

VERTICAL AND TEMPORAL DISTRIBUTION OF COCCINELLIDAE (COLEOPTERA) IN FLIGHT OVER AN AGRICULTURAL LANDSCAPE

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Abstract

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Twenty-one species of Coccinellidae were trapped in flight between 0.8 and 14.3 m from 1992 to 1995 in New Brunswick, Canada. Catches were larger at 0.8 m, with a rapidly decreasing capture rate leading, on average, to more than 50% of the catches at or below 3.8 m every year. The capture rate at 14.3 m was lower than at any of the nine other levels. *Hippodamia convergens* Guérin-Ménéville flights were distributed close to the ground, with more than 50% of catches at 0.8 m, whereas *Mulsantina hudsonica* Casey flights were similar at all levels. The strong decreasing gradient of flight as a function of height for Coccinellidae (-0.825) was strongly influenced by that of *H. convergens* (-1.809) and of *Coccinella septempunctata* L. (-0.921) and *Coccinella trifasciata perplexa* Mulsant (-0.715). All other species had a slope of less than -0.5 . The temporal distribution of flights was species specific, with maximum activity before the end of June for most, but this was not reflected in the frequency of catches for the entire family, which did not differ throughout the season, although they tended to be lower after mid-August. The weekly vertical flight distribution differed from the average distribution pattern only occasionally, probably during periods of long-distance dispersal. These profiles and known catches from a single trap location can be used to estimate dispersal activity at different heights.

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Résumé

Vingt et une espèces de Coccinellidae ont été capturées en vol entre 0,8 et 14,3 m de 1992 à 1995 au Nouveau Brunswick, Canada. Les captures étaient plus élevées à 0,8 m. Par la suite, le taux de capture diminuait rapidement pour en arriver à ce que plus de 50% des captures soient, chaque année, à ou sous 3,8 m. Le taux de capture à 14,3 m était plus bas que celui des neuf autres niveaux. Les vols de *Hippodamia convergens* Guérin-Ménéville étaient distribués près du sol avec plus de 50% des captures à 0,8 m, tandis que ceux de *Mulsantina hudsonica* Casey étaient semblables à tous les niveaux. Le gradient négatif prononcé pour le vol des coccinelles en fonction de la hauteur ($-0,825$) est dû en grande partie aux gradients très prononcés de *H. convergens* ($-1,809$) et de *Coccinella septempunctata* L. ($-0,921$) et *Coccinella trifasciata perplexa* Mulsant ($-0,715$). Toutes les autres espèces ont un gradient de moins de $-0,5$. La distribution temporelle des vols était spécifique à chaque

espèce avec le plus haut niveau d'activité avant la fin de Juin pour la plupart; toutefois cela ne se reflète pas dans la fréquence de capture pour la famille, laquelle ne diffère pas pendant la saison, mais est moins élevée après la mi-août. Occasionnellement, la distribution verticale hebdomadaire varie du patron moyen de distribution, probablement durant les moments de dispersion sur de longues distances. Ces profils et captures connues d'un seul piège peuvent être utilisés pour estimer l'activité de dispersion à différentes hauteurs.

Introduction

The use of biological control for the management of insect pests in agriculture is often equated to the introduction or encouragement of Coccinellidae (Coleoptera). In North America, this close association goes back to the introduction of the vedalia beetle, *Rodolia cardinalis* (Mulsant), against the cottony cushion scale in California (Flint and van den Bosch 1981). The rapid range expansions of two recently introduced species, the seven spotted lady beetle, *Coccinella septempunctata* L., and the multicoloured Asian lady beetle, *Harmonia axyridis* (Pallas) (Gordon and Vandenberg 1991; Coderre *et al.* 1995), indicate their successful acclimatization. However, the value of these species as biological control agents of insect pests and their possibly deleterious interactions with native species are still under investigation.

The migratory flights of Coccinellidae to common overwintering sites is well documented (*e.g.*, Hodek 1973; Hodek and Honek 1996). The vertical distribution of flight frequency at high altitude for insects including Coccinellidae has received some attention (*e.g.*, Johnson 1969), but the vertical distribution close to the crops has not (Ewert and Chiang 1966; Fluke 1925, 1929; Hodek 1973). Although they frequently occupy centre stage in biological control, the effectiveness of entomophagous Coccinellidae against insect pests of field crops has been difficult to assess critically. This can be attributed partly to the rapid fluctuations in the abundance of prey in the case of aphidophagous Coccinellidae and to the difficulty of accurately sampling these insects (Frazer and Raworth 1985). The rate of arrivals and departures in mass releases or in natural populations is difficult to estimate because species have different propensities to fly and different flight patterns. Trap height is an important consideration for accurate sampling.

We were interested in describing and contrasting the vertical distribution of Coccinellidae found over an agricultural landscape within the air layer near the ground. Taylor (1965) calculated that insects retain control over their flight within the first 14 m above the ground. Within this space wind speed increases with height and determines the general profile of the flight frequency distribution curve (Taylor 1965). The first objective of this project was to determine a general vertical flight distribution curve for Coccinellidae and to assess the variation between species. The second objective was to determine a general temporal flight distribution pattern for Coccinellidae and to assess the variation among species. The existence and extent of these deviations must be determined before sampling methods can be selected to measure their importance in the potato agroecosystem.

Materials and Methods

Sampling Tower. A 15 m high tower was erected in the early spring of 1992 at the Potato Research Centre (45°55'15"N latitude, 66°36'30"W longitude), Fredericton, New Brunswick, Canada. The tower was located in the middle of a 0.22-ha meadow area surrounded by level fields except for a forest at approximately 130 m on one side. Nearby crops included potatoes, alfalfa, timothy, and clover. The tower was used to hold 40 window traps, 10 on each side. The structure was made up of 10 typical construction scaffolding units, each approximately 1.5 m × 2.4 m × 1.5 m (width × length

TABLE 1. Logarithm-transformed density versus height regression profile parameters for Coccinellidae (Coleoptera) trapped in flight at 10 different heights along a 15-m tower over 4 years (1992–1995), New Brunswick, Canada

Taxa	r^2	Slope	Height of 50% capture (m)	n
<i>Hippodamia convergens</i>	0.972	-1.8086	0.8	279
<i>Coccinella septempunctata</i>	0.8738	-0.9209	3.8	349
Coccinellidae	0.9596	-0.825	3.8	1841
<i>Coccinella trifasciata perplexa</i>	0.8088	-0.7148	3.8	159
<i>Scymnus brullei</i>	0.8273	-0.4801	3.8	44
<i>Harmonia axyridis</i>	0.5692	-0.4584	3.8	32
<i>Chilocorus stigma</i>	0.5667	-0.4512	3.8	35
<i>Anisosticta bitriangularis</i>	0.3443	-0.221	3.8	22
<i>Hyperaspis bigeminata</i>	0.6355	-0.4975	5.3	71
<i>Anatis mali</i>	0.5545	-0.3535	5.3	77
<i>Adalia bipunctata</i>	0.3359	-0.2996	5.3	551
<i>Psyllobora vigintimaculata</i>	0.297	-0.3323	6.8	66
<i>Calvia quatuordecimguttata</i>	0.3483	-0.2951	6.8	57
<i>Mulsantina hudsonica</i>	0.0483	0.1274	9.8	53

× height). The sides of the structure were oriented according to the compass. Window traps on the north and south sides of the tower were fixed to the built-in ladder structure of the scaffolding units, in the centre of each unit. Window traps on the eastern and western sides were bolted on the cross bars of the scaffolding units, in the centre of each unit. The structure was kept as simple as possible to prevent modification of the wind patterns which could affect the flight of the insects that we were attempting to catch with the device. Scouts monitoring the traps were protected by a harness and rope system fixed from the top of the structure. Each window trap was made of a 61 × 69 cm section of plywood painted yellow (British Colour Council, buttercup yellow No. 53; peak reflectance 570 nm) and held perpendicular to the ground. A plastic gutter, capped at both ends, leaving a 61 × 61 cm section of the yellow board free for trapping, was attached on one side of the board. The gutter was filled with a 40% mixture of antifreeze and water (four parts antifreeze to six parts water). In 1992–1994 catches were removed on a daily basis, whenever possible, sorted, identified to species, and recorded. Catches were sorted by morphotypes and general keys used for preliminary identification. Representative specimens were identified by the second author. In 1995, catches were removed on a weekly basis. The traps were operated between 17 May and 26 September in 1992 and between 1 June and 4 October in 1993–1995.

Data Analysis. A regression analysis was applied to the average percentage of flights over the 10 elevations sampled to determine the flight gradient for the family and each species. An analysis of variance and a mean separation test were applied to the average weekly catches over the 4 years of the project. An arcsine transformation was applied to percentage data but reconverted values are presented. Specific vertical profiles for the three most abundant species were contrasted using the χ^2 test and the catch ratio between the upper and lower halves of the sampling tower for the average vertical profile (Coccinellidae) for expected ratio. The temporal distribution of flights for each species was represented graphically for the cumulative catches over the 4 years because of the wide range of abundance between years within a species.

TABLE 2. Weekly vertical flight frequency distribution for three species of Coccinellidae (Coleoptera) wick, Canada

	Week No.								
	1	2	3	4	5	6	7	8	9
<i>Adalia bipunctata</i>									
Height 0.8–6.8	8		5	13	18		58	40	28
Height 8.8–14.3	16		7	9	16		26	17	8
χ^2 for ratio 62:38	8.540		2.164	0.093	1.254		1.652	1.523	3.694
<i>P</i>	0.003		0.141	0.760	0.263		0.199	0.217	0.055
<i>Coccinella septempunctata</i>									
Height 0.8–6.8	10	9		16	10		29		16
Height 8.8–14.3	5	4		9	8		4		4
χ^2 for ratio 78:22	1.108	0.573		2.824	5.244		1.897		0.050
<i>P</i>	0.293	0.449		0.093	0.022		0.168		0.824
<i>Hippodamia convergens</i>									
Height 0.8–6.8	0	0	0	0	0		8		
Height 8.8–14.3	0	0	0	0	0		0		
χ^2 for ratio 95:5	—	—	—	—	—		0.455		
<i>P</i>	—	—	—	—	—		0.500		

NOTE: Data are from 1992 for *A. bipunctata* and *C. septempunctata* and from 1995 for *H. convergens*.

Results

Vertical Flight Frequency Distribution. The vertical flight frequency distribution pattern for Coccinellidae was similar to the general distribution pattern for insects suggested by Taylor (1965) with a strong negative gradient (Table 1). More than 50% of the flights occurred at or below 3.8 m and decreased throughout the tower (Table 1) from base to top. The specific distribution pattern for the 13 most abundant of the 21 species trapped over the years (Fig. 1; Table 1) ranged from a near even likelihood of flight at each elevation for *Mulsantina hudsonica* Casey to more than 50% of flights at the first trap level for *Hippodamia convergens* Guérin-Ménéville. More than 50% of insects in flight were captured at or below 3.8, 5.3, or 9.8 m for 7, 3, and 3 of the 13 species, respectively.

Flight activity for *Adalia bipunctata* L., *H. convergens*, and *C. septempunctata* was high enough in 1992, 1995, and 1992, respectively, to draw vertical profiles at different times throughout the cropping season. The weekly profiles did not differ significantly from the average specific profiles except for the first sampling week with *A. bipunctata* and for the middle of June (weeks 5 and 6) with *C. septempunctata* (Table 2).

Flight Seasonality. The relative abundance of the different beetle species varied between years even with species generally associated with agricultural landscapes such as *H. convergens* or *C. septempunctata* (Table 3). The distribution of average flight activity for Coccinellidae over the sampling period was not different ($F_{19,53} = 1.40$, $P < 0.16$) (Fig. 2). Flight activity in early summer was caused by more beetle species than in mid and late summer. Nine of the 13 most abundant species reached their maximum weekly flight frequency by June 23 (week 6, Table 3), but some did not reach it until early August (week 12) or late September (week 19), and some reached it later in some years. Maximum weekly flight activity occurred at the same time in all years for *Calvia quatuordecimguttata* (L.), *Hyperaspis bigeminata* Randall, *Scymnus brullei* Mulsant, and *Coccinella trifasciata perplexa* Mulsant. It differed between years for

compared with the average distribution pattern for that species (week 1 = 17–23 May), New Brun-

Week No.										
10	11	12	13	14	15	16	17	18	19	20
27	18	----- 14 -----	-----	-----	-----	----- 10 -----	-----	-----	0	0
10	5	----- 4 -----	-----	-----	-----	----- 5 -----	-----	-----	0	0
1.810	2.501	----- 1.847 -----	-----	-----	-----	----- 0.124 -----	-----	-----	—	—
0.178	0.113	----- 0.174 -----	-----	-----	-----	----- 0.724 -----	-----	-----	—	—
38	39	-----	-----	-----	----- 18 -----	-----	-----	-----	—	—
6	17	-----	-----	-----	----- 2 -----	-----	-----	-----	—	—
1.817	2.24	-----	-----	-----	----- 1.693 -----	-----	-----	-----	—	—
0.178	0.134	-----	-----	-----	----- 0.193 -----	-----	-----	-----	—	—
-----	53	77	0	74	-----	-----	----- 12 -----	-----	-----	-----
-----	2	2	0	1	-----	-----	----- 0 -----	-----	-----	-----
-----	0.327	1.257	-----	2.410	-----	-----	----- 0.682 -----	-----	-----	-----
-----	0.567	0.262	-----	0.12	-----	-----	----- 0.409 -----	-----	-----	-----

A. bipunctata, *Anatis mali* Say, *M. hudsonica*, *Psyllobora vigintimaculata* (Say), *Hippodamia convergens*, and *C. septempunctata*.

Discussion

The flight profile gradient for Coccinellidae with a slope of -0.825 is similar to that for Coleoptera at -1.0442 obtained by Taylor (1974). Similar or steeper slopes were found in only three of the 13 lady beetle species, leaving 77% with a slope of -0.498 or less. However, 50% of the flights for seven of the 13 species were at or below 3.8 m. This pattern is characteristic of the trivial flights of insects within or close to the boundary layer. The relative dispersal activity of these coccinellid beetles can be estimated from traps located at one height, but this would underestimate flight activity for species like *H. convergens* and overestimate it for species like *M. hudsonica*.

Deviations from the Coccinellidae pattern were not related to the size of the different species. The size of the beetles sampled in this project ranged from 2.5 to 9 mm in body length. There was no significant relation between wing loading estimated by body length (Price 1997) and the height at which each species reached a cumulative 50% flight frequency ($y = -0.198x + 4.607$, $r^2 = 0.0627$). Differences in flight behaviour or ecology are more likely to explain deviations from the Coccinellidae pattern than differences in body size.

It is difficult to compare the results obtained here with those of other ecosystems because no other complete vertical profiles have been published. Our results confirm that *H. convergens* disperses close to the ground during its trivial flights (Ewert and Chiang 1966) and extend its recorded flight height to 14.3 m. The flight distribution frequency for this species does not represent an inability to fly higher because this species was reported to take off at a vertical angle and rapidly climb out of sight for long-distance dispersal (Hodek 1973). The different take-off angle would allow these beetles to clear the traps on the tower when dispersing farther. Ewert and Chiang (1966) reported that *Hippodamia tredecimpunctata* L. flew up to 3.6 m with 90% of flights at 0.9 m in a way similar to that of *H. convergens*. Only six *H. tredecimpunctata* were captured in our project, making it impossible to determine the pattern. Similarly, *Hippodamia parenthesis* Say, reported to fly as high as 9 m (Fluke 1929), was captured

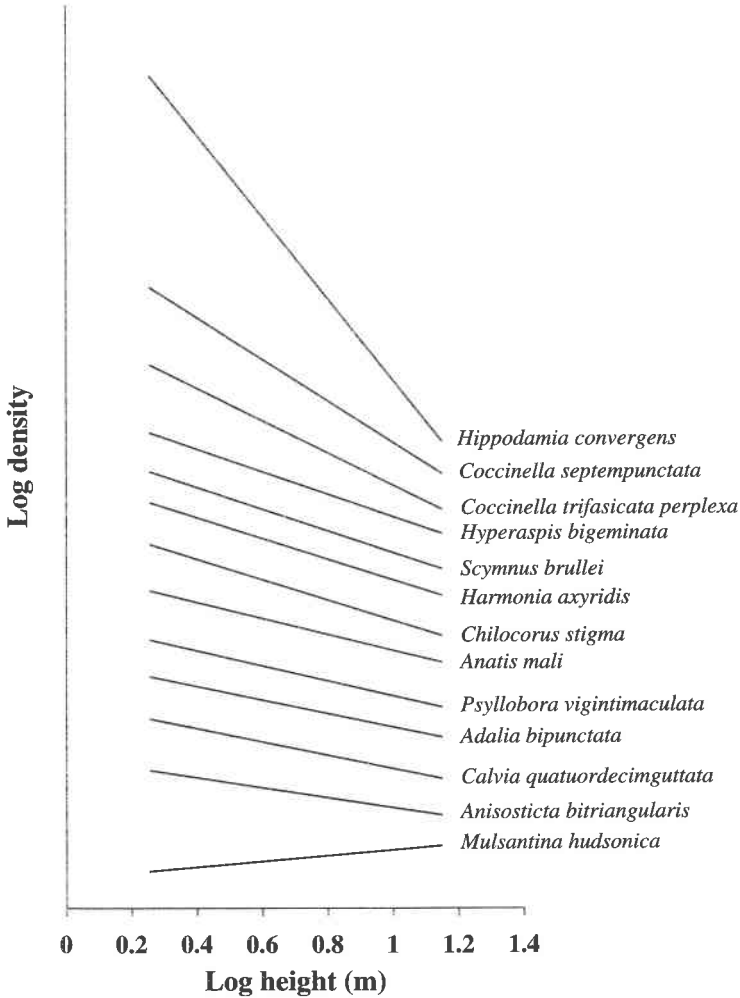


FIGURE 1. Regression profiles for 13 species of Coccinellidae (Coleoptera) trapped over a 4-year period in a New Brunswick agroecosystem. The vertical scales are staggered.

too infrequently to determine its profile. Ewert and Chiang did not capture *Coleomegilla maculata* DeGeer above the 0.9-m trap, suggesting that it would have a distribution pattern even lower than that for *H. convergens*. *Coleomegilla maculata* is rare in New Brunswick. It was not trapped in this project nor was it trapped between 1979 and 1981 (Boiteau 1983). Ewert and Chiang suggested that phytophagous species may have less of a need to disperse than aphidophagous species such as *H. convergens* and *H. tredecimpunctata*. It is possible that these species, like *H. convergens*, have a steeper take-off angle for long-distance dispersal than for trivial flights and that they escape traps at relatively low elevation.

Harmonia axyridis is the most recent coccinellid introduction to establish itself in Canada and was reported for the first time in Quebec in 1994 (Coderre *et al.* 1995). In New Brunswick, *H. axyridis* was not trapped in the tower until 1995, although its presence was noted elsewhere in New Brunswick the same year (A.G. Wheeler Jr., personal

TABLE 3. Seasonal distribution of all species of Coccinellidae (Coleoptera) trapped between 1992 and 1995 with total catch greater than 20 (week 1 = 17-23 May), New Brunswick, Canada

Species	No. of individuals per year					Week No.																				
	1992	1993	1994	1995	year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
<i>Anisosticta bitriangularis</i>	19	0	1	2	7*	2	3	1	3	2	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Chilocorus stigma</i>	0	4	3	28	0	0	18*	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	5*	5*
<i>Hyperaspis bigeminata</i>	7	7	10	47	0	0	16	30*	11	7	0	0	0	0	0	0	3	0	1	2	0	1	0	0	0	0
<i>Mulsantina hudsonica</i>	31	9	3	10	0	0	2	17*	7	5	3	0	0	4	6	7*	0	0	1	0	0	1	0	0	1	0
<i>Anatis mali</i>	27	1	9	40	1	0	16	20*	8	1	0	3	3	14*	5	2	2	1	0	0	0	0	0	1	0	0
<i>Scymnus brullei</i>	0	9	10	25	0	0	7	5	5	8*	3	2	0	0	0	1	0	2	3	0	4	2	1	1	1	1
<i>Coccinella trifasciata perplexa</i>	86	33	27	13	15	5	20	47*	26	17	5	1	2	3	2	3	0	3	0	3	2	1	2	4	0	1
<i>Coccinella septempunctata</i>	244	32	20	53	15	5	15	33*	26	14	5	38	20	62	75*	16	8	4	2	1	4	2	1	4	2	0
<i>Calvia quatuordecimguttata</i>	26	13	13	5	3	1	4	10	8	13*	7	6	1	2	1	1	0	0	0	0	0	0	0	0	0	0
<i>Adalia bipunctata</i>	362	69	51	32	19	6	24	40	56	40	95*	87	57	52	28	15	8	4	8	2	1	3	5	1	1	1
<i>Psyllobora vigintimaculata</i>	0	5	23	38	0	0	0	8	10	5	15*	4	12	6	4	1	0	1	0	1	0	0	0	0	0	0
<i>Hippodamia convergens</i>	5	15	30	229	0	0	1	1	1	1	0	1	0	6	55	79*	0	76*	9	1	7	14	16	11	11	11
<i>Harmonia axyridis</i>	0	0	0	32	0	0	0	0	0	0	0	0	0	1	2	5*	2	0	5	2	0	8*	2	2	2	3

NOTE: Less abundant species (i.e., ≤20) are as follows: *Propylea quatuordecimpunctata*, *Hippodamia tredecimpunctata*, *Mysia pullata randalli*, *Coccinella hieroglyphica kirbyi*, *Hyperaspis undulata*, *Brachyacantha ursina*, and *Hippodamia parenthesis*.

*Weeks of maximum abundance.

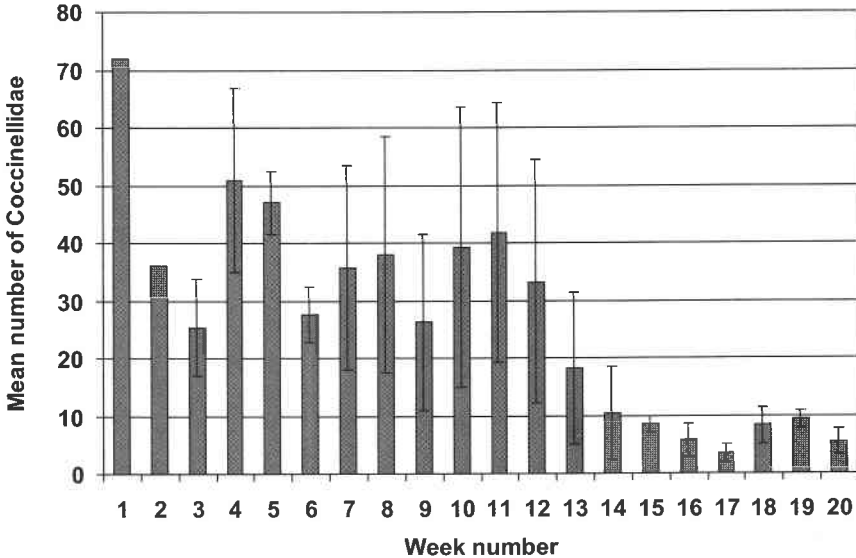


FIGURE 2. Average flight frequency (\pm SE) for Coccinellidae (Coleoptera) in New Brunswick between 1992 and 1995. Week 1 = 17–23 May; weeks 1 and 2 were monitored only in 1992.

communication). The vertical flight frequency distribution profile of *H. axyridis* is similar to that of Coccinellidae.

Mulsantina hudsonica is not an insect of economic importance but showed an even distribution of flight frequency over height. Not enough is known about the species to explain the pattern. One could speculate that it is a strong flyer that retains full control over its dispersal as the impact of the wind increases with height.

The flight frequency for most coccinellid species in most years was too low to study the seasonal variations of the vertical flight frequency distribution. However, data from *A. bipunctata*, *C. septempunctata*, and *H. convergens* demonstrate that seasonal variation does exist and varies between species, although it is probably limited to periods of long dispersal. Therefore, the vertical flight distribution during the crop season varies little. *Adalia bipunctata* frequently overwinters at the edge of forests from which it recolonizes the fields each spring (Laroche 1979). We suggest that the significantly different flight profile observed in the first week of observations reflects the end of the spring long-distance dispersal. In the case of *C. septempunctata*, a significantly different profile occurred about 1 month later than that for *A. bipunctata*. This species is more cosmopolitan and the profile change may still reflect long-distance dispersal from one type of overwintering site or from a spring host. In the case of *H. convergens*, it is likely that migratory flights from the overwintering sites occurred outside of our monitoring period.

Overall flight activity recorded in this project is made up of localized trivial flights as coccinellids move among plants or crops in a fashion that may reflect prey abundance. The relative abundance of prey at the study site and the particular combination of crops probably explain the variations in flight activity within each species between years. Peak flight activity is also probably dependent on crop phenology and prey availability. Flight activity for most species and peak activity for more than 50% of the species start in early spring as vegetation resumes growth, suggesting that their flight is well adapted to relatively low ambient temperatures. The introduced multicoloured Asian lady beetle, *H. axyridis*, was not trapped until the warm temperatures of July in 1995, but it inhabits a wide range of environments throughout the world (e.g., Coderre

et al. 1995). This suggests that the species captured for the first year in New Brunswick did not build up a significant population in the area before the middle of summer.

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