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## ORIGINAL PAPER

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**Contributions of female oviposition patterns and larval behavior to group defense in conifer sawflies (hymenoptera: diprionidae)**

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**Abstract** We studied the effects of adult oviposition and larval interactions on the defensive potential of gregarious behavior in conifer sawflies. Aggregation size and distribution initially reflected adult host plant selection and oviposition behavior. The contagious distribution of egg clusters resulted in part from the utilization of individual trees by multiple females, and of single host shoots by several females. Trees with the greatest degree of prior defoliation received the most eggs, even though the potential for larval crowding made resource depletion possible. Foliar monoterpene and nitrogen contents explained only a small proportion of variability in female host utilization. Conifer needle architecture restricted the size of larval subgroups within aggregations, and limited the degree of defensive cohesiveness between subgroups. Subgroup turnover was frequent and independent of local food depletion. Risk of predation from wood ants varied with larval aggregation size and predator foraging level. When ant activity was high, large aggregations suffered greater numerical losses, but showed lower per capita predatory risk, than small groups. Results suggest that female oviposition patterns are influenced in part by the defensive benefits gained by offspring in large aggregations. Against ants, dilution effects and defensive synchrony due to gregariousness contribute to the overall antipredator strategy of sawfly larvae.

**Key words** Defense · Gregariousness · Oviposition · *Formica* · *Neodiprion*

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**Introduction**

Gregarious behavior can confer a variety of benefits on herbivorous insects. Group living can accelerate development by increasing feeding rates (Ribeiro 1989; Lawrence 1990; Stamp and Bowers 1990a), water uptake (Lockwood and Story 1986), or the efficiency of thermoregulation (Seymour 1974; Stamp and Bowers 1990b). Gregariousness can also increase survivorship by facilitating parental care (Eickwort 1981), overcoming host plant defenses (Raffa and Berryman 1983), or providing protection from natural enemies (Vulinec 1990). These advantages must be evaluated against such potential costs as increased disease transmission (Mohamed et al. 1985), resource depletion (Prokopy et al. 1984), and conspicuousness to some natural enemies (Bertram 1978) to fully understand the role of gregarious behavior in life history.

Specific antipredator benefits to gregarious insect prey may include dilution of per capita risk (Hamilton 1971; Treisman 1975), increased ability to detect predators (Terhune and Foster 1982), or the amplification of either aposematic signals (Fisher 1930; Sillen-Tullberg 1988) or defense behavior (Prop 1960). The defensive efficacy of gregariousness likely varies with such natural enemy traits as size, sensory modalities used in prey location, and retrieval methods (Curio 1976; Stamp and Bowers 1988), and also with the changing suite of prey characteristics through the life cycle (Cornell et al. 1987). Thus, gregariousness may serve a complex, changing role in prey defense and comprise but one part of a multicomponent repertoire (Pearson 1989; Vulinec 1990).

The gregarious behavior of many conifer sawfly (Hymenoptera: Diprionidae) larvae has long been viewed as an antipredator adaptation (Fisher 1930; Carpenter and Ford 1933; Cott 1940), although additional benefits, such as the facilitation of feeding (Ghent 1960; but see Kalin and Knærer 1977) and thermoregulation (Seymour 1974), are likely. Although some species are solitary (Larsson et al. 1993), most occur in colonies during most or all of

the larval period. Colony sizes range from small groups containing only a fraction of a female's clutch to large aggregations formed from the fusion of smaller groups (Atwood 1962). Gregariousness in these sawflies is part of a multiple defense strategy that includes physical (Prop 1960) and chemical (Eisner et al. 1974; Bjorkman and Larsson 1991; Codella and Raffa in press a) components.

In many gregarious insects, parental oviposition decisions determine the initial size and distribution of larval aggregations (Stamp 1980; Courtney 1984; Subinprasert and Svenson 1988). Thus, examination of egg clusters can provide a "snapshot" of larval social structure in the early instars (Lyons 1964). Diprionid females use serrated ovipositors to cut individual egg pockets in host foliage. In most species, females cluster their eggs (generally 50–150 total; Coppel and Benjamin 1965; Larsson et al. 1993) by producing a series of such slits in each of several adjacent needles. The emerging larvae remain aggregated and feed collectively. Sawfly oviposition behavior thus has implications for both adult and offspring and may reflect a series of conflicts and compromises.

Diprionid larvae are attacked by a diversity of arthropod and vertebrate predators (references in Codella and Raffa 1993). Previous studies of conifer sawfly gregariousness have considered defensive efficacy in light of bird (Sillen-Tullberg 1990) and pentatomid bug (Tostowaryk 1972) predation. However, the mechanisms and efficacy of defense may be predator-dependent (Curio 1976).

Ants (Hymenoptera: Formicidae) are considered major selective agents for the evolution of arthropod defenses (Pasteels et al. 1983). The wood ants (*Formica rufa* species group) are widely distributed in forested habitats and frequently attack diprionid sawflies and other herbivores under natural conditions (Lyons 1964; Ilnytsky and McLeod 1965; McNeil et al. 1978; Knerer and Wilkinson 1990; Olofsson 1992; additional references in Codella and Raffa 1993). The socially facilitated foraging behavior and worker site fidelity of these predators (reviewed by Traniello 1989) likely provides special challenges to sedentary prey aggregations. However, there has been little study of how gregarious defense specifically affects ant behavior or the outcome of predator-prey interactions.

The purpose of this study was to examine the antipredator consequences of sawfly gregarious behavior and the ecological factors which influence aggregations. Our specific objectives were: first, to examine female sawfly host selection and oviposition patterns in terms of impact on offspring aggregation size and distribution; second, to examine the dynamics of movement and interaction within aggregations; and third, to determine the efficacy of sawfly gregarious behavior as a strategy against wood ant predation.

## Materials and methods

### Study species

We studied three sawfly congeners, one of which was present at each of our field sites. The European pine sawfly, *Neodiprion sertifer* Geoffr., and the red pine sawfly, *N. nanulus nanulus* Schedl, share many aspects of life history, including dark larval coloration and a relatively narrow host range. In contrast, the redheaded pine sawfly, *N. lecontei* (Fitch), is a brightly colored polyphage (Larsson et al. 1993; Codella and Raffa in press a). Females of all three species cluster their eggs, and larval feeding aggregations are often large (Haack and Matsson 1993; Larsson et al. 1993).

### Oviposition patterns

Observations of diprionid host selection and oviposition were conducted in Sawyer County, Wisconsin, United States, during 1987–1988. Records of the Wisconsin Department of Natural Resources (Prey et al. 1985) indicated that high population levels of *N. lecontei* had been present in the area for several years. This species lays its eggs in clusters in 1-year-old foliage and generally oviposits in only one of the two needles in each pine fascicle (Benjamin 1955; Griffiths 1958).

In 1988, a managed stand of young red pine (*Pinus resinosa* Ait.) was selected for intense study. The site is on sandy soil with a southeast-facing incline of approximately 30°. Trees were originally planted with a 1.8-m spacing. No wood ant mounds were present at the site. We selected and mapped a 0.07-ha area and tagged all trees [ $n = 105$ ; mean height of  $1.80 \pm 5.69$  (SEM) m]. Each tree was placed in one of five classes on the basis of estimated prior defoliation from sawflies: 1 = no apparent defoliation; 2 =  $\leq 25\%$ ; 3 = 26–50%; 4 = 51–75%; 5 =  $> 75\%$ . Defoliation levels were assessed independently by two observers, who then compared their estimates for corroboration. The site was later sampled (9.3 m<sup>2</sup> sample plot size) to assess the spatial dispersion of prior defoliation and current oviposition using the methods of Southwood (1984) and Zar (1984).

Trees were examined weekly for *N. lecontei* eggs from 3 June through 27 July. Needle clusters were tagged, eggs were counted, and the bases of egg-bearing needle fascicles were marked with colored paint pens. Previously tagged shoots were rechecked weekly to determine if they were subsequently used by additional females, and any new egg-bearing needles were marked in distinct colors. The unusually hot and dry conditions prevailing in northern Wisconsin during the study period resulted in a high rate of hatch failure (Codella 1994).

Foliage was collected for analysis of monoterpene and nitrogen content on 11 June. Monoterpenes have been implicated in host defenses for several conifer-herbivore systems (Raffa and Berryman 1982; Cates et al. 1987; Cates and Redak 1988; Geri et al. 1993), may provide host location cues for ovipositing females (Leather 1985; Geri et al. 1993), and are a volatile component of diprionid defensive regurgitant (Eisner et al. 1974; Codella and Raffa in press a). Nitrogen is a limiting nutritional factor in many insects, and dietary content is often correlated with herbivore feeding and growth rates (Scriber 1984). One-year-old shoots were clipped from the southern quadrant of the upper-third crown to control for within-crown variability (Kossuth and Muse 1986) and stored at  $-20^{\circ}\text{C}$  until analysis. Pentane extracts of chopped foliar samples were analyzed for total monoterpene content with a Shimadzu GC-9APF gas chromatograph equipped with a 25 m $\times$ 0.25 mm bonded fused silica open tubular polydimethylsiloxane polar column (Carbowax 20-M; Alltech Associates, Deerfield, Ill.). Injector and detector temperatures were 225°C. Oven temperature was 60°C (isothermal) for 17 min. The flow rate of the carrier gas (helium) was 1 ml/min. Quantitative determinations were made by comparison of total peak areas with that of 0.1% *p*-cymene, an added internal standard (Raffa and Steffek 1988). Total foliar nitrogen content was determined by semi-micro Kjeldahl analysis of oven-dried samples by the Soil and Plant

Analysis Laboratory, University of Wisconsin-Madison (Schulte et al. 1987).

*N. lecontei* larvae were collected from nearby sites and reared on clipped pine foliage in plastic boxes at 22°C and 18:6 L:D (Knerer 1984). Newly spun cocoons were housed under similar conditions and misted periodically with distilled water. Emerging virgin females were dissected, and their eggs counted.

#### Dynamics within aggregations

Late-instar aggregations of *N. n. nanulus* were observed on mature (c 30-year-old) *P. resinosa* in Sauk County, Wisconsin during May 1991. Counts were made of the number of larvae within aggregations and the number of larvae per needle (henceforth subgroups) within each aggregation. To assess the degree of defensive integration between subgroups, we waved a pair of forceps near needles bearing six larvae. Defensive response, as indicated by whipping, arching or regurgitation (Prop 1960), was recorded. We also noted responses of unharassed larvae on a previously selected, adjacent needle.

To evaluate movements of larvae within aggregations, eight uniquely marked late-instar *N. lecontei* were placed on an upright shoot of jack pine (*Pinus banksiana* Lamb.) within a 0.125-m<sup>3</sup> ventilated plexiglass cage at 25°C and 16:8 L:D in the laboratory. Beginning at 0600 hours (lights on), we observed the larvae for 1-h periods at 3-h intervals over 24 h. During dark periods, observations were conducted under red light. Preliminary observations indicated three general categories of larval behavior: stationary (motionless on needle substrate), feeding, and crawling. We recorded these behaviors, the composition of larval subgroups, and the occurrence of defensive movements using instantaneous and scanning methods (Martin and Bateson 1986).

#### Effect of group size on ant predation

Field studies on the effect of sawfly gregarious behavior on ant predation were conducted in June 1991 in a Scots pine (*Pinus sylvestris* L.) Christmas tree plantation in Waushara County, Wisconsin. Western thatching ants, *Formica obscuripes* Forel, are abundant in the area, forage widely for a variety of arthropod prey, and are known to attack diprionid larvae (Weber 1935; Bradley 1972; Williamson 1973; Finnegan 1977; O'Neill 1988). At the study site, several trunk trails (*sensu* Oster and Wilson 1978) radiated from mounds and generally led to trees on which workers tended homopterans for honeydew and foraged for prey. Hundreds of ants were present on trees throughout the day. In contrast, trail activity dropped during midday, when soil temperatures often exceeded 40°C (S.G. Codella and K.F. Raffa, unpublished work). Although sawfly larvae were not observed at the site, there was a history of activity in the area (see below).

We selected a single ant mound (1.3 m diameter×0.2 m high) for the experiments. After mapping trails with small flags, two active trails, which led to separate trees 9.6 and 7.1 m distant by trail from the mound, respectively, were selected. Four aphid-bearing shoots were selected on each tree, because wood ant predation is known to increase in association with tended homopterans (Campbell 1990). Two-year-old foliage was stripped from each selected branch to facilitate observations. We placed groups of 5 or 40 late-instar *N. sertifer* larvae on the shoots (one group size/tree). This species was present in nearby plantations during the study period, and had been present at the study site in the past, as evidenced by empty cocoons in the topsoil. From 1600 to 2000 hours, aggregations were checked every 30 min. We recorded the number of remaining larvae, the number of workers present on the branch, and worker foraging rate on both the branch and the trail. Foraging rates were measured by counting the number of workers passing in both directions at the midpoint of the trail or branch over a 2-min interval.

To further examine the effect of ant activity levels on the efficacy of diprionid gregarious defense, we conducted laboratory ex-

periments with *F. obscuripes* using a 1.2×1.5 m wooden foraging arena lined with acrylic sheeting. The periphery of the arena was surrounded by a 10 cm acrylic wall coated with "Teflon" resin 30 solution (E. I. DuPont de Nemours & Co., Wilmington, Del. USA) to prevent ant escape (Codella and Raffa in press b). Workers foraged for honey water (simulating the presence of aphids) and insect prey on two elevated foraging stations equidistant from the nest entrance. Honey water (10% v/v) was supplied in a recessed 8-ml reservoir. Beyond this was a 15-cm circular area supporting a 10-cm clipped shoot of *P. banksiana* foliage upon which sawfly larvae and other prey were placed.

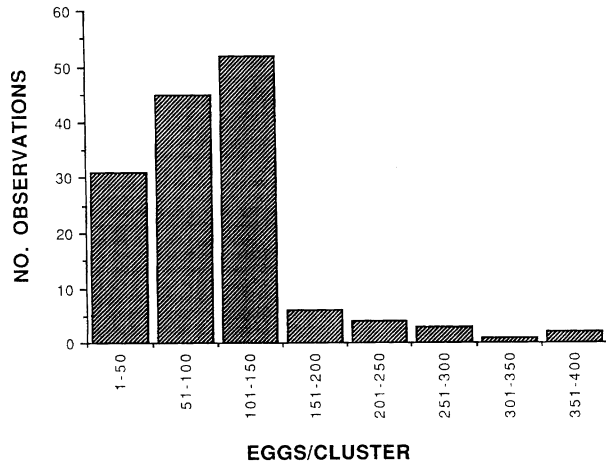
We experimentally skewed the activity levels at the two stations by consistently providing food more frequently and in greater abundance at one of the stations during the pre-experimental period. Wood ants adjust laboratory foraging activity in response to resource availability (Cosens and Toussaint 1986; S.G. Codella, unpublished work). For 3 weeks prior to the experimental period, the "high activity" station received 8 ml honey water daily and six mealworm fragments three times weekly. In contrast, the "low activity" station received 4 ml honey water and three prey fragments, both twice weekly in a haphazard pattern. Uneaten food was removed from both stations at the end of the day. Foraging rates to the stations were measured by counting the total number of workers passing the midpoint of the ramp leading to the feeding platform (both directions combined) over a 5 min interval. After the acclimation period, foraging rates averaged about 40 workers/5 min at the high traffic station 2 h after the provisioning of food and about 20 workers/5 min at the low traffic station under the same conditions.

We evaluated the interaction between ant activity level and sawfly aggregation size in 8-h assays. Honey reservoirs were filled at 0800 hours. After 2 h, equal numbers of late-instar *N. lecontei* larvae were placed at both the high- and low-activity stations. At 1700 hours, the number of larvae remaining at each station was counted, and all food was removed. Foraging rate was not assessed during the experiment. The experiment was replicated twice each for five, ten, twenty and forty larvae/aggregation. For both high and low activity stations, we tested the ordered hypothesis that sawfly mortality increases with group size; i.e.,  $H_A: X_5 < X_{10} < X_{20} < X_{40}$  (Jonckheere test for ordered alternatives; Siegel and Castellan 1988).

## Results

### Oviposition patterns

In 1988, 46 (43.8%) of the trees at the site bore a total of 145 egg-bearing shoots [ $\bar{x} = 3.2 \pm 0.4$  (SEM) egg-bearing shoots/tree;  $R = 1-15$ ]. The total egg count at the site was 14,102. Egg number per infested shoot was highly variable, averaging  $97.2 \pm 5.5$ , with a range of 2 to 392 eggs/shoot (Fig. 1). Since dissected virgin females carried a mean of  $104.0 \pm 4.0$  eggs ( $R = 50-155$ ;  $n = 58$ ), and since females tend to deposit their entire clutch (Coppel and Benjamin 1965), the range of egg cluster size suggests that individual females split their clutches among several shoots, and that several females may oviposit on a common shoot. Among all shoots, 31 (21.4%) bore 50 or fewer eggs; 13 of these (8.9% of total) had 25 eggs or less. Likewise, 16 shoots (11.0% of all egg-bearing shoots at site) bore eggs in excess of the upper range indicated by dissections. The preliminary data from 1987 indicated that 59 of 162 total shoots (36.4%) exceeded a single female's clutch range. Five of these clusters (3.1% of total) had more than 500 eggs.



**Fig. 1** *Neodiprion lecontei* egg cluster size distribution in young *Pinus resinosa* plantation

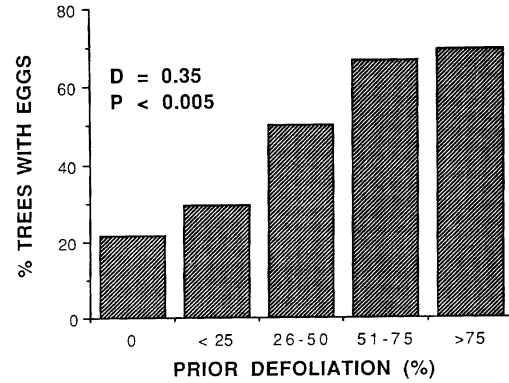
**Table 1** Oviposition dispersion patterns of *Neodiprion lecontei* in a young *Pinus resinosa* stand.  $S^2/\bar{x}$  = variance: mean ratio;  $I_D$  of dispersion (Southwood 1984), where  $I_D = (S^2/\bar{x})N-1$  for  $N = 15$  samples.  $I_D$  values were compared to  $\chi^2(0.05 < P < 0.95, df = 14)$ ; values within this range indicate random distributions, while those above or below indicate contagious and uniform dispersions, respectively (Southwood 1984)

Sampled unit	$s^2/\bar{x}$	$i_D$	Conclusion
All trees	1.21	16.94	Random
Trees with eggs	1.29	18.06	Random
All eggs	996.90	13,956.60	Contagious
All egg-bearing trees	5.10	71.40	Contagious

In 1988, sequential marking of egg-bearing fascicles in shoots confirmed multiple female visitations. At least 19 shoots (13.1% of total) on 13 trees were visited by two ( $n = 15$ ) or three ( $n = 4$ ) females; the additional females added  $22.7 \pm 4.0$  eggs ( $R = 3-90$ ) to shoots already bearing  $127.1 \pm 24.3$  ( $R = 13-375$ ) eggs. The

**Table 2** Association between *Pinus resinosa* defoliation level due to prior *Neodiprion lecontei* herbivory and 1) *N. lecontei* oviposition (per tree); 2) foliar chemistry (total quantity). Monoterpenes

Dependent variable	Prior defoliation					$r_s$	P	
	None	$\leq 25\%$	26-50%	51-75%	$> 75\%$			
<b>Oviposition (n = 46)</b>								
No. eggs	$\bar{x}$	75.7	208.3	287.4	410.2	395.5	0.31	<0.05
	SE	12.4	41.9	100.5	139.4	103.7		
	n	3	12	9	6	16		
Shoots with eggs	$\bar{x}$	1.0	2.5	2.9	3.5	4.1	0.29	<0.05
	SE	0	0.4	0.9	1.2	0.9		
	n	3	12	9	6	16		
<b>Chemistry</b>								
Monoterpenes (n = 30)	$\bar{x}$	0.72	0.67	0.81	0.77	1.0	0.62	<0.001
	SE	0.02	0.04	0.06	0.03	0.07		
	n	3	9	5	3	10		
Nitrogen (N = 46)	$\bar{x}$	0.98	1.14	1.14	1.22	1.19	0.28	<0.1
	SE	0	0.06	0.02	0.05	0.03		
	n	3	12	9	6	16		



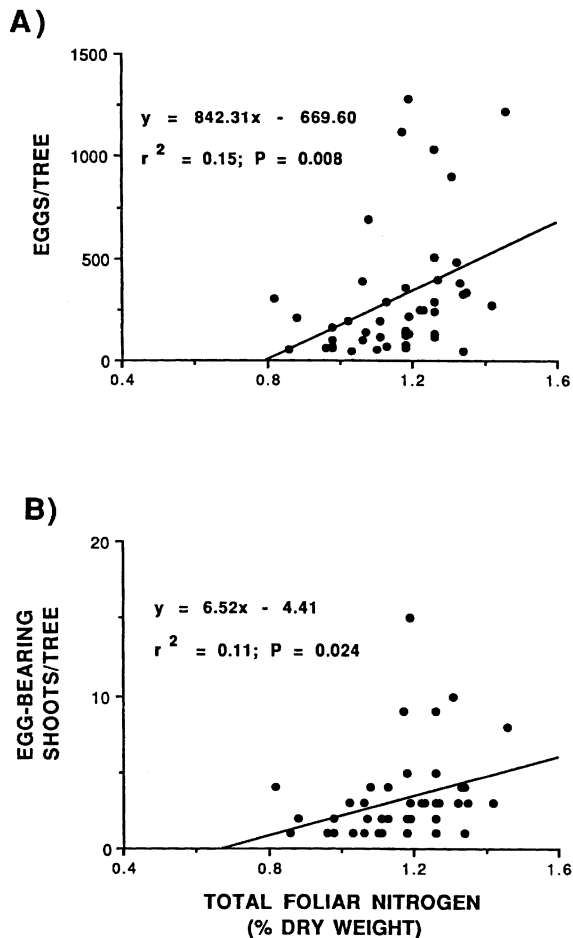
**Fig. 2** Association between current *N. lecontei* oviposition and *P. resinosa* prior defoliation level.  $D$  = statistic for Kolmogorov-Smirnoff two-sample test (Siegel and Castellan 1988)

somewhat elevated mean of these initial egg counts suggests that at least some of the shoots were visited by more than one female before our first census.

Despite the initial uniform planting of the plantation (1.8 m x 1.8 m), living pines were randomly dispersed at the time of the study due to prior mortality from various factors (Table 1). Egg-bearing trees were also randomly distributed. However, both eggs and egg-bearing shoots displayed highly contagious distributions (Table 1). Fifteen trees bore more than 300 eggs, for a total of 9715 eggs ( $\bar{x} = 647.15 \pm 93.24$ ) and 89 egg-bearing shoots ( $\bar{x} = 5.93 \pm 0.91$ ). Thus, 32.6% of the egg-bearing trees at the study site held 68.9% of the total eggs and 61.1% of the egg-bearing shoots.

Oviposition was strongly associated with prior defoliation. Highly defoliated trees were significantly more likely to bear eggs (Fig. 2). Also, both egg-bearing shoots and total eggs per tree increased significantly with prior defoliation (Table 2). Of the 15 trees with more than 300 eggs, 10 (66.7%) showed greater than 50% prior defoliation, yet 6 of these (40.0%) were adjacent to at

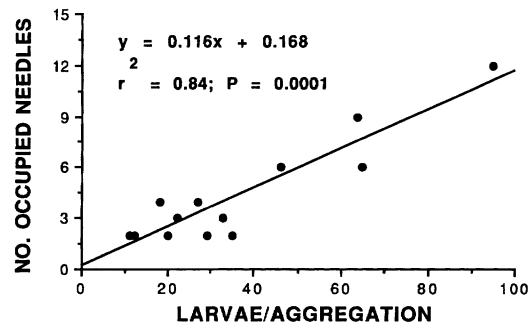
and Nitrogen were determined by gas-liquid chromatography and semi-micro Kjehldahl analysis, respectively



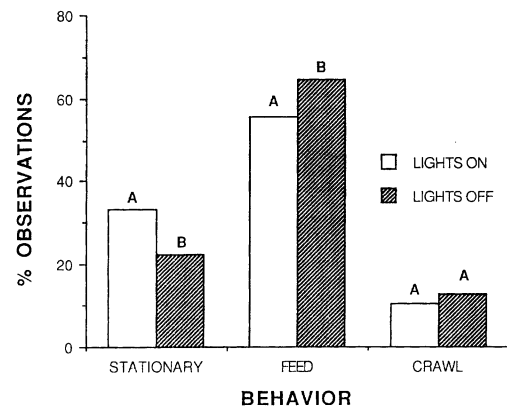
**Fig. 3** Association between total foliar nitrogen content of *P. resinosa* and *N. lecontei* oviposition for **A** Total eggs per tree; **B** egg-bearing shoots per tree

least one tree that lacked eggs entirely and showed less than 25% prior defoliation. When the extremes of defoliation were compared for egg-bearing trees (classes 1 + 2 vs. class 5), the highly defoliated trees showed a trend, though insignificant, toward greater egg number (classes 1 + 2:  $\bar{x} = 181.7 \pm 36.2$  eggs/tree,  $n = 15$ ; class 5:  $\bar{x} = 395.5 \pm 103.7$ ,  $n = 16$ ; Mann-Whitney test:  $U = 160.5$ ,  $P < 0.20$ ).

Among egg-bearing trees, total monoterpene content (mg monoterpene/g dry weight of foliage) was significantly positively correlated with prior defoliation (Table 2), but not with total eggs/tree ( $r^2 = 0.001$ ,  $n = 30$ ,  $P = 0.86$ ) or with egg-bearing shoots/tree ( $r^2 = 0.0004$ ,  $n = 30$ ,  $P = 0.92$ ). In contrast, total foliar nitrogen (percentage of foliar dry weight) showed weak though highly significant positive correlations with numbers of eggs (Fig. 3A) and numbers of shoots with eggs (Fig. 3B), but not with prior defoliation (Table 2). When trees with eggs were compared to those without eggs, egg-bearing pines had significantly higher nitrogen levels (with eggs:  $\bar{x} = 1.16 \pm 0.02\%$ ,  $n = 46$ ; without eggs:  $\bar{x} = 1.09 \pm 0.02\%$ ,  $n = 59$ ;  $t$ -test:  $t = 2.48$ ,  $df = 103$ ,  $P = 0.015$ ) but not monoterpene levels ( $\bar{x} = 8.20 \pm 0.40$  mg/g,  $n = 30$  vs.



**Fig. 4** Association between *N. nanulus nanulus* aggregation size and colony subdivision



**Fig. 5** *N. lecontei* larval behavior (late instar) under light and dark conditions. Within behavioral categories, differing letters indicate significant differences at  $P < 0.05$  (Mann-Whitney  $U$ -test)

$\bar{x} = 8.40 \pm 0.40$  mg/g,  $n = 36$ ;  $t$ -test:  $t = -0.45$ ,  $df = 64$ ,  $P = 0.66$ ). Total monoterpenes and total nitrogen were not associated ( $r^2 = 0.004$ ,  $n = 66$ ,  $P = 0.61$ ).

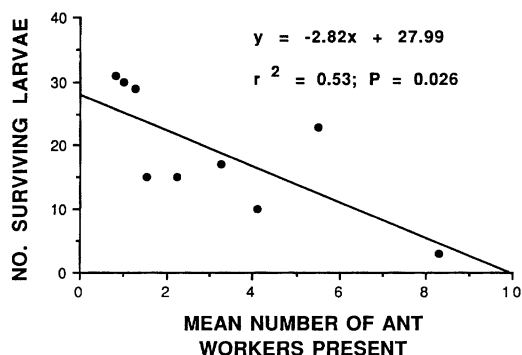
#### Dynamics within aggregations

The number of *P. resinosa* needles occupied by *N. nanulus* larvae was significantly correlated with aggregation size (Fig. 4). In contrast, mean subgroup size ( $\bar{x} = 8.4 \pm 0.58$  larvae/needle for  $n = 60$  total needles) within an aggregation was not ( $r^2 = 0.02$ ,  $n = 14$ ,  $P = 0.64$ ). All larval subgroups ( $n = 25$ ) responded defensively when disturbed by forceps. Subgroups on adjacent needles also reacted defensively in 17 (68.0%) of these cases (one-tailed binomial test,  $P = 0.054$ ; Siegel and Castellan 1988).

In laboratory observations, late-instar *N. lecontei* larvae on *P. banksiana* spent the majority of time (nearly 60% overall) feeding. Within categories, the frequency of behaviors varied with light conditions; larvae fed more and were stationary less often with lights off versus on (Fig. 5). Defense behaviors such as arching and regurgitation were not observed, even though larvae frequently contacted each other. Sawflies moved frequently among subgroups and generally abandoned needles be-

**Table 3** Effect of aggregation size on survival of *Neodiprion sertifer* larvae subjected to *Formica obscuripes* predation during 4-h field assays ( $N = 9$  for each aggregation size). Values are mean (standard error of mean). Statistical comparisons are within columns

Aggregation size	No. larvae taken	% Survival
5	4.11 (0.39)	17.78 (7.78)
40	20.78 (3.24)	48.06 (8.09)
	$U = 76$	$U = 66$
	$P = 0.001$	$P < 0.05$



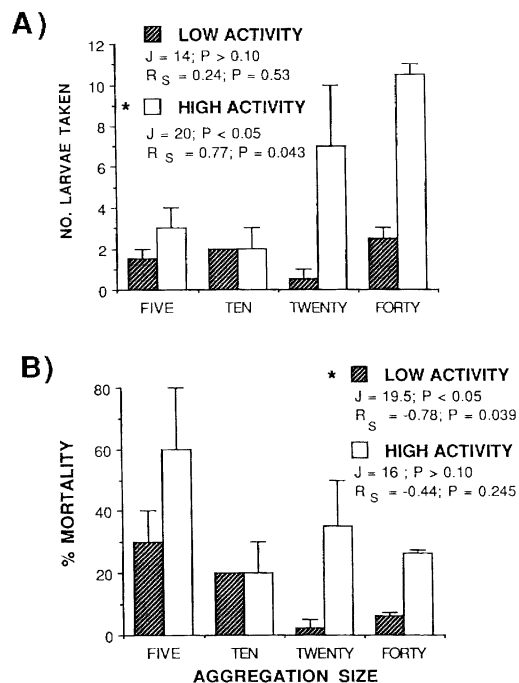
**Fig. 6** Association between *Formica obscuripes* foraging activity and *N. sertifer* larval mortality in field experiments

fore available food was exhausted. Subgroup size ( $\bar{x} = 2.3$  for  $n = 93$  observed combinations) ranged from 1 to 4 larvae per needle. Within the range of 1 to 3 individuals/subgroup (97.8% of observations), the eight larvae combined in 37 of the 92 possible combinations (38.0%) and changed subgroups an average of  $9.75 \pm 1.84$  ( $R = 1-17$ ) times. In five observed instances, larvae attempting to join an existing subgroup were unable to do so because of crowding on the needle; three of these cases involved subgroups already containing three or four individuals.

#### Effect of group size on ant predation

In field experiments, large sawfly aggregations lost significantly more individuals to ant predation than did small groups, but members of large groups had a significantly lower individual probability of mortality (Table 3). In large groups, the number of surviving larvae was negatively correlated with the mean number of workers present on the shoot during the 4-h experiment (Fig. 6), but not with mean foraging rates on either the branch or the trail leading to the tree. In small groups, predation losses were uniformly high (Table 3), and survival did not correlate with any of our measures of ant activity.

In laboratory foraging experiments, sawfly mortality was significantly affected by both predator activity level and prey gregariousness. At the high activity station, the number of sawflies removed by ants increased with prey aggregation size (Fig. 7A). In contrast, numerical losses to ants remained constant at the low activity station



**Fig. 7** Defensive efficacy of *N. lecontei* larval gregariousness as a function of *F. obscuripes* foraging intensity in laboratory experiments **A** number of larvae taken; **B** percent survival.  $J$  = statistic for Jonckheere test for ordered alternatives (Siegel and Castellan 1988);  $r_s$  = Spearman rank-order correlation coefficient. \* significant at  $P < 0.05$

(Fig. 7A). Larvae at the low activity station also had a significantly reduced individual probability of mortality when in large aggregations (Fig. 7B).

#### Discussion

We considered larval gregariousness in diprionid sawflies from three perspectives: the effect of female oviposition decisions on initial colony size, the dynamics of larval movement within aggregations, and the relationship between aggregation size and escape from wood ant predation. Both adult and larval behavior affect the size, distribution and behavioral options of aggregations and hence contribute to the mechanism and efficacy of gregarious defense (Codella and Raffa 1993).

Parental oviposition behavior affects the distribution of progeny among host trees and within individual crowns. In our study, *N. lecontei* egg cluster dispersion was highly contagious at the host tree level, as has been observed in *N. sertifer* (Hattemer et al. 1969; Wilson 1975). Pines with numerous egg clusters were often located near hosts bearing few or no eggs (Warren and Coyne 1958; Boeve 1991). At the shoot level, the size of some clusters indicated clutch splitting or fusion.

Contagious oviposition patterns have implications for all diprionid life stages. From the female's perspective, egg clustering reflects several constraints. Females are generally weak fliers and live only several days in the

field (Coppel and Benjamin 1965; Coppel et al. 1974). For most Diprionidae, oviposition is a multicomponent, stereotypic behavior (Ghent and Wallace 1958; Ghent 1959); our observations indicate that females can take 5 min to deposit a single egg. These constraints may favor rapid initiation of oviposition upon adult emergence. Diprionids generally spin cocoons in the topsoil below the tree on which they completed larval development (Coppel and Benjamin 1965; Bjorkman and Gref 1993). Emerging females that oviposit on or near this same tree will minimize the energetic and temporal costs of flight and host selection.

The frequency with which sawfly females split their clutches (Warren and Coyne 1958; Wilkinson et al. 1966; Becker and Benjamin 1967; Knerer and Atwood 1973; Coppel et al. 1974; Codella 1994) or fuse them with those of other females (Warren and Coyne 1958; Lyons 1964) determines the size of the egg mass. There may be costs to female egg clustering, and these may be especially magnified during outbreak periods (Haack and Mattson 1993; Larsson et al. 1993). For example, during the egg stage, high densities increase conspicuousness to natural enemies, such as ichneumonid egg parasites (Lyons 1962) and great tits (Olofsson 1986). Large larval colony size facilitates viral pathogen transmission (Mohamed et al. 1985; Young and Yearian 1990), and may increase conspicuousness to certain predators and parasites due to amplified visual or chemical cues (Vine 1973; Heinrich and Collins 1983; Vulinec 1990). Crowding can also cause foliar resource depletion, and larvae migrating to new trees are exposed to high soil temperatures and predators (Benjamin 1955; Smirnov 1960; Ives 1963; Teras 1982). Larval coloniality can lead to dense cocoon aggregations in the topsoil below host trees (Stark and Dahlsten 1961; McLeod 1966), where small mammals exert heavy predation pressure (Olofsson 1987).

Our results suggest that the potential costs of female egg clustering are offset in part by the defensive benefits of larval gregariousness. In our field experiments, large colonies suffered greater numerical losses to wood ants than did small aggregations, but percent survival was greater in large groups. Using our survival rates from Table 3, a 40-egg clutch subdivided into eight colonies of five will produce about eight survivors if all colonies are discovered by predators. In contrast, about 20 larvae will survive if the eggs are placed in a single cluster. Although small colonies may be less conspicuous, the ubiquitous distribution and high foraging activity of wood ants suggests that a majority of clusters will be located. Clutch splitting might facilitate female avoidance of predators; however, it could ultimately reduce fitness through increased offspring predation.

Sawfly egg clustering was also influenced by host chemistry. In this study, foliar nitrogen showed some correlation with both prior defoliation and the degree of oviposition. How this might ultimately affect fitness is unclear, however, since the relationship between nitrogen fertilization and sawfly performance appears highly vari-

able (Smirnov and Bernier 1973; Krol 1985; Popp et al. 1986; Geri et al. 1993). Monoterpene content also increased significantly with sawfly defoliation level (in contrast to lodgepole pine defoliated by the pine beauty moth; Watt et al. 1991), but this had no significant effect on host selection. Although monoterpene concentrations were not associated with nitrogen levels, Bjorkman et al. (1991) demonstrated a positive effect of nitrogen fertilization on another foliar terpene component, diterpene resin acids. Resin acids have a detrimental effect on diprionid performance (Larsson et al. 1986), but late-instar larvae preferentially accept high-resin tissue (Bjorkman and Larsson 1991; Codella and Raffa in press a). This may reflect a conflict between the defensive benefit and developmental cost of resin intake (Bjorkman and Larsson 1991; Codella and Raffa in press a).

Gregariousness likely confers additional, nondefensive benefits, particularly to early-instar larvae (Ghent 1960; Kalin and Knerer 1977; Nakamura 1980, 1981; Codella and Raffa 1993). For example, aggregates of newly hatched *Neodiprion pratti banksianae* larvae are better able to sever the tough epidermis of pine needles than are solitary individuals (Ghent 1960). Aggregation behavior might also facilitate thermoregulation, as seen in pergid sawflies (Seymour 1974) and many lepidopteran larvae (Stamp and Bowers 1990b).

Larval behavior affects the mechanism of sawfly defense. Larvae change subgroup alliances frequently, resulting in a high turnover rate at the aggregation periphery. This concurs with models of gregarious defense which interpret prey aggregation as the summation of individual cover-seeking behavior (Hamilton 1971; Treisman 1975; Vulinec 1990). Aggregation may also be viewed at the tree level (Boeve 1991; Codella and Raffa 1993), and the superclustering of eggs on some trees may reduce individual risk. Treisman (1975) elaborated Hamilton's (1971) selfish herd model to include the role of additional defenses, such as the chemical repellency seen in our system. Aggregate living facilitates the synchronization of diprionid allomone regurgitation (Tostowaryk 1972) and defensive movements (Prop 1960; Sillen-Tullberg 1990) and may magnify aposematic signaling (Fisher 1930; Vulinec 1990). The high frequency of active feeding observed in the chemically-defended, conspicuously-colored *N. lecontei* contrasts with observations of many cryptic lepidopteran larvae (Heinrich 1979; Heinrich and Collins 1983; S. G. Codella and R. C. Lederhouse, unpublished work) that punctuate long stationary periods with relatively short feeding bouts. The increased nocturnal feeding observed in *N. lecontei* in this study has been noted in other sawflies (Heitland and Pschorn-Walcher 1993) and is a common strategy of temporal escape from diurnal predators (Heinrich 1979; Lederhouse 1990).

Despite potential advantages, the defensive efficacy of sawfly colonial behavior is constrained by several factors. Intracolony movement may be restricted in very large aggregations due to increased interference among larvae (Tostowaryk 1971). Conifer foliar architecture di-



vides aggregations into subgroups which occupy adjacent needles. We found the degree of defensive cohesiveness between these subgroups to be somewhat limited, with adjacent units failing to respond defensively about 30% of the time. Subgroup size can be limited by interspecific host differences in needle length, as egg number per needle correlated with needle length (Ghent 1955; Griffiths 1960). Short needles may also restrict movement between subgroups due to increased crowding.

In our both our field and laboratory experiments, numerical losses to ants increased with group size at a faster rate than did percent survival. This outcome was modulated by the intensity of ant foraging, since our low activity foraging station showed a large increase in dilution benefits as aggregation size increased. Predation pressure on sawflies is likely to be especially intense near ant mounds, where foraging activity is high (Laine and Niemela 1980). These results suggest that defensive synchrony is a major benefit of gregariousness against initial scout workers, when collective responses by prey can abort localized attraction to prey and prevent the escalation of attack (Codella and Raffa in press b). Ultimately, the dynamics and outcome of group defense will vary with the characteristics of the natural enemies encountered.

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