

## Diversity and Seasonal Activity of Ground Beetles (Coleoptera: Carabidae) in Two Vineyards of Southern Quebec, Canada

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**ABSTRACT** From 1997 to 1999, 11,435 specimens of ground beetles representing 124 species were captured in pitfall traps at two commercial vineyards in southern Quebec, Canada. Taking into account only the species breeding or likely breeding in the two vineyards, the carabid diversity was similar over the 3-yr period in both sites. The number of species was similar (51 and 54) in both vineyards, but the most common species were ranked differently in a position that was consistent over the 3-yr period. *Chlaenius sericeus* (Forster) and *Clivina fossor* (L.) occurred mainly on the clay loam vineyard, and *Amara latior* (Kirby) and *Harpalus herbivagus* Say on the gravel and sand loam vineyard. The Shannon diversity and evenness indexes were greater at the gravel and sand loam vineyard. Two recently introduced European species, *Harpalus rufipes* (Duftschmid) and *Pterostichus vernalis* (Panzer), became more prevalent between 1997 and 1999 and are likely to affect the rank position at each site. Diversity at the clay loam vineyard was equal to another unsprayed and annually cultivated site on clay in the ecozone. It shared with the unsprayed site a similar number of species for an equal sample size, Shannon and evenness indexes, and for most species, ranking of the most commonly trapped species.

**KEY WORDS** Carabidae, biodiversity, bioindicator, diversity, ranking

IN SOUTHERN QUEBEC, CANADA, ≈300 species of ground beetles have been recorded (Lindroth 1961, 1963, 1966, 1968, 1969a; Larochelle 1975). In this ecozone, up to 250 species have been recorded over an area of 25–36 km<sup>2</sup>. Among these beetles, 60–70 species probably breed in cultivated agricultural sites with annual crops (Rivard 1966, Frank 1971, Levesque and Levesque 1994, Raworth et al. 1997). Therefore, in this ecozone, ≈25% of the species of an ecologically diverse region are likely to occur in typical agricultural sites. Each species of ground beetle has specific environmental requirements (Lindroth 1961, 1963, 1966, 1968, 1969a; Larochelle 1975). Knowledge of these requirements helps in recognizing species typical of a study site from those wandering through it.

Ground beetles also are good indicators of habitat types and environmental quality in terms of the effects of pesticides (Lindroth 1945, Rainio and Niemela 2003). Adults and larvae of most species are predators

(Kromp 1999), a few species are omnivorous (Baldur 1935, Lund and Turpin 1977a, Larochelle 1990), and a few others feed on seeds (Alcock 1976, Lund and Turpin 1977b, Thiele 1977).

Our study of ground beetles is part of a larger study on beneficial and harmful insects at the northern end of the production area of commercial vineyards in North America (Bostanian et al. 2003). Ground beetles were singled out for environmental assessment of two vineyards where research was supported by their owners. Our study aimed to (1) record variation in abundance and diversity within each vineyard over three consecutive seasons; (2) compare species diversity between the two vineyards based on ranking of the 10 most-frequently captured species; (3) compare species diversity, diversity, and evenness indexes and ranking of commonly trapped species in these vineyards with other sprayed and unsprayed agricultural sites; and (4) discuss the significance of fallow or hay fields as sources of ground beetles in agricultural ecosystems.

### Materials and Methods

The study was done in two commercial vineyards, i.e., Dietrich-Jooss (45° 16' N 73° 11' W) and L'Orpailleur (45° 07' N 72° 51' W) vineyards near Iberville and Dunham, respectively, Quebec, Canada. The study plot at Dietrich-Jooss was on clay loam. It

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Table 1. Number of carabid specimens captured in pitfall traps positioned in two commercial vineyards in southern Quebec

Vineyard	Year	Sampling period	No. pitfall traps	No. specimens	No. species
Dietrich-Jooss	1997	10 June–17 Sept.	23	1,242	42
	1998	6 May–2 Sept.	34	3,077	59
	1999	6 May–2 Sept.	34	3,340	51
	Total			7,659	81
L'Orpailleur	1997	10 June–17 Sept.	16	460	33
	1998	6 May–2 Sept.	20	1,199	56
	1999	6 May–2 Sept.	20	2,098	66
	Total			3,776	89
Grand Total				11435	124

was surrounded by vines on three sides and a fallow band ( $\approx 15$  m in width) with a creek near the edge of the south side. The study plot at L'Orpailleur was on sand and gravel loam, had a large fallow field and a small bushy site on the west side, an apple orchard on the north side, and cultivated vines on the east and south sides. In both vineyards, the soil was managed similarly. The topsoil was cultivated twice a year; in the spring to uncover the short vines, and in the fall, to cover their basal stocks (Bostanian et al. 2003). Weeds were managed by cultivation. Up to 1996, the research sites were treated with pesticides against mites, insects, weeds, and fungi. During our study, only fungicides Captan (Captan 50 WP), metaxyl (Ridomil 72 WP), metiram (Polyram 80 WP), and myclobutanil (Nova 40 WP) were applied at label rates as registered in Canada against powdery and downy mildew (Bostanian et al. 2003).

Data from the Dietrich Jooss vineyard were compared with data from an oat field near Wakefield, Quebec ( $45^{\circ} 44' 04''$  N  $75^{\circ} 49' 09''$  W) in 2001. This site is in a valley ( $\approx 1$  km<sup>2</sup>) that had never been treated with pesticides. We also studied a soybean field at the Central Experimental Farm in Ottawa, Ontario ( $45^{\circ} 22' 46''$  N  $75^{\circ} 43' 04''$  W) in 1999. This site has a long and complex history of pesticide use since the early 1960s. In the past 10 years, the main pesticides sprayed have been herbicides. The soil at the three latter sites was classified as clay loam.

Pitfall traps were used to collect adult ground beetles at all sites mentioned above. Captures may be affected by numerous variables (Greenslade 1964, Thiele 1977), but they adequately reflect the diversity of ground beetles of a site. The pitfall traps used in both vineyards were designed by L. LeSage and consisted of a 1.3-cm-thick plywood frame (outside dimensions 19.5 by 26.5 cm; inside dimensions 11.8 by 18.7 cm). The upper surface of the wood frame was routed along the inner side to form a 1-cm-wide and 0.25-cm-deep groove. The outer frame edges were cut at  $45^{\circ}$  to ease the junction between the frame and soil. A transparent rectangular (18.5 by 11.5 cm, and 5.5 cm in depth) vinyl container was painted bright yellow on the outside surface. The pitfall trap doubled its role as a yellow pan trap. The edge of the vinyl container had a flat 6–7-mm-wide rim fitting into the plywood. This pitfall trap was effective in dry as well

as in wet periods. Ethylene glycol was used as a preservative. At the Ottawa and Wakefield sites, respectively, nine and 20 ramp traps were used (Bouchard et al. 2000).

In Table 1 we summarized the sampling periods and the number of pitfall traps used for each year and site. The traps were placed 4–6 m apart to prevent an excessive sampling of specimens in the area. The number of captures for the same trapping period varied between sites and between years within each site. The larger the sample, the more likely it would have a greater diversity of species. However, the relationship between the number of specimens captured and the species diversity was nonlinear. The diversity between sites or between years within a site was compared by rarefaction calculations (Simberloff 1978). These calculations were done according to Brzustowski (2004).

The Shannon index ( $H'$ ), the evenness index ( $J'$ ), and the Chao-1 nonparametric estimator of species richness were used to evaluate the diversity of ground beetles at each site. Species richness was based on the number of species represented by one or two specimens at a site and a given period (Chao 1984, 1987; Colwell and Coddington 1994) by using a procedure available at Brzustowski (2004). All specimens were kept at the Canadian National Collection, Agriculture and Agri-Food Canada, Ottawa.

## Results and Discussion

**Species and Data Considered.** Adults of 11,435 specimens representing 124 species were captured from 1997 to 1999 inclusive. Among these, 7,659 specimens (81 species) were captured at Dietrich-Jooss and 3,776 specimens (89 species) at L'Orpailleur (Table 1). Based on habitat preferences (Lindroth 1961, 1963, 1966, 1968, 1969a; Larochelle 1975), 53 species were unlikely to breed in the two vineyards. These unexpected species, listed in Table 2, represented 42% of the total diversity but only 1.7% of total captures (192 specimens), and were not considered further in the biodiversity analyses. Table 3 contains the basis for the following analyses, and only species likely to breed with the number of captures in the 3-yr period at each site are listed. At the Dietrich-Jooss and L'Orpailleur vineyards, respectively, 7,535 specimens (51 species)

Table 2. Species, its typical habitat, and number of carabids captured but unlikely to breed at each vineyard

Carabid species	Habitat	Vineyard	
		L'Orpailleur	Dietrich-Jooss
<i>Acupalpus alternans</i> (LeConte)	Marshes	1	
<i>Acupalpus pauperculus</i> Dejean	Marshes	1	10
<i>Agonum gratiosum</i> (Mannerheim)	Marshes	1	
<i>Agonum palustre</i> Goulet	Marshes	1	
<i>Agonum retractum</i> LeConte	Leaf litter	2	
<i>Agonum trigeminum</i> Lindroth	Marshes		6
<i>Amara obesa</i> (Say)	Sand and gravel pits	4	1
<i>Amara quenseli</i> (Schonherr)	Sand and gravel pits	1	1
<i>Amphasia interstitialis</i> (Say)	Wet places	2	
<i>Anisodactylus discoideus</i> Dejean	Marshes		1
<i>Anisodactylus nigrita</i> Dejean	Marshes		1
<i>Anisodactylus rusticus</i> (Say)	Sand and gravel pits	5	
<i>Apristus subsulcatus</i> (Dejean)	Sand and gravel pits	3	1
<i>Atranus pubescens</i> (Dejean)	Beaver houses	1	1
<i>Badister notatus</i> Haldeman	Leaf litter	1	1
<i>Bembidion frontale</i> (LeConte)	Marshes		1
<i>Bembidion concretum</i> Casey	Marshes	1	
<i>Bembidion minus</i> Hayward	Wet clay bank	6	15
<i>Bembidion patruale</i> Dejean	Wet clay bank		8
<i>Bembidion versicolor</i> (LeConte)	Wet clay bank	7	48
<i>Bradycellus nigriceps</i> LeConte	Sand and gravel pits	1	
<i>Chlaenius lithophilus lithophilus</i> Say	Marshes		1
<i>Chlaenius pennsylvanicus pennsylvanicus</i> Say	Marshes		6
<i>Chlaenius sericeus sericeus</i> (Forster)	Wet clay bank	3	
<i>Cicindela duodecimguttata</i> Dejean	Wet sand banks		1
<i>Cymindis cribricollis</i> Dejean	Sand and gravel pits	1	
<i>Diplocheila impressicollis</i> (Dejean)	Marshes		1
<i>Dyschirius brevispinus</i> LeConte	Gravel creek banks		1
<i>Dyschirius integer</i> LeConte	Wet clay bank		1
<i>Dyschirius politus</i> Dejean	Wet sand banks		2
<i>Dyschirius sphaericollis</i> (Say)	Wet sand banks		1
<i>Polyderis laevis</i> (Say)	Wet clay bank	1	
<i>Elaphrus californicus</i> Mannerheim	Wet clay bank		2
<i>Harpalus erraticus</i> Say	Sand and gravel pits	1	
<i>Loricera pilicornis pilicornis</i> (F.)	Marshes		2
<i>Notiobia terminata</i> (Say)	Sand and gravel pits	1	
<i>Omophron americanus</i> Dejean	Wet sand banks		1
<i>Paratachys rhodeanus</i> (Casey)	Marshes	2	
<i>Perigona nigriceps</i> (Dejean) <sup>a</sup>	Moist organic habitats		1
<i>Porotachys bisulcatus</i> (Nicolai) <sup>a</sup>	Moist organic habitats	8	1
<i>Pseudamara arenaria</i> (LeConte)	Leaf litter	1	
<i>Pterostichus coracinus</i> (Newman)	Leaf litter	1	
<i>Pterostichus luctuosus</i> (Dejean)	Wet places	1	
<i>Pterostichus mutus</i> (Say)	Leaf litter	3	
<i>Selenophorus opalinus</i> (LeConte)	Sand and gravel pits		1
<i>Sphaeroderus stenostomus lecontei</i> Dejean	Leaf litter	1	
<i>Stenolophus ochropezus</i> (Say)	Marshes	1	5
<i>Stenolophus plebejus</i> Dejean	Marshes	1	
<i>Synuchus impunctatus</i> (Say)	Leaf litter	1	
<i>Tachyta angulata</i> Casey	Under tree bark	2	
<i>Tetragonoderus fasciatus</i> (Haldeman)	Wet sand banks		1
<i>Trechus apicalis</i> Motschulsky	Leaf litter	1	
<i>Trichotichmus vulpeculus</i> (Say)	Leaf litter	1	

<sup>a</sup> Accidentally introduced species.

and 3,685 specimens (54 species) likely to breed were captured (Table 4).

**Species Diversity between Sampling Seasons within Each Vineyard.** As the sampling period and the number of traps used varied between seasons at each site (Table 1), the trapping efficiency was expressed as the number of specimens per trap per week because almost 1 mo of data were missing in spring 1997. A summary of captured carabids and species for the complete season and the restricted season is reported in Tables 4 and 5.

**Trapping Rate.** At both sites, the 1997 season had the least and 1999 the highest mean number of captures (Table 4). The range between seasons in the number of specimens per trap per week was smaller at the Dietrich-Jooss than at the L'Orpailleur vineyard (Table 4). A possible explanation may be a more pronounced effect of hot and dry weather in summer 1999 on activity and/or abundance of ground beetles at L'Orpailleur than at Dietrich-Jooss.

**Diversity.** At Dietrich-Jooss, the diversity for 1997 was 1 standard deviation lower than the expected

Table 3. Number of carabids captured over a 3-yr period and expected to breed in each vineyard

Carabid species	Dietrich-Jooss			L'Orpailleur		
	1997	1998	1999	1997	1998	1999
<i>Agonum cupripenne</i> (Say)		1			2	
<i>Agonum muelleri</i> (Herbst) <sup>a</sup>		3 <sup>S</sup>				
<i>Agonum nutans</i> (Say)		1 <sup>S</sup>				
<i>Agonum placidum</i> (Say)	8	32	41	3	65	75
<i>Amara aenea</i> (DeGeer) <sup>a</sup>	5	9	20		19	15
<i>Amara angustata</i> (Say)				5 <sup>S</sup>	1 <sup>S</sup>	7 <sup>S</sup>
<i>Amara apricaria</i> (Paykull) <sup>a</sup>		1	3	1	2	3
<i>Amara aulica</i> (Panzer) <sup>a</sup>	2	5	3	22 <sup>F</sup>	29 <sup>F</sup>	13 <sup>F</sup>
<i>Amara avida</i> (Say)	3 <sup>F</sup>	6 <sup>F</sup>	9 <sup>F</sup>			2
<i>Amara bifrons</i> Gyllenhal <sup>a</sup>						1 <sup>S</sup>
<i>Amara convexa</i> LeConte					2 <sup>S</sup>	
<i>Amara cupreolata</i> Putzeys					1 <sup>S</sup>	
<i>Amara familiaris</i> (Duftschmid) <sup>a</sup>		2	5		2	4
<i>Amara impuncticollis</i> (Say)				9 <sup>S</sup>	13 <sup>S</sup>	
<i>Amara latior</i> (Kirby)	38			87 <sup>F</sup>	165 <sup>F</sup>	188 <sup>F</sup>
<i>Amara littoralis</i> Mannerheim	20	8	17	3	10	24
<i>Amara musculus</i> (Say)						1 <sup>S</sup>
<i>Amara patruelis</i> Dejean				1 <sup>S</sup>		
<i>Amara rubrica</i> Haldeman			3 <sup>S</sup>			
<i>Anisodactylus harrisii</i> LeConte	4	6	1	9	11	18
<i>Anisodactylus nigerrimus</i> (Dejean)					2 <sup>S</sup>	
<i>Anisodactylus sanctaerucis</i> (F.)	181	343	342	28	92	321
<i>Bembidion nitidum</i> (Kirby)					1 <sup>S</sup>	1 <sup>S</sup>
<i>Bembidion obscurellum</i> (Motschulsky) <sup>a</sup>		3 <sup>S</sup>	3 <sup>S</sup>			
<i>Bembidion obtusum</i> Audinet-Serville <sup>a</sup>		1				1
<i>Bembidion quadrimaculatum oppositum</i> Say	80	175	360	27	50	205
<i>Bembidion tetracolum</i> Say <sup>a</sup>		2 <sup>S</sup>	2 <sup>S</sup>			
<i>Blemus discus</i> (F.) <sup>a</sup>		3 <sup>S</sup>	6 <sup>S</sup>			
<i>Bradycellus neglectus</i> (LeConte)	1		2	1		
<i>Bradycellus nigriceps</i> LeConte		3	4			2
<i>Bradycellus rupestris</i> (Say)		3	5	5 <sup>F</sup>	18 <sup>F</sup>	23 <sup>F</sup>
<i>Calathus opaculus</i> LeConte					1 <sup>S</sup>	
<i>Carabus granulatus granulatus</i> L. <sup>a</sup>			1 <sup>S</sup>			
<i>Chlaenius sericeus sericeus</i> (Forster)	15 <sup>S</sup>	30 <sup>S</sup>	44 <sup>S</sup>			
<i>Chlaenius tricolor</i> Dejean	6	27	14	6	18	15
<i>Cicindela punctulata punctulata</i> Olivier			3			
<i>Cicindela sexguttata sexguttata</i> F.	7 <sup>F</sup>	4 <sup>F</sup>	4 <sup>F</sup>	1	2	
<i>Clivina fossor</i> (L.) <sup>a</sup>	49 <sup>F</sup>	270 <sup>F</sup>	249 <sup>F</sup>	15	24	33
<i>Cymindis americanus</i> Dejean				1 <sup>S</sup>	1 <sup>S</sup>	
<i>Diplocheila obtusa</i> (LeConte)	1	5			9 <sup>F</sup>	16 <sup>F</sup>
<i>Dyschirius globulosus</i> (Say)		4	1		7	1
<i>Elaphropus anceps</i> (LeConte)					6	27
<i>Elaphropus incurvus</i> (Say)	2	7	22	8	13	10
<i>Harpalus affinis</i> (Schrank) <sup>a</sup>	36	89	199	13	59	106
<i>Harpalus compar</i> LeConte		31 <sup>F</sup>	25 <sup>F</sup>	1		4
<i>Harpalus erythropus</i> Dejean		1	4	1	2	4
<i>Harpalus fallax</i> LeConte	1			4 <sup>F</sup>	3 <sup>F</sup>	5 <sup>F</sup>
<i>Harpalus faunus</i> Say		2	4	1	3	
<i>Harpalus herbivagus</i> Say	3	7	4	8 <sup>F</sup>	22 <sup>F</sup>	38 <sup>F</sup>
<i>Harpalus indigens</i> Casey					5 <sup>S</sup>	
<i>Harpalus longicollis</i> LeConte		1				1
<i>Harpalus pennsylvanicus</i> (DeGeer)	125	268	652	36	164	525
<i>Harpalus plenalis</i> Casey						2 <sup>S</sup>
<i>Harpalus reversus</i> Casey	1 <sup>S</sup>					
<i>Harpalus rubripes</i> (Duftschmid) <sup>a</sup>						1 <sup>S</sup>
<i>Harpalus rufipes</i> (DeGeer) <sup>a</sup>	1	1	2	2 <sup>F</sup>	34 <sup>F</sup>	124 <sup>F</sup>
<i>Harpalus somnulentus</i> Dejean						1 <sup>S</sup>
<i>Lebia fuscata</i> Dejean						1 <sup>S</sup>
<i>Lebia grandis</i> Hentz						1 <sup>S</sup>
<i>Lebia solea</i> Hentz		1 <sup>S</sup>				
<i>Patrobus longicornis</i> (Say)	1 <sup>S</sup>	2 <sup>S</sup>	1 <sup>S</sup>			
<i>Poecilus chalcites</i> (Say)		8 <sup>S</sup>	5 <sup>S</sup>			
<i>Poecilus lucublandus</i> (Say)	17	98	53	16	32	43
<i>Pterostichus melanarius</i> (Illiger) <sup>a</sup>	422	1,401	1,069	82	192	54
<i>Pterostichus vernalis</i> (Panzer) <sup>a</sup>	1 <sup>F</sup>	16 <sup>F</sup>	8 <sup>F</sup>		1	3
<i>Selenophorus gagatinus</i> Dejean						1 <sup>S</sup>
<i>Stenolophus comma</i> (F.)	188	152	87	53	94	138
<i>Stenolophus conjunctus</i> (Say)	1 <sup>S</sup>		3 <sup>S</sup>			
<i>Stenolophus lineola</i> (F.)	1 <sup>S</sup>					
<i>Syntomus americanus</i> (Dejean)				1 <sup>S</sup>		
<i>Trechus rubens</i> (F.) <sup>a</sup>			1 <sup>S</sup>			

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Table 3. (Continued)

Carabid species	Dietrich-Jooss			L'Orpailleur		
	1997	1998	1999	1997	1998	1999
Total of specimens	1,220	3,032	3,281	450	1,177	2,058
Three-years total of specimens			7,535			3,685
Total no. of species	29	41	40	30	39	42
Three-year total of species			51			54
No. of species shared between the two vineyards	20	28	26	20	28	26
% of species shared	69	68	65	67	72	62
Total of species shared			65			61
Shannon index of diversity (H')	2.20	2.07	2.21	2.69	2.87	2.65
Shannon index of diversity (H') (3 yr)			2.22			2.84
Evenness index (J')	0.59	0.51	0.56	0.77	0.71	0.63
Evenness index (J') (3 yr)			0.51			0.63

<sup>a</sup> Accidentally introduced species.

<sup>b</sup> S, species found in one site only.

<sup>c</sup> F, species that is at least five times more captured at one site than at the other.

mean as estimated in the rarefaction calculations. However, there was a marked decrease for 1999 as the diversity was >2 standard deviations below the expected mean, as estimated in the rarefaction calculations (Table 5). When capture rates for 1999 were compared with those of 1998, there was a reduction in number of species captured weekly and of specimens captured per trap per week after mid-July 1999 (Table 4).

At L'Orpailleur, there were no significant differences in the estimated diversity for 1997 and 1998, but there was a marked decrease for 1999 because the observed diversity was >3 standard deviations below the expected mean, as estimated in the rarefaction calculations (Table 5). When weekly capture rates for 1999 were compared with those for 1998, there was a decrease in the number of species weekly and of specimens captured per trap per week during July and August. The number of specimens per trap per week in summer was 4.7 or ≈30% lower than the 6.1 for the complete season (Table 4). In 1999, adults of a number of species such as *Pterostichus melanarius* (Illiger), a summer-active species, were captured in markedly lower numbers than in previous years.

The decrease of the observed diversity in 1999 at both sites was significant, especially at L'Orpailleur (Table 5). The average number of specimens per trap

per week was higher for the complete season than the restricted season, but this difference supports a more significant decrease during the summer period, especially at L'Orpailleur.

Adults of some species may have been less mobile at both sites because the weather in 1999 was exceptionally hot and dry. Species with mesic adaptations may have been more affected at L'Orpailleur because the sand and gravel loam dried even earlier. This is supported by samples from Wakefield, where in mid-July capture rates decreased to ≈20% of expected captures in 2001 (H.G., unpublished). The period between mid-July and early August 2001 had the highest recorded temperatures in the region in addition to severe drought conditions. Ground beetles at Wakefield may have started a dormancy period, moved away, or died.

Despite the cessation of pesticide use, there was no increase in species diversity from 1997 to 1999 at each vineyard. The decrease in diversity observed at both sites in 1999 was more likely the result of a hot and dry period, during the summer, on the mobility rate of adults of some species.

*Indexes of Diversity and Evenness.* The Shannon diversity and evenness indexes showed consistently higher values at L'Orpailleur (Table 3). The higher diversity index also is supported by higher estimated

Table 4. Total number of carabid specimens and species captured at each vineyard yearly, and mean number of adults captured per trap per week

Vineyard	Year	No. traps	Complete season			10 June–2 Sept.		
			No. wk	No. adults	No. adults/trap/wk	No. wk	No. adults	No. adults/trap/wk
Dietrich-Jooss	1997	23	15	1,220	3.5	14	1,132	3.5
	1998	34	17	3,034	5.3	14	2,461	5.2
	1999	34	17	3,281	5.7	14	2,476	5.2
	Total	30.3 <sup>a</sup>	49	7,535	5.1	42	6,064	4.8
L'Orpailleur	1997	16	14	451	2.0	14	424	1.9
	1998	20	17	1,176	3.5	14	900	3.2
	1999	20	17	2,058	6.1	14	1,321	4.7
	Total	18.7 <sup>a</sup>	48	3,685	4.1	42	2,645	3.4

<sup>a</sup> This is avg no. of traps used over the 3-yr period at a vineyard.

**Table 5.** Estimated diversity of carabid species (calculated rarefaction values) for the number of specimens captured each year at each vineyard, and the observed diversity of species recorded each year at each vineyard for a shared period between 6 May and 2 September for 1998 and 1999, and between 10 June and 2 September for 3 yr at each vineyard

Vineyard	Year	6 May–2 Sept.				10 June–2 Sept.			
		Sample size	Observed diversity	Estimated diversity	Std. dev.	Sample size	Observed diversity	Estimated diversity	Std. dev.
Dietrich-Jooss	1997	— <sup>a</sup>	—	—	—	1,132	28 <sup>SD1b</sup>	30.75	2.39
	1998	3,026	40	41.96	1.72	2,461	39	38.29	2.11
	1999	3,289	41 <sup>SD1</sup>	42.55	1.64	2,476	34 <sup>SD2</sup>	38.35	2.11
L'Orpailleur	1997	—	—	—	—	424	29	29.45	2.15
	1998	1,176	39	39.89	2.34	900	34	35.38	2.14
	1999	2,058	42 <sup>SD2</sup>	46.25	1.97	1,321	31 <sup>SD3</sup>	38.79	2.07

<sup>a</sup> Data not used, as incomplete for the period in 1997.

<sup>b</sup> SD1, SD2, and SD3 denote a difference of 1, 2, or 3 standard deviations between the observed and the estimated diversity values.

diversity calculated from the Chao-1 nonparametric estimator (Table 6). The higher evenness value at L'Orpailleur was due to a lower number of specimens of the few dominant and mostly adventive species than at Dietrich-Jooss. At Dietrich-Jooss, adults of *P. melanarius* were dominant because this species represented 34–43% of all captures, whereas at L'Orpailleur there were no species representing >20% of the total captures. Although we have no hard evidence, the marked dominance of few adventive species may have displaced native species, leading to lower diversity and evenness indexes.

**Estimated Diversity.** Based on the Chao-1 nonparametric estimator of species richness, 60–76 species were estimated for the 3 yr at L'Orpailleur (Table 6). This is a reliable diversity estimate compared with Lindroth (1961, 1969a, b) and Laroche (1975). The estimates between seasons were all <75 species and were reliable diversity estimates (Lindroth 1961, 1969a, b; Laroche 1975). Comparable but lower values (31–59) were recorded for the period between 10 June and 2 September (based on individual years as the 3-yr calculations with 120–265 were not realistic values). Similarly, 36–64 species (based on individual years because it could not be calculated for the 3-yr periods because of lack of species recorded in the two specimen class) were estimated for 3 yr at Dietrich-Jooss (Table 6). Similar values (51–68 species) were calculated for the period between 10 June and 2 September. Thus, within a 3-yr period, a high proportion

of the expected diversity of ground beetles was captured at each site (i.e., between 80 and 100% at Dietrich-Jooss and between 70 and 90% at L'Orpailleur).

**Species Diversity between the Two Vineyards.** *Shared species.* In 1998 and 1999, 83 and 85% of species were shared at Dietrich-Jooss, and 69 and 74% of the species were shared at L'Orpailleur, respectively (Tables 3 and 9). Thus, there was a high degree of similarity between the observed diversity each year within each site. In the 3-yr period, 61–72% of species were shared by both vineyards (Table 3). There was a greater proportion of shared species between seasons at each site than between sites, indicating a difference in the diversity between both sites.

*Ranking of Species.* Table 7 shows the ground beetle capture rankings at Dietrich-Jooss for the 3-yr period. *P. melanarius* was consistently the most commonly captured species. The 10 most commonly captured species showed a moderate range in ranking positions. For example, the capture rank of *Anisodactylus sanctaecrucis* (F.) placed this species between the second and fourth position over the 3-yr period. This rather consistent ranking among more commonly trapped species supported our hypothesis that ground beetles were likely to be good biological indicators of the environmental quality of agricultural sites. Some commonly captured species showed a much wider range of rankings over the years. For example, *Amara littoralis* Mannerheim was less often captured in 1998

**Table 6.** The Chao-1 nonparametric estimator of species richness (i.e., estimate of the maximal species diversity) based on the distribution of expected carabid species represented by one and two specimens for the entire season (6 May–2 Sept.) and a share period (i.e., between 10 June and 2 Sept.) yearly and for the 3-yr study at each vineyard

Vineyard	Year	Complete season			10 June–2 Sept.		
		Observed diversity	Estimated diversity	Standard deviation	Observed diversity	Estimated diversity	Standard deviation
Dietrich-Jooss	1997	29	49.6	13.9	28	35.2	6.5
	1998	41	47.1	4.9	39	71.7	18.1
	1999	40	44.2	4.0	34	36.1	3.1
	Total	51	n/a <sup>a</sup>	n/a	47	59.5	8.3
L'Orpailleur	1997	30	46.0	11.8	29	41.2	9.6
	1998	39	43.1	3.4	34	45.7	7.9
	1999	42	62.2	12.7	31	47.0	11.7
	Total	54	68.0	8.0	47	192.5	72.9

<sup>a</sup> The estimator could not be calculated because there were no species represented by two specimens.

**Table 7.** Ranking of carabids captured at the Dietrich-Jooss vineyard for the most commonly trapped species with a narrow range of relative position, followed by species showing marked range variations in relative position from 1997 to 1999

Species	Year			Avg rank <sup>a</sup>	Range in rank <sup>b</sup>
	1997	1998	1999		
Species with consistent rank					
<i>Pterostichus melanarius</i> (Illiger) <sup>c</sup>	1	1	1	1.0	1-1 (1)
<i>Anysodactylus sanctaecrucis</i> (F.)	3	2	4	3.0	2-4 (3)
<i>Harpalus pensylvanicus</i> (DeGeer)	4	4	2	3.3	2-4 (3)
<i>Bembidion quadrimaculatum oppositum</i> Say	5	5	3	4.3	3-5 (3)
<i>Clivina fossor</i> (L.) <sup>c</sup>	6	3	5	4.6	3-6 (4)
<i>Stenolophus comma</i> (F.)	2	6	7	5.0	2-7 (6)
<i>Harpalus affinis</i> (Shrank) <sup>c</sup>	8	8	6	7.3	6-8 (3)
<i>Poecilus lucublandus</i> (Say)	10	7	8	8.3	7-10 (4)
<i>Chlaenius sericeus sericeus</i> (Forster)	11	11	9	10.3	9-11 (3)
<i>Agonum placidum</i> (Say)	12	9	10	10.3	9-12 (4)
Species with marked changes in rank					
<i>Amara littoralis</i> Mannerheim	9	15	14	12.6	9-15 (7)
<i>Pterostichus vernalis</i> (Panzer) <sup>c</sup>	21	13	17	17	13-21 (9)
<i>Harpalus compar</i> LeConte	30	10	11	17	10-30 (21)

<sup>a</sup> The "avg rank" is the sum of the rank position each year divided by 3.

<sup>b</sup> The "range in rank" is the lowest and highest rank recorded in the 3-yr period followed by the number of rank positions (in parentheses) within the range.

<sup>c</sup> Accidentally introduced species.

and 1999 and *Harpalus compar* LeConte, a regularly trapped species in 1998 and 1999, was not captured in 1997. *Pterostichus vernalis* (Panzer) is an unusual species. It was reported near Montreal, Quebec, by Beaulne (1914). Since then, it had not been recorded despite the efforts of numerous collectors. It was assumed that Beaulne's specimen was mislabeled, as were those of many other species that he reported (Lindroth 1969b). The nearly simultaneous discovery of this species in 1997 south of Montreal at Dietrich-Jooss and in Vermont 3 km south of the Canadian border (Byers et al. 2000) suggests that it had recently become established. Many more specimens were captured in 1998 and 1999. We assume that the species is in the process of establishing its rank position among other species of ground beetles in both vineyards.

The rankings for many species at L'Orpailleur (Table 8) were similar to those at Dietrich-Jooss, but some of the most commonly captured species were almost peculiar to this site [e.g., *Amara latior* (Kirby)], and other species were less commonly seen at Dietrich-Jooss (Table 7). L'Orpailleur has a different soil type. It consists of organic matter, sand, and gravel. Such a site is more suitable to ground beetles requiring very well drained habitats. This site had a diverse array of *Amara* and *Harpalus* species. Four species showed a greater range of rank positions. The variation of the *P. melanarius* capture rates was unexpected. Captures of this species, ranked in previous years in the first and second position, fell drastically in 1999 to ninth position. Perhaps the hot and dry conditions in 1999 caused this species to become less

**Table 8.** Ranking of carabids captured at the L'Orpailleur vineyard for the most commonly trapped species with a narrow range of relative rank positions, followed by species showing marked range variations in relative rank from 1997 to 1999

Species	Year			Avg rank <sup>a</sup>	Range in rank <sup>b</sup>
	1997	1998	1999		
Species with consistent rank					
<i>Amara latior</i> (Kirby)	1	2	4	2.3	1-4 (4)
<i>Harpalus pensylvanicus</i> (DeGeer)	4	3	1	2.6	1-4 (4)
<i>Stenolophus comma</i> (F.)	3	4	5	4.0	3-5 (3)
<i>Anisodactylus sanctaecrucis</i> (F.)	5	5	2	4.0	2-5 (4)
<i>Bembidion quadrimaculatum oppositum</i> Say	6	8	3	5.6	3-8 (6)
<i>Harpalus affinis</i> (Shrank) <sup>c</sup>	10	7	7	8.0	7-10 (4)
<i>Poecilus lucublandus</i> (Say)	8	10	10	8.6	8-10 (3)
<i>Clivina fossor</i> (L.) <sup>c</sup>	9	12	12	11.0	9-12 (4)
<i>Harpalus herbivagus</i> Say	14	13	11	12.6	11-14 (4)
Species with marked changes in rank					
<i>Pterostichus melanarius</i> (Illiger) <sup>c</sup>	2	1	9	4.0	1-9 (9)
<i>Agonum placidum</i> (Say)	19	6	8	11.0	6-19 (14)
<i>Harpalus rufipes</i> (DeGeer) <sup>c</sup>	21	9	6	12.0	6-21 (16)
<i>Amara aulica</i> (Panzer) <sup>c</sup>	7	11	20	12.6	7-20 (14)

<sup>a</sup> The "avg rank" is the sum of the rank position each year divided by 3.

<sup>b</sup> The "range in rank" is the lowest and highest rank recorded in the 3-yr period followed by the number of rank positions (in parentheses) within the range.

<sup>c</sup> Accidentally introduced species.

active, to move elsewhere, to die or enter into aestivation. *Amara aulica* (Panzer), a species well adapted to dry conditions, is a European species that may require more mesic conditions and, for reasons mentioned under *P. melanarius*, it may have become less common in 1999. *Agonum placidum* (Say) and *Harpalus rufipes* (DeGeer) were more commonly captured after 1997. *H. rufipes* was the more interesting of the two species. In 1997 at both sites, we captured the first specimens of this European species in southern Quebec. It was previously recorded from northeastern United States (Zhang et al. 1994, 1997), the Maritime regions and the Gaspé peninsula. L'Orpailleux was the vineyard where the species became markedly common. In 1998, *H. rufipes* was often captured (position 9), and by 1999, it had become the sixth most commonly captured species of ground beetle at this site while remaining rare at the Dietrich-Jooss site. The L'Orpailleux site had a rank order that was consistent for at least nine species.

Among the more commonly trapped species, *Chlaenius sericeus* (Forster) and *Clivina fossor* (L.) best characterized the Dietrich-Jooss site, and *A. latior* and *Harpalus herbivagus* Say, the L'Orpailleux site. Other less commonly captured species that were restricted to or almost entirely restricted to each site are listed in Table 3. If a species in this list had a capture frequency greater than four, it was probably a characteristic species of this site. Below this frequency, a species may not have been restricted to a site as it was probable that it could be found at both sites, given a larger sample size. Thus, the diversity of the 10 most commonly trapped species and their ranking was consistent from year to year at each site. Such ranking is a practical way for comparing sites.

**Comparison of the Vineyard Sites with Other Agricultural Sites.** Because the ground beetle diversity at each vineyard basically remained similar over the 3-yr period, we did not know whether the observed diversity at each vineyard was rich or impoverished after a long period of intensive use of pesticides. Therefore, we compared ground beetle capture data from two other agricultural sites, one in Ottawa and another at Wakefield. Because ground beetles are sensitive to the type of soil, we could not consider the L'Orpailleux data, because there were no ground beetle data recorded from another site with sand and gravel loam soil in the same ecozone.

**Diversity at a Pesticide-Free Site.** At Wakefield, only the period 7 May to 14 July was considered because after mid-July the capture rate of most species of ground beetles markedly dropped after an extremely hot and dry period. Twenty-eight species were trapped at Wakefield for that period. The rarefaction calculations were based on the Dietrich-Jooss sample for the same period and gave a mean of 27.18 species and a standard deviation of 2.22 for a subsample size equal to that of Wakefield (688 specimens). The Shannon diversity ( $H' = 2.06$ ) and the evenness indexes ( $J' = 0.57$ ) were also similar for samples from both sites (Table 3). Except for the commonly trapped *Bembidion obtusum* Audinet-Serville and *Bembidion*

Table 9. Number of carabid species shared between seasons within each vineyard for 1998 and 1999

Vineyard	No. shared species	1998		1999	
		No. species	% shared species	No. species	% shared species
Dietrich-Jooss	34	41	83	40	85
L'Orpailleux	29	39	74	42	69

*quadrinaculatum oppositum* Say, the species rank of ground beetles at Wakefield was similar to that of the Dietrich-Jooss vineyard. The observed difference in rank of these two spring and day active species may be due to pesticide use in the general vicinity of the Dietrich-Jooss vineyard. The crops in the vineyard region are corn and soybean that are sprayed with herbicides in the spring. As sprays are applied, adults of these species could be directly exposed to the sprays or their drift.

Gregoire-Wibo (1983) showed that herbicides increase the number of many small day active ground beetles as adults prefer open habitats, but there were no observations about the long-term effect at her research sites. In southern Quebec, the following species, *Agonum placidum* (Say), *Bembidion tetracolum* Say, *B. obtusum*, and *Syntomus americanus* (Dejean) are much rarer today than they were in the early 1960s (H.G., unpublished) after the establishment of commercial corn crops in the region between 1970 and 1980. This crop has an herbicidal protocol and it replaced much of the alfalfa, a very widespread crop in the region. Muller (1971) clearly showed the toxic effect of many herbicides on ground beetles. Despite different herbicides in use today, the above-mentioned species are rarely or are no more captured. Thus, present day herbicides are very suspect in absence toxicological studies.

**Diversity at a Site with Long-Term Pesticide Use.** At the Ottawa site, we captured 3,767 specimens that represented 27 species. This sample extended over a similar sampling period to the Dietrich-Jooss vineyard. At the Dietrich-Jooss vineyard, we captured 3,034 specimens that represented 41 species in 1998 and 3,281 specimens that represented 40 species in 1999. The rarefaction calculations for the Ottawa sample suggested 25.35 species with a standard deviation of 1.16 for a subsample of 3,034 specimens, and 25.93 species with a standard deviation of 0.97 for a subsample of 3,281 specimens. The diversity observed at the Ottawa site was highly significantly lower than the observed diversity at Dietrich-Jooss for 1998 and 1999. The Shannon diversity ( $H' = 1.18$ ) and evenness indexes ( $J' = 0.36$ ) for the Ottawa site relative to those of Dietrich-Jooss showed a marked decrease value (Table 9). Thus, at the Ottawa site common species were even more common whereas other species were much more uncommon. The main change in the species diversity at the Ottawa site is the absence or the near absence of specimens of species with a spring reproductive cycle. The Dietrich-Jooss vineyard sample was much more diverse for every year of the study.

Therefore, the diversity observed in 1998 and 1999 at Dietrich-Jooss was as diverse as an unsprayed site immediately after the termination of pesticide sprays in the fall of 1996. This also seemed to be the case in 1997, although early season data were missing. This was unexpected as numerous studies in Europe clearly have shown that sites with heavy pesticide use have a remarkably reduced diversity of species (Thiele 1977). Moreover, all types of pesticides have been shown to affect negatively ground beetle diversity and abundance (Muller 1971, Thiele 1977, Freitag 1979, Gregoire-Wibo 1983). The most likely hypothesis is that the ground beetles at both vineyards came from a rich and unsprayed source area during fall 1996 and spring 1997. Such a source area, namely, a fallow field with a similar species assemblage of ground beetles, was adjacent to each of our research sites. The diversity of ground beetles at the Central Experimental Farm in Ottawa after long-term use of pesticides is markedly reduced. Contrary to the Dietrich-Jooss vineyard, the Central Experimental Farm site is surrounded by other sprayed fields and is far from any source area to compensate for specimen or species losses.

**Significance of Fallow Sites as a Source of Ground Beetles.** As observed in Europe, the fauna of fallow fields was similar to that of cultivated land with similar soil and drainage conditions (Thiele 1977). The species of ground beetles found in numerous agricultural and fallow fields sampled in southern Quebec for a period of 5 yr in the early 1960s confirm the European observations (H.G., unpublished).

Normally fallow and hay fields are not sprayed. However, fallow fields are left unused for several years, and hay fields are cut at least once a year. The fallow field along the Dietrich-Jooss vineyard was a 15–20-m-wide band with a creek in the middle. The fallow field at the L'Orpailleur vineyard was much larger. In Europe, hedgerows are important, and their elimination has a marked negative effect on the diversity and abundance of ground beetles and other insects (Kromp 1999). Most European hedgerows consist of trees or large bushes with leaf litter. They act as corridors for the wildlife and forest adapted insects. They are excellent refuges and hibernation sites for ground beetles (Thiele 1977). However, marsh and forest edges are not as ideal as fallow or hay fields because they are unsuitable for ground beetles breeding in southern Quebec. Adults of most field adapted species of ground beetles do not occur on wet soil or in the forest leaf litter during the breeding season (H.G., unpublished), unless the marsh is dried up or the ground under these forest edges is exposed to light with a rich layer of herbs. Therefore, fallow or hay fields are important as obvious source areas that could replenish many of the ground beetle species in depleted agricultural sites (Kromp 1999).

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#### References Cited

- Alcock, J. 1976. The behaviour of the seed-collecting larvae of a carabid beetle (Coleoptera). *J. Nat. Hist.* 10: 367–375.
- Balduf, W. V. 1935. The bionomics of entomophagous Coleoptera. John S. Swift, New York.
- Beaulne, J.-L. 1914. Les coléoptères du Canada. II Carabiques. *Nat. Can.* 40–43.
- Bostanian, N. J., C. Vincent, H. Goulet, L. LeSage, J. Lasnier, J. Bellemare, and Y. Mauffette. 2003. The arthropod fauna of Quebec vineyards with particular reference to the pests. *J. Econ. Entomol.* 96: 1221–1229.
- Bouchard, P., T. A. Wheeler, and H. Goulet. 2000. Design for a low-cost, covered, ramp pitfall trap. *Can. Entomol.* 132: 387–389.
- Brzustowski, J. 2004. Rarefaction calculator. <http://www.biology.ualberta.ca/jbrzusto/rarefact.php>.
- Byers, R. A., G. M. Barker, R. L. Davidson, E. R. Hoebeke, and M. A. Sanderson. 2000. Richness and abundance of Carabidae and Staphylinidae (Coleoptera), in northeastern dairy pastures under intensive grazing. *Great Lakes Entomol.* 33: 81–105.
- Chao, A. 1984. Nonparametric estimation of the number of classes in a population. *Scand. J. Stat.* 11: 265–270.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43: 783–791.
- Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B* 345: 101–118.
- Frank, J. H. 1971. Carabidae (Coleoptera) of an arable field in central Alberta. *Quaest. Entomol.* 7: 237–252.
- Freitag, R. 1979. Carabid beetles and pollution. In T. L. Erwin, G. E. Ball, and D. R. Whitehead (eds.), *Carabid beetles: their evolution, natural history, and classification*. Dr. W. Junk, The Hague, The Netherlands.
- Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *J. Anim. Ecol.* 2: 301–310.
- Gregoire-Wibo, C. 1983. Incidence écologique de traitements phytosanitaires en culture de betteraves sucrière. II. Acariens, polydesmes, staphylinins, cryptophagides et carabides. *Pedobiologia* 25: 93–108.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impact and enhancement. In M. G. Paoletti (ed.), *Invertebrate biodiversity as bioindicators of sustainable landscape*. *Agric. Ecosyst. Environ.* 74: 187–228.
- Larochelle, A. 1975. Les Carabidae Québec et du Labrador. Département de Biologie du Collège Bourget, Rigaud, Qc, Canada. Bull. 1.
- Larochelle, A. 1990. The food of carabid beetles (Coleoptera: Carabidae, including Cicindelinae). *Fabrerias Suppl.* 5: 1–132.
- Levesque, C., and G. Levesque. 1994. Abundance and seasonal activity of ground beetles (Coleoptera: Carabidae)

- in a raspberry plantation and adjacent sites in southern Quebec (Canada). *J. Kans. Entomol. Soc.* 67: 73–101.
- Lindroth, C. H. 1945. Die Fennoskandischen Carabidae. Eine Tiergeographische Studie. I. Spezieller Teil. Elanders Boktryckeri Aktiebolag, Goteborg, Sweden.
- Lindroth, C. H. 1961, 1963, 1966, 1968, 1969a, 1969b. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, part 2. *Opusc. Entomol. Suppl.* 20: 1–200; 24: 201–408; 29: 409–648; 33: 649–944; 34: 945–1192; 35: I–XLVIII.
- Lund, R. D., and F. T. Turpin. 1977a. Serological investigation of Black Cutworm larval consumption by ground beetles. *Ann. Entomol. Soc. Am.* 70: 322–324.
- Lund, R. D., and F. T. Turpin. 1977b. Carabid damage to weed seeds found in Indiana cornfields. *Environ. Entomol.* 6: 695–698.
- Muller, G. 1971. Laboruntersuchungen zur Wirkung von Herbiziden auf Carabiden. *Arch. Pflanzenschutz* 7: 351–364.
- Rainio, J., and J. Niemela. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers. Conserv.* 12: 487–506.
- Raworth, D. A., S. J. Clements, C. Cirkony, and Y. Bousquet. 1997. Carabid beetles in commercial raspberry fields in the Fraser Valley of British Columbia and a sampling protocol for *Pterostichus melanarius* (Coleoptera: Carabidae). *J. Entomol. Soc. B. C.* 94: 51–58.
- Rivard, I. 1966. Ground beetles (Coleoptera, Carabidae) in relation to agricultural crops. *Can. Entomol.* 98: 189–195.
- Simberloff, D. S. 1978. Use of rarefaction and related methods in ecology, pp. 150–165. *In* K. L. Dickson, J. Cairns, Jr., and R. J. Livingston (eds.), *Biological data in water pollution assessment: quantitative and statistical analyses*. Am. Soc. Test. Mat. STP 652, Philadelphia, PA.
- Thiele, H.-U. 1977. Carabid beetles in their environments. A study on habitat selection by adaptation in physiology and behavior. Springer, Berlin, Germany.
- Zhang, J., F. Drummond, and M. Liebman. 1994. Spread of *Harpalus rufipes* DeGeer (Coleoptera: Carabidae) in eastern Canada and the United States. *Entomol. Trends Agric. Sci.* 2: 67–71.
- Zhang, J., F. Drummond, M. Liebman, A. Hartke. 1997. Biology of *Harpalus rufipes* DeGeer, an exotic ground beetle invading Maine and Northeastern North America. *Trends Entomol.* 1: 63–70.

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