

# Density-dependent and density-independent responses of three species of *Telenomus* parasitoids of hemlock looper eggs

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Accepted: 29 September 2010

**Key words:** density dependence, Geometridae, Lepidoptera, Hymenoptera, Scelionidae, egg parasitization, population regulation, sex ratio, IPM, *Lambdina fiscellaria*

## Abstract

We examined patterns of host exploitation by natural populations of three *Telenomus* species (Hymenoptera: Scelionidae) parasitizing hemlock looper, *Lambdina fiscellaria* Guenée (Lepidoptera: Geometridae), eggs in sentinel traps in eastern Quebec and western Newfoundland (Canada). The percentage of eggs parasitized by *Telenomus flavotibiae* Pelletier and *Telenomus coloradensis* Crawford in autumn, and by *Telenomus droozi* Muesebeck in spring either were not or only weakly related to host egg density. In contrast, the percentage of eggs parasitized by *T. coloradensis* in the spring was positively related to host egg density. *Telenomus flavotibiae* and *T. droozi* parasitized eggs in fewer traps than *T. coloradensis*, suggesting that they were less abundant or less efficient locating host patches. Eggs parasitized by *T. droozi* only occurred in traps with eggs parasitized by *T. coloradensis*, suggesting that it may be responding to kairomones emitted by *T. coloradensis*. In contrast, neither the number nor sex ratio of *T. coloradensis* emerging from eggs in traps with *T. droozi* differed from those in traps without this congeneric. Secondary sex ratios of all three species were significantly female biased. Our study suggests that only *T. coloradensis* has the potential to regulate hemlock looper populations.

## Introduction

Understanding the role of natural enemies in the population dynamics of eruptive pest insects remains an essential aspect of contemporary integrated pest management (Fraser et al., 2008). In the case of parasitoids, elucidation of host finding and host exploitation capabilities are necessary to gain a full understanding of their role in host population dynamics (Morrison & Strong, 1980, 1981). The ability of parasitoids to locate a high percentage of hosts

and to respond in a positive density-dependent manner to increases in host density is vital to the reduction of host populations (Stiling, 1987; Orr, 1988).

Laboratory studies have shown that female parasitoids can preferentially parasitize high-density host patches when there is a large variation in density among patches (Hassell, 1971). This aggregation pattern has, in many species, been linked to chemical stimuli, such as kairomones from host eggs (Morrison, 1986; Reznik & Umarova, 1991), honeydew (Bouchard & Cloutier, 1984), and host pheromones (Vet et al., 1991). Not surprisingly, this pattern is not as evident when host patches are more uniform in density (van Lenteren et al., 1976). Once located, numerous factors can affect the extent to which a parasitoid will exploit a host patch. These factors may be

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abiotic, such as changes in photoperiod (Roitberg et al., 1992) or barometric pressure (Roitberg et al., 1993), biotic, such as the age of the female (Wajnberg, 2006), or related to patch characteristics, such as the presence of direct (Hassell, 1971) or indirect competition (Goubault et al., 2005), number of hosts (Hassell, 1971; Morrison & Lewis, 1981; Field, 1998), host age (Hirose et al., 2003), and density of host traces [e.g., kairomones (Waage, 1978); see Wajnberg, 2006 for a review].

Within a patch, female parasitoids choose how many hosts to parasitize and many are capable of controlling, to some degree, the sex of their progeny. Sex allocation by parasitoids can be influenced by numerous factors including host quality, patch size, competition between foundress females (Ode & Hardy, 2008; West, 2009), time between mating and parasitism (King, 1987), and the sequence of egg laying (Kapranas et al., 2009).

In this study, we report the patterns of host patch exploitation by three species of *Telenomus* (Hymenoptera: Scelionidae) that parasitize eggs of hemlock looper, *Lambdina fiscellaria* Guenée (Lepidoptera: Geometridae) throughout eastern Quebec and western Newfoundland (Canada). In north-eastern North America, the hemlock looper is an important pest of balsam fir, *Abies balsamea* (L.) Mill (Pinaceae) (Otvos & Bryant, 1972). Defoliation by hemlock looper can result in significant growth losses and tree mortality (Carroll, 1956); however, populations of this defoliator have remained difficult to track due to their patchy distribution within the canopy and across sites (Carroll, 1956; Otvos et al., 1979), and the often rapid rise and fall of population densities (Hébert et al., 2006).

Hébert et al. (2001) reported that the crash of an outbreak population of hemlock looper in Quebec was associated with very high levels of egg parasitism in late spring by *Telenomus* spp. However, the individual patterns of host exploitation and the relative importance of each egg parasitoid species in the *Telenomus* complex (Pelletier & Piché, 2003) have yet to be determined. Almost all (>88%) identified egg parasitoids observed during a period of very low hemlock looper density in eastern Quebec and Newfoundland (Carleton et al., 2009) were one of three *Telenomus* species identified by Pelletier & Piché (2003). *Telenomus flavotibiae* Pelletier parasitized hemlock looper eggs in the autumn, *Telenomus droozi* Muesebeck parasitized eggs during the spring, and *Telenomus coloradensis* Crawford parasitized hemlock looper eggs in both autumn and spring, with the vast majority of parasitism by *T. coloradensis* occurring during the spring (Carleton et al., 2009). It remains unclear, however, whether all or only a subset of these parasitoid species can contribute to suppressing hemlock looper populations. Following a review of classical biological control programs, Denoth et al. (2002) con-

cluded that multiple-agent release programs were less likely to gain establishment than single species release; and furthermore, in those cases where successful control was attained after multiple-agent release, the success was attributed largely to one agent.

We carried out a field study to evaluate the attack rate and sex ratio responses of *T. flavotibiae*, *T. droozi*, and *T. coloradensis* to a range of hemlock looper egg densities in eastern Quebec and western Newfoundland. As hemlock looper densities were extremely low at all sites, we evaluated the level of parasitism using sentinel traps (described by Carleton et al., 2009) that contained a range of egg densities.

## Materials and methods

In summer 2006, 10 mature balsam fir stands were selected in both eastern Quebec and western Newfoundland (Carleton et al., 2009). Hemlock looper populations were very low during the study, as mean ( $\pm$  SE) branch egg densities per site were only  $0.30 \pm 0.13$  in Quebec and  $0.11 \pm 0.04$  in Newfoundland. Within each stand, 10 balsam fir trees were selected at 5–10 m intervals along a single transect during each sampling period and a sentinel trap was stapled to the base of these trees at breast height (Hébert et al., 2006). Sentinel traps consisted of white polyurethane foam disks (6 cm in diameter and 1 cm thick), with hemlock looper eggs from the same province embedded. To produce hemlock looper eggs, adult moths were mated and provided water, a sucrose solution, and a foam disk as an oviposition site [see Carleton et al. (2009) for complete details]. Sentinel trap egg densities ranged from 1 to 120 eggs, and were haphazardly selected for each tree. To identify any density-dependent response by *T. flavotibiae* or *T. coloradensis* to hemlock looper eggs, ‘autumn’ sentinel traps were placed in stands from the beginning of looper flight in late August and removed at the end of the looper flight period in early November (Carleton et al., 2009). Spring traps were subsequently placed in these same stands to test for density-dependent responses to looper egg density in the spring. In Newfoundland, ‘spring’ traps were placed in the stands in mid-April, before mean daily temperatures exceeded 3 °C, the minimum threshold temperature for hemlock looper (Hartling et al., 1999), and were removed just prior to egg hatch (i.e., ca. 175 DD<sub>-3°C</sub>; Hartling et al., 1999). In Quebec, where winter temperatures are lower and sites were less accessible, spring traps were placed on study trees in early November (when autumn traps were removed) and removed just before egg hatch in spring.

After collection, autumn sentinel traps were placed in darkness in an environmentally controlled chamber for no

less than 13 weeks at  $2.2 \pm 0.1$  °C. Thereafter, all eggs were reared at  $22.0 \pm 0.5$  °C,  $75 \pm 2\%$  r.h., and L16:D8 photoperiod, and checked daily for looper hatchlings or adult parasitoid emergence. Emerged parasitoids were identified to species in both provinces and sexed (for Newfoundland sites only) based on morphological characteristics (Pelletier & Piché, 2003). Eggs that did not hatch were dissected to determine egg state (i.e., undeveloped or containing a pharate hemlock looper larva or parasitized but not emerged). Parasitoids that did not emerge, or that were damaged (14.3% of 1 624 parasitized hemlock looper eggs) and could not be identified to the species level are not reported here. Several unidentified factors may affect the behavioral patterns of a given species during various periods throughout the year. Such factors could include but are not limited to: alternate generations of the species, changes in primary host species, and changes in strategies for host patch exploitation. Given that we cannot accurately account for these potential factors, species that were collected in both autumn and spring were analyzed separately.

#### Statistical analysis

Two-sample t-tests were used to determine whether looper egg densities differed between Newfoundland and Quebec traps for the same collection period. For spring data, Fisher's exact tests were used for each province to determine whether attacks by *T. coloradensis* and *T. droozi* were independent (attacks by *T. coloradensis* in autumn were too infrequent to test independence with *T. flavotibiae*).

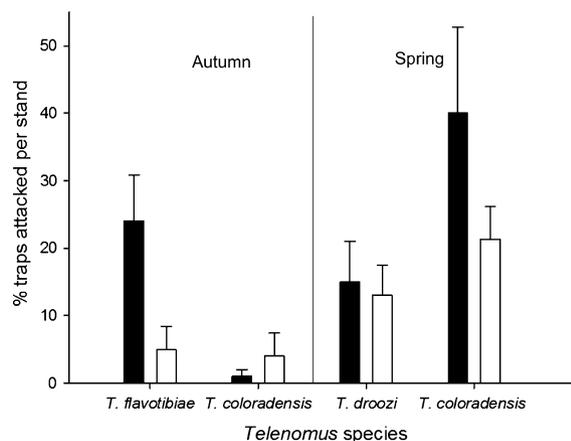
For each *Telenomus* species, and for *T. coloradensis* separately for spring and autumn, a series of generalized linear models were fit (using SAS Proc GLIMMIX; SAS v9.2, SAS Institute, Cary, NC, USA) testing the influence of egg density (number of eggs per trap) and province on parasitism rate. These models used a logit link function, assumed a binomial error (as we modeled the count of parasitized eggs given the number of available eggs), and included stand as a random variable nested within province. First, traps were scored as parasitized (at least one *Telenomus* emerging from any egg in the trap) or unparasitized, asking whether parasitism rate at the trap level differed between provinces. Second, individual eggs were scored as parasitized or unparasitized, asking whether parasitism rate at the egg level depended on province, egg density, or their interaction. Third, we tested whether the presence of *T. droozi* affected spring parasitism by *T. coloradensis*, repeating the egg-level parasitism rate analysis using only traps with at least one *T. coloradensis* egg and including as an additional factor the presence or absence of *T. droozi* in each trap.

The effects of egg density on sex ratio were also examined for each *Telenomus* species in Newfoundland (Quebec parasites were not sexed). These tests used the same generalized linear model framework as the parasitism rate tests, except that counts of females among total wasps were modeled using only data from traps with at least one emerging wasp. The population-level sex ratio was also calculated, across all traps in all stands, for each *Telenomus* species, using binomial confidence intervals to test the null hypothesis of a 1:1 sex ratio.

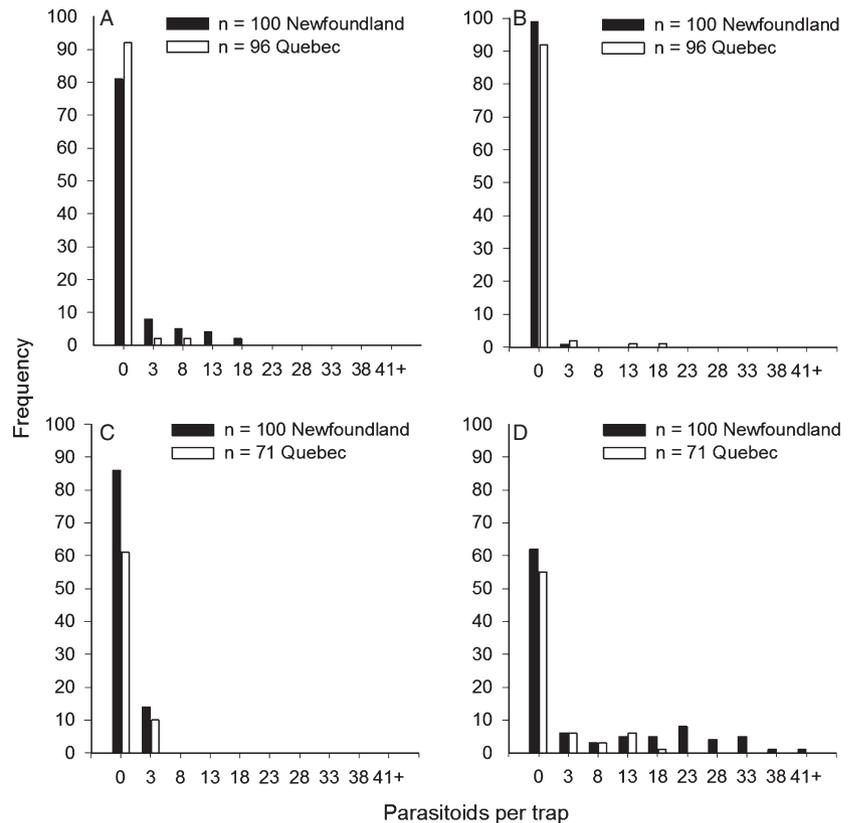
#### Results

Mean ( $\pm$  SE) sentinel trap egg densities in autumn 2006 were slightly but significantly lower in Newfoundland ( $29.0 \pm 1.0$ ) than in Quebec ( $34.8 \pm 1.1$ ) ( $t = 3.79$ , d.f. = 191,  $P < 0.01$ ). In contrast, in spring 2007, mean sentinel trap egg densities were significantly higher in Newfoundland ( $29.2 \pm 1.2$ ) than in Quebec ( $17.2 \pm 1.6$ ) ( $t = -5.98$ , d.f. = 141,  $P < 0.01$ ).

*Telenomus coloradensis* (spring) parasitized eggs in more traps than *T. coloradensis* (autumn), *T. droozi*, or *T. flavotibiae* (Figure 1). The highest number of eggs attacked in a single sentinel trap was 11, 57, 17, and 5 by *T. coloradensis* (autumn), *T. coloradensis* (spring), *T. flavotibiae*, and *T. droozi*, respectively. The modal egg-density class of eggs parasitized per trap was only 1–5 eggs for all species, in both provinces and both seasons, with the exception of *T. coloradensis* in Newfoundland in the spring, where the modal egg-density class was 20–25 eggs (Figure 2). During the spring, *T. droozi* only parasitized eggs in sentinel traps containing eggs parasitized by *T. coloradensis*. This positive association differed significantly from that expected if



**Figure 1** Mean ( $\pm$  SE) percentage of sentinel traps attacked by three species of *Telenomus* in Newfoundland (black bars) and Quebec (white bars) in autumn 2006 and spring 2007.



**Figure 2** Frequency histogram describing the number of hemlock looper eggs attacked per sentinel trap by (A) *Telenomus flavotibiae*, (B) *T. coloradensis* (autumn), (C) *T. droozi*, and (D) *T. coloradensis* (spring) in Newfoundland (black bars) and Quebec (white bars) in autumn 2006 and spring 2007. Values on the x-axis represent the median value for the respective ranges; e.g., 3 = 1–5 parasitoids per trap.

parasitism was independent in both Quebec ( $n = 71$ ) and Newfoundland ( $n = 100$ ) (both d.f. = 1,  $P < 0.01$ ).

The percentage of traps with at least one hemlock looper egg parasitized by *T. flavotibiae* was significantly higher in Newfoundland than in Quebec ( $F_{1,18} = 6.13$ ,  $P = 0.024$ ); however, for *T. droozi* and for *T. coloradensis* in spring and autumn there was no significant difference between provinces in parasitism at the trap level ( $F_{1,18} = 0.0$ , 1.21, and 1.49, respectively;  $P = 0.97$ , 0.29, and 0.24).

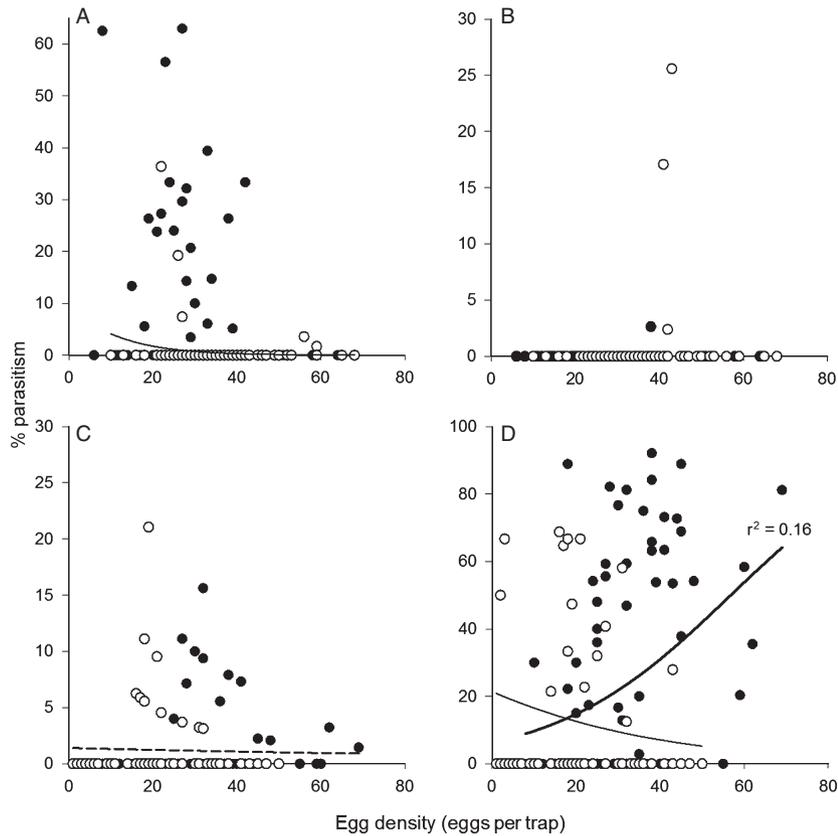
In autumn, the rate of attack by *T. coloradensis* on looper eggs did not depend significantly on egg density, province, or their interaction (Table 1, Figure 3A), although attacks were so uncommon that our analysis has limited power. For *T. flavotibiae*, the dependence of attack rate on egg density differed between provinces: it declined weakly with egg density in Quebec but was independent of egg density in Newfoundland (Table 1, Figure 3B).

In spring, *T. droozi* attack rate declined weakly with egg density (with no evidence for effects of province or its interaction with egg density), although the egg-density effect was of marginal significance (Table 1, Figure 3C). For *T. coloradensis* in spring, the dependence of attack rate on egg density was very different between provinces: attack rate declined very weakly with egg density in Quebec but

**Table 1** Summary of generalized linear model analyses evaluating effects of province (Quebec or Newfoundland) and *Lambdina fiscellaria* egg density on *Telenomus* spp. attack rates

Season	Species	Factor	d.f.	F	P
Autumn	<i>Telenomus flavotibiae</i>	Egg density	1,174	19.4	<0.0001
		Province	1,18	0.53	0.48
		Egg*province	1,174	12.2	0.0006
Autumn	<i>Telenomus coloradensis</i>	Egg density	1,174	0.13	0.71
		Province	1,18	1.21	0.29
		Egg*province	1,174	0.59	0.44
Spring	<i>Telenomus droozi</i>	Egg density	1,147	4.30	0.040
		Province	1,18	2.05	0.17
		Egg*province	1,147	2.37	0.13
Spring	<i>Telenomus coloradensis</i>	Egg density	1,147	4.12	0.044
		Province	1,18	1.48	0.24
		Egg*province	1,147	26.8	<0.0001

increased with egg density in Newfoundland (Table 1, Figure 3D). In traps that contained at least one *T. coloradensis*, the mean percentage of eggs parasitized by *T. coloradensis* did not differ significantly in the presence or absence of *T. droozi* in Quebec (48.2 vs. 41.3%) or in Newfoundland (60.4 vs. 53.3%) ( $F_{1,39} = 0.18$ ,  $P = 0.67$ ).



**Figure 3** Relationships between the density of *Lambdina fiscellaria* eggs in sentinel traps and the percentage of eggs parasitized by (A) *Telenomus coloradensis* (autumn), (B) *T. flavotibiae* (autumn), (C) *T. droozi* (spring), and (D) *T. coloradensis* (spring), in Quebec (open circles) and Newfoundland (solid circles). Raw data are shown, but statistical analyses and fitted curves are from generalized linear models with binomial errors and a logit link. Fitted curves are shown only for datasets where egg density has significant explanatory power, and are calculated separately for the two provinces when the egg density\*province interaction was significant (Table 1; thin solid line for Quebec, thick solid line for Newfoundland, and dashed line for *T. droozi* where a model pooling across provinces was appropriate). The  $r^2$  estimate for Newfoundland *T. coloradensis* in spring is calculated based on residuals from the fitted curve on the plotted arithmetic scale; such  $r^2$  estimates for all other fitted curves were  $\leq 0.016$ . Note the scale differences on the vertical axes among the four panels.

For *T. coloradensis* in autumn, we did not have enough data to test for effects of egg density on parasite sex ratio. For *T. coloradensis* and *T. droozi* in spring, and *T. flavotibiae* in the fall, parasite sex ratio appeared independent of egg density (*T. coloradensis*:  $F_{1,33} = 0.20$ ,  $P = 0.66$ ; *T. droozi*:  $F_{1,9} = 0.66$ ,  $P = 0.44$ ; *T. flavotibiae*:  $F_{1,14} = 0.16$ ,  $P = 0.69$ ). For all three species, 95% confidence intervals around the secondary sex ratio excluded 50% [*T. coloradensis*: 60.8% (59.0–65.9); *T. droozi*: 75.0% (56.5–88.5); *T. flavotibiae*: 74.5% (66.8–81.2)].

## Discussion

Of the three parasitoids studied, only *T. coloradensis* parasitizing hemlock looper eggs during spring in Newfoundland displayed a positive, density-dependent response to egg densities in sentinel traps. In that province, the density

of hemlock looper eggs in traps where *T. coloradensis* (spring) parasitized one or more eggs was higher than in traps where they did not parasitize eggs, suggesting that the ability to find high-density host patches contributed, at least in a limited manner, to the positive density-dependent response by *T. coloradensis*. Other parasitoids respond to increased concentrations of kairomones emitted by host eggs in patches with higher host egg densities (Morrison, 1986; Reznik & Umarova, 1991). *Telenomus droozi* may have responded to kairomones associated with previous foraging or parasitism by *T. coloradensis*, as it only parasitized eggs in traps containing eggs parasitized by *T. coloradensis*.

Usually *T. flavotibiae*, *T. coloradensis* (autumn), and *T. droozi* only parasitized 1–5 eggs in individual sentinel traps, regardless of host egg density, resulting in no effect or only a very weak positive relationship between

percent parasitism and host egg density. In contrast, in a similar analysis the percentage of eggs parasitized by *T. coloradensis* (spring) in Newfoundland was positively related to host egg density. Although most *T. coloradensis* only parasitized 1–5 eggs per trap in Quebec, the modal egg-density class of eggs parasitized per trap was 20–25 eggs in Newfoundland. The high rates of parasitism by *T. coloradensis* in Newfoundland may have been due, in part, to individual females parasitizing more eggs per trap, or to a greater number of *T. coloradensis* females locating and parasitizing eggs in the same sentinel trap. The latter assumption is more likely given the higher proportion of traps parasitized by *T. coloradensis* than either of the other species investigated.

The same modal egg-density class for number of eggs parasitized per trap for all three species in each province (except for *T. coloradensis* in Newfoundland in spring) suggests that all three species, which are of similar size and shape (Pelletier & Piché, 2003), parasitized a similar number of hosts per patch visit. Although there is no published study describing the number of host eggs that the three *Telenomus* species studied here can parasitize, females of other *Telenomus* species usually parasitize 30–180 eggs during their 2- to 25-day lifetime, generally parasitizing the majority of their hosts within the first 24–48 h (Orr & Boethel, 1990), with a range of 2–13 eggs per day (Bosque & Rabinovich, 1979; Orr et al., 1985, 1986; Navasero & Oatman, 1989; Orr & Boethel, 1990; Chabi-Olaye et al., 1997, 2001; Ballal & Ramani, 1999; Foerster & Butnariu, 2004).

The secondary sex ratios (Godfray, 1994) reported in Newfoundland, where parasitoid populations were probably higher than in Quebec, were strongly female biased in all three species. These are typical sex ratios of hymenoptera under local mate competition (West, 2009), where we would expect significant sibling mating prior to dispersal. These results should be interpreted with some caution, as we did not directly observe females on host patches, nor were we able to assess potential differential mortality of the sexes (King, 1987).

The apparent density-dependent response of *T. coloradensis* to various host egg densities in sentinel traps suggests that it may be capable of responding quickly to increases in hemlock looper densities. This could explain why hemlock looper populations have reportedly been reduced by *Telenomus* spp. so rapidly after reaching outbreak levels (Hébert et al., 2001). The mechanisms involved in such a rapid response are unclear; however, it appears that *T. coloradensis* may have a wider distribution throughout the forest landscape than *T. flavotibiae* or *T. droozi*, even when hemlock looper populations are low (see Carleton et al., 2009). *Telenomus coloradensis* may have more alternate

hosts or alternative hosts that are more abundant than *T. flavotibiae* or *T. droozi*.

Hébert et al. (2001) reported that a hemlock looper outbreak in eastern Québec ended suddenly due to extremely high rates of parasitism of hemlock looper eggs in spring. Based on the frequency of parasitoid specimens that they subsequently identified, Pelletier & Piché (2003) concluded that *T. coloradensis* was the parasitoid primarily responsible for the population decline of hemlock looper previously reported by Hébert et al. (2001). Although the present study was carried out in low density hemlock looper populations, the rapid positive density-dependent response of *T. coloradensis* to artificially increased host egg densities and the lack of such a response by the other egg parasitoids support this conclusion. This study further suggests that *T. coloradensis* could play an important role in hemlock looper population dynamics even when host populations are low.

### Acknowledgements

We thank J. Baker, G. Butt, Y. Dubuc, A. Labrecque, K. McCarthy, and G. Pelletier for technical assistance and G. Boiteau, E. Eveleigh, R. Johns, and two anonymous reviewers for comments on an earlier version of the manuscript. Financial support was provided by a collaborative research development grant from NSERC with Abitibi Bowater, Corner Brook Pulp and Paper, Department of Natural Resources of Newfoundland & Labrador, Société de Protection des Forêts contre les Insectes et les Maladies (SOPFIM), and Forest Protection contributing as industrial partners, and by NSERC Discovery Grants to Dan Quiring and Steve Heard. The Canadian Forest Service provided additional logistical support, as well as a graduate scholarship (from CFS-Atlantic) to Drew Carleton.

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