Ecological applications of pheromone trapping of *Malacosoma disstria* and *Choristoneura conflictana*

Brad C. Jones,[1] Maya L. Evenden

Department of Biological Sciences, CW 405, Biological Sciences Centre, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Abstract—The forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), and large aspen tortrix, *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae), are important pests of trembling aspen, *Populus tremuloides* Michx. (Salicaceae), in western Canada. Populations of both species can be monitored with sex pheromone-baited traps as part of an integrated pest management program. Moths captured in pheromone traps can also be used for ecological studies. Captured males of each species were examined to test the effect of population density, geographic region, and collection date on moth quality. Moth quality was assessed on the basis of wing area and level of infection with microsporidian parasites. The level of microsporidian infection of *M. disstria* was strongly dependent on geographic region but not on population density. Male *M. disstria* from high-density populations had smaller wings than males from endemic populations. Wing area of male *M. disstria* decreased throughout the flight period. Neither collection date nor microsporidian infection level affected wing area of male *C. conflictana.* Collection date also did not affect the level of microsporidian infection of *C. conflictana*. These data support pheromone trapping as a tool to detect microsporidian infections and examine their temporal and density-dependent effects on wing size in *M. disstria* and *C. conflictana* populations.

Résumé—La livrée des forêts, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), et la tordeuse du tremble, *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae), sont d'importants ravageurs du tremble, *Populus tremuloides* Michx. (Salicaceae), dans l'ouest du Canada. Il est possible de suivre les populations des deux espèces au moyen de pièges munis de phéromones sexuelles dans le cadre d'un programme de lutte intégrée (IPM). On peut aussi utiliser les papillons récoltés dans des pièges pour des études écologiques. Nous avons examiné des mâles de chacune des espèces capturés dans les pièges pour vérifier l'effet de la densité de population, de la région géographique et de la date de récolte sur la qualité des papillons. La qualité des papillons se mesure par la surface alaire et le degré d'infection par les microsporidies parasites. Le degré d'infection aux microsporidies chez *M. disstria* est fortement dépendant de la région géographique, mais non de la densité de population. Les mâles de *M. disstria* des populations de forte densité ont les ailes plus petites que ceux des populations endémiques. La surface alaire des mâles de *M. disstria* diminue au cours de la période de vol. Ni la date de récolte, ni le degré d'infection par les microsporidies n'affectent la taille de l'aile chez les mâles de *C. conflictana*. La date de récolte n'affecte pas non plus le degré d'infection par les microsporidies chez *C. conflictana*. Ces données valident l'utilisation des pièges à phéromones comme outils pour déceler les infections à microsporidies et elles mettent en lumière les effets temporels et les effets dépendants de la densité sur la taille des ailes dans les populations de *M. disstria* et de *C. conflictana.*

[Traduit par la Rédaction]

Introduction

The forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), and large aspen tortrix, *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae), are both serious defoliators of trembling aspen, *Populus tremuloides* Michx. (Salicaceae), in the Nearctic boreal forest. Repeated defoliation of trembling aspen by *M. disstria* is associated with reduced

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[1]Corresponding author (e-mail: bcjones@ualberta.ca).

tree growth (Hildahl and Reeks 1960; Churchill *et al.* 1964) and even mortality (Candau *et al.* 2002). Defoliation by *C. conflictana* is less severe and may cause loss of tree vigor and reduction of incremental growth (Ives and Wong 1988; Cerezke 1992). Populations of both species can be monitored with sex pheromone-baited traps (Schmidt and Roland 2003; Evenden 2005) as part of an integrated pest management program. However, male moths captured in monitoring traps are also a potential source of specimens for ecological studies. Pheromone traps can be checked at intervals throughout the flight season to examine temporal effects on insect quality. Insect body size (Klemola *et al.* 2004) and parasite load (Fitzgerald 1995) may indicate the stage of infestation of insect populations that undergo cyclical changes in population density. In this study we demonstrate some ecological applications of pheromone trapping using male moths captured in sex pheromone-baited traps designed to attract both *M. disstria* and *C. conflictana* (Evenden 2005; Jones 2007). Males of these two outbreaking forest pests were examined to assess moth quality on the basis of size and parasitic infection level.

Microsporidia (Protozoa: Microsporidia) are unicellular parasites that affect many forest Lepidoptera (Maddox *et al.* 1998). Microsporidia occur as resistant spores in the environment until ingested by larvae. However, most microsporidian species can be transmitted either horizontally or vertically via transovariole transmission from mother to offspring (Maddox *et al.* 1998). Microsporidia are found in natural populations of both *M. disstria* (Thomson 1959) and *C. conflictana* (Wilson and Burke 1971). Sublethal microsporidian infections of Lepidoptera are associated with decreased host body size, fecundity, and longevity (Thomson 1958*b*; Gaugler and Brooks 1975; Wilson 1977*a*, 1979; Bauer and Nordin 1989; Evenden *et al.* 2006). The level of microsporidian infection in *M. disstria* increases as population outbreaks progress and insect density increases (Fitzgerald 1995). Thus, the incidence and level of infection potentially have implications for population dynamics of forest Lepidoptera.

Wing area of Lepidoptera is a useful measure of moth quality because adult body size is associated with fecundity (Honek 1993; Evenden *et al.* 2006) and wing size is related to flight ability (Hill *et al.* 1999). Moth wing measurements are indicators of population quality (Bellinger *et al.* 1990; Du Merle and Cornic 1991; Hoffman *et al.* 2002), as insect body size generally decreases during population outbreaks (Elkinton and Liebhold 1990; Klemola *et al.* 2004). In addition, microsporidian infection level and wing area are not independent of each other (Bauer and Nordin 1989). Pheromone trapping can yield specimens for examining moth quality and studying the effects of various factors on the state of adult male Lepidoptera.

We examined the effect of flight period, geographic region, and population density on the quality of male *M. disstria* and *C. conflictana*. Male moths were collected with a combined pheromone-based monitoring system (Evenden 2005; Jones 2007) that attracted both species simultaneously. We hypothesized that both flight period and population density would affect moth quality. Specifically, we predicted that males captured at sites with high population densities would have smaller wings and higher levels of microsporidian infection than males captured at low-density sites. We also expected to see smaller males with a higher level of microsporidian infection later in the flight period (Eveleigh *et al.* 2007). These factors are not independent of each other; thus, we predicted an effect of the interaction between collection date and infection level on wing area. These data provide ecological information on two important forest pests and demonstrate a nontraditional application of pheromone trapping.

Methods and materials

Study sites

Field sites were established in 2005 and 2006 as part of a larger pheromone-based monitoring study of *M. disstria* and *C. conflictana* in central Alberta, Canada (Jones 2007). In 2005 we established 23 field sites in three areas with different densities of *M. disstria* and *C. conflictana* populations. Sites with a high population density of one species served as low-density sites for the other, with additional low-density sites for both species. Stands with greater than 70% defoliation of the canopy were considered severely defoliated and the local population to be at outbreak level. Seven sites were located north of Wabasca, Alberta (56°18′N, 113°45′W), where an outbreak of *M. disstria* was in its fourth year ($\text{Wabasca}_{\text{high density}}$ region). Five sites with endemic populations of both species were established approximately 70 km south of the *M. disstria* infestation (55°37′N, 113°26′W)

(Wabasca$_{\text{low density}}$ region). Nine sites targeting high-density *C. conflictana* populations were established between Rocky Mountain House, Alberta (52°22′N, 114°55′W), and Drayton Valley (53°13′N, 114°59′W) (Rocky–Drayton region). In 2006 we established five additional sites approximately 150 km east of the Wabasca infestation, near Fort McMurray, Alberta (56°17′N, 111°39′W), to target a moderate-density population of *M. disstria* (Fort McMurray). All study sites were at least 1 km apart and stands were dominated by *P. tremuloides*.

Pheromone trapping

Pheromone traps were baited with lures containing a combination of components from each species' identified pheromone. The *M. disstria* blend consisted of (*Z*5,*E*7)-dodecadienal (*Z*5*E*7–12:Ald), (*Z*5,*Z*7)-dodecadienal (*Z*5*Z*7–12:Ald), and *Z*7-dodecanal (*Z*7–12:Ald) in the ratio 100 µg : 1 µg : 10 µg (Schmidt *et al.* 2003). The ratio of components was 100:0.65:10 in 2005 and 100:3.1:10 in 2006. The amount of the *Z*5*Z*7–12:Ald isomer in the *M. disstria* blend cannot be controlled during synthesis and thus varied among years. However, blends containing 1%–10% of *Z*5*Z*7–12:Ald are known to attract male *M. disstria* (Palaniswamy *et al.* 1983; Schmidt *et al.* 2003; Evenden 2005). The individual diene aldehydes cannot be purified, therefore the *E*5*E*7–12:Ald isomer occurred at 13% of the main component in 2005 and 2% in 2006. However, the *E*,*E* isomer is not known to elicit a behavioral response in male *M. disstria* (Chisholm *et al.* 1982). We used 100 µg of (*Z*11)-tetradecenal (*Z*11–14:Ald) for *C. conflictana* (Evenden and Gries 2006) (>99% isomerically pure in both years). Pheromone blends for each species were obtained from Pherotech International Inc., Delta, British Columbia, in HPLC-grade hexane and we loaded both species' pheromones into pre-extracted grey rubber septa (Pherotech International Inc.) lures in the laboratory. Previous work showed no antagonistic effects of heterospecific pheromone components on males' response in either species, since the combined lure was as attractive to male moths as each species' pheromone alone (Evenden 2005; Jones 2007). We used nonsaturating bucket-style Unitraps (Pherotech International Inc.) to accommodate large numbers of captured males at high-density sites and to ensure moths that were in a suitable condition for measurement and dissection after capture. Traps were baited at each site with the combined lure before flight occurred for either species in 2005 and 2006. Traps remained in the field throughout the flight period of both species (June–August). Captured males were collected at approximately 2-week intervals in 2005 and 3-week intervals in 2006. Moths were stored at –20 °C until used for data collection.

Measuring moth quality

Male samples

To assess moth quality we examined male *M. disstria* and *C. conflictana* captured at each site on each collection date. Five moths per site were sampled on each collection date when possible, for a cumulative sample of 30 males of each species per region and collection date in each year. Males were randomly selected from bags containing frozen specimens sorted by site and date. If a selected male had damaged wings it was discarded and another selected. The same male moth was used to measure wing area and determine microsporidian-spore load. The high-density population of *C. conflictana* collapsed in 2005, so density-dependent effects on quality could not be studied for this species. Therefore, only *C. conflictana* collected in the Rocky–Drayton region were assessed for both years. In 2005, insufficient numbers of male *M. disstria* were captured at any site to measure quality indices. *Malacosoma disstria* from all regions were examined in 2006. The Rocky–Drayton region had a substantially larger geographic area than any of the other three regions. Therefore, only *M. disstria* captured at sites near Rocky Mountain House (55°22′N, 114°59′W) in the Rocky–Drayton region were measured so that a similarly sized geographic area in each of the four regions was used.

Wing area

To determine wing area of captured male *M. disstria* and *C. conflictana*, we removed the right forewing with forceps from randomly selected males. Wings were glued onto white paper and scanned with a HP Scanjet 4070 Photosmart scanner. ImageJ 1.34s (United States National Institutes of Health) was used to convert wing images to 8-bit grayscale and then binary, which produced black wing images with sharper edges. Using ImageJ, wings were automatically measured to the nearest 0.001 cm^2.

Microsporidian infection level

To assess microsporidian infection level, we removed abdomens of male *M. disstria* and

C. conflictana and placed them individually into 1 mL microcentrifuge tubes with 0.2 mL of distilled water. Abdomens were ground with a Teflon rod and the solution was homogenized with a vortex. We placed 25 µL of the solution onto a glass microscope slide. Slides were examined under 500× magnification for the presence of microsporidian spores. Large spores (approximately 2.0 × 4.5 µm) from *M. disstria* were found and were presumably of the genus *Nosema* (Thomson 1959). Microsporidian spores from *C. conflictana* were markedly smaller (approximately 1.5 × 2.5 µm) and morphologically similar to those of the genus *Cystosporogenes* (van Frankenhuyzen *et al.* 2004). Ten fields of view were examined for each slide and the level of infection was scored for each male as none, low (1–10 spores per field of view), or high (>10 spores per field of view).

Statistical analyses

Because of few collection dates throughout the flight period, date was treated as a categorical variable. We tested the effect of collection date and geographical region on wing area of male *M. disstria* and the effect of collection date and microsporidian infection level on wing area of male *C. conflictana* using a GLM (SPSS® version 11.0.3; SPSS Inc. 2005) followed by Tukey's HSD test for pairwise comparisons of region and date. A χ^2 likelihood test was employed to test for independence between infection level and collection date.

Results

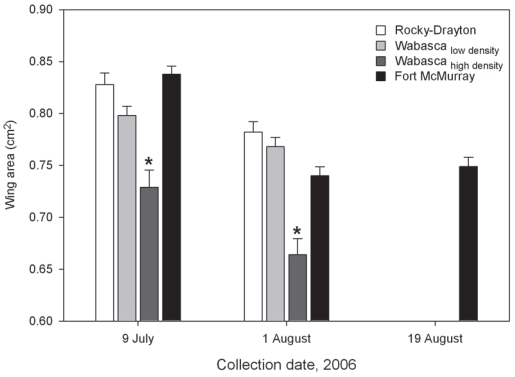
Measuring moth quality

Malacosoma disstria

In 2006, all male *M. disstria* examined from sites in the Rocky–Drayton region were highly infected with microsporidia but all males examined from sites in Fort McMurray and both Wabasca regions were not infected. Therefore, we did not perform further analyses of microsporidian infection for *M. disstria*.

Geographical region and collection date (9 July and 1 August 2006) both had strong effects on *M. disstria* wing area (Fig. 1). Wing area decreased between 9 July and 1 August 2006 in all four regions (Fig. 1). On 19 August 2006, males were captured only in traps in the Fort McMurray region. Collection date had strong effect on wing area ($F_{2,166} = 42.50$, $P < 0.001$) when moths collected on 9 July, 1 August, and 19 August 2006 were included in a separate analysis of data from the Fort McMurray region (moderate population density), but wing area did not decrease further after 1 August (Tukey's HSD test, $P = 0.76$) (Fig. 1). Wing areas of males collected in the Wabasca$_{\text{high density}}$ region (high population density) were smaller than those from all three other regions (Fig. 1). Traps in the Fort McMurray region attracted males with the largest wing area on 9 July 2006, but Fort McMurray males were smaller than both Rocky–Drayton (low population density) and Wabasca$_{\text{low density}}$ (low population density) males on 1 August (Fig. 1) as demonstrated by a significant interaction effect between area and date.

Fig. 1. Effects of collection date ($F_{1,419} = 54.35$, $P < 0.001$) and geographical region ($F_{3,419} = 36.10$, $P < 0.001$) and their interaction ($F_{3,419} = 3.34$, $P = 0.011$) on right forewing area (mean ± SE) of male *Malocosma disstria* in 2006. The wing areas of males from the Wabasca$_{\text{high density}}$ region (*) differ from those of males in all three other regions (Tukey's HSD test, $P < 0.001$). Wing areas of males captured in Fort McMurray on 19 August 2006 are not included in the analysis.



Choristoneura conflictana

Neither collection date nor microsporidian infection level affected wing area of male *C. conflictana* in either 2005 (Fig. 2A) or 2006 (Fig. 3A). Collection date did not affect microsporidian infection level in 2005 (Fig. 2B) or 2006 (Fig. 3B).

Discussion

These data support pheromone trapping as an approach to examining morphological characters and parasitic infections of forest Lepidoptera. We found high levels of microsporidian infection in all male *M. disstria* from the Rocky–Drayton

Fig. 2. (A) Effect of collection date ($F_{3,105}$ = 1.41, P = 0.25) and microsporidian infection level ($F_{2,105}$ = 0.36, P = 0.70) with no interaction ($F_{6,105}$ = 1.05, P = 0.40) on right forewing area (mean ± SE) of male *Choristoneura conflictana* in 2005. (B) Effect of collection date on microsporidian infection level (χ^2_6 = 10.17, P = 0.12).

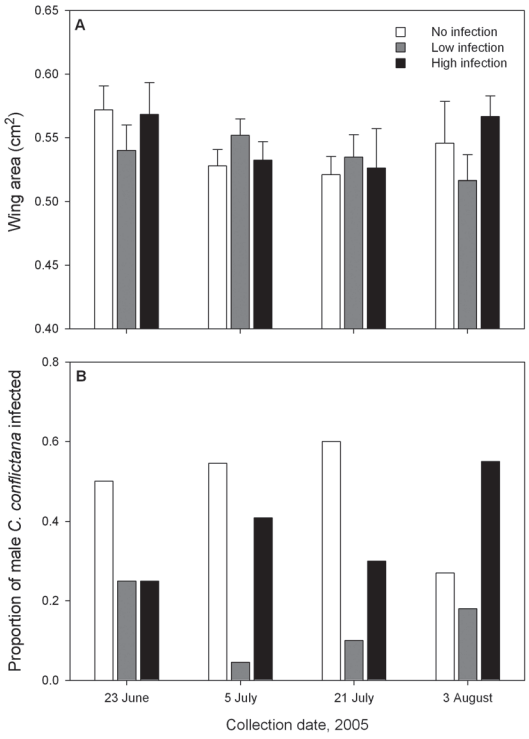
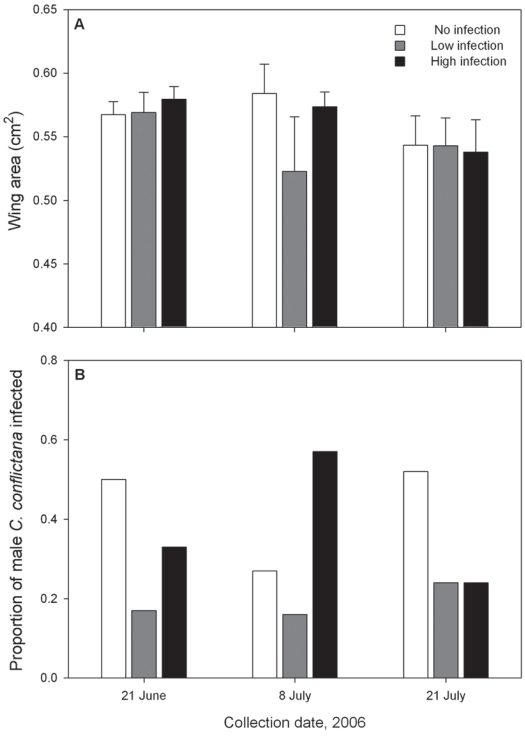


Fig. 3. (A) Effect of collection date ($F_{2,93}$ = 1.32, P = 0.27) and microsporidian infection level ($F_{2,93}$ = 0.98, P = 0.38) with no interaction ($F_{4,93}$ = 0.64, P = 0.63) on right forewing area (mean ± SE) of male *Choristoneura conflictana* in 2006. (B) Effect of collection date on microsporidian infection level (χ^2_4 = 8.85, P = 0.065).



region on both collection dates in 2006. Conversely, spores were not found in male *M. disstria* in any other region on any collection date. We expected to capture highly infected male *M. disstria* in the Wabasca$_{\text{high density}}$ region because population density has been at epidemic levels since 2001 in this region and microsporidian infection increases with population density (Thomson 1958*a*; Wilson 1977*b*; Fitzgerald 1995). Spores accumulate in the environment from silk, feces, or larval carcasses and increase the probability of horizontal transmission (Maddox *et al.* 1998). In 2005 and 2006, microsporidia were found in *C. conflictana*, at varying infection levels, at all sites in the Rocky–Drayton region throughout the flight period. These results show that the incidence and level of microsporidian infection vary among regions for *M. disstria* populations and within and among regions for *C. conflictana*.

Our findings are in accord with previous studies which showed that the incidence of microsporidian infection varies greatly among sites for the moths *C. conflictana* (Wilson and Burke 1971; Burke and Percy 1982), *Malacosoma americanum* (Fabr.) (Lepidoptera: Lasiocampidae) (Nordin 1976), *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) (Wilson 1977*b*), and *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae) (Hill and Gary 1979). In several of these studies larval samples were used, although infection level may be highest at the adult stage, owing to ingestion of spores by developing larvae. Accordingly, using adults is a reliable method to detect infection that would otherwise go undetected if only early-instar larvae were examined. Microsporidian infections do, however, cause larval and pupal mortality in forest Lepidoptera and if samples of adults are used, it is possible that only sublethal effects of infection will be assessed (Wilson 1977*a*; Bauer and Nordin 1989). In future studies, larval and pupal stages of

M. disstria and *C. conflictana* should be sampled to compare microsporidian infection levels with those in pheromone-trapped adult males.

Contrary to our prediction, microsporidian infection level was not affected by flight period for either *M. disstria* or *C. conflictana*. We expected an increase in infection level over the duration of the flight period as a result of slower development of infected individuals as has been observed in *C. fumiferana* (Thomson 1958*a*; Wilson 1977*b*; Eveleigh *et al.* 2007). If adults flying later in the season is a result of slower growth of larvae in a population, then longer periods of foliage consumption will increase exposure to spores in the environment (Wilson 1977*b*). Alternatively, since microsporidian infections slow larval growth in both *M. disstria* (Wilson 1977*a*) and *C. fumiferana* (Thomson 1958*b*), moths that fly later in the season could be expected to be already infected. The variation in infection level in captured male *C. conflictana* indicates that a proportion of highly infected males develop and fly as well as less or uninfected males. Similarly, in the laboratory, microsporidian infection in *C. fumiferana* did not affect flight duration or response to calling females (Sanders and Wilson 1990). For both *M. disstria* and *C. conflictana*, however, larval mortality and reduced flight capability due to microsporidian infection may prevent the capture of a proportion of highly infected males in sex pheromone-baited traps.

We found no evidence that microsporidian infection affected wing size in males of either *M. disstria* or *C. conflictana*. Male *M. disstria* from the Rocky–Drayton region were all highly infected and no infection existed in moths sampled from the other regions. Therefore, region and infection are confounded and it is not possible to conclude whether or not infection would reduce wing size. However, the heavily infected male *M. disstria* from the Rocky–Drayton region had the second largest mean wing size among males from all four regions on 9 July 2006 and the largest on 11 July 2006, suggesting that infection alone does not influence moth size. An effect of microsporidian infection on wing area may be difficult to observe if highly infected males are not captured because of reduced flight capability or pheromone responsiveness. Alternatively, the most highly infected individuals may not survive to eclose as adults and are therefore not represented in the pheromone-trap catch. This hypothesis is supported by findings that *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae) highly infected with a protozoan parasite, *Ophryocystis elektroscirrha* McLaughlin and Myers (Apicomplexa: Neogregarinida), had smaller wing areas than uninfected individuals (Altizer and Oberhauser 1999). However, low to moderate infection levels did not affect wing area of *D. plexippus* (Bradley and Altizer 2005).

Trap-captured male *M. disstria* from the $\text{Wabasca}_{\text{high density}}$ region had significantly smaller wings than males from other regions on both collection dates in 2006. High population density can reduce individual body size (Elkinton and Liebhold 1990) and wing length (Carter *et al.* 1991) in *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). Body size of the autumnal moth, *Epirrita autumnata* (Borkhausen) (Lepidoptera: Geometridae), is smaller at high population densities than at low population densities (Klemola *et al.* 2004). Possible causes of reduced body size at high defoliator densities are a quantitative shortage of foliage, short-term and delayed induced chemical defenses of the host tree, and larval-crowding effects (Klemola *et al.* 2004). In 2006 the $\text{Wabasca}_{\text{high density}}$ outbreak was in its fifth year, thus captured male *M. disstria* may be smaller for all of these reasons.

Wing area of *M. disstria* decreased significantly throughout the flight season and there was a similar nonsignificant trend in *C. conflictana*. Foliage quality of *P. tremuloides* declines over the growing season through an increase in plant defensive compounds, including phenolic glycosides and condensed tannins, as well as constitutive changes such as increased leaf toughness and decreased nitrogen concentration and water content (Hunter and Lechowicz 1992; Osier *et al.* 2000). In addition, short-term induced resistance from herbivory changes foliage chemistry (Clausen *et al.* 1989). These factors adversely affect the development of *M. disstria* (Hemming and Lindroth 1999; Kopper and Lindroth 2003) and *C. conflictana* larvae (Bryant *et al.* 1987; Clausen *et al.* 1989). Larvae that hatch late or grow slowly will obtain lower quality food than those that hatch early or grow quickly (Witter and Waisanen 1978; Hunter and Lechowicz 1992; Jones and Despland 2006). In insects, adult size is determined by larval size, so adults that eclose later in the season are usually smaller than those that eclose earlier (Eveleigh *et al.* 2007).

Our data support the use of pheromone trapping to assess the quality of adult male *M. disstria* and *C. conflictana*. Pheromone traps can be used to detect the level of microsporidian

infection in populations of either species. Furthermore, we demonstrated temporal and density-dependent effects on wing area of captured male *M. disstria*. Future work should involve analysis of other wing dimensions such as length and width. Wing length is a possible predictive factor for monitoring *L. dispar* populations (Bellinger *et al.* 1990; Carter *et al.* 1991) and might be a valuable addition to the development of a combined tool (Evenden 2005; Jones 2007) for monitoring these important aspen defoliators.

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