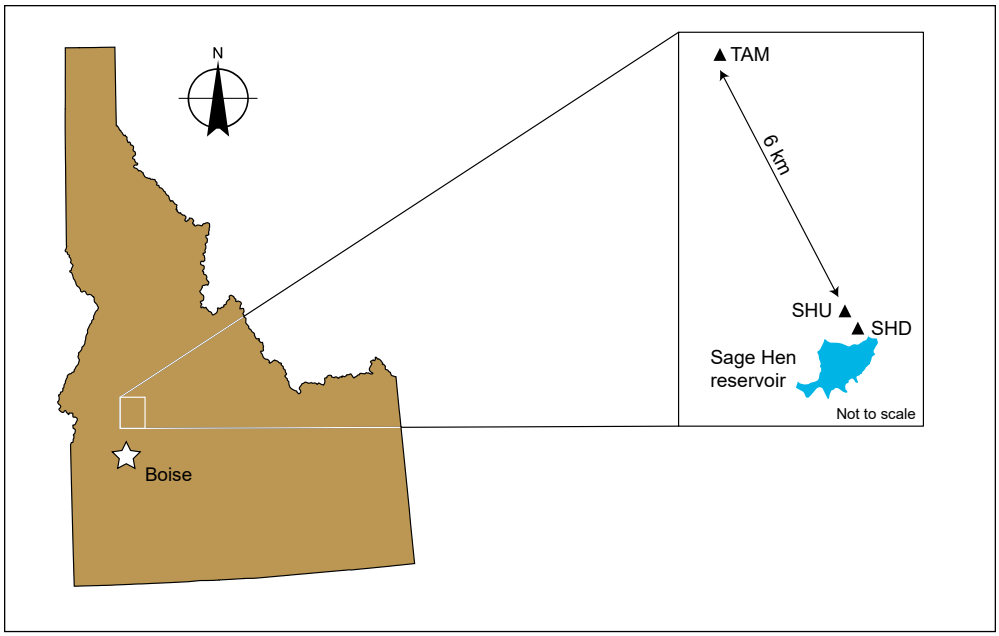

Figure 1—Map of field sites in the Sage Hen Reservoir area of Idaho. Sage Hen Down (SHD) and Sage Hen Upper (SHU) are marked. The distance between the reservoir and Tamarack Flats (TAM) is 6 km (3.7 mi).

at these study sites reached outbreak level in the 2 years following our experiment, allowing us to make qualitative assessments of outbreak synchrony relative to our experimental results.

Experiment Design

In order to test the effects of different factors on the predation rates of DFTM larvae, we stocked branches in the field with lab-reared larvae. We set up larvae on 48 branches (16 branches per site) so that some sets of larvae would experience different conditions:

1) Enclosed by bag vs. not enclosed by bag

We enclosed 24 of the branches in fabric bags to exclude flying predators, such as birds and wasps. This allowed us to quantitatively assess the impact of these predators in particular. Bags also confined experimental larvae to the foliage on that branch (~1 m in length, with some variation in the amount of foliage). On branches that were not covered with bags, we applied a ring of Tanglefoot®[2] Insect Barrier, a sticky resin, to the base of the branch to prevent movement of larvae away from the study branch.

[2] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

2) Beaten branch vs. unbeaten branch

We beat 24 of the experimental branches with batons, shaking potentially predatory arthropods off the branches before deploying larvae on them. This should have reduced the impact of non-flying, branch-dwelling predators on these branches, allowing us to also quantify losses due to this class of generalist predator (table 1). While we did not inspect the organisms that were knocked off during the experimental beating, earlier use of the beating sticks during larval collection showed them to be effective at dislodging spiders, ants, and other branch-dwelling arthropods.

Table 1—Treatments: selected branches could be covered with a bag to exclude flying predators, or beaten to dislodge branch-dwelling predators. Some branches received a single treatment, others received both treatments, and others received no treatment.

	Beaten		Not beaten	
	Flying predators	Branch-dwelling predators	Flying predators	Branch-dwelling predators
Enclosed by bag	Protected	Protected	Protected	Exposed
Not enclosed by bag	Exposed	Protected	Exposed	Exposed

3) Higher vs. lower density

On 24 of the branches, we deployed 20 larvae per branch. On the other 24, we deployed only 5 larvae each.

Our experimental setup was fully crossed within each site, with two replicates for each combination of treatments. At each field site, we selected 16 lower branches from Douglas-fir trees. These branches were accessible from the ground without the use of a ladder and were in partial sunlight. Before larvae were applied to any branch, the branch was visually inspected for wild larvae from the building outbreak and such larvae were manually removed. We chose branches with similar foliage area to one another, albeit with some variation. No two replicates of the same treatment were ever placed on the same tree, although some trees did carry multiple experimental branches.

All larvae used in the experiment were reared to the third instar in the lab from egg masses that had been collected from the Sage Hen Reservoir area earlier in the season. We deployed all larvae on 11 July 2017. At that time, we also observed third instar larvae in the field, indicating that our experimental larvae were developmentally appropriate for that point in the season.

Seven days after we deployed the larvae in the field (18 July 2017), we recovered larvae by removing each experimental branch and visually inspecting

it for approximately 20 minutes. All recovered surviving larvae were placed in plastic cups and returned to the laboratory where they were placed on an agar-based caterpillar diet and observed for 23 days for signs of parasitism or baculovirus infection. We recorded the total numbers of larvae recovered from each branch, specifically the number recovered alive. Because the bagged branches were enclosed, almost all of the caterpillars that had been initially placed could be recovered—including both live individuals and cadavers. Because recovery of cadavers usually requires finding them in the bags, as opposed to on foliage, cadavers were unlikely to be recovered from the exposed branches. Thus, we assumed that dead insects on the exposed branches likely fell from the branch. We therefore expected a higher fraction of recovered caterpillars from the bagged branches and performed all analyses (below) using only the number of living larvae as a proportion of total larvae initially placed on the branch. We did not find any larvae that had become trapped in the Tanglefoot® ring on exposed branches.

Data Analysis

We performed all statistical analyses using R (R Core Team). Generalized linear models (GLMs) were derived using the *glm* function in the base R stats package, producing log-logit models. The data were input as proportions (larvae recovered alive/initial number of larvae deployed), which weighted the final numbers by the initial numbers in each treatment. Factors in the initial, global, GLM included the site, whether the branch was bagged, whether the branch was beaten, and the density. If the habitat for predators varies between sites, we would expect to see differences in predator prevalence and composition between sites, perhaps including more or fewer flying predators relative to branch-dwelling predators, which would cause the efficacy of bagging in deterring predation to vary from site to site. The prevalence of predators at different sites could also contribute to varying effects of prey density. Additionally, if branch-dwelling and flying predators have different responses to prey density, then we would expect the effect of bagging a branch, excluding flying predators, to interact with the effect of prey density. As a result, we included the two-way interactions between site and bagging, site and density, and bagging and density, as well as the three-way interaction between site, bagging, and density, in our models. Removing factors from successive models, we calculated the $qAIC_c$ score for each model in order to compare the models, while taking into account our small sample sizes and the overdispersion of our data, given that there were only two true replicates of each treatment. We considered factors meaningful if their inclusion resulted in a model with a $qAIC_c$ score that was at least 2 points lower than that of a model without them (Burnham and Anderson 2004).

Results

At both the TAM and SHU sites, a greater proportion of larvae survived on the bagged branches than the proportion of larvae that was on the exposed branches (fig. 2), suggesting the successful exclusion of predators. The survival rate at the TAM site differed by (mean ± se) 0.531 ± 0.095 on enclosed vs. exposed branches, whereas SHU had a mean difference in proportions of 0.306 ± 0.104. No significant effect of bagging was observed at the SHD site (0.081 ± 0.120).

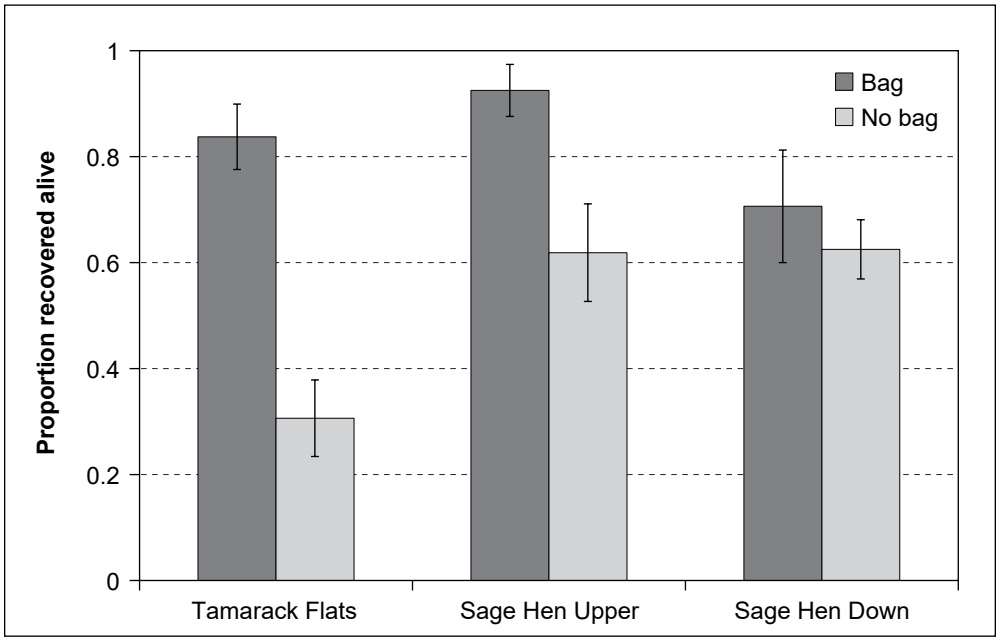

Figure 2—Difference in total larval survival (mean ± se) at each site on branches with bags to deter avian predation and on branches without bags. Differences in survival between enclosed and unenclosed treatments varied among sites as shown by a site x bag interaction term in the best fit generalized logit model (table 2).

The site differences were included in the best fit generalized logit model for the data, which also included effects of flying predator exclusion and the interaction between site and predator exclusion as factors (table 2). This model fit the data better than models without any interaction terms ($\Delta qAIC_c = 18.75$) or consisting of site effects alone ($\Delta qAIC_c = 59.44$), or exclusion effects alone ($\Delta qAIC_c = 22.82$). Our density treatments apparently did not affect survival in that the density term was not included in the best model, nor did it have a detectable effect in interaction with other factors (fig. 3, table 2). Prior removal of arthropod predators also had no detectable effect as indicated by exclusion of that term from the best model. None of the live caterpillars or cadavers that were recovered showed any signs of parasitism

or baculovirus infection. In the 2 years following the experiment, the populations at the sites reached outbreak levels, and all three crashed at the end of the larval season in 2019 as a result of a combination of baculovirus infection and parasitoid attacks on cocoons (likely Tachinidae).

Table 2—Structure of candidate generalized logit models for analysis of factors affecting survival of Douglas-fir tussock moth larvae at varying density and predator treatments, and resultant explanatory power of each model.

Site effect	Bag effect	Beat effect	Density effect	Site x bag	Site x density	Bag x density	Site x bag x density	Num. Params.	Max log likelihood	$\Delta qAIC_c$ [a]
Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	13	-42.75	29.04
Yes	Yes	No	Yes	Yes	Yes	Yes	Yes	12	-47.44	26.95
Yes	Yes	Yes	Yes	No	No	No	No	6	-60.65	13.93
Yes	**Yes**	**No**	**No**	**Yes**	**No**	**No**	**No**	6	-52.43	0
Yes	Yes	No	No	No	No	No	No	4	-67.52	18.75
Yes	No	No	No	No	No	No	No	3	-93.23	59.44
No	Yes	No	No	No	No	No	No	2	-73.19	22.82

"Yes" or "no" indicates inclusion of the term in a model. "Site" indicates distinction between the three study sites. "Bag" and "beat" refer to the overall effect of avian predator exclusion and arthropod predator removal, respectively.

[a]Calculated using the 13-parameter global model as the highest parameter baseline for c-hat, c-hat = 1.179.

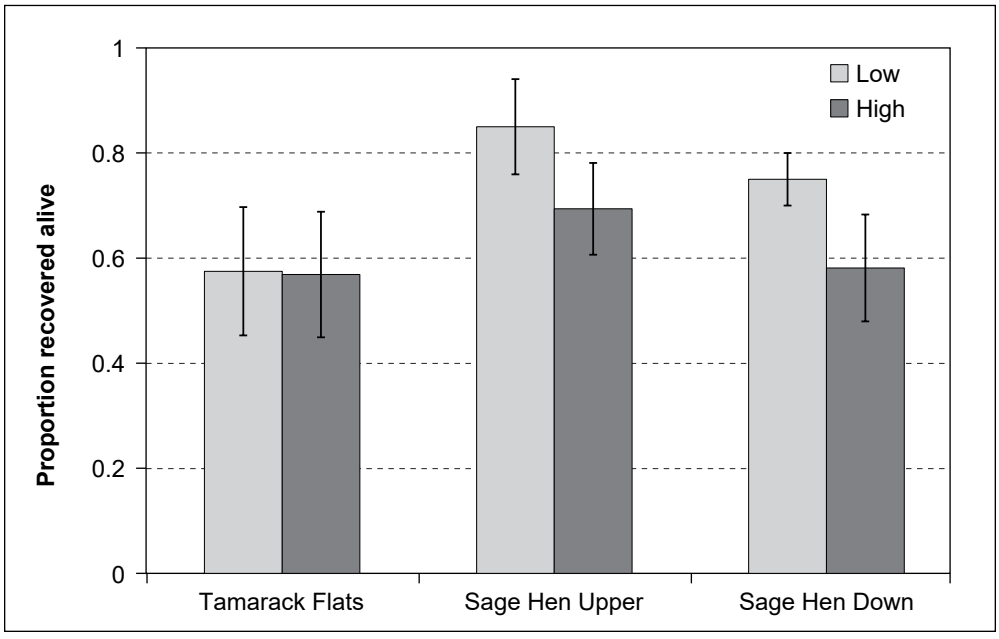

Figure 3—The proportion of larvae (mean ± se) that survived at each study site as a function of larval density. "Low" density = 5 larvae per branch; "high" density = 20 larvae per branch. Larval survival varied among sites, but did not vary significantly with density (table 2).

Discussion

Our experimental design enabled us to make a distinction among two predator guilds (flying vs. branch-dwelling predators) and to examine density dependence in predation rate (Dwyer et al. 2004). The effect of excluding flying predators on DFTM larvae varied from site to site and is consistent with a scenario in which variation in predation rates affects outbreak cycles at sites even as close as 5 to 10 km apart. Models and data from other study systems suggest that this variation may disrupt spatial synchrony in population cycles, such as the outbreaks of defoliating lepidopteran insects (Dwyer et al. 2004). Thus, our experiment allows us to generate hypotheses about mechanisms regulating synchrony of DFTM outbreaks at larger spatial scales.

Field experiments enable examination of predation intensity and spatio-temporal variation. Mason et al. (1983) estimated total predation rates by monitoring populations throughout the larval season. This led to an estimate of a cumulative survival rate of 2.4 percent, compared with 68 percent survival on branches covered to exclude predators. That survival rate is lower than the results from baculovirus infection in some observed populations undergoing natural epizootics (Mihaljevic et al. 2020). This is consistent with the finding of Dwyer et al. (2004) that predators may have stronger regulation over populations at sub-outbreak density. Our experiment was shorter in duration, but differentiated between the effects of two predator guilds using avian exclusion, arthropod removal, or both. Mason and Torgersen (1983) ran a similar experiment over an entire season of larval development; their data suggested that larval predation risk switched from arthropods in early instars to avian predation in later instars, which is supported by the strong short-term effect we observed of avian predators on third instar DFTM larvae.

The lack of a detectable effect of larval density on predation rate in our results contrasts with prior studies of the gypsy moth, another forest-defoliating lepidopteran (Allstadt et al. 2013). However, the observation of heavier predation mortality on exposed larvae at the TAM site relative to the other two sites (fig. 2) could suggest a role for prey insect density. Adult trapping at the end of the larval season in 2017 indicated that adult density at the TAM site was 10-fold greater than at the SHU or SHD sites (Eidson et al., 2017). Given the apparent high density of adult DFTMs at TAM, it is possible that TAM initially had a high density of wild DFTM larvae, and that this sustained locally high densities of predators, which may have led to higher predation rates on the experimental larvae. However, adult trapping densities are not always the best indicator of total population density

because at high density fewer adults are sometimes trapped because males find actual females more easily (Lowrey 2019).

Our results regarding larval density could also have been due to the duration of the experiment, or possibly because density-dependent predation occurs at spatial scales larger than individual branches (e.g., stand or whole site). It is also possible that the experimental stocking densities on branches did not consist of a sufficient range to demonstrate density dependence. When the populations reached outbreak density in the 2 years subsequent to the experiment at these sites, measured densities reached 36 to 63 larvae per branch (unpublished data), approximately two to three times higher than the highest density used in our experiment. However, predation at the lower densities might still generate spatial variation in outbreak periodicity. Increasing predation pressure via high predator density may cause Allee effects in the prey insect population, increasing the time interval between defoliator outbreaks and thus disrupting spatial synchrony between them (Bjørnstad et al. 2010).

Detectable variation in predation rates among sites may be due to local variation in habitat quality for predatory birds; for instance, standing dead wood often creates preferred roost sites for birds that feed on DFTMs (Torgersen et al. 1990). Apart from noting qualitative differences in stand composition above regarding the relative proportion of Douglas-fir and grand fir (see "Study Sites"), we did not quantify habitat differences for flying predators nor predator density. Much of the range of the DFTM is subject to periodic wildfire that may affect habitat quality for avian predators of DFTM larvae (Saab and Dudley 1998, Stuart-Smith et al. 2006) and the quality of those tree species as host plants for the larvae. Host plant quality further interacts with natural enemies of defoliating insects to influence population dynamics, particularly as the defoliator population becomes large (Gallagher and Dwyer 2019).

Synchrony in outbreaks often decays with distance (Peltonen et al. 2002) and variation in generalist predator density/activity is a driving mechanism of variation in that periodicity (Abbott and Dwyer 2009, Dwyer et al. 2004). However, despite the variation in generalist predation found at our study sites, DFTM populations reached outbreak levels there in the subsequent 2 years, then crashed synchronously, as did the outbreak across the wider area that includes the Boise National Forest. The differences in predation rates among sites were at sub-outbreak density, which could also explain why the onset of outbreaks is less synchronous than their termination (Shepherd et al. 1988). If the factor controlling low population densities, which is typically generalist predation, was more spatially variable than the factor curtailing high population densities, which is generally

viral infection (Dwyer et al. 2004), then we would expect that the beginnings of outbreaks would be less synchronous than their finales. DFTMs are difficult to observe at low population density and it is therefore difficult to collect data on the spatial synchrony of early-stage, building outbreaks.

Dispersal of early instars interacting with predators and the pathogen adds further complexity to the spatial variation in outbreak periodicity. An increased rate of dispersal from patches of high predator density to patches of lower predator density is predicted to cause the two patches to converge on similar periodicity between outbreaks (Bjørnstad et al. 2010). However, both Bjørnstad et al. (2010) and Haynes et al. (2012) found that overall bioclimatic characteristics of the forests or individual weather events had higher explanatory power for outbreak synchrony than did dispersal. Parasitoids cause substantial reductions in larval populations and may also be involved in feedbacks with outbreak cycles. At a fourth site we monitored during 2017, we observed a rate of larval parasitism ranging from 8 to 21 percent during the course of the season that terminated the DFTM outbreak at that site that year (unpublished data). Parasitoid activity also appeared to be the primary factor in terminating the outbreaks on the Boise National Forest in 2019 (Eidson et al. 2019) despite relatively low infection rates (unpublished data) during the epizootics. Therefore, more empirical evidence is needed regarding the interaction between predation, parasitism, the pathogen, and larval dispersal in outbreaks of moth species with flightless females, such as the gypsy moth and the DFTM.

Despite their small spatial scale, our experimental data suggest that predation may vary considerably across landscapes. However, the effects of this variation remain unaddressed by long-term field observation or by mathematical modeling. Particularly in the absence of long-term data on the effects of variation in predation on insect population dynamics, mathematical models that incorporate spatial variation of predation rate could be important. Such models would allow us to explore the impacts of this variation on dynamics that take place over decades, the scale at which outbreaks occur.

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U.S. Equivalents

When you know:	Multiply by:	To get:
Meters (m)	3.28	Feet
Kilometers (km)	0.621	Miles

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