

**GROUND-DWELLING WEEVIL
(COLEOPTERA: CURCULIONIDAE) COMMUNITIES IN
FRAGMENTED AND CONTINUOUS HARDWOOD FORESTS
IN SOUTH-CENTRAL ONTARIO**

E. PROCTOR¹, R. S. ANDERSON², E. NOL³,
J. M. GIRARD⁴ AND S. RICHMOND⁵

Department of Environmental and Life Sciences, Trent University
1600 West Bank Drive, Peterborough, ON, Canada K9J 7B8
email: eproctor@trentu.ca

Abstract

J. ent. Soc Ont. 141: 69- 83

Weevils (Coleoptera: Curculionidae) are the largest family in the animal kingdom and can be found in any habitat where plants grow. Many species not native to North America have invaded both anthropogenic and natural habitats, and the aim of this paper is to determine whether forest landscape continuity has discouraged introduced species. We compared the ground-dwelling weevil communities of hardwood forest fragments to those in hardwood stands in a continuously forested landscape, with the prediction that the fragments would have more introduced species. Pitfall traps caught 5090 individuals from 26 species. Both landscapes were dominated by introduced weevils (96% of all individuals), but forest fragments were dominated by *Barypeithes pellucidus* (Boheman), while *Sciaphilus asperatus* (Bonsdorff) represented 74% of all weevils caught in the continuous forest. Sixty-four percent of the introduced species were parthenogenetic, and all parthenogenetic species were polyphagous and flightless. Fifteen native species were captured but they accounted for only 4% of total individuals, and the only numerous native species, *Hormorus undulatus* (Uhler), was absent from the continuous forest. Seven native species were each represented by a single individual, one of which, *Sirocalodes sericans* (LeConte) is the first record for Ontario. Ground-dwelling weevil communities in central Ontario's forests are composed largely of non-native species, and relatively intact forests do not provide conservation protection for this group of invertebrates.

Published November 2010

¹ Author to whom all correspondence should be addressed

² Canadian Museum of Nature, email: randerson@mus-nature.ca

³ Biology Department, Trent University, email: enol@trentu.ca

⁴ Biology Department, Carleton University, email: jphilli8@connect.carleton.ca

⁵ Faculty of Forestry, University of Toronto email: sonya.richmond@utoronto.ca

Introduction

The family Curculionidae (Coleoptera), hereafter weevils, is the largest family in the animal kingdom and contains about 51000 species worldwide, in 4600 genera (Anderson 1997; Oberprieler et al. 2007). As larvae and adults, almost all weevils are phytophagous, although a few species are saprophagous. While most of the phytophagous species are associated with angiosperms, weevils can be found in association with almost any terrestrial or freshwater plant species, and any plant part (Anderson 2002; Oberprieler et al. 2007). The largest subfamily, Entiminae, have larvae that mostly live in the soil and feed on roots. Both adult and larval entimines are largely polyphagous, feeding on many species of host plants. The other 17 subfamilies contain species whose larvae tend to live and feed inside plant parts including stems, leaves, roots and reproductive structures. These subfamilies also tend to have a more restricted range of host plants (monophagous or oligophagous), some limited to a single family, genus or species (Anderson 2002).

There are about 600 described weevil species in Canada, many of which are introduced (McNamara 1991). Most of the introduced species are of European origin (Langor et al. 2009) and most introductions are attributed to the importation of ornamental plants and other products, or to dry ballast (rock, soil and sand) dumped by British ships at North American seaports at the turn of the nineteenth century (Anderson 2002; Majka et al. 2007). Introduced weevils are prevalent in forested habitats. Pinski et al. (2005a) found 66.4% of all adult Curculionidae caught in northern hardwood forests in the Great Lakes region to be an introduced species (*Phyllobius oblongus* L.) and Coyle et al. (2008) reported a suite of nine invasive root-feeding weevils from this same region. Maerz et al. (2005) found one introduced weevil, *Barypeithes pellucidus* (Boheman), to be more abundant than all other beetle taxa combined in mature forest stands in New York and Pennsylvania. These past studies show the prevalence of introduced weevils in forests, but it is not known whether any large forest stands in Ontario provide refuge for native species.

Niemelä and Mattson (1996) argue that European phytophagous insects are better at invading North American forests than their North American counterparts are at invading European forests, especially in disturbed or fragmented landscapes where the plant communities are partially European in origin (Burke and Nol 1998). Periods of glaciation, more severe in Europe due to its topography than elsewhere in the world (Huntley 1993), and the past 6000 years of human habitation and exploitation (Ledig 1992) resulted in a long history of expansion and contraction of European forests. Through this volatility, traits having high survival-value in patchy landscapes were selected over those adapted to expansive forests. Armed with such traits as phenotypic plasticity, high reproductive potential, and stress-tolerance mechanisms, many introduced species have become the dominant phytophagous insects in their invaded niches (Niemelä and Mattson 1996).

Our objective is to compare the ground-dwelling weevil assemblages among forest fragments in an agricultural landscape and continuous forest in central Ontario, Canada. We predicted that forest fragments would have a greater proportion and higher abundances of introduced weevil species than stands found in a continuously forested landscape. We discuss the life history attributes of the weevils in light of their ability to become established in continuously forested landscapes.

Materials and Methods

Study Sites

Forest Fragments – Twenty-two mature deciduous woodlots in the southern portion of Peterborough County (44° 17' N, 78° 20' W) in central Ontario, Canada were selected as part of a broader study on forest-breeding birds. The region is part of the Great Lakes-St. Lawrence lowlands, at the southern edge of the Canadian Shield, in the Mixedwood Plains Ecozone of the Ecological Land Classification of Canada (AAFC 2010). The region experiences an average of 124 frost-free days a year, and 84 cm of precipitation (Environment Canada 2008). Elevation ranges from 75 to 408 m with an average of 305 m (Wickware and Rubec 1989). Though the soils in this region are variable in composition, all woodlots were located in well-drained loam or sandy-loam soils with layers of organic material 8-10 cm thick (Webber et al. 1946; Gillespie and Acton 1981). The landscape is composed of agriculture and forest fragments, interspersed with farms, housing developments, and wetlands (Phillips et al. 2005). On average, intensive agriculture (row-crops) accounted for 28% of the landscape within 2 km of the woodlots, less-intensive agriculture (hay, old fields, and pastures) accounted for 30%, and forest cover accounted for 24% (Richmond 2006). All 22 woodlots were dominated by *Acer saccharum* (Aceraceae), with *Fraxinus americana* (Oleaceae), *Ostrya virginiana* (Betulaceae), *Thuja occidentalis* (Cupressaceae), *Fagus grandifolia* (Fagaceae) and *Tilia americana* (Tiliaceae) all occurring as frequent canopy species. The woodlots ranged from 6.7 to 280.4 ha, with a mean of 37.1 ha. None of the woodlots had been recently exposed to grazing, logging, fire or construction (Phillips et al. 2005, Richmond 2006). The understory plant communities at the sampling points in forest fragments were largely native (S. Richmond, pers. obs.).

Continuous Forest – Nine mature hardwood stands in the southern portion of Algonquin Provincial Park (45° 35' N, 78° 29' W) in central Ontario, Canada were selected as part of a larger study on sustainable forest management. Algonquin Park lies in a transition zone between the boreal forest to the north and the Great Lakes-St. Lawrence lowlands to the south (Rowe 1972), in the Boreal Shield Ecozone of the Ecological Land Classification of Canada (AAFC 2010). The park covers an area of 7700km², the western two-thirds of which (about 4600km²) consists of tolerant hardwood forests over rugged terrain, interspersed with numerous lakes (Quinn 2004). Mean elevation is 396m, with the western portion of the park experiencing an average of 84 frost-free days a year, and 100cm of precipitation (Strickland 2006). Soils characteristic of the hardwood forests are fresh to moist, medium to coarse loams, with an average organic matter layer of 10cm (Chambers et al. 1997). All nine stands were characterized by canopies dominated by *Acer saccharum*, with lesser amounts of *Fagus grandifolia*, *Betula alleghaniensis* (Betulaceae), *Prunus serotina* (Rosaceae), and *Tsuga canadensis* (Pinaceae). Sites ranged from 14.4 to 54.8ha, with a mean of 35.8ha. Few non-native plant species occurred in these stands (E. Proctor, pers. obs.).

Insect Sampling

Ground-dwelling invertebrates were sampled in all sites using pitfall traps, which consisted of 500ml containers dug into the ground so that the lips of the containers were

flush with the soil. The containers were filled halfway with water, a pinch of salt (as a preservative) and a few drops of dish soap (to disrupt surface tension). Each trap was covered with a wire grate to reduce small mammal and amphibian by-catch, and to discourage larger mammals from disturbing them.

Sampling in Peterborough County took place in the spring and summer of 2001, 2003 and 2004, and the number and layout of pitfall traps varied from year to year. In 2001, one trap was placed every 20m along a 100m transect that extended from the edge of the woodlot into the interior, for a total of six pitfalls per site. Traps were active from mid May until mid August, for a total of approximately 8800 trap-days. In 2003 and 2004, the transect was 50m long, with one trap placed every 5m from 0 to 20m, and then every 10m from 20 to 50m, for a total of eight traps per site. In 2003, sampling went continuously from late-May to late-July, for a total of approximately 8500 trap-days. In 2004, trapping began in June and continued until August, and traps were left inactive for six to seven days following each collection. This resulted in approximately 3600 trap-days. Thus, in the fragmented forest we had a sampling effort of 20,900 trap-days.

Sampling in Algonquin Provincial Park took place in the spring and summer of 2006 and 2007. Each of the nine stands had 12 pitfalls, placed in a three-by-four grid, with 10m between traps. Pitfalls were located in the centre of each stand and were active for two seven-day periods: once in late May and again in mid June, for a total of approximately 1500 trap-days per year for a total of 3000.

All invertebrates were rinsed and preserved in 70% ethanol upon collection. Weevils were later separated from the rest of the samples and identified to species. Voucher specimens were deposited at Trent University and the Canadian Museum of Nature. We characterized dominant species as those that represented 5% or more of the total number of specimens for a region.

Analysis

To determine whether parthenogenesis or flightlessness were more prevalent in the introduced weevil species than in the native species caught in this study, we used Fisher's exact tests. When comparing communities, problems arise if sample sizes differ because larger samples are expected to contain a greater number of species. The Peterborough County sites were sampled more intensively than those in Algonquin Park, with sampling taking place throughout the growing season as compared to a week each in late-May and mid-June. We used rarefaction to standardize all samples to a common sample size by estimating the number of species expected in a random sample of individuals taken from a collection (Krebs 1999). We used EcoSim (Gotelli and Enstminger 2009) to estimate the number of species expected in Peterborough County had we caught 1000 weevils there during the same time periods as those in Algonquin and to compare species richness between the two regions.

Results

In total, 5090 weevil specimens were collected from 10 subfamilies, 21 genera, and 26 species. The fragmented forest sites yielded 24 species, 11 of which were introduced,

and the continuous forest sites yielded five species, 3 of which were introduced.

More than 4000 individuals were captured in the Peterborough County pitfall traps (Table 1). Most individuals collected were of introduced species (95.1%) even though fewer than half the species were introduced (11 out of 24). The three dominant species were *Barypeithes pellucidus* Boheman (63.7% of total), *Otiorhynchus raucus* Fabricius (17.7%), and *Phyllobius oblongus* L. (6.1%). Of the 13 native species, *Hormorus undulatus* Uhler was the most abundant (3.2%). All other native species represented 0.6% of the specimens, or less. Five natives (*Anametus granulata* Say, *Rhyncolus brunneus* Mannerheim, *Grypus equiseti* Fabricius, *Listronotus sparsus* Say, and *Listronotus oregonensis* LeConte) were each represented by a single individual.

One thousand weevils from five species were caught in the Algonquin Park pitfall traps (Table 1). The three dominant species were all introduced and accounted for 99.8% of the total: *Sciaphilus asperatus* Bonsdorff (74%), *P. oblongus* (20%), and *Otiorhynchus ovatus* L. (5.8%). The two native species, *Nemocestes horni* Van Dyke and *Sirocalodes sericans* LeConte, were each represented by a single individual, and were not caught in the forest fragments. *Otiorhynchus ovatus*, *P. oblongus*, and *S. asperatus* were found in both forest types, and were collected every year. Five species (*H. undulatus*, *O. raucus*, *B. pellucidus*, *Polydrusus sericeus* Schaller, and *Trachyphloeus bifoveolatus* Beck) were only caught in the forest fragments, but were caught in all three years.

More than half of the species (57.7%) and 98.7% of the individuals caught in this study were from the subfamily Entiminae. Of these, 13 were flightless (86.7%) and nine were parthenogenetic (60%). All but one of the introduced species was from this subfamily. Seven out of 11 introduced entimines (63.6%) were parthenogenetic and flightless, three were bisexual and capable of flight (27.3%), and one was bisexual and flightless. The proportion of parthenogenetic introduced species was significantly greater than the proportion of parthenogenetic native species [7 out of 11 (63.6%) parthenogenetic introduced; 2 out of 15 (13.3%) parthenogenetic native; Fisher's exact test, $P = 0.01$]. The proportion of flightless introduced species was not significantly greater than the proportion of flightless native species [8 out of 11 (72.7%) flightless introduced; 6 out of 15 (40%) flightless native; Fisher's exact test, $P = 0.10$].

Peterborough County sites caught 2016 weevils from 18 species during the weeklong periods in late-May and mid-June that corresponded to Algonquin's sampling. Using the rarefaction method, in a random sample of 1000 weevils from this subsample of Peterborough County, we would expect to see between 13 and 18 species (95% confidence). The Peterborough County sites therefore have higher species richness than the Algonquin sites (1000 individuals from five species).

Discussion

Contrary to our prediction, introduced weevils overwhelmingly dominated both the fragmented and continuously forested landscapes of central Ontario but the assemblages of the two regions were distinct and species richness was higher in the fragmented sites. Most of the weevils in both regions were flightless, but introduced species were more likely to be parthenogenetic.

TABLE 1. Subfamilies, status in North America (native or introduced), flight capability, mode of reproduction in North America, and known host plants of weevils (Coleoptera: Curculionidae) captured in pitfall traps in 22 hardwood forest fragments in Peterborough County, Ontario and 9 hardwood stands in Algonquin Provincial Park, Ontario.

Subfamily ^a	Species	Peterborough			Algonquin		Total
		2001	2003	2004	2006	2007	
Dryophthorinae	<i>Sphenophorus minimus</i> Hart		19	5			24
	<i>S. parvulus</i> Gyllenhal		10				10
Erirhinae	<i>Grypus equiseti</i> Fabricius		1				1
Curculioninae	<i>Tychius picirostris</i> Germar		1	1			2
Baridinae	<i>Stethobaris ovata</i> LeConte		3	1			4
Ceutorhynchinae	<i>Sirocalodes sericans</i> LeConte					1	1
Cossoninae	<i>Rhyncolus brunneus</i> Mannerheim				1		1
Cryptorhynchinae	<i>Acalles carinatus</i> LeConte		15	3			18
Cyclominae	<i>Listronotus oregonensis</i> LeConte	1					1
	<i>L. sparsus</i> Say		1				1
Entiminae	<i>Hormorus undulatus</i> Uhler	55	51	25			131
	<i>Otiorhynchus ovatus</i> L.	12	38	14	5	53	122
	<i>O. raucus</i> Fabricius	90	256	378			724
	<i>O. rugosostriatus</i> Goeze	1					1
	<i>O. singularis</i> L.	2					2
	<i>Nemocestes horni</i> Van Dyke					1	1
	<i>Phyllobius oblongus</i> L.	90	124	37	133	67	451
	<i>Polydrusus sericeus</i> Schaller	4	1	4			9
	<i>Barypeithes pellucidus</i> Boheman	295	1799	512			2606
	<i>Sciaphilus asperatus</i> Bonsdorff	39	71	67	118	622	917
	<i>Sitona lineelus</i> Bonsdorff		2				2
	<i>Cathormiocerus aristatus</i> Gyllenhal ^c		30	16			46
	<i>Trachyphloeus bifoveolatus</i> Beck	3	3	2			8
<i>Anametis granulata</i> Say	1					1	
<i>Phyxelis rigidus</i> Say	1	3				4	
Molytinae	<i>Conotrachelus posticatus</i> Boheman		2				2
	TOTAL	594	2430	1066	256	744	5090

TABLE 1. continued...

Species	Status ^b	Flight	Reproduction	Known Host Plants	Sources
<i>S. minimus</i>	Native	Yes	Sexual	Poaceae, Cyperaceae	Vaurie 1951
<i>S. parvulus</i>	Native	Yes	Sexual	Poaceae, Cyperaceae	Vaurie 1951
<i>G. equiseti</i>	Native	Yes	Sexual	Equisetaceae	Cawthra 1957; Anderson 2002
<i>T. picirostris</i>	Introduced	Yes	Sexual	Fabaceae (<i>Trifolium</i>)	Anderson and Howden 1994
<i>S. ovata</i>	Native	Yes	Sexual	Orchidaceae	Blatchley and Leng 1916; Howden 1988
<i>S. sericans</i>	Native	Yes	Sexual	Papaveraceae, Fumariaceae	Anderson 2002; Korotyayev 2008
<i>R. brunneus</i>	Native	Yes	Sexual	Downed woody debris	Anderson 1997; Anderson 2002
<i>A. carinatus</i>	Native	No	Sexual	Downed woody debris	Anderson 2002; LaChowska et al. 2009
<i>L. oregonensis</i>	Native	Yes	Sexual	Apiaceae	Campbell et al. 1989
<i>L. sparsus</i>	Native	Yes	Sexual	Asteraceae, Chenopodiaceae	Boivin 1999; Anderson 2002
<i>H. undulatus</i>	Native	No	Sexual	Liliaceae	Blatchley and Leng 1916; Champlain and Null 1921
<i>O. ovatus</i>	Introduced	No	Asexual	Polyphagous	Takenouchi 1965; Anderson 2002
<i>O. raucus</i>	Introduced	No	Asexual	Polyphagous	Anderson 2002
<i>O. rugosostriatus</i>	Introduced	No	Asexual	Polyphagous	Wheeler 1999; Anderson 2002
<i>O. singularis</i>	Introduced	No	Asexual	Polyphagous	Campbell et al. 1989
<i>N. horni</i>	Native	No	Asexual	Polyphagous	Anderson 2002
<i>P. oblongus</i>	Introduced	Yes	Sexual	Polyphagous	Pinski et al. 2005a
<i>P. sericeus</i>	Introduced	Yes	Sexual	Polyphagous	Pinski et al. 2005a
<i>B. pellucidus</i>	Introduced	No	Sexual	Polyphagous	Takenouchi 1965; Galford 1987
<i>S. asperatus</i>	Introduced	No	Asexual	Polyphagous	Pinski et al. 2005a
<i>S. lineelus</i>	Native	No	Sexual	Polyphagous	Loan 1963
<i>C. aristatus</i> ^c	Introduced	No	Asexual	Polyphagous	Piper et al. 2001
<i>T. bifoveolatus</i>	Introduced	No	Asexual	Polyphagous	Brown 1965; Piper et al. 2001
<i>A. granulata</i>	Native	No	Sexual	Polyphagous	Campbell et al. 1989; McLain 1998
<i>P. rigidus</i>	Native	No	Asexual ^d	Brassicaceae, Rosaceae	Levesque and Levesque 1994; Shellhorn and Sork 1997
<i>C. posticatus</i>	Native	Yes	Sexual	Fagaceae (<i>Quercus</i>)	Anderson 2002
TOTAL					

a) Subfamily classification based on Anderson 2002

b) Sources: McNamara 1991; Anderson 1997

c) Formerly *Trachyphloeus*

d) No males in Canadian Museum of Nature or Royal Ontario Museum collections

Barypeithes pellucidus dominated the forest fragments in Peterborough County while *S. asperatus* dominated the continuously forested sites in Algonquin Park. Both of these entomine weevils are flightless and polyphagous as larvae and adults (Witter and Fields 1977; Galford 1987; Anderson 2002) but *B. pellucidus* reproduces sexually (Takenouchi 1965), while *S. asperatus* reproduces through apomictic parthenogenesis (Suomalainen et al. 1987). Many parthenogenetic organisms are successful colonizers due to their abilities to continually propagate even at low population numbers, and to rapidly adapt because of more frequent random mutations (Ledig 1992; Langor et al. 2009). With asexual reproduction and a preference for *Acer saccharum* and other deciduous trees (Witter and Fields 1977), *S. asperatus* has been able to colonize not only the continuous hardwood forests of Algonquin Park, but also those in Michigan and Wisconsin (Werner and Raffa 2000; Pinski et al. 2005a; Coyle et al. 2008). It is a widespread species (McNamara 1991; Bright and Bouchard 2008) and has been found as far north as Iroquois Falls, Ontario (48° 45' N, 80° 41' W), and Edmonton, Alberta (53° 32' N, 113° 29' W; Bright and Bouchard 2008).

Barypeithes pellucidus, with a preferred diet that includes *Quercus rubra* (Fagaceae), *Aster spp.* (Asteraceae), *Medicago spp.* (Fabaceae), *Trifolium spp.* (Fabaceae), and weedy herbaceous plants (Galford 1987; Campbell et al. 1989) is the dominant species in the forest fragments in this study and in New York and Pennsylvania (Maerz et al. 2005). High numbers have been found in agricultural sites such as vineyards (Bouchard et al. 2005), berry plantations (Bomford and Vernon 2005), residential areas (Balsbaugh 1988) and continuous forests of Wisconsin and Michigan (Werner and Raffa 2000).

We suggest several explanations for why this adaptable colonizing species was absent from the Algonquin Park samples. Weevil abundance can vary considerably seasonally, from year to year, and from place to place (Balsbaugh 1988; Bouchard et al. 2005) and it is possible that *B. pellucidus* is established in the sites in Algonquin Park but the small sampling effort failed to detect them. In Quebec, Bouchard et al. (2005) caught over 1000 individuals of *B. pellucidus* in one vineyard but caught only 19 in another vineyard 30km away. They hypothesized that the high clay-content soils of the depauperate vineyard were less favourable to this species' pupation, but none of the soils in our study contained much clay (Webber et al. 1946; Gillespie and Acton 1981; Chambers et al. 1997). *Barypeithes pellucidus* are univoltine (Campbell et al. 1989). Adults usually emerge early in spring and disappear by mid-summer (Galford 1987; Maerz et al. 2005), and have only been found in the milder parts of Canada, such as southern British Columbia, around the Great Lakes, and in the Maritimes (Bright and Bouchard 2008). Specimens have been collected from as far north as Sault Sainte Marie, Ontario (46° 30' N, 84° 20' W; Takenouchi 1965) and Montreal, Quebec (45° 32' N, 73° 38' W; Bright and Bouchard 2008) but the frost-free periods in both these locations (120d and 140d, respectively), and in Peterborough County (124d), are much longer than in Algonquin (84d; Marsan 1990; Strickland 2006; Environment Canada 2008; MRCC 2009). The short frost-free period in Algonquin may be insufficient for one generation to find mates, lay eggs, and for the larvae of the next generation to hatch and grow to a sufficient size to survive the winter. If *B. pellucidus* is present in Algonquin Park, the combination of its flightlessness, sexual reproduction, and the short frost-free period, all likely contribute to limiting its numbers there.

Otiorhynchus raucus, like *B. pellucidus*, was abundant in Peterborough County,

but absent from the Algonquin Park samples. This species is flightless, polyphagous, and parthenogenetic in North America (Mazur 1992; Bright and Bouchard 2008), and has been found as far north as Calgary, Alberta (51° 07' N, 114° 19' W; Bright and Bouchard 2008). It was first reported in North America in 1936 at a nursery in Fonthill, Ontario (Hicks 1947), and the larvae are serious pests of garden vegetables, while adults feed on the foliage and shoots of fruit trees (Campbell et al. 1989). According to Mazur (1992), in Europe *O. raucus* is a common component in anthropogenic habitats such as urban parks, gardens, and roadsides, and it is probably absent from Algonquin Park due to the lack of cultivated plants on which it prefers to feed in both its native and introduced range.

Phyllobius oblongus was a dominant species in both landscapes. Unlike the aforementioned species, *P. oblongus* is capable of flight, and thus is a good disperser. It is established in continuous hardwood forests in the Great Lakes Region (Pinski et al. 2005a; Coyle et al. 2008) and in Nova Scotia (McCorquodale et al. 2005). Host plants include a wide variety of trees and shrubs, especially *Acer saccharum* (Witter and Fields 1977) and *Ostrya virginiana* (Pinski et al. 2005b). These tree species were common in both landscapes.

Otiorhynchus ovatus was present in both regions and in all five years, and was a dominant species in Algonquin. Commonly known as the strawberry root weevil, it is abundant, widely distributed, and can be found wherever plants occur (Bright and Bouchard 2008). It is flightless, parthenogenetic, extremely fecund, and has a very broad range of hosts, including conifers (Warner and Negley 1976; Campbell et al. 1989). This broad niche and the capability of overwintering as adults or larvae (Campbell et al. 1989), have likely facilitated *O. ovatus*' ability to colonize as far north as Fairbanks, Alaska (64° 50' N, 147° 38' W; Bright and Bouchard 2008). Why it was collected less frequently in the forest fragments than its congener *O. raucus* is unknown. *Otiorhynchus raucus* (5.5 to 7.5 mm) is larger than *O. ovatus* (4 to 5.5 mm; Bright and Bouchard 2008) and since pitfalls select for larger, more active individuals (Baars 1979), the high catches of *O. raucus* may not reflect the true proportions of these two species.

The only introduced weevil species caught in this study not in the subfamily Entiminae was *Tychius picirostris* Fabricius (subfamily Curculioninae). Commonly known as the clover-seed weevil, its larvae feed inside the reproductive structures of naturalized and cultivated clovers (*Trifolium spp.*; Anderson and Howden 1994; Anderson 2002). Though there are a few species of clover native to Ontario (e.g. *T. reflexum*), most are introduced from Europe (e.g. *T. repens* and *T. pratense*), and have been spread throughout the continent for their use as forage and in crop rotation (Taylor 1985; Voss 1985). Majka et al. (2007) suggest *T. picirostris* was introduced to North America in dry ballast, and with the ability to fly and the widespread distribution of its host plants (i.e. introduced clovers), it has become established throughout the continent (Anderson and Howden 1994).

Hormorus undulatus was the only abundant native weevil species captured in this study, and it was only caught in the Peterborough sites. Little is known of this entimine species beyond that it reproduces sexually, is flightless, and has been found on members of the Liliaceae family (*Convallaria*, *Maianthemum* and *Polygonatum*; Blatchley and Leng 1916; Champlain and Knull 1921). In Canada, it has been recorded as far north as Wawa, Ontario (47° 59' N, 84° 46' W; Bright and Bouchard 2008), and three were collected from raspberry (*Rubus idaeus*) in a Quebec plantation (Levesque and Levesque 1994). A few individuals

were collected in continuous hardwood forests in the Great Lakes Region compared to the thousands of introduced specimens (Coyle et al. 2008). Though sampling was not as intensive in Algonquin Park as it was in Peterborough County, the absence of *H. undulatus* from the Park's samples indicates that it is not an abundant species there. If it ever had been a significant component of the weevil community in this forest and those elsewhere, it is possible that the competitive abilities of the invasive European species already mentioned have displaced them. The short growing season may also have prevented *H. undulatus* from establishing in Algonquin Park and may explain the substantially lower species richness of the weevil communities of the park as compared to the more southerly forest fragments.

All parthenogenetic species caught in this study were flightless and polyphagous. With parthenogenetic reproduction and a polyphagous diet, these weevils do not need to find mates nor travel far to find food. The high proportion of introduced species that were parthenogenetic (63.6%) emphasizes the superior colonizing ability of these flightless weevils over flightless sexual species like *B. pellucidus*. The proportion of flightless introduced species (72.7%), however, was not significantly greater than the proportion of flightless native species (40%), which suggests that flightlessness alone does not affect colonizing ability. Therefore the polyphagous diets of entimines, in combination with either parthenogenetic reproduction or the ability to fly, have made these introduced weevils dominate the forested sites of this study.

Species richness was lower in the continuous forest sites than in the forest fragments. We found only five species in 1000 individuals in Algonquin, whereas we would expect 13 to 18 species in a same-sized sample from Peterborough County for the same time period. With three common species in Peterborough County (*B. pellucidus*, *O. raucus*, and *H. undulatus*) all seeming to be absent from Algonquin Park, it is likely that the shorter frost-free period, as well as the lack of agricultural and anthropogenic habitats are limiting others species as well.

This is the first report of *Sirocalodes sericans* for Ontario. Though it is generally distributed in the western and southern regions of the United States, in Canada it has only been documented in Manitoba (McNamara 1991; Anderson 2002). Other *Sirocalodes* species are associated with Papaveraceae and Fumariaceae, with larvae mining the stems or crowns of the host plants (Anderson 2002). *Dicentra cucullaria* (Fumariaceae) is a common spring ephemeral in northern hardwood forests (Walton and Hufford 1994), and is a possible host for this weevil. Further targeted sampling around this plant might help to elucidate more of this species' biology.

Pitfall traps are useful in assessing relative abundance of invertebrates active at the ground level, and are the most efficient method to assess ground-dwelling invertebrate communities (Prasifka et al. 2007). Further research on the weevil communities in these areas would benefit from additional sampling techniques such as flight-intercept traps, emergence traps, and sweep-netting.

The life histories and effects of invasive weevils are thoroughly studied in agricultural systems (e.g. *Otiorhynchus sulcatus* Fabricius; Moorhouse et al. 1992) because of the economic damage they can cause, but forest-invaders are poorly understood. We lack information on native weevil assemblages in forests prior to the invasions (Pinski et al. 2005a) and studying the tolerances and below-ground herbivory of introduced larval entimines is difficult (Coyle et al. 2008). There is ample scope for further study of the

functional role of these adaptable insects in our forested ecosystems.

Acknowledgements

We thank the many field and lab assistants, D. R. Coyle, D. Beresford, and two anonymous reviewers for their helpful comments. Funding for this work was provided by the National Science and Engineering Research Council, the Forestry Futures Trust Grant, the Ontario Ministry of Natural Resources, Environment Canada and Trent University.

References

- Agriculture and Agri-Food Canada (AAFC). 2010. National Ecological Framework for Canada. http://atlas.agr.gc.ca/agmaf/index_eng.html. Viewed 5 October 2010.
- Anderson, R. S. and A. T. Howden. 1994. *Tychius meliloti* Stephens new to Canada with a brief review of the species of *Tychius* Germar introduced into North America (Coleoptera: Curculionidae). *The Canadian Entomologist* 126: 1363-1368.
- Anderson, R. S. 1997. Weevils (Coleoptera: Curculionoidea, excluding Scolytinae and Platypodinae) of the Yukon. pp. 523-562 in H. V. Danks and J. A. Downes (eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa, Ontario.
- Anderson, R. S. 2002. Curculionidae Latreille 1802. pp. 722-815 in R. H. J. Arnette et al. (eds.), *American Beetles, Volume 2: Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, Florida.
- Baars, M. A. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41: 25-46.
- Balsbaugh Jr., E. U. 1988. Distributions for two holarctic weevils which are new household pests (Coleoptera: Curculionidae). *Entomological News* 99: 102-104.
- Blatchley, W. S. and C. W. Leng. 1916. *Rhynchophora or Weevils of North Eastern America*. The Nature Publishing Company. Indianapolis, Indiana. 682 pp.
- Boivin, G. 1999. Integrated management for carrot weevil. *Integrated Pest Management Reviews* 4: 21-37.
- Bomford, M. K. and R. S. Vernon. 2005. Root weevil (Coleoptera: Curculionidae) and ground beetle (Coleoptera: Carabidae) immigration into strawberry plots protected by fence or portable trench barriers. *Environmental Entomology* 34: 844-849.
- Bouchard, P., L. Lesage, H. Goulet, N. J. Bostanian, C. Vincent, A. Zmudzinska and J. Lasnier. 2005. Weevil (Coleoptera: Curculionoidea) diversity and abundance in two Quebec vineyards. *Annals of the Entomological Society of America* 98: 565-574.
- Bright, D. E. and P. Bouchard. 2008. *Coleoptera, Curculionidae, Entiminae. The Insects and Arachnids of Canada. Part 25*. NRC Research Press, Ottawa, Ontario. 327 pp.
- Brown, W. J. 1965. *Trachyphloeus* Germar (Coleoptera: Curculionidae) in North America. *The Canadian Entomologist* 97: 189-192.
- Burke, D. M. and E. Nol. 1998. Edge and fragment size effects on the vegetation of deciduous

- forests in Ontario, Canada. *Natural Areas Journal* 18: 45-53.
- Campbell, J. M., M. J. Sarazin and D. B. Lyons. 1989. Canadian beetles (Coleoptera) injurious to crops, ornamentals, stored products, and buildings. Agriculture Canada, Ottawa, Ontario. Publication 1826. 491 pp.
- Cawthra, E. M. 1957. Some notes on *Grypidius equiseti* F. (Col.: Curculionidae) with a description of its larva. *Proceedings of the Royal Entomological Society of London* 32: 96-106.
- Chambers, B. A., B. J. Naylor, J. Nieppola, B. Merchant and P. Uhlig. 1997. Field guide to the forest ecosystems of central Ontario. Queen's Printer for Ontario. Ottawa, Ontario. 200 pp.
- Champlain, A. B. and J. N. Knull. 1921. Notes on Coleoptera in Pennsylvania, New York and Connecticut. *Ecological News* 32: 270-273.
- Coyle, D. R., W. J. Mattson and K. F. Raffa. 2008. Invasive root-feeding insects in natural forest ecosystems of North America. pp. 134-149 in S. N. Johnson and P. J. Murray (eds.), *Root Feeders: An Ecosystem Perspective*. CABI Press. London, UK.
- Environment Canada. 2008. National climate data and information archive: Canadian climate normals, Peterborough, Ontario (1971-2000). http://www.climate.weatheroffice.gc.ca/climate_normals/index_e.html. Viewed January 2010.
- Galford, J. R. 1987. Feeding habits of the weevil *Barypeithes pellucidus* (Coleoptera: Curculionidae). *Entomological News* 98: 163-164.
- Gillespie, J. E. and C. J. Acton. 1981. Soils of Peterborough County, Report no. 45. Ontario Institute of Pedology and Agriculture Canada. Ottawa, Ontario. 61 pp.
- Gotelli, N. J. and G. L. Entsminger. 2009. EcoSim: null models software for ecology, version 7. Acquired Intelligence Inc. and Kesey-Bear. Jericho, Vermont.
- Hicks, S. D. 1947. *Brachyrhinus raucus* (Fab.), a European weevil new to North America. *The Canadian Entomologist* 79: 171.
- Howden, A. T. 1988. Structures related to oviposition in Curculionoidea. *Memoirs of the Entomological Society of Washington* 14: 53-100.
- Huntley, B. 1993. Species-richness in north-temperate zone forests. *Journal of Biogeography* 20: 163-180.
- Korotyaev, B. A. 2008. Distribution of the weevil subfamily Ceutorhynchinae (Coleoptera, Curculionidae). *Entomological News* 88: 928-947.
- Krebs, C. J. 1999. *Ecological Methodology*, 2nd edition. Addison-Wesley Educational Publishers, Inc. Menlo Park, California. 678 pp.
- LaChowska, D., M. Rozek and M. Holecova. 2009. Chromosome similarities and differences among three sibling species of the *Acalles echinatus* group (Coleoptera, Curculionidae, Cryptorhynchinae). *Zootaxa* 1985: 63-68.
- Langor, D. W., L. J. DeHaas and R. G. Foottit. 2009. Diversity of non-native terrestrial arthropods on woody plants in Canada. *Biological Invasions* 11: 5-19.
- Ledig, F. T. 1992. Human impacts on genetic diversity in forest ecosystems. *Oikos* 63: 87-108.
- Levesque, C. and G.-Y. Levesque. 1994. Abundance and seasonal activity of weevils (Coleoptera: Curculionidae) in a raspberry plantation and adjacent sites in southern Quebec (Canada). *The Great Lakes Entomologist* 27: 23-37.
- Loan, C. C. 1963. The bionomics of *Sitona scissifrons* (Coleoptera: Curculionidae) and

- its parasite *Microctonus sitonae* (Hymenoptera: Braconidae). *Annals of the Entomological Society of America* 56: 600-612.
- Maerz, J. C., J. M. Karuzas, D. M. Madison and B. Blossey. 2005. Introduced invertebrates are important prey for a generalist predator. *Diversity and Distributions* 11: 83-90.
- Majka, C. G., R. S. Anderson and D. B. McCorquodale. 2007. The weevils (Coleoptera: Curculionoidea) of the Maritime provinces of Canada, II: New records from Nova Scotia and Prince Edward Island and regional zoogeography. *The Canadian Entomologist* 139: 397-442.
- Marsan, J.-C., 1990. *Montreal in Evolution: Historical Analysis of the Development of Montreal's Architecture and Urban Environment*. McGill-Queen's Press. Montreal, Quebec. 456 pp.
- Mazur, M. 1992. Description of male of *Otiorhynchus raucus* (Fabricius, 1777) with some remarks on the geographical origin of the species (Coleoptera: Curculionidae). *Genus* 14: 241-248.
- McLain, D. K., 1998. Sexual selection and community structure: an island biogeographic analysis with beetles. *Oikos* 82: 271-281.
- McNamara, J. 1991. Family Curculionidae: snout beetles or weevils. pp. 329-56 in Y. Bousquet (ed.), *Checklist of Beetles of Canada and Alaska*. Agriculture Canada Publication 1861/E. Ottawa, Ontario.
- McCorquodale, D. B., B. L. Musgrave, S. Atkins, C. Majka and R. S. Anderson. 2005. New records of native and introduced weevils (Coleoptera: Curculionidae) for Nova Scotia from Cape Breton Island. *The Coleopterists Bulletin* 59: 27-34.
- Midwest Regional Climate Center (MRCC). 2009. *Historical Climate Data: Growing Season Summary*, Sault Sainte Marie, Michigan. <http://climate.geo.msu.edu/stations/7366/gss.txt>. Viewed 10 January 2010.
- Moorhouse, E. R., A. K. Charnley and A. T. Gillespie. 1992. A review of the biology and control of the vine weevil *Otiorhynchus sulcatus* (Coleoptera, Curculionidae). *Annals of Applied Biology* 121: 431-454.
- Niemelä, P. and W. J. Mattson. 1996. Invasion of North American forests by European phytophagous insects. *BioScience* 46: 741-753.
- Oberprieler, R. G., A. E. Marvaldi and R. S. Anderson. 2007. Weevils, weevils, weevils everywhere. pp. 491-520 in Z.-Q. Zhang and W. A. Shear (eds.), *Linnaeus Tercentenary: Progress in Invertebrate Taxonomy*. Magnolia Press. Auckland, NZ.
- Phillips, J., E. Nol, D. Burke and W. Dunford. 2005. Impacts of housing developments on wood thrush nesting success in hardwood forest fragments. *The Condor* 107: 97-106.
- Pinski, R. A., W. J. Mattson and K. F. Raffa. 2005a. Composition and seasonal phenology of a nonindigenous root-feeding weevil (Coleoptera: Curculionidae) complex in northern hardwood forests in the Great Lakes Region. *Environmental Entomology* 34: 298-307.
- Pinski, R. A., W. J. Mattson and K. F. Raffa. 2005b. Host breadth and ovipositional behavior of adult *Polydrusus sericeus* and *Phyllobius oblongus* (Coleoptera: Curculionidae), nonindigenous inhabitants of northern hardwood forests. *Environmental*

- Entomology 34: 148-157.
- Piper, R. W., S. G. Compton, J.-Y. Rasplus and S. Piry. 2001. The species status of *Cathormiocerus britannicus*, an endemic, endangered British weevil. *Biological Conservation* 101: 9-13.
- Prasifka, J. R., M. D. Lopez, R. L. Hellmich, L. C. Lewis and G. P. Dively. 2007. Comparison of pitfall traps and litter bags for sampling ground-dwelling arthropods. *Journal of Applied Entomology* 131: 115-120.
- Quinn, N. W. S. 2004. The pre-settlement hardwood forests and wildlife of Algonquin Provincial Park: a synthesis of historic evidence and recent research. *The Forestry Chronicle* 80: 705-717.
- Richmond, S. 2006. The importance of local versus landscape scale features in the demography of three forest breeding songbirds. M.Sc. Thesis. Trent University, Peterborough, Ontario. 76 pp.
- Rowe, J. S. 1972. Forest regions of Canada. Canadian Forestry Service. Publication 1300. Ottawa, Ontario, 172 pp.
- Schellhorn, N. A. and V. L. Sork. 1997. The impact of weed diversity on insect population dynamics and crop yields in collards, *Brassica oleraceae* (Brassicaceae). *Oecologia* 111: 233-240.
- Strickland, D. 2006. Trees of Algonquin Provincial Park. The Friends of Algonquin Park. Whitney, Ontario. 40 pp.
- Suomalainen, E., A. Saura and J. Lokki. 1987. Cytology and Evolution in Parthenogenesis. CRC Press. Boca Raton, Florida. 216 pp.
- Takenouchi, Y. 1965. Chromosome survey in thirty-four species of bisexual and parthenogenetic weevils of Canada. *Canadian Journal of Genetics and Cytology* 7: 663-687.
- Taylor, N. L. 1985. Clovers around the world. pp. 1-6 in E. N. Taylor (ed.), *Clover Science and Technology*. The American Society of Agronomy. Madison, Wisconsin.
- Vaurie, P. 1951. Revision of genus *Calendra* (formerly *Sphenophorus*) in the United States and Mexico (Coleoptera: Curculionidae). *Bulletin of the American Museum of Natural History* 98: 33-186.
- Voss, E. G. 1985. Michigan flora: part II, dicots (Saururaceae-Cornaceae). Regents of the University of Michigan. Ann Arbor, Michigan. 744 pp.
- Walton, G. B. and L. Hufford. 1994. Shoot architecture and evolution of *Dicentra cucullaria* (Papavaraceae, Fumarioidea). *International Journal of Plant Sciences* 155: 553-568.
- Warner, R. E. and F. B. Negley. 1976. The genus *Otiiorhynchus* in America north of Mexico (Coleoptera: Curculionidae). *Proceedings of the Entomological Society of Washington* 78: 240-262.
- Webber, L. R., F. F. Morwick and N. R. Richards. 1946. Soil survey of Durham County. Report no. 9, Ontario Soil Survey. Ontario Agricultural College. Guelph, Ontario. 68 pp.
- Werner, S. M. and K. F. Raffa. 2000. Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. *Forest Ecology and Management* 139: 135-155.
- Wheeler Jr., A. G. 1999. *Otiiorhynchus ovatus*, *O. rugosostriatus*, and *O. sulcatus*

- (Coleoptera: Curculionidae): exotic weevils in natural communities, mainly mid-Appalachian shale barrens and outcrops. *Proceedings of the Entomological Society of Washington* 101: 689-692.
- Wickware, G. M. and C. D. Rubec. 1989. Ecoregions of Ontario. Ecological lands classification series no. 26. Sustainable Development Branch, Environment Canada. Toronto, Ontario. 34 pp.
- Witter, J. A. and R. D. Fields. 1977. *Phyllobius oblongus* and *Sciaphilus asperatus* associated with sugar maple reproduction in northern Michigan. *Environmental Entomology* 6: 150-154.