

Pupation Site Selection and Enemy Avoidance in the Introduced Pine Sawfly (*Diprion similis*)

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Abstract - Insects that pupate on the branches of trees and shrubs suffer mortality from both predators and parasitic wasps. Which natural enemy represents the greater threat and therefore the stronger selection force on pupation site selection depends upon the time of year, the relative abundance of predators versus parasitoids, and the availability of alternative prey or hosts. Predation by foraging birds and mammals is likely to occur most commonly in winter when leaves have fallen, cocoons are conspicuous, and higher quality prey are scarcer. Inaccessibility and crypsis of pupation sites may provide protection from visually hunting predators. Attacks by parasitic wasps, which take place only during warmer months, may not be as easily avoided by inaccessibility or crypsis. We studied the patterns and mortality risks of pupation site selection in *Diprion similis* (Hymenoptera: Diprionidae; Introduced Pine Sawfly). Cocoons that were smaller than average and situated in relatively inaccessible sites (thinner branches, underside of branches) were less likely to be attacked by predators; background matching in terms of branch size proved not to improve survival. In contrast, the probability that a cocoon would be attacked by parasitic wasps (primarily *Monodontomerus dentipes*; Hymenoptera: Torymidae) was unaffected by location along branches, indicating that parasitoids are more difficult to escape through pupation site selection. Because Pine Sawflies were twice as likely to be killed by predators than by parasitoids during the cocoon stage, inaccessibility may be the most important factor for selecting pupation sites.

Introduction

Predators and parasites can regulate the population size of herbivorous insects, influence their population structure, and act as a selective force on the evolution of morphology, behavior, and life-history traits (Bernays and Graham 1988, Fagan and Hurd 1994, Lill 2001, Sillen-Tullberg and Leimar 1988). However, pressure from natural enemies does not occur evenly across different life stages (Olofsson 1987). In insects that undergo complete metamorphosis, the highest mortality rates often occur when insects are immobile during the pupal or cocoon stage (Tauber et al. 1986). For insects that pupate on the branches of deciduous trees and shrubs, the risk of predation likely rises once leaves have fallen and cocoons are more conspicuous to vertebrates. The selection of safe pupation sites by larvae during the summer or fall may reduce the probability of predation by rodents and birds during the winter, which is a significant source of mortality in the

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few insect species in which it has been studied (e.g., Limacodidae [slug caterpillars]; Murphy and Lill 2010).

Parasitic wasps can also serve as powerful selective forces on pupation site selection by insect larvae (Ohsaki and Sato 1999, Osawa 1992, West and Hazel 1982). However, to the extent that parasitoids use chemical cues to find hosts, inaccessibility or visual crypsis in pupation site selection may not reduce the risk of parasitism (Gross 1993).

In general, cocoons in exposed sites are especially vulnerable to both vertebrate predators and parasitoids (Battisti et al. 2000, Ohsaki and Sato 1999). Cocoons of *Neodiprion sertifer* Geoffroy (European Pine Sawfly) experimentally placed in trees suffered higher mortality than those in leaf litter (Hanski and Parviainen 1985, see also Shin et al. 2012). However, for the vast majority of insect species, the patterns and consequences of pupation site selection remain unknown.

We examined the effects of pupation site selection on the risk of predation and parasitism in *Diprion similis* Hartig (Hymenoptera: Diprionidae; Introduced Pine Sawfly, hereafter Pine Sawfly). We were able to reconstruct the consequences of pupation site selection by larval Pine Sawflies by taking advantage of the conspicuousness of their cocoons following leaf fall and the persistent and diagnostic evidence of their success or failure. The tough, leathery cocoons of Pine Sawflies remain tightly attached to branches throughout the winter, sometimes persisting for several winters.

We tested 3 predictions: (1) If predation by vertebrates is the main factor influencing pupation site selection by larval Pine Sawflies and inaccessibility is an effective defense, cocoons would be expected to be located away from the trunk, on slender twigs, and on the undersides of branches. As a corollary, mortality from predators should be lower in inaccessible sites. (2) If predation by vertebrates is the main factor and crypsis is the main defense against them, cocoons would be expected to be situated on the undersides of branches (as in the first prediction) but also in the forks of branches. In addition, the diameter of cocoons should closely match the diameter of branches chosen as pupation sites. (3) If parasitoids are a more important source of mortality for Pine Sawflies and if parasitoids locate cocoons mainly by using chemical cues (Rostás et al. 2003), selecting unpredictable pupation sites may be the best strategy for Pine Sawflies. Under these conditions, we would expect to find high variation in the sites where Pine Sawfly cocoons were situated but no relation between mortality risk and pupation site.

Methods

Study species

Pine Sawflies were accidentally introduced from Europe to Connecticut in 1914 and quickly spread across eastern North America, laying their eggs and feeding as larvae on five-needled pines, especially *Pinus strobus* (Eastern White Pine; Baker et al. 1988, Wilson 1966). Usually there are 2 generations per year. In the summer and fall, wandering larvae locate pupation sites and spin their cocoons on the host tree where they fed, in leaf litter, or on the trunks and branches of nearby trees and

shrubs (Wilson 1966). Cocoons remain firmly attached to the branches where they are spun, often closely matching the color of the bark at their pupation site. In the overwintering generation, pupae (technically prepupae; Bjorkman et al. 1997) enter diapause in the fall; adults generally eclose (successfully emerge) the following spring, but pupae may remain in diapause for up to 3 years (Wilson 1966).

Parasitoids of Pine Sawflies include tachinid flies and hymenopterans of at least 6 families. In northeastern North America, the most common parasitic wasp species is *Monodontomerus dentipes* Dalman (Torymidae), which attacks Pine Sawflies during the cocoon stage (Drooz et al. 1985). Known vertebrate predators include *Sorex cinereus* Kerr (Common Shrew), *Blarina brevicauda* Say (Northern Short-tailed Shrew), *Peromyscus maniculatus* Wagner (North American Deer Mouse), and *Poecile atricapillus* Kaup (Black-capped Chickadee) (Holling 1959, Wilson 1966).

Study sites and field methods

We quantified Pine Sawfly pupation site selection and its consequences at 11 predominantly mixed coniferous–deciduous forest sites in Brunswick, ME (43°54'39"N, 69°57'47"W). Although cocoons can be found in any season, they are much more conspicuous in winter, which is why we conducted this study during 29 January–4 March 2016. Within each study site, we haphazardly chose individual White Pines, surveying the understory woody vegetation beneath them for Pine Sawfly cocoons from ground level to 2.4 m above ground. We measured the diameter at breast height (DBH) of each focal White Pine (to 1 cm).

For each cocoon that we found, we recorded the following variables: (1) plant species on which it occurred, (2) DBH (to 1 cm) of the plant, (3) distance of the cocoon above the ground (to 10 cm), and (4) fate of the cocoon. If the cocoon was situated on a branch, we also estimated (5) horizontal distance from the trunk (to 4 cm) and (6) distance from the tip of the branch (to 2 cm), used calipers to measure (7) diameter of the branch at the pupation site and (8) at the base of the branch, as well as (9) cocoon diameter (to 1 mm), and noted (10) position on the branch (trunk, or top, side, bottom or fork of the branch). Successful cocoons were those from which an adult Pine Sawfly had eclosed, which was evidenced by a neatly cut terminal opening in the cocoon. We were not able to differentiate between cocoons that had eclosed during a summer generation or during the previous spring after overwintering. Death caused by parasitoids was revealed by a single small (~1–2 mm) hole from which the wasps had emerged. Death caused by vertebrate predators was indicated by a larger, ragged hole in the cocoon (Fig. 1). We verified the accuracy of these fate assignments by noting the shape of holes left by eclosing Pine Sawflies raised in the laboratory, by parasitoids raised in the laboratory, or by chickadees observed preying on intact cocoons on their original branches.

To answer the question of whether Pine Sawfly larvae make non-random decisions about where to pupate, we compared observed versus available (random) pupation sites in the commonest tree species on which cocoons were found. Based on a sample of 611 cocoons, the 4 most common plant species were *Acer rubrum* (Red Maple), *Quercus rubra* (Red Oak), *Prunus serotina* (Black Cherry), and White Pine. After determining the median DBH for each tree species in our sample,

we haphazardly selected a typical-sized individual of each species. All branches and twigs were cut from these 4 trees and laid end-to-end. The diameter of available pupation sites in each plant was measured (to 1 mm) at 10-cm intervals to produce frequency distributions of potential pupation sites for each plant species.

In an attempt to rear Pine Sawflies, determine sex ratios, and quantify rates of parasitism, we collected and placed in gelatin capsules (size 00) 180 cocoons that were intact (i.e., no evidence of eclosion, parasitism, or predation). Capsules were individually labeled with a fine permanent marker and stored in a terrarium at 23 °C and 71% relative humidity under natural light cycles.

In February 2000 and 2007, we collected preliminary data on the microhabitats and fates of Pine Sawfly cocoons in the same area. Although we quantified the density of cocoons in only 1 of the 3 years of this study (2007), our impression (based on the relative difficulty of finding cocoons) was that population densities

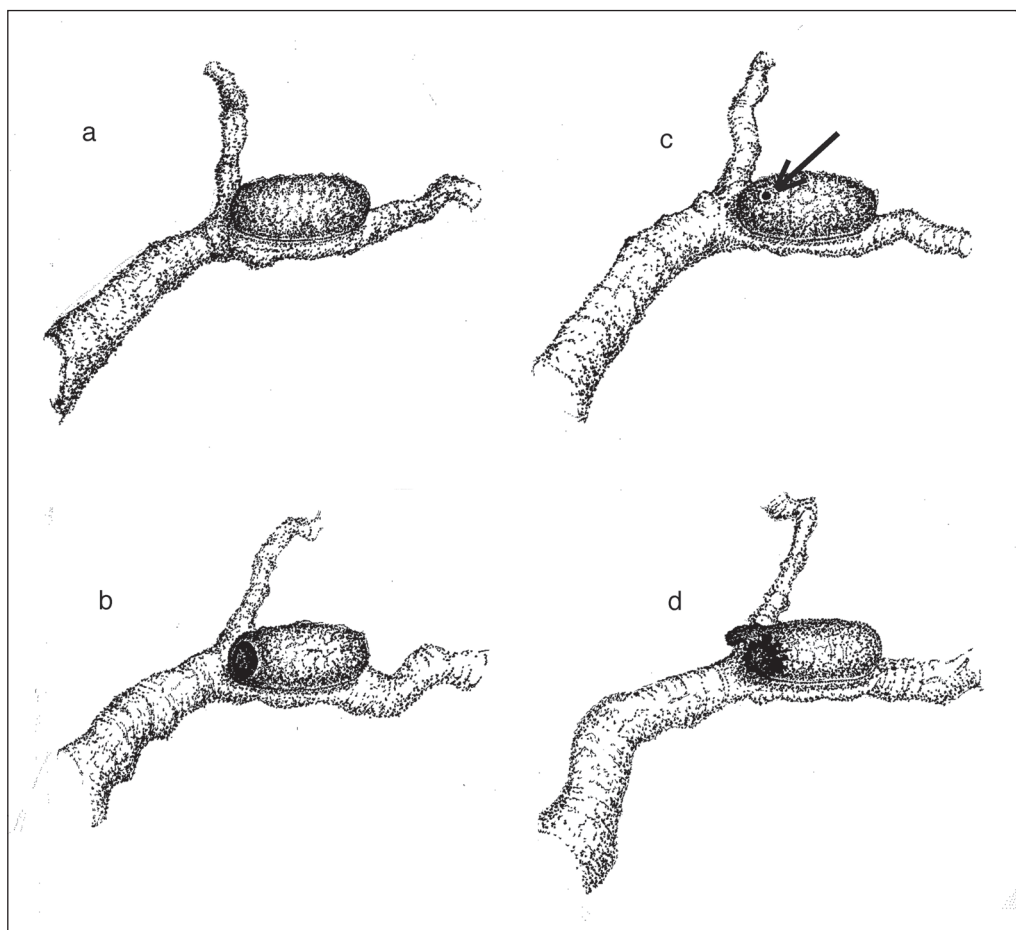


Figure 1. Fates of overwintering cocoons of Pine Sawflies: (a) intact, (b) successful emergence indicated by neatly cut terminal opening, (c) mortality caused by parasitoids indicated by small offset hole (see arrow), (d) mortality caused by vertebrate predators indicated by larger ragged hole (drawings by Sarah A. McCarthy).

were much lower in 2016 than in 2000 or 2007. In 2007, we determined the density of trees and shrubs within 10 m x 10 m quadrats beneath White Pines to test whether Pine Sawflies selected deciduous versus coniferous plants randomly with respect to their availability as pupation sites. In the 2007 pilot study, a smaller sample of Pine Sawflies and their parasitoids were reared from cocoons after storing them in plastic bags kept indoors under conditions similar to our 2016 experiment.

Statistical analyses

We performed a series of binary logistic regressions to estimate the effects of all measured variables (categorical as well as continuous) on the success or failure of cocoons (IBM SPSS 2015). We did not include intact cocoons in the regression analysis because a portion of those were likely parasitized, with the parasitoid having not yet emerged. Microhabitat variables that were not normally distributed were log-transformed. Models were run on different combinations of variables, and we selected the final model based on the percentage of cases that were correctly classified and how much variation in success could be explained by the model using the Nagelkerke R^2 value. We dropped from the model variables with P -values greater than 0.05 or those that contributed little to the model (as indicated by no increase in Nagelkerke R^2 values). Rejected variables included the species and DBH of the tree or shrub on which the cocoon was found; distance of the pupation site from the trunk and from the branch tip; and diameter of the branch at its base. Using a simpler dataset from 2007, we repeated the same analyses. We performed additional statistical tests using SPSS and R (R Core Team 2015). Descriptive results are given as means \pm 1 SD.

Results

Pine Sawfly cocoons were found on 20 different shrub and tree species beneath White Pines. The seven most common species are listed in Table 1. Deciduous woody plants were preferred over conifers for pupation sites, based on quadrat surveys in 2007 ($\chi^2(1) = 6.99$, $P = 0.008$, $n = 520$ deciduous shrubs and trees and 142 conifers examined for cocoons). Within individual plants, observed pupation sites were a non-random subset of available sites with respect to branch diameter within 3 of the 4 plant species where cocoons were most commonly found, and marginally non-random for a fourth (Red Maple, Red Oak, White Pine: $P < 0.01$; Black Cherry; $P = 0.055$; Fig. 2). Larval Pine Sawflies preferred to spin their cocoons on the bottom of branches (32%) and in the forks of twigs (32%) ($n = 611$).

The frequency of successful eclosion (28%) was approximately equal to that of predation (31%), whereas parasitism (17%) was less common. One quarter of the cocoons that we found were intact ($n = 611$). There was high variability in most of the quantitative characteristics of the cocoons' microhabitat (Table 1).

The best logistic regression model used microhabitat features to explain 22.1% of the variance in success of cocoons (Nagelkerke R^2 ; $\chi^2(9) = 81.63$, $P < 0.001$; Table 2). The model correctly classified 86.0% of unsuccessful outcomes but only 48.8% of successful eclosions (overall classification rate = 72.3%). Significant

predictors of success were small cocoon diameter, thin branches where cocoons were situated, and cocoons positioned on the underside of branches. No other variables significantly influenced success (Table 2). We repeated the logistic regression model to identify important risk factors separately for parasitism versus predation. Although the model focusing on parasitism was significant overall (Nagelkerke $R^2 = 0.14$; $\chi^2(10) = 19.79$, $P = 0.031$), no individual variable was a significant predictor of success (all $P > 0.08$). In the model focusing on predation by vertebrates, cocoons

Table 1. Mean characteristics of Pine Sawfly cocoons and their pupation sites and frequency by plant species ($n = 611$).

Trait	Mean \pm SD
Cocoon diameter (mm)	4.38 \pm 0.50
Branch diameter at pupation site (mm)	3.91 \pm 3.72
Branch diameter at branch base (mm)	10.13 \pm 9.96
Cocoon height above ground (m)	1.38 \pm 0.60
Cocoon mass (g)	0.03 \pm 0.02
Distance from pupation site to branch tip (cm)	21.36 \pm 20.16
Distance from pupation site to trunk (cm)	64.12 \pm 79.92
Plant species selected for pupation sites	No. cocoons (%)
<i>Acer rubrum</i> L. (Red Maple)	166 (27.2%)
<i>Quercus rubra</i> L. (Northern Red Oak)	127 (20.8%)
<i>Prunus serotina</i> Ehrh. (Black Cherry)	99 (16.2%)
<i>Pinus strobus</i> L. (Eastern White Pine)	42 (6.9%)
<i>Fagus grandifolia</i> Ehrh. (American Beech)	35 (5.7%)
<i>Ilex verticillata</i> (L.) A. Gray (Winterberry Holly)	33 (5.4%)
<i>Betula papyrifera</i> Marshall (White Birch)	23 (3.8%)
Other species ($n = 13$)	86 (14.0%)

Table 2. Binary logistic regression estimating the effect of 6 variables on success (survival) or failure (mortality) of Pine Sawfly cocoons. The probability of success was higher when the cocoon was smaller, when the diameter of the branch at the pupation site was small, and when the cocoons were positioned on the bottom of branches (versus top, in a fork, or on the trunk; bottom = reference). No other variables included in the model significantly influenced success.

Variable	B	S.E.	Wald	df	P	Exp(B)	95% C.I. for Exp(B)	
							Lower	Upper
Pupation site diameter	-0.330	0.070	21.960	1	<0.001	0.719	0.626	0.825
Cocoon diameter	-0.623	0.222	7.840	1	0.005	0.536	0.347	0.830
Position (bottom)	-	-	12.411	4	0.015	-	-	-
Position (side)	0.237	0.529	0.201	1	0.654	1.268	0.450	3.573
Position (top)	-0.180	0.614	0.086	1	0.770	0.836	0.251	2.786
Position (fork)	-0.158	0.532	0.089	1	0.766	0.853	0.301	2.422
Position (trunk)	-0.742	0.528	1.980	1	0.159	0.476	0.169	1.339
Cocoon height	-0.083	0.057	2.111	1	0.146	0.920	0.823	1.029
Log(distance from trunk + 1)	-0.371	0.244	2.311	1	0.128	0.690	0.428	1.113
DBH of pine	0.005	0.006	0.620	1	0.431	1.005	0.992	1.018
Constant	4.035	1.128	12.785	1	<0.001	56.539		

were significantly more likely to survive if they were small in diameter, on thin branches, and on the bottom or side of branches, as found in the overall model (Nagelkerke $R^2 = 0.25$; $\chi^2(10) = 53.52$, $P < 0.001$). Although we could not measure the mass of pupae from cocoons that had been parasitized or preyed upon, cocoon diameter was a good predictor of mass, based on a regression of mass versus diameter in intact cocoons ($n = 110$, $r^2 = 0.28$, $P < 0.01$).

A logistic regression using 2007 data that included only 3 microhabitat variables (height above ground, branch diameter at pupation site, position on branch)

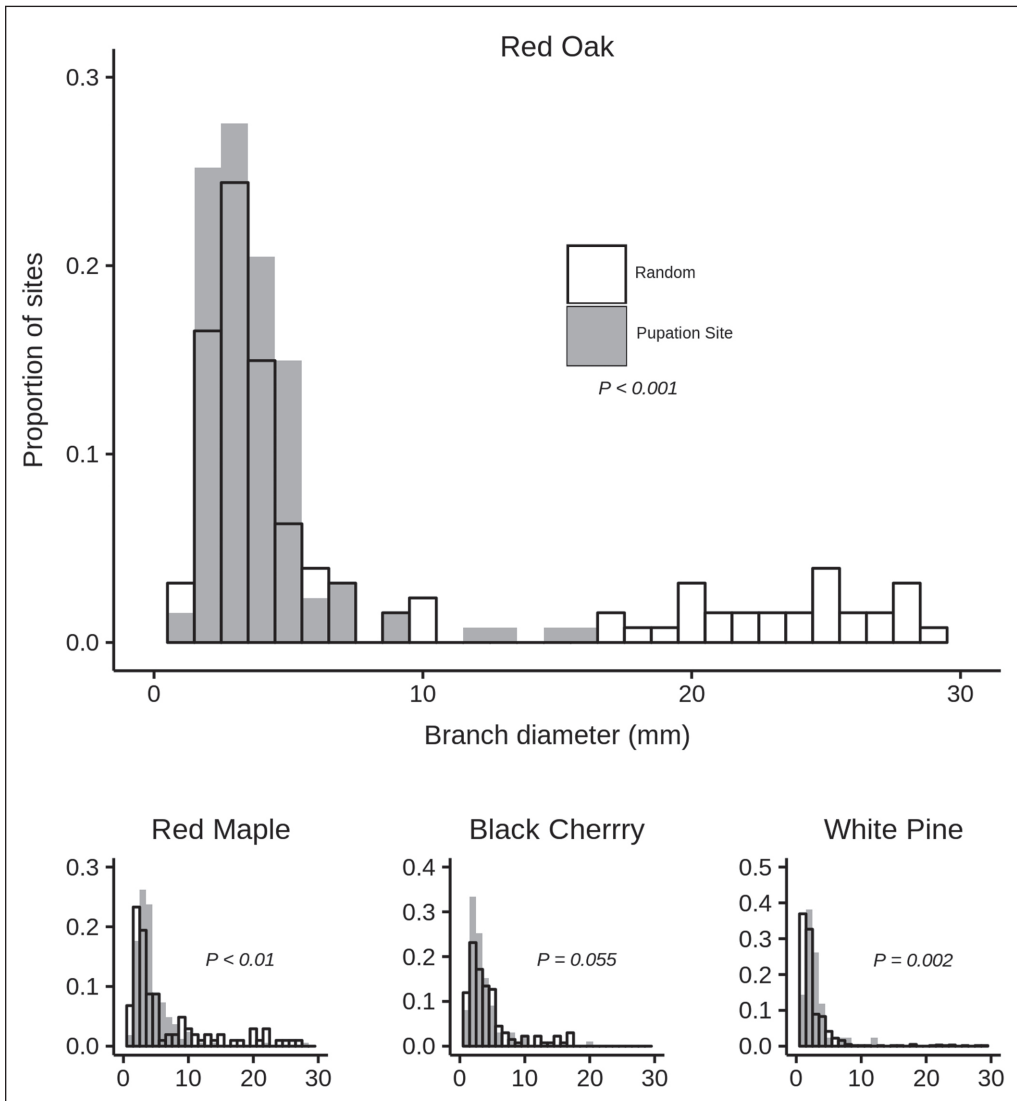


Figure 2. Frequency distribution of the diameters of available (random) pupation sites (white bars) versus observed Pine Sawfly pupation sites (gray bars). In the 4 most commonly selected plant species, Pine Sawflies tended to prefer sites that were 2–4 mm in diameter while avoiding stouter sites (P -values = results of Kolmogorov-Smirnov tests).

proved not to be significant. Although the model correctly classified 98.1% of successful cases (representing 79% of 138 cocoons), it misclassified 89.7% of unsuccessful cases (Nagelkerke $R^2 = 0.048$; $\chi^2(5) = 4.28$, $P = 0.51$).

Cocoons from which Pine Sawflies eclosed were significantly smaller than cocoons that were parasitized ($P = 0.002$) or preyed upon ($P < 0.001$). There were no differences in size, however, as a function of the source of mortality ($P > 0.05$). Cocoons of female Pine Sawflies collected in 2007 were larger in diameter on average than those of males (4.8 ± 1.8 mm vs. 4.0 ± 2.2 mm; t -test: $P < 0.001$, $n = 5$ females and 5 males). Female mass was nearly triple that of males (F vs. M: 31 ± 18 mg vs. 9 ± 4 mg; t -test: $P = 0.03$). These results suggest that rates of predation and parasitism may be higher for female than male Pine Sawflies.

Pine Sawflies that spun large cocoons tended to choose pupation sites of larger diameter (Spearman Rank test: $r_s = 0.26$, $P < 0.001$). Nonetheless, cocoons and pupation sites were not closely matched in size (Fig. 3). Branch diameters at pupation sites averaged 0.47 mm smaller than cocoon diameters. In accordance with the results of the logistic regression, pupation site diameter differed among fates of cocoons (Kruskal-Wallis tests: $P < 0.001$). Cocoons that had been preyed upon

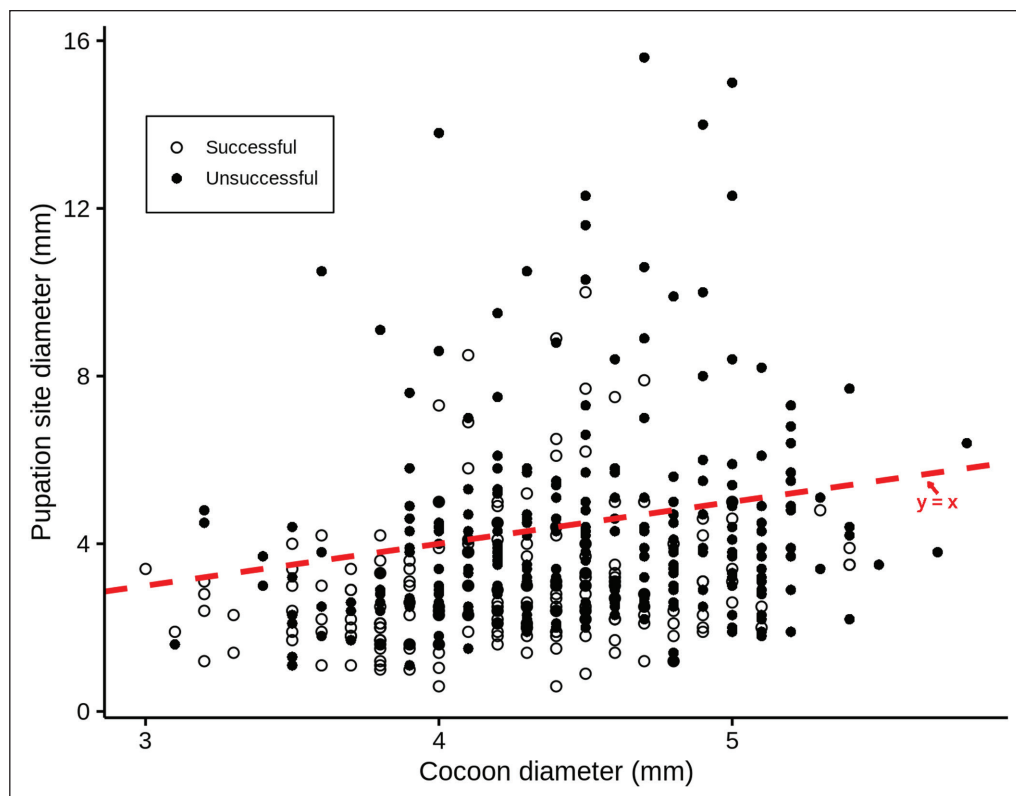


Figure 3. Pine Sawfly cocoon diameter versus branch diameter at pupation sites. Successful cocoons are indicated by open circles ($n = 171$), unsuccessful cocoons by filled circles ($n = 294$). Five outliers with a pupation site diameter greater than 20 mm are not included. Dashed line indicates cocoons and pupation sites of equal diameter.

were found on branches of larger diameter than parasitized or successful cocoons (adjusted pairwise comparisons: both $P < 0.001$). Parasitized cocoons were also found at significantly larger-diameter sites than cocoons from which a Pine Sawfly had successfully emerged ($P = 0.004$). Of the cocoons that were smaller in diameter than their pupation site (i.e., above the line of equality in Fig. 3), 80.5 % failed ($n = 118$), compared to 57.4% of cocoons that were larger in diameter than their pupation site ($n = 345$; $\chi^2(1) = 19.24$, $P < 0.001$).

Results from data collected at the same sites in 2000 were similar: there was no evidence of larval Pine Sawflies selecting branch diameters to match their cocoon size, and branch diameters at pupation sites averaged 0.23 mm smaller than cocoons ($n = 259$). As in 2016, the mean branch diameter at the pupation site of cocoons attacked by predators was significantly larger than that of parasitized or successful cocoons (4.6 ± 2.0 mm vs. 3.7 ± 2.1 mm, $n = 79$ and 180, respectively; t -test: $P = 0.001$).

The position of the pupation site along a branch influenced the risk of predation. Cocoons on the bottom of branches were most likely to be successful, whereas cocoons located in forks were typically unsuccessful (Fig. 4). The probability of success, parasitism, or predation depended upon how far out along the branch a cocoon was situated (Fig. 5). Note, however, that the results of the logistic regression presented above suggest that differences in survival were mainly due to differences in branch thickness rather than distance from the trunk per se.

Our attempts to rear Pine Sawflies and their parasitoids in the laboratory demonstrated that very few of the intact cocoons collected in January 2016 contained living Pine Sawfly pupae. Of 112 intact cocoons, only 3 had living Pine Sawflies. Fifteen had been parasitized (including 2 by unidentified Diptera). We could not

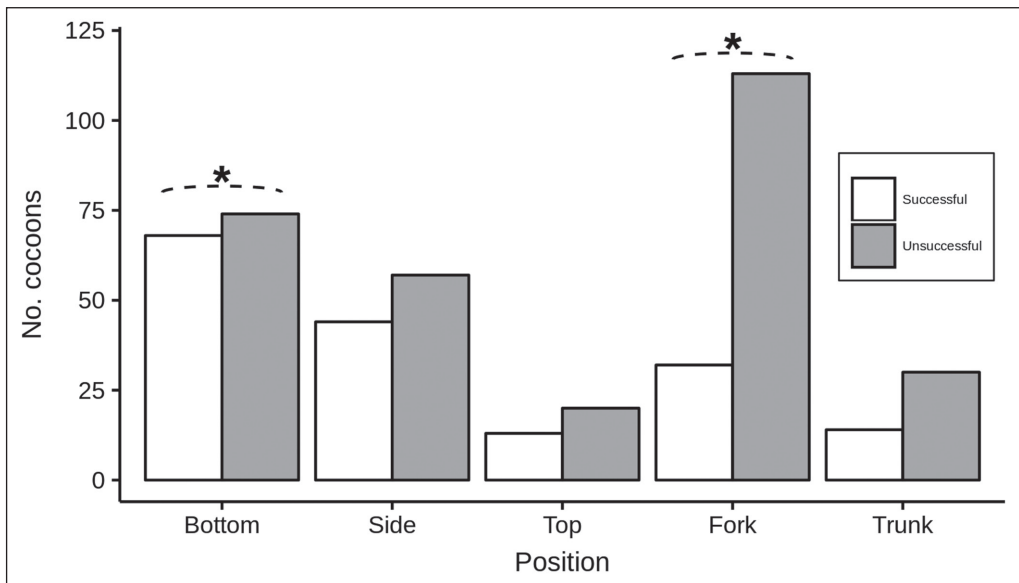


Figure 4. The probability of being parasitized or preyed upon differed as a function of where cocoons were situated on branches (chi-square test: $\chi^2(4) = 23.6$, $P < 0.0001$). Survival was highest on the bottom of branches and lowest in forks (z test: $P < 0.05$ for both).

determine the cause of death of the remaining larvae and pupae, although 14 were covered in white fungal hyphae. Of 68 intact cocoons collected in March 2016, none contained living Pine Sawflies and 11 contained parasitic wasps; the cause of death of the remaining pupae could not be determined. The only species of parasitic wasp that we reared from cocoons in the lab was *M. dentipes*. A mean of 9.7 ± 3.3 wasps emerged per cocoon in 2007 ($n = 6$) and 8.9 ± 5.2 in 2016 ($n = 22$; range = 2–22). Brood sex ratios of wasps were highly female-skewed, averaging 0.23 males per female in 2007 and 0.19 males per female in 2016, with one brood consisting of 0 males and 18 females.

We observed Black-capped Chickadees and *Baeolophus bicolor* (L.) (Tufted Titmouse) preying on cocoons on branches that we had attached next to a bird feeder. In one instance, 2 different chickadees repeatedly displaced each other while alternately hammering at the same cocoon. Finally, after investing more than 2 minutes of pecking, with numerous interruptions over a 14-minute period, one of the birds was able to extract and eat the larva. Chickadees and titmice appeared

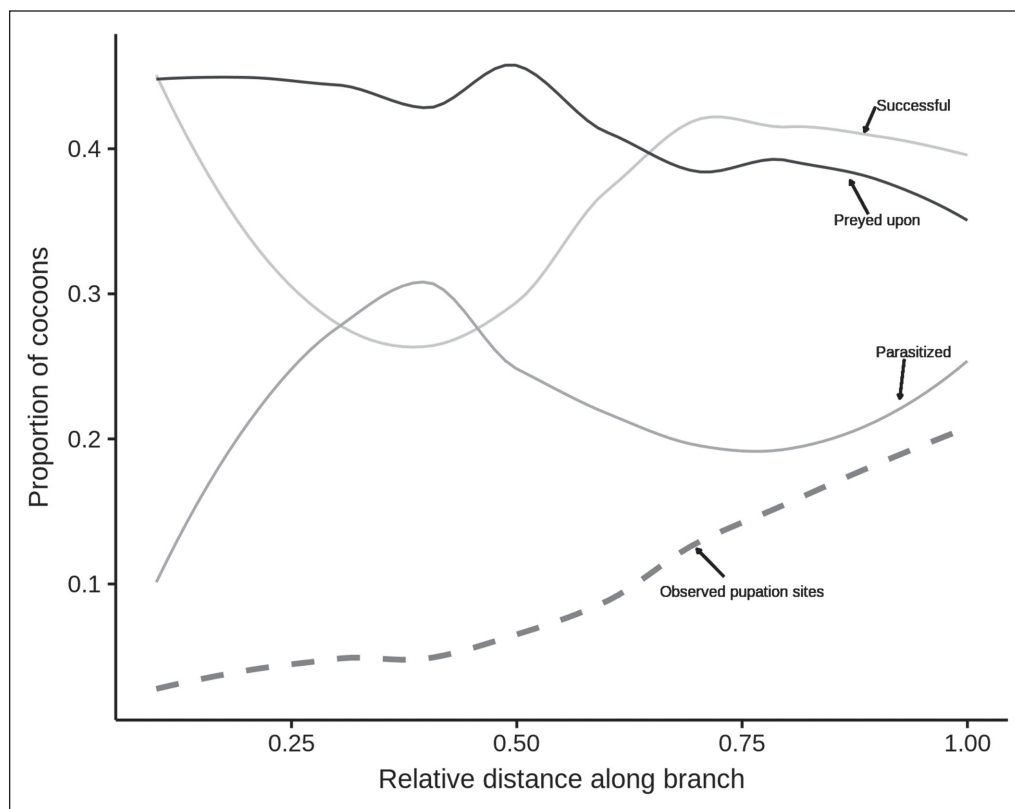


Figure 5. Proportion of successfully emerged, preyed upon, and parasitized cocoons as a function of relative location of pupation sites along a branch (0.0 = trunk, 1.0 = branch tip). To illustrate mortality risks, curves were smoothed along bins of proportional frequency (bin width = 0.1) using an LOESS function. Pine Sawflies preferentially pupate on the outer portions of branches where predation rates are lower, as illustrated by the dashed line showing observed relative frequencies of cocoons ($n = 611$).

to be able to distinguish cocoons with living Pine Sawfly pupae from cocoons that contained dead Pine Sawflies or parasitic wasps, based on later dissections of the rejected cocoons, as well as an observation of a titmouse that pulled a cocoon off a branch but then discarded it.

Discussion

More than half of all Pine Sawflies in our study failed to survive the cocoon stage during the fall and winter. Based on the evidence of distinct holes in their persistent cocoons, the insects were killed by 2 different types of natural enemies: parasitic wasps and vertebrate predators. Pine Sawflies were twice as likely to be killed by predators as by parasitoids. Because parasitoids and vertebrates hunt for their prey in distinct ways, they likely select for distinct pupation site-selection strategies on the part of Pine Sawfly larvae.

Our results suggest that there may be no easy solution to the problem of avoiding parasitic wasps. We found generally equivalent rates of parasitism on cocoons located on thick versus thin branches, and on the top, bottom, side, and forks of branches. Parasitic wasps such as *M. dentipes*, the major parasitoid of Pine Sawflies in our study area, probably rely mainly on olfactory cues to locate their hosts (cf. Rostás et al. 2003). Consequently, visual crypsis (e.g., by closely matching branch and cocoon diameters) may not provide Pine Sawflies a refuge from parasitoids. Likewise, positioning cocoons on thin twigs may not be effective because of the wasps' ability to reach the tips of branches. The fact that Pine Sawfly cocoons are located on such a wide diversity of plant species and microhabitats may reflect a bet-hedging strategy against parasitic wasps, which forage widely and efficiently (Gross 1993). In Europe, *M. dentipes* parasitizes cocoons of the *Diprion pini* L. (European Pine Sawfly) on branches and trunks with equal likelihood but rarely parasitize cocoons in leaf litter (Herz and Heitland 2005).

Although targeted pupation site selection may not be effective against parasitic wasps, Pine Sawflies can increase the probability of escaping vertebrate predators by positioning their cocoons in inaccessible locations. Selecting a pupation site at a thin point along a branch or on the bottom of the branch reduced predation risk. Such pupation sites also turned out to be favored by Pine Sawflies, presumably because of their relative inaccessibility to chickadees and other vertebrate predators. Most avian and mammalian predators are heavy enough to have difficulty reaching cocoons on thin branches, especially cocoons situated on the underside. However, picking a pupation site whose diameter closely matched cocoon diameter, which might be expected to increase crypsis, provided no advantage. Although we did not measure background color matching, Pine Sawfly cocoons are often strikingly similar in color to the branches on which they are located and, to the human eye at least, visually well-camouflaged. We did not search for Pine Sawfly cocoons in the leaf litter, which might provide a refuge from predators or parasitoids.

Our results indicate that inaccessibility may be a more important consideration for Pine Sawflies selecting pupation sites than closely matching branch and cocoon

diameters. Cocoons tucked in the forks of branches often seemed to the human eye to be particularly cryptic, yet that location was associated with the highest predation rates. Birds and small mammals may develop a search image for such locations or find it easier to attack the tough cocoons in a well-anchored fork of a branch. Our study did not record mortality of cocoons that might have been removed entirely from branches.

Although we observed variation in population density of Pine Sawflies between years, sources of mortality in 3 different years remained generally consistent. Parasitoids are a major source of mortality for Pine Sawflies and may regulate their population sizes (cf. Herz and Heitland 1999). However, the selection of pupation sites evident in this study, especially the preference for small diameter branches near the tip, appear to be shaped mainly by predation by birds and possibly small mammals.

Unlike Murphy and Lill (2010), we found that small cocoons were more successful than large ones. Smaller cocoons may be difficult to attack or may not be worth the energetic investment of pecking or biting through them to get at the pupa. Alternatively, the larger cocoons of female Pine Sawflies may make them a bigger or more attractive target for natural enemies, resulting in sex-specific mortality (cf. Ercit 2014). Depending upon the intensity of predation and the reproductive value of targeted individuals, sex-selective predation could have a disproportionate effect on population dynamics (see Hoy et al. 2015) and potentially favor sex-specific strategies in pupation site selection in Pine Sawflies.

Acknowledgments

We thank T. Dwyer and J. Walters (2000) and A. Benders, T. Buehrens, R. Dunlavey, C. Jeffrey, M. Taylor, A. Lee, and S. McFarlane (2007) for the use of unpublished data; J. Reblin for help in the lab; K. Raffa for references and information about Pine Sawfly biology; B. Sandercock and J. Fitzgerald for statistical advice; and S. Smedley, T. Wickman, and several anonymous reviewers for helpful comments on our manuscript.

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