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## Modeling flight activity and population dynamics of the pine engraver, *Ips pini*, in the Great Lakes region: effects of weather and predators over short time scales

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**Abstract** Ascertaining the relative effects of factors such as weather and predation on population dynamics, and determining the time scales on which they operate, is important to our understanding of basic ecology and pest management. In this study, we sampled the pine engraver *Ips pini* (Say) (Coleoptera: Scolytidae) and its predominant predators *Thanasimus dubius* (F.) (Coleoptera: Cleridae) and *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae) in red pine plantations in Wisconsin, USA, over 2 years. We sampled both the prey and predators using flight traps baited with the synthetic aggregation pheromone of *I. pini*. Flight models were constructed using weather variables (temperature and precipitation), counts of bark beetles and their predators, and temporal variables to incorporate possible effects of seasonality. The number of *I. pini* per weekly collection period was temperature dependent and decreased with the number of predators, specifically *T. dubius* in 2001 and *P. cylindrica* in 2002. The number of predators captured each week was also weather dependent. The predators had similar seasonal phenologies, and the number of each predator species was positively correlated with the other. Including a term for the number of prey did not improve the model fits for either predator for either year. Our results suggest that exogenous weather factors strongly affect the flight activity of *I. pini*, but that its abundance is also affected by direct density-dependent processes acting over weekly time scales.

Adult predation during both colonization and dispersal are likely processes yielding these dynamics.

**Keywords** Direct density dependence · Density independence · Flight models · Weather effects · *Thanasimus dubius* · *Platysoma cylindrica*

### Introduction

Studies on population dynamics are often performed by examining predator and prey densities at multiple time points. A common goal is to partition the relative effects of endogenous variables, such as food, and exogenous variables, such as predation or weather, on prey population densities (Rothery et al. 1997; Kamata 2000). Partitioning the relative effects of biotic and abiotic factors, however, may be complicated by a number of factors. For example, separate feedback processes due to predators and weather may act at different temporal and/or spatial scales (Cappuccino 1992; Saitoh et al. 1999, 2003; Williams and Liebhold 2000; Teder et al. 2000). Second, environmental noise may obscure organism generation times, which are necessary for discrete-time growth models (Rothery et al. 1997; Barlow et al. 2002). Third, different sampling strategies for predators and prey may be necessary due to their respective biologies. Differences in sampling method may lead to abundance estimates on different scales or may introduce different measurement errors (Goldwasser and Roughgarden 1997; Kruger 2002; Graham 2002; Williams et al. 2003; Rutz 2003). Such observation errors can lead to spurious detections of density dependence (Solow 2001).

The pine engraver *Ips pini* (Say) (Coleoptera: Scolytidae) is endemic across North America, colonizing weakened pines and occasionally spruce and tamarack (Clemens 1916; Thomas 1961). In the Great Lakes region, it is a significant pest of red pine plantations (Schenk and Benjamin 1969; Klepzig et al. 1991; Kegley

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et al. 1997). Males select suitable hosts and bore through the bark to create nuptial chambers. While boring, they emit a stereoisomeric blend of ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) and, in some populations such as in the Great Lakes region, lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one). These compounds function as aggregation pheromones (Wood 1982; Miller et al. 1997). Males typically mate with two or three females, which then construct ovipositional galleries. The brood develops in the phloem and sapwood before emerging to seek new hosts (Clemens 1916; Thomas 1961). The mean generation time in pines in the Great Lakes region is approximately 35 days (Aukema et al. 2004).

Two of the most abundant predators in this region are *Thanasimus dubius* (F.) (Coleoptera: Scolytidae) and *Platysoma cylindrica* (Coleoptera: Histeridae). Both are highly efficient at exploiting the aggregation pheromones of *I. pini* to locate their prey (Raffa and Klepzig 1989; Herms et al. 1991; Aukema et al. 2000a; Ayres et al. 2001). Both predators prey on adults and larvae. *T. dubius* preys exophytically on bark beetles arriving at the tree, before ovipositing at the entrances to their galleries. The larvae disperse throughout the galleries and prey endophytically on developing brood (Thatcher and Pickard 1966; Mignot and Anderson 1969; Aukema and Raffa 2002). *P. cylindrica* adults enter bark beetle galleries, where they consume adult prey (Aukema and Raffa 2004a). Like *T. dubius*, *P. cylindrica* larvae forage throughout the subcortical habitat on developing bark beetle brood.

Previous field studies have suggested that these predators may reduce *I. pini* in a delayed density-dependent manner, both within and between years (Erbilgin et al. 2002). However, there is also strong seasonal correlation among the abundances of these two predators in field data. Complementary laboratory studies conducted at prey and predator densities that occur in the field, aimed at separating the effects of *T. dubius* and *P. cylindrica*, demonstrate that each predator species reduces prey reproduction. The joint effects of these predators are both substitutable and additive (Aukema et al. 2004; Aukema and Raffa 2004b). Further, predator effects persist after accounting for mortality due to intraspecific herbivore competition (Aukema and Raffa 2002). Despite these studies, however, the potential impacts of *T. dubius* and *P. cylindrica* in the field remains uncertain for a variety of reasons.

First, the effects of density-independent factors, such as temperature or precipitation, on *I. pini* population dynamics and flight activity have not been characterized. It seems likely that *I. pini* populations are affected by additional forces other than bottom-up trophic dynamics, since beetles are aggregated in weakened trees within stands, yet stand-level seasonal trap catches are not correlated with the number of stressed trees within stands (Klepzig et al. 1991; Erbilgin and Raffa 2002). The effects of weather and predation have never been studied in concert. Second, these predators may be

considered habitat specialists in that they feed exclusively on the fauna within trees killed by bark beetles, but are feeding generalists in that they feed on several coexisting bark beetle species, some of which compete with *I. pini* (Erbilgin and Raffa 2001a). Lagged feedback generally arises from specialist predator-prey interactions (Jiang and Shao 2003). Third, neither *I. pini* nor its predator populations have been observed to oscillate as in some other bark beetle systems (Turchin et al. 1999). This suggests that factors other than delayed, density-dependent predation may also be exerting effects. Fourth, *I. pini* and predator population dynamics have never been studied at finer time scales than triennial counts or across years, which may skip generations of the herbivore (Erbilgin et al. 2002). Choice of time scale can be important to elucidating factors that regulate polyvoltine species (Lewellen and Vessey 1998). This problem is compounded by the fact that weather may not only affect beetle population density, but also the proportion of beetles flying at a particular time.

In this experiment, we exploited the attraction of both the herbivore *I. pini* and its predators *T. dubius* and *P. cylindrica* to the aggregation pheromones of *I. pini* to sample these insects in flight traps in red pine plantations over 2 years. We then modeled the direct counts of the insects captured each year. Because the number of traps and the study area remained constant, the direct counts reflected insect population density. We had three primary objectives. First, we wanted to determine if we could model bark beetle and predator flight on weather variables. Such models have potential applications to pest management. Second, we tested whether there was evidence of predator impacts on *I. pini* populations over brief time scales, allowing for weather effects. Third, if such predator effects were found, we sought to characterize them as direct or delayed density dependence.

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## Materials and methods

We selected two homogenous red pine plantations, approximately 45 years old, near Mirror Lake State Park, Wisconsin, USA (43°34'N, 89°53'W and 43°33'N, 89°51'W). Within each plantation, we deployed four 12-unit funnel traps (Lindgren 1983) in a 15 m × 100 m rectangle. We baited each trap with a bubble-cap lure of 50(+)/50(-) ipsdienol (release rate 110 µg/day at 25°C) and a similar lure of lanierone (release rate 100 µg/day at 25°C) (Pherotech, Delta, BC, Canada). This combination is optimally attractive to *I. pini*, and also attractive to *T. dubius* and *P. cylindrica*, but the latter prefer more (+) and (-) blends, respectively (Aukema et al. 2000a,b). As such, our trap counts were likely conservative for the number of predators. We placed a 2 cm × 2 cm piece of revenge bug strip (18.6% 2-2-dichlorovinyl dimethyl phosphate; Roxide International, New Rochelle, N.Y., USA) in each trap cup to kill arriving insects and prevent destruction of trap contents by predators.

We sampled insects throughout the duration of their flight period over 2 years, from 25 May to 12 October 2001, and 22 April to 21 October 2002. Sampling in 2001 was performed on exact 7 day intervals, for a total of 21 collection dates. We sampled 26 times in 2002. Twenty of these collections sampled 7 day intervals, five were within 2 days of this target. One collection spanned a 16 day gap. New lures were deployed each spring and in early July of each year, to maintain constant emission rates.

The weather, temporal, and insect variables for our analyses are defined in Table 1. Temperature and precipitation weather data were obtained from the National Climatic Data Center (Asheville, N.C., USA) for the Wisconsin Dells weather station (43°37'N and 89°46'W; altitude 254.5 m), which is approximately 10 km from the plantations. A program was written in the statistical language R (<http://www.r-project.org>; Ihaka and Gentleman 1996; R Development Core Team 2004) to retrieve user-defined weather variables (Table 1) for each collection period. Temporal variables included “period”, the number of days in the collection period (to potentially control for the 16 day period in 2002), and “days”, the number of days after the first collection each year, with the first collection numbered as one. This latter variable was included to incorporate possible seasonality effects. Insect variables included the mean number of *I. pini*, *T. dubius*, and *P. cylindrica* per trap for a given sample period.

Insect variables were square root transformed to satisfy assumptions of normality for our regression models.

We regressed the number of *I. pini*, *T. dubius*, and *P. cylindrica* per trap per sample period on the weather, temporal, and insect variables listed in Table 1, using backward elimination and setting  $\alpha=0.05$ . Because one variable can mask the effect of another if highly correlated (i.e., if multicollinearity is present), we also examined some additional models by retaining the variable that would otherwise be eliminated by backward elimination but removing a correlated variable (i.e., one with a similar low *t* and high *P* value) at an elimination step and proceeding as above. Using these methods, in a few instances we found two models that fit the data well for a given insect and present both (see Results). A key assumption of simple linear regression is that the errors are independent. For all models, to check for temporal dependence among the weekly trap catches, we examined the autocorrelation and partial autocorrelation functions for evidence of first- or higher-order autocorrelation among the models' residuals. In two instances where autocorrelation was detected, a lagged insect term improved the model fit (see Results) and removed the significant autocorrelation among the errors. All coefficients in final models, with the possible exception of the intercept, were significant using  $\alpha=0.05$ . The overall significance of final models was judged by *F* ratios, again using  $\alpha=0.05$ .

**Table 1** Variables defined for constructing flight models of *I. pini* and predators in south-central Wisconsin, 2001–2002 (each variable is specific to the collection period)

Variable	Explanation	2001			2002		
		Min	Mean	Max	Min	Mean	Max
IP	Mean number of <i>I. pini</i> captured/trap/sample period	0.0	69.2	284.0	0.0	45.3	121.9
TD	Mean number of <i>T. dubius</i> captured/trap/sample period	0.0	3.2	30.4	0.0	2.3	19.3
PC	Mean number of <i>P. cylindrica</i> captured/trap/sample period	0.0	1.0	14.0	0.0	0.8	3.8
MaxT	Maximum temperature (°C)	19.4	29.3	35.6	12.8	29.2	37.2
MinT	Minimum temperature (°C)	−6.7	6.2	13.3	−6.1	4.7	14.4
MeanHi	Mean maximum daily temperature (°C)	15.1	24.9	32.9	8.7	24.0	31.6
MeanLo	Mean minimum daily temperature (°C)	2.3	11.0	19.4	−1.9	9.8	18.2
MeanT	Mean temperature	8.9	18.1	26.2	3.5	17.0	25.0
Hdd <sup>a</sup>	Beetle heating degree days (21°C)	0.0	31.3	96.9	0.0	39.7	139.7
Cdd <sup>a</sup>	Beetle cooling degree days (21°C)	0.0	8.3	41.4	0.0	8.4	53.4
Raindays	Number of days with > 13 mm of rain	0.0	1.0	3.0	0.0	0.5	2.0
Prcp	Total precipitation	0.0	32.7	99.1	0.0	23.7	61.0
MeanPrcp	Mean daily precipitation	0.0	4.1	12.4	0.0	2.8	7.6
Days <sup>b</sup>	Number of days after first collection of the year	1	–	141.0	1	–	183.0
Period	Number of days in collection period	7.0	7.0	7.0	5.0	7.3	16.0

<sup>a</sup>Heating or cooling degree days are calculated from the first sample period of the season (25 May 2001 or 11 April 2002) and an arbitrarily chosen 21°C threshold

<sup>b</sup>A quadratic term, days<sup>2</sup>, was included to allow for a concave or convex pattern in a species' abundance through the flight season

Due to concerns of the possible effects of sample interval variations on detecting lagged feedback in 2002, appropriate continuous-time autoregressive models were also constructed using generalized least-squares procedures (Pinheiro and Bates 2002). Suitability of these maximum likelihood models with similar fixed effect structures (i.e., weather, temporal, and insect variables listed in Table 1) but different autoregressive structures were judged by Akaike Information Criterion (Akaike 1973) comparisons and inspection of autocorrelation and partial autocorrelation functions. Comparison of nested models with different fixed effect structures were performed using likelihood ratio tests (Pinheiro and Bates 2002). However, models constructed using generalized least-squares procedures provided results similar to the ordinary least-squares models (i.e., no differences in significance of coefficient estimates). Hence, we report only the ordinary least-square regression results. Assumptions of normality and homogeneity of variances were checked with residual and normal scores plots. All data analysis was performed using R.

## Results

Over the 2 years, we captured more than 22,609 insects from 30 species within 13 families (Table 2). The most common insect was *I. pini*, of which we captured 20,630. As in previous studies (Aukema et al. 2000a,b; Erbilgin and Raffa 2001b), the two most common predators were *T. dubius* (1,004) and *P. cylindrica* (336). Because all other insects were substantially less abundant, they were not included in flight models. The flight patterns of *I. pini* (Fig. 1), *T. dubius* (Fig. 2), and *P. cylindrica* (Fig. 3) were slightly different from year to year. More insects were captured in 2001 than 2002 (Table 2), and peak flights occurred during different months each year (Fig. 1), or were spread over longer periods (Fig. 3). Despite these inter-annual variations, our fitted models provided high quality approximations of flight patterns for all three species (Table 3). In general, trap catches of *I. pini* could be explained by temperature, precipitation, temporal, and predator variables (Fig. 1). In contrast, trap catches of the predators could be explained by temperature, temporal, and corresponding predator but not prey variables (Figs. 2,3).

### *Ips pini*

In 2001, two models provided quality explanations of the number of *I. pini* captured during weekly intervals ( $R^2_{\text{adj}} > 90\%$ ; Table 3). In both models, the number of *I. pini* increased with temperature, doubled with the number of days of rain above 13 mm during the preceding week, but decreased with the total precipitation. These two models differed by the inclusion of one of two variables. Trap catch of *I. pini* decreased with the number of *T. dubius* simultaneously captured in one

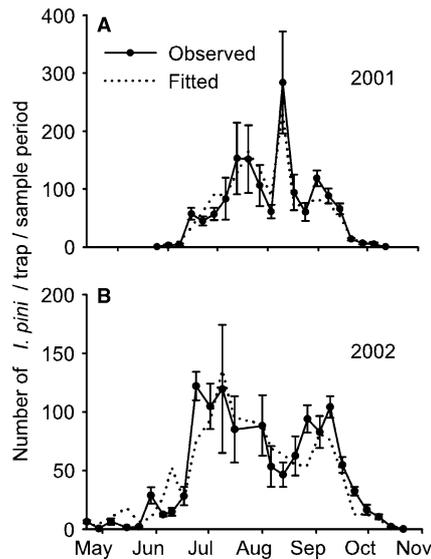
model, and increased as the number of days into the flight season increased in the other model. The correlation between these two variables ( $r = -0.48$ ) can be seen in Fig. 2, as *T. dubius* peaks in early spring and then wanes. In 2002, the number of *I. pini* captured during a 1-week interval likewise increased with a temperature variable, the mean low temperature. Similar to the 2001 model, trap catch of *I. pini* decreased with increasing numbers of a predator species, this time *P. cylindrica*.

### Predators

The observed number of one predator species captured during a sample period could be predicted from tem-

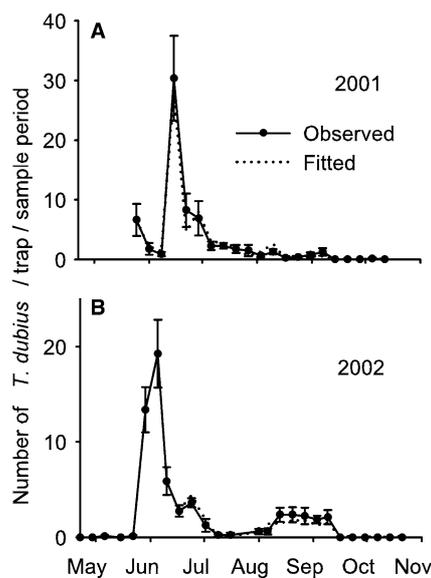
**Table 2** Total numbers of insects captured in red pine plantations in south-central Wisconsin, 2001–2002

Order Family	Year	
	2001	2002
Coleoptera		
Buprestidae	0	2
Cerambycidae		
<i>Monochamus scutellatus</i> (Say)	0	1
<i>Monochamus titillator</i> (F.)	0	4
<i>Rhagium inquisitor</i> (L.)	0	2
Other	9	3
Scolytidae		
<i>Dendroctonus valens</i> LeConte	4	3
<i>Dryocoetes autographus</i> (Ratzeburg)	1	0
<i>Gnathotrichus materarius</i> (Fitch)	0	5
<i>Hylastes</i> spp.	15	1
<i>Orthotomicus caelatus</i> (Eichhoff)	1	0
<i>Ips grandicollis</i> (Eichhoff)	0	28
<i>Ips perroti</i> Swaine	0	5
<i>Ips pini</i> (Say)	11,210	9,420
Males	5,638	4,405
Females	5,572	5,015
Curculionidae		
<i>Dryophthorus americanus</i> (Bedel)	0	77
Carabidae		
<i>Plochionus pallens</i> (F.)	22	55
Cleridae		
<i>Enoclerus nigrifrons</i> (Say)	25	4
<i>Enoclerus nigripes</i> (Say)	4	9
<i>Phlogistosternus dislocatus</i> (Say)	3	0
<i>Thanasimus dubius</i> (F.)	531	473
<i>Thanasimus undulatus</i> (Say)	29	5
<i>Zenodosus sanguineus</i> (Say)	8	23
Cucujidae	24	24
Histeridae		
<i>Platysoma cylindrica</i> (Paykull)	176	160
<i>Platysoma parallelum</i> (Say)	43	40
Staphylinidae	14	20
Tenebrionidae		
<i>Corticeus parallelus</i> (Melsheimer)	11	15
Trogossitidae		
<i>Tenebroides marginatus</i> Beauvois	31	33
<i>Tenebroides collaris</i> Sturm	2	0
<i>Grynocharis quadrilineata</i> (Melsheimer)	0	5
Hymenoptera		
Pteromalidae		
<i>Tomicobia tibialis</i> Ashmead	3	2
Other	24	0

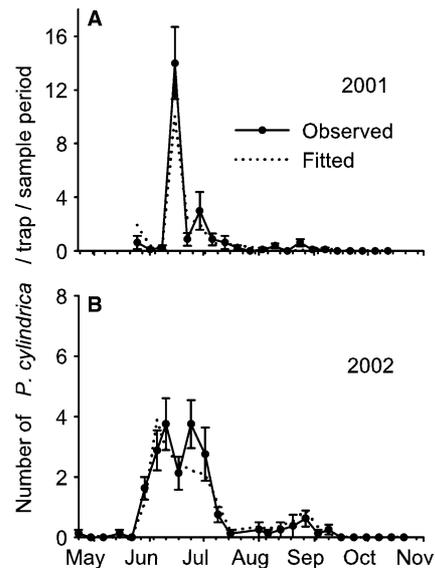


**Fig. 1** Observed and fitted catches of *I. pini* per trap per sample period in Wisconsin (USA) red pine plantations, **A** 2001 and **B** 2002. Equations for fitted models are given in Table 3 (fitted model for **A** is the first *I. pini* 2001 model listed). Error bars for observed catches are one SE ( $n=8$  traps)

perature variables, temporal variables, the number of the other predator species in the same period, and, in 2002, the numbers of conspecifics from an earlier time point (Table 3). For example, in 2001, we found two models that explained the number of *T. dubius* captured during a 1-week interval. The number of *T. dubius* was directly related to mean high temperatures and the number of *P. cylindrica* captured. A quadratic temporal



**Fig. 2** Observed and fitted catches of *T. dubius* per trap per sample period in Wisconsin (USA) red pine plantations, **A** 2001 and **B** 2002. Equations for fitted models are given in Table 3 (fitted model for **A** is the first *T. dubius* 2001 model listed). Error bars for observed catches are one SE ( $n=8$  traps)



**Fig. 3** Observed and fitted catches of *P. cylindrica* per trap per sample period in Wisconsin (USA) red pine plantations, **A** 2001 and **B** 2002. Error bars for observed catches are one SE ( $n=8$  traps)

function, indicative of fewer *T. dubius* during the middle of the flight season, also improved the models. One of the two models also incorporated mean temperature and heating degree days. In 2002, mean low temperature and heating degree days were the only temperature variables used. Similar to 2001, the number of *T. dubius* captured was positively correlated with the number of *P. cylindrica* captured. The 2002 model for *T. dubius* was improved by incorporating approximately one-fifth the number of *T. dubius* captured 2 months previously (Table 3).

The number of *P. cylindrica* was positively correlated with the number of captured *T. dubius*, in both 2001 and 2002 (Table 3). In 2002, the best model also incorporated the number of *P. cylindrica* captured the previous week, as well as two temperature coefficients: mean high temperature, and mean temperature of the sample period (Table 3).

## Discussion

These experiments suggest that predators exert direct negative impacts on *I. pini* within time periods shorter than prey generation times. These relationships persist after accounting for density-independent processes that affect flight activity, such as temperature and precipitation (Table 3). The possibility that *I. pini* counts were artifactually reduced by predation within the confines of the traps is precluded by two things. First, the pesticide strips quickly killed arriving insects. Second, *P. cylindrica* must prey subcortically and cannot feed on *I. pini* in open containers (Aukema and Raffa 2004a). Thus, it appears that predation on bark beetle adults that are

**Table 3** Regression models containing temperature, precipitation, temporal, and predator-capture variables that explain the observed number of *I. pini*, *T. dubius*, and *P. cylindrica* per trap per sample period captured in red pine plantations in south-central Wisconsin, 25 May to 12 October 2001 ( $n = 21$  collections, 7 day durations) and 22 April to 21 October 2002 ( $n = 26$  collections, approximate 7 day durations). For each model, standard errors are provided below each parameter estimate

Insect <sup>a</sup>	Year	Regression variables <sup>b</sup>										Model summary											
		Intercept					Temperature					Precipitation		Temporal		Insects <sup>a</sup>		$R^2_{\text{adj}}$	$s^2$	F	df	P	
		MeanHi	MeanLo	MeanT	Hdd		Raindays	Prcp	days	days <sup>2</sup>	TD	PC											
Herbivore <i>I. pini</i>	2001	-16.349 ±1.784	0.995 ±0.072				1.913 ±0.585	-0.061 ±0.018											0.9077	1.85	50.19	4,16	<0.0001
		-19.323 ±1.904	0.990 ±0.066				2.308 ±0.546	-0.077 ±0.017	0.029 ±0.007										0.9212	1.58	59.44	4,16	<0.0001
Predators <i>T. dubius</i>	2002	3.890 ±0.423		0.658 ±0.071															0.8057	2.44	52.83	2,23	<0.0001
	2001	-0.860 ±0.710	0.129 ±0.040																0.9306	0.11	68.03	4,16	<0.0001
<i>P. cylindrica</i>	2002	2.343 ±1.678	0.174 ±0.071																0.9430	0.09	56.14	6,14	<0.0001
	2001	3.752 ±0.713		-0.258 ±0.054															0.8435	0.08	23.91	4,13	<0.0001
	2002	0.992 ±0.355	-0.190 ±0.059	0.211 ±0.066															0.8391	0.11	105.30	1,19	<0.0001
																			0.9024	0.04	56.45	4,20	<0.0001

<sup>a</sup>Square root transformation applied to insect counts

<sup>b</sup>Not all variables defined in Table 1 were useful in explaining predator or prey trap catch, such as single maximum and minimum temperature, cooling degree days, average precipitation, length of sample period, and the number of *I. pini* captured per trap per collection. These variables are thus excluded here

<sup>c</sup>Number of *T. dubius*, lagged eight sample periods

<sup>d</sup>Number of *P. cylindrica* from previous sample period

colonizing new trees (Aukema and Raffa 2004c), and/or those about to disperse after mating and establishing galleries within a host (Reid and Roitberg 1994; Aukema and Raffa 2004a), are important processes.

Predator flight models were not improved by incorporation of a term for the prey, *I. pini*. This is likely because any numerical responses of predators to prey were likely obscured over the long time lags requisite for predator generations. The generation times of these predators are much greater than our 1 week sample intervals, being a minimum of 5 weeks for *P. cylindrica* and 8 weeks for *T. dubius* under laboratory conditions (Aukema et al. 2004). In studies where delayed density dependence has been detected with *T. dubius* and a bark beetle prey, each sampling interval spanned several prey generations (Turchin et al. 1991, 1999; Erbilgin et al. 2002). These differences highlight the importance of time scale in the analysis of delayed density-dependence (Lewellen and Vessey 1998). One predator model was improved by incorporation of a term with a long lag time. The number of *T. dubius* in 2002 was related to the number captured 2 months previously. Although these predators are believed to be univoltine in the field, this model suggests that some *T. dubius* in Wisconsin may be bivoltine (Fig. 2b).

All predator models were improved by incorporating terms for the other species of predator captured simultaneously in the same trap. *T. dubius* and *P. cylindrica* exhibit very similar seasonal phenologies, with peak abundances in the spring and lower numbers in late summer and fall (Erbilgin et al. 2002) (Figs. 2, 3). In contrast, numbers of *I. pini* are usually higher in the summer and fall than spring (Erbilgin et al. 2002) (Fig. 1). High late-season trap catches of *I. pini* could result from progeny from two previous generations having peak flights in July and August (Fig. 1a). Late summer populations of *I. pini* may obtain some temporal escape from predators. These hypotheses are supported by the two similar models for *I. pini* in 2001, which differ only in the inclusion of one of two correlated variables: the number of *T. dubius*, and the number of days into the flight season.

Despite the predator effects, *I. pini* flight appears to be most dependent upon temperature when analyzed at high resolution, i.e., weekly, time scales. Our finding that the dependence of insect flight upon temperature is certainly not new, and has been previously noted among bark beetles (McCambridge 1971; Thompson and Moser 1986; Poland et al. 2002) and other insects (Forsse et al. 1992; Lehane et al. 1992; Jonsson and Anderbrant 1993; Zhang et al. 1998; Tuda and Shima 2002). *I. pini* flight seems to be less dependent upon precipitation, although terms for precipitation were significant in 2001 models when the catch of *I. pini* doubled with each day of rain more than 13 mm (0.5 inches) during the preceding week. This likely reflects a delay in beetle flight until after a rainstorm, similar to the precipitation-delayed phenology noted in fall webworm moths (Zhang et al. 1998). Total precipitation during the trapping period

was associated with a decrease in bark beetles captured (Table 3). Similar results have been noted in trap catches of the southern pine beetle, *Dendroctonus frontalis* Zimmermann in Louisiana, USA (Moser and Dell 1980). Our results and those of Moser and Dell (1980), however, indicate that the flight of the predator, *T. dubius*, is less affected by rainfall. This could be due to the larger size of this predator, as smaller parasitoids in other systems exhibit flight activity that is negatively correlated with precipitation (Weisser et al. 1997; Schworer et al. 1999). It is likely that other climatic factors that we did not measure, such as humidity, wind velocity, and wind direction, also affect flight activity of these forest insects (Franklin and Grégoire 2001; Östrand and Anderbrant 2003).

The flight models presented here are exploratory in nature and have not been validated over other years. However, the ability to satisfactorily model large flight responses (i.e., >100 *I. pini*/trap/week) on short time scales (i.e., 7 days intervals) may be useful for pest monitoring approaches and studies in population dynamics (Moser and Dell 1979; Aukema et al. 2000b; Tuda and Shima 2002). In addition to weather and predator effects, density-dependent dispersal and habitat structure play important roles in population dynamics and flight activity (Denno 1994; Cronin et al. 2000; Tuda and Shima 2002). Current work is focusing on characterizing the dispersal of *I. pini* and its associates within and between red pine plantations to augment the current and other studies in population dynamics.

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