Seasonal Occurrence of Adult Carabid Beetles (Coleoptera: Carabidae) in West-Central Illinois[1]

Kenneth W. McCravy[2] and Jason E. Willand[3]

Department of Biological Sciences, Western Illinois University, 1 University Circle, Macomb, Illinois 61455 USA

J. Entomol. Sci. 55(3): 329–343 (July 2020)

Abstract The Carabidae is a diverse family of beetles with many species of interest in conservation and biological control. Carabid beetle adult seasonal activity patterns were studied in a west-central Illinois forest/reconstructed tallgrass prairie matrix over a 2-yr period using pitfall traps. We found a threefold or greater difference in carabid abundance between years. Despite lower abundance, a second year of sampling yielded seven previously undetected species. Abundance and species richness were greatest in May–July and lower in August–October. Relative abundance and species richness were consistent among months between years. Shannon diversity and effective number of species were lowest in June and July. *Cyclotrachelus sodalis* (LeConte) and *Chlaenius platyderus* Chaudoir were the two most abundant species, comprising 54.3% of total captures. These species were most abundant in July and June, respectively. Most species showed greatest abundance in spring or early summer, and declined thereafter. Collections of several species were suggestive of bimodal seasonal patterns. Carabid species composition differed significantly among months, but not between years. Our results document seasonal variation in carabid abundance and species composition, and show that sampling throughout the growing season, and multiple sampling years, provide substantial benefits for assessments of carabid diversity in this region.

Key Words carabid seasonality, ground beetles, biodiversity, species composition

Carabid beetles (Coleoptera: Carabidae), including ground beetles and tiger beetles, comprise a highly diverse family with ~40,000 described species (Lövei and Sunderland 1996). Most species are generalist predators (Larochelle and Larivière 2003), although phytophagy (Honek et al. 2003) and fungivory (Johnson and Cameron 1969) are also well represented in the family. Many carabids have close associations with specific environments and are important as bioindicators, and the family includes important biological control agents of agricultural pests (McCravy 2018, Willand et al. 2011). In addition, carabids have become model organisms for field studies examining functional traits (characteristics that contribute to short-term performance or long-term adaptation) such as trait reassembly during prairie restoration (Barber et al. 2017). Despite a large amount of research on

[1]Received 18 July 2019; accepted for publication 25 August 2019.
[2]Corresponding author (email: KW-McCravy@wiu.edu).
[3]Department of Biology and Environmental Health, Missouri Southern State University, 3950 E. Newman Road, Joplin, MO 64801 USA.

carabids of the midwestern United States (McCravy and Lundgren 2011), relatively few studies have focused on temporal activity patterns.

Information on seasonal patterns of carabid species diversity is important for several reasons. Knowledge of temporal patterns can facilitate optimization of sampling periods for studies of carabid ecology and conservation (Werner and Raffa 2003), inform analyses of carabid co-occurrence with pest species for biological control purposes (Suenaga and Hamamura 2001), and provide information on potential impacts of exotic species on native carabids with which they may overlap temporally (Niemelä et al. 1997). Potential impacts of activities such as pesticide applications and prescribed burning may also be evaluated in relation to carabid activity. Carabids are an important food resource for many vertebrates (Larochelle 1975a, 1975b, 1980) which could be adversely affected by changes in carabid seasonal activity patterns. Carabid behaviors such as diel activity patterns can also vary with season (Willand and McCravy 2006). Furthermore, studies of carabid seasonal activity patterns can provide important information on potential effects of anthropogenic climate change. Evidence suggests that there have been major changes in the composition of the British carabid fauna associated with climate change (Coope 1978, 1987) and that carabids will likely respond to climate change via distributional shifts rather than physiological adaptation (Butterfield 1996). Knowledge of carabid temporal activity patterns could be useful in predicting interactions within new carabid assemblages.

Like much of the midwestern United States, the Illinois landscape has undergone dramatic changes due to cultivation. Over 80% of Illinois has been converted to cropland or pasture over the past 160 yr (Iverson 1988). The resulting landscape is dominated by an agricultural matrix with habitat fragments. Carabids are a focal group from both conservation and applied biological control standpoints in the Midwest (McCravy and Lundgren 2011). In this study, we examined seasonal activity of adult carabids in west-central Illinois in a habitat matrix of forest and reconstructed tallgrass prairie. Our objectives were to characterize the seasonal occurrence of carabids in west-central Illinois and to compare carabid species composition and diversity across months.

Materials and Methods

Carabids were collected in pitfall traps during May–October 2005 and 2006 at Western Illinois University's Alice L. Kibbe Life Science Research Station (N 40°21′52″, W 91°24′19″) in Hancock Co., IL. Each pitfall trap consisted of two 473-ml plastic cups (Dart Container Corp., Mason, MI), one nested inside the other, and placed in the ground with the rim flush with the ground surface. Traps were filled with approximately 150 ml of a 50/50 mixture of propylene glycol and water. A total of 162 pitfall traps were set in 18 3 $\times$ 3 arrays, encompassing an area of approximately 60 ha of reconstructed tallgrass prairie, oak–hickory forest, and early successional forest, with a variety of prescribed burning regimes. Traps within arrays were 5 m apart, and each array was 40–75 m from the nearest array. Traps were operated for seven consecutive days each month (08–15 May, 04–11 June, 09–16 July, 06–13 August, 10–17 September, and 08–15 October 2005; 12–19 May, 08–15 June, 13–20 July, 10–17 August, 16–23 September, and 09–16

October 2006) (see Willand et al. [2011] for further site and trapping details). Carabids were identified using Lindroth (1961–1969) and a synoptic reference collection.

Spearman correlation analyses were conducted to test for associations of monthly carabid abundance between years and species richness between years, using SigmaPlot, Version 13. Pitfall trap collections are a function of carabid activity levels as well as density, and so are best viewed in terms of "activity-density" (Maelfait and Baert 1975, Thiele 1977). Herein, "abundance" is used in this sense.

Shannon indices (H) (Shannon 1948) were calculated for all months combined and for each month, and compared between months using the t test developed by Hutcheson (1970). Holm's step-down procedure (Holm 1979) was used to adjust for paired comparisons by comparing the nth smallest P value with 0.05/number of comparisons $+ 1 - n$. The Shannon index is a diversity measure that quantifies the uncertainty or entropy of a community based on the number of species (species richness) and the relative abundance of the species (evenness). Greater Shannon values indicate greater diversity. Evenness values were obtained by dividing the Shannon value by the natural logarithm of species richness. Evenness can range from 0 to 1, with greater values representing greater evenness. Effective number of species (ENS) for each month and for all months combined was derived using exp(H). H and other entropy measures are nonlinear, making interpretation problematic. ENS is the number of equally abundant species necessary to produce the observed Shannon value, eliminating nonlinearity and allowing more meaningful comparisons of effect size (Jost 2007).

One-factor permutational multivariate analysis of variance (PerMANOVA; Anderson 2001) was used to compare species composition (species present and their relative abundances) among months. PerMANOVA is a multivariate analysis of variance that provides a test for differences in mean within-group distances among groups, using a permutation-based F test. For PerMANOVA, species with fewer than three nonzero cells were excluded from analysis to reduce sparsity, and values for each species were relativized by the maximum value to reduce heterogeneity and effects of dominant species (Peck 2016). PerMANOVA was conducted using PC-Ord, Version 7. Spearman correlations, using SigmaPlot Version 13, were conducted to compare species composition between years, both within months and overall.

Results

A total of 2,712 carabids were collected overall, representing 27 genera and 54 species (Table 1). In 2005, 2,073 carabids were collected, representing 25 genera and 47 species; in 2006, 639 carabids were collected, representing 22 genera and 32 species. Abundance and species richness of carabids were consistently greater in 2005 than in 2006, and were greater in May–July than in August–October. Monthly abundance was significantly correlated between years ($\rho = 1.000$, $P = 0.00278$, $n = 6$), but richness was not ($\rho = 0.771$, $P = 0.103$, $n = 6$).

Shannon index values and ENS were similar between years overall, but varied substantially between years among months (Table 2). In August and October Shannon values were significantly higher in 2005, but the 2006 value was highest in

Table 1. Numbers of carabids collected in pitfall traps during 1-week periods each month from May through October 2005 and 2006 at Alice L. Kibbe Life Science Research Station, Hancock Co., IL.

	May		June		July		August		September		October		Total	
Species	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
Amara cupreolata Putzeys	20	4	5	5	2	4	0	0	0	0	0	0	27	13
Amara exarata Dejean	0	0	0	1	1	0	0	0	0	0	0	1	1	2
Amara obesa (Say)	0	0	0	0	0	0	0	0	3	0	1	0	4	0
Amphasia interstitialis (Say)	2	1	2	1	0	0	0	0	1	0	0	0	5	2
Anisodactylus agricola (Say)	6	0	7	0	0	0	0	0	0	0	0	0	13	0
Anisodactylus caenus (Say)	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Anisodactylus carbonarius (Say)	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Anisodactylus furvus LeConte	0	1	1	1	1	0	0	0	0	0	0	0	2	2
Anisodactylus nigerrimus (Dejean)	2	0	0	0	0	0	0	0	0	0	0	0	2	0
Anisodactylus ovularis (Casey)	1	0	0	0	0	0	0	0	1	0	0	0	2	0
Apenes sinuatus (Say)	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Bembidion affine Say	0	2	0	4	0	0	0	0	0	0	0	0	0	6
Bembidion pedicellatum LeConte	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Bradycellus badipennis (Haldeman)	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Calathus gregarius Say	0	0	0	0	0	1	0	0	0	1	0	0	0	2
Calathus opaculus LeConte	0	0	4	0	16	0	2	0	37	10	2	0	61	10
Calleida punctata LeConte	1	0	0	0	0	0	0	0	0	0	0	0	1	0

Table 1. Continued.

Species	May		June		July		August		September		October		Total	
	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
Chlaenius emarginatus Say	6	0	15	15	3	6	0	0	0	0	0	0	24	21
Chlaenius nemoralis Say	0	0	9	0	3	0	4	0	0	0	0	0	16	0
Chlaenius pennsylvanicus Say	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Chlaenius platyderus Chaudoir	140	32	466	34	23	1	9	1	2	0	2	0	642	68
Chlaenius pusillus Say	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Chlaenius tricolor Dejean	0	0	2	0	0	0	2	0	0	0	0	0	4	0
Cicindela punctulata Olivier	0	0	0	0	2	0	1	0	0	0	0	0	3	0
Cicindela sexguttata Fabricius	10	5	34	49	2	7	0	1	0	0	0	0	46	62
Clivina bipustulata (Fabricius)	2	1	1	1	0	0	0	0	0	0	0	0	3	2
Cyclotrachelus seximpressus (LeConte)	0	0	38	0	2	0	2	0	3	0	3	0	48	0
Cyclotrachelus sodalis (LeConte)	66	11	91	60	284	123	69	39	12	1	6	1	528	235
Cymindis americanus Dejean	0	0	0	1	0	0	3	0	0	0	1	0	4	1
Dicaelus dilatatus Say	2	1	0	1	1	0	1	0	0	0	0	0	4	2
Dicaelus elongatus Bonelli	4	2	19	7	0	2	0	1	0	0	0	0	23	12
Dicaelus furvus Dejean	0	0	2	0	0	0	0	0	0	0	0	0	2	0
Dicaelus politus Dejean	1	0	2	0	0	0	0	0	0	0	0	0	3	0
Dicaelus purpuratus Say	4	1	12	1	4	1	0	1	0	1	0	0	20	5

Table 1. Continued.

Species	May		June		July		August		September		October		Total	
	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
Galerita janus (Fabricius)	22	6	51	6	17	2	3	0	0	0	0	0	93	14
Harpalus compar LeConte	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Harpalus herbivagus Say	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Harpalus protractus Casey	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Megacephala virginica L.	0	0	0	0	51	7	2	0	0	0	0	0	53	7
Notiobia nitidipennis (LeConte)	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Notiobia terminata Say	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Notiophilus novemstriatus LeConte	1	2	0	1	0	0	0	0	3	9	5	11	9	23
Platynus decentis (Say)	88	34	35	25	4	9	4	0	0	2	4	2	135	72
Poecilus chalcites (Say)	4	0	0	0	0	0	0	0	0	2	1	0	5	2
Poecilus lucublandus (Say)	1	3	20	5	17	0	5	2	1	0	0	0	44	10
Pterostichus permundus (Say)	0	0	5	1	0	0	0	0	54	14	20	0	79	15
Pterostichus stygicus (Say)	0	1	19	24	6	2	2	0	36	3	11	0	74	30
Scaphinotus elevatus Haldeman	0	2	2	0	0	0	0	0	8	6	10	0	20	8
Scaphinotus fissicolis (LeConte)	0	0	0	0	0	0	0	0	0	1	1	1	1	2
Scarites subterraneus Fabricius	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Stenolophus plebejus Dejean	0	0	1	0	0	0	0	0	0	0	0	0	1	0

Table 1. Continued.

Species	May		June		July		August		September		October		Total	
	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
Synuchus impunctatus (Say)	0	0	3	0	1	0	3	0	23	0	2	0	32	0
Trichotichnus autumnalis (Say)	0	0	0	0	0	2	0	0	0	0	0	0	0	2
Trichotichnus fulgens (Csiki)	21	3	9	2	0	0	0	0	0	0	0	0	30	5
Total	405	112	860	248	441	168	112	45	184	50	71	16	2073	639
Species richness	22	18	31	24	20	14	15	6	13	11	16	5	47	32
Total (both years)	517		1108		609		157		234		87		2712	
Species richness (both years)	26		39		24		18		18		17		54	

Table 2. Species richness, Shannon index values, evenness, and effective numbers of species (ENS) for carabids collected in pitfall traps during 1-week periods each month from May through October 2005 and 2006 at Alice L. Kibbe Life Science Research Station, Hancock Co., IL.

Diversity Measure	May		June		July		August		September		October		Total	
	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
Species richness	22	18	31	24	20	14	15	6	13	11	16	5	47	32
Species richness (years pooled)	26		39		24		18		18		17		54	
Shannon index*	2.002	2.097	*1.892*	*2.284*	1.437	1.191	*1.612*	*0.601*	1.911	1.981	*2.275*	*1.037*	2.370	2.347
Shannon index (years pooled)**	2.068a		2.112a		1.448b		1.424b		2.063a		2.318a		2.434	
Evenness	0.648	0.726	0.551	0.719	0.480	0.451	0.595	0.335	0.745	0.826	0.821	0.644	0.616	0.677
Evenness (years pooled)	0.635		0.576		0.456		0.493		0.714		0.818		0.610	
ENS	7.404	8.142	6.633	9.816	4.208	3.290	5.013	1.824	6.760	7.250	9.728	2.821	10.70	10.45
ENS (years pooled)	7.908		8.261		4.255		4.155		7.872		10.153		11.410	

* Within months, values in italics are significantly different from each other (*t* tests, $P < 0.05$).

** Among months, values followed by the same letter are not significantly different (*t* tests, with Holm's step-down correction for multiple paired comparisons).

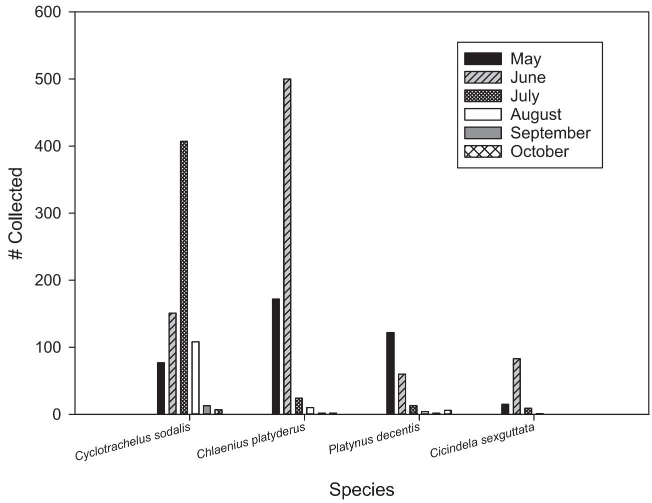

Fig. 1. Numbers of four species of carabids collected in pitfall traps during 1-week periods each month from May through October 2005 and 2006 (years pooled) at Alice L. Kibbe Life Science Research Station, Hancock Co., IL.

June. When yearly data were pooled, Shannon index values were lower in July and August than in the remaining months, as were ENS and evenness (Table 2). There was no significant correlation of monthly values between years for Shannon values or for ENS ($\rho = 0.143$, $P = 0.803$, $n = 6$, each comparison). There was also no significant correlation of monthly ENS and species richness ($\rho = 0.029$, $P = 0.919$, $n = 6$).

PerMANOVA revealed significant differences in carabid species composition among months ($F = 2.1867$; df $= 5, 6$; $P = 0.0044$). Variation in species composition among months accounted for 37.238% of total variation. All pairwise comparisons between months were nonsignificant ($P \geq 0.3268$, each comparison). Species composition was significantly correlated between years overall ($\rho = 0.573$, $P < 0.0001$, $n = 54$), and for May and June (May: $\rho = 0.492$, $P = 0.0110$, $n = 26$; June: $\rho = 0.414$, $P = 0.00912$, $n = 39$), but not for the remaining months (July: $\rho = 0.305$, $P = 0.145$, $n = 24$; August: $\rho = 0.116$, $P = 0.638$, $n = 18$; September: $\rho = 0.315$, $P = 0.198$, $n = 18$; October: $\rho = 0.0446$, $P = 0.861$, $n = 17$).

Of the 17 species for which at least 40 individuals were collected (Figs. 1–4), all but two (*Cicindela sexguttata* F. and *Notiophilus novemstriatus* LeConte) were most abundant in 2005 (Table 1). *Cyclotrachelus seximpressus* (LeConte) and *Synuchus impunctatus* (Say) were collected exclusively in 2005. The two most abundant species, *Cyclotrachelus sodalis* (LeConte) and *Chlaenius platyderus* Chaudoir, comprised 54.3% of total captures, with *C. sodalis* numbers peaking in July and *C. platyderus* in June (Fig. 1).

Most species showed greatest abundance in spring or early summer (Figs. 1 – 4). *Platynus decentis* (Say), *Amara cupreolata* Putzeys, and *Trichotichnus fulgens* (Csiki) showed greatest overall numbers in May, declining thereafter (Figs. 1, 3, 4).

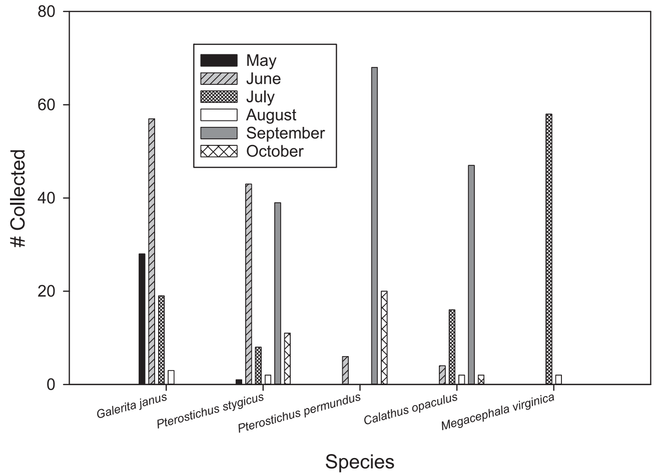

Fig. 2. Numbers of five species of carabids collected in pitfall traps during 1-week periods each month from May through October 2005 and 2006 (years pooled) at Alice L. Kibbe Life Science Research Station, Hancock Co., IL.

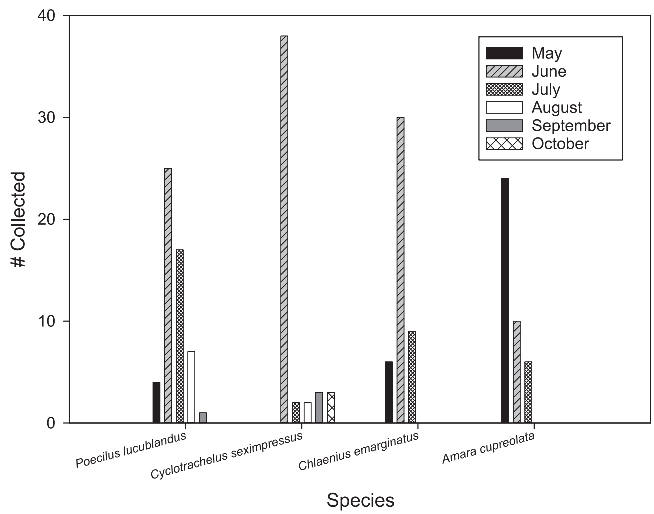

Fig. 3. Numbers of four species of carabids collected in pitfall traps during 1-week periods each month from May through October 2005 and 2006 (years pooled) at Alice L. Kibbe Life Science Research Station, Hancock Co., IL.

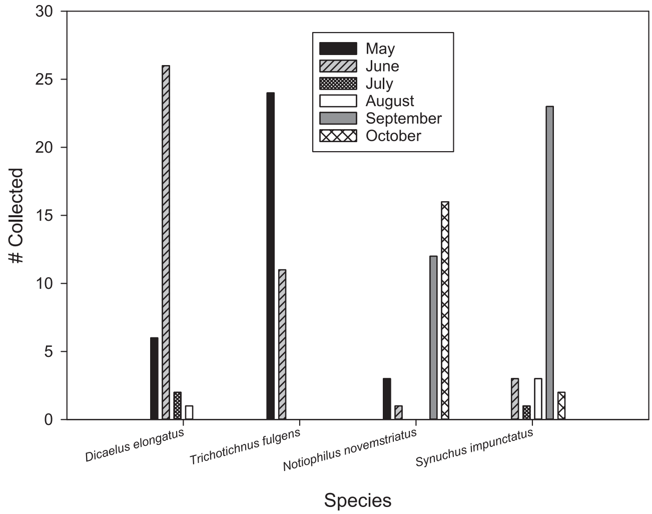

Fig. 4. Numbers of four species of carabids collected in pitfall traps during 1-week periods each month from May through October 2005 and 2006 (years pooled) at Alice L. Kibbe Life Science Research Station, Hancock Co., IL.

The tiger beetle *Cicindela sexguttata* was most common in spring, especially June, and absent from fall collections, as was *Galerita janus* (F.) (Figs. 1, 2). *Poecilus lucublandus* (Say), *Cyclotrachelus seximpressus*, *Chlaenius emarginatus* Say, and *Dicaelus elongatus* Bonelli were most abundant in June (Figs. 3, 4), and *Pterostichus stygicus* (Say) was most abundant in June and September samples (Fig. 2).

Among later season species, almost all of the tiger beetle *Megacephala virginica* L. were collected in July (Fig. 2). Most *Pterostichus permundus* (Say) and *N. novemstriatus* were collected in September and October, with relatively small numbers collected in the spring (Figs. 2 and 4). Most *S. impunctatus* were collected in September (Fig. 4).

Discussion

Numbers of carabids collected varied greatly between years. This is not unusual; pitfall trap collections of carabids can vary by more than an order of magnitude in different years (Jones 1979). Even though carabid numbers were substantially lower in 2006 than in 2005, the second year of sampling yielded seven previously undetected species overall, and from one to eight previously undetected species each month. This suggests that 2 yr of sampling provided substantial benefits in documenting the carabid fauna of Kibbe Station. Likewise, monthly sampling proved to be important since species composition varied significantly among months, and many carabid species showed strongly seasonal activity patterns at this site. Relative abundance and species richness among months were consistent between years overall, with both of these measures highest in May–July and lower in August–October. June sampling yielded the greatest abundance and species richness; about two-thirds and three-fourths of total species richness were collected during this month in 2005 and 2006, respectively. Other studies of carabids in the U.S. Upper Midwest (Epstein and Kulman 1990, Werner and Raffa 2003), Alberta, Canada (Niemelä et al. 1992), and northwestern Arkansas Ozark Highlands (Hamilton et al. 2018) have also obtained greatest trap catches early in the season. These seasonal patterns suggest that trapping throughout the growing season is necessary to sufficiently sample carabid diversity at this location, but for limited monitoring early season sampling is best. The relatively low numbers collected in August suggest low activity at that time. Temperate carabid activity is often low in summer, when some species may enter aestivation (Lövei and Sunderland 1996).

Shannon index values and corresponding evenness and ENS values also showed a seasonal pattern with lower values in July and August. This pattern appears to have been driven by the dominance of *C. sodalis*, which accounted for about two-thirds of all carabid captures during these months. Shannon and ENS values were relatively high in October, when species richness was low, but evenness was high. This may in part be a result of relatively low sample sizes and consequent lower limits on variation in relative species abundances. ENS values did not correlate well with species richness, again probably due to the dominance/evenness factors described above. Monthly Shannon (and associated ENS) values also did not correlate significantly between years, probably due in large part to the much lower 2006 values for August and October. These low values corresponded to very low species richness (six and five species, respectively) for these 2 mo.

Species composition varied significantly among months, further underscoring the importance of sampling throughout the activity season. Species composition was consistent between years overall, but only for May and June among particular months. Relatively low sample sizes in the later months could be a reason. It is also possible that carabid communities increase in entropy as the season progresses, and that this occurs at variable rates in different years.

Among individual species, seasonal activity patterns generally agreed with those reported in the literature. It should be noted that, because our sampling was restricted to a 1-week period near the middle of each month, our data represent discrete samples rather than continuous samples as has been done in most other studies. Therefore, comparisons with other studies should be done with caution. In southeastern Minnesota, Epstein and Kulman (1990) found *C. sodalis* to be most common from late June through July, and again from mid-August to mid-September, when their sampling ended. In our study, *C. sodalis* numbers peaked in July samples, with few individuals collected in September and October. Epstein and Kulman (1990) suggest that this species, as well as *S. impunctatus*, overwinter as larvae. They collected *S. impunctatus* adults in greatest numbers in July and August, with declining numbers in September. Werner and Raffa (2003) found a similar pattern in northeastern Wisconsin and the Upper Peninsula of Michigan, although they did not sample in September. In our study, *S. impunctatus* was only collected in 2005, with 23 of 32 specimens collected in September, perhaps due to the longer growing season in west-central Illinois.

Cicindela sexguttata was collected predominantly in June in our study. This species also has a seasonal peak in June in South Dakota and Nebraska (Carter 1989, Spomer et al. 2008). *Cicindela sexguttata* is unusual among North American

Cicindelinae in that adults are observed almost exclusively in spring/early summer, and rarely in fall (Knisley and Schultz 1997). This species has a 2-yr life cycle, but adults remain in the pupal burrows, emerging the following spring (Knisley and Schultz 1997, Shelford 1908). *Platynus decentis* was collected primarily in May and June in our study, with similar patterns found in southeastern Minnesota (Epstein and Kulman 1990), northeastern Wisconsin and the Upper Peninsula of Michigan (Werner and Raffa 2003), and Alberta, Canada (Niemelä et al. 1992). This is a forest species that overwinters as adults in forests and forest edges, under embedded stones, in leaf litter, and in tree stumps (Larochelle 1972, Larochelle and Larivière 2003). Gravid females of this species have been found in Illinois in mid-May (Gilbert 1957). *Amara cupreolata* and *Poecilus lucublandus* also overwinter as adults (Epstein and Kulman 1990, Larochelle and Larivière 2003). We collected *A. cupreolata* exclusively in May–July, with greatest numbers in May. Epstein and Kulman (1990) collected this species primarily throughout May and to a lesser extent in June. *Poecilus lucublandus* had distinct spring and late-season activity periods in southeastern Minnesota, with none captured from early July to mid-August (Epstein and Kulman 1990). We collected relatively large numbers of this species in our mid-July 2005 sampling, with numbers declining in later samples. It is possible that a period of activity could have occurred between our July and August samplings. We collected *C. seximpressus* in 2005 only. Allen and Thompson (1977) found a bimodal activity pattern for this species in northwestern Arkansas woodlands, with relatively large numbers in June and July, and then again in September and October. In our study, 38 of 48 *C. seximpressus* were collected in June. The remainder were distributed throughout the later samples, with no apparent peak.

The relatively large numbers of *Pterostichus stygicus* collected in June and September samples in our study suggests a bimodal seasonal pattern, particularly during 2005 when sample size was greatest. Gilbert (1957) suggested that, in northeastern Illinois (Cook Co.), females of this species either oviposited in the current spring, or in the previous year and then overwintered even though they had already reached sexual maturity. Collections of *P. permundus* likewise were suggestive of a bimodal pattern in our study, although only 6% of specimens were collected in June. Allen and Thompson (1977) found a bimodal activity pattern for this species in woodlands of northwestern Arkansas, but with greatest numbers in June. *Megacephala virginica* is a summer tiger beetle, with peak abundance in August according to Knisley and Schultz (1997). In Nebraska, Carter (1989) recorded greatest numbers in August and especially September. In our study, almost all *M. virginica* were collected in July.

Our results show that west-central Illinois carabid communities vary temporally, with abundance and species richness greatest early in the season. Species composition was fairly consistent across years. Abundance and species richness differed greatly between years, but relative numbers among months were similar between years. Carabid species showed distinct seasonal patterns of occurrence, but for the most part were similar to patterns found for these species in other midwestern U.S. studies.

Acknowledgments

The authors thank Seán Jenkins (Western Illinois University), Ben Wodika (Illinois State University), and Jamie Palmer (Purdue University) for assistance with field work, and Robert Davidson (Carnegie Museum of Natural History) for identification of unknown carabids. We thank Dean Corgait (Illinois Department of Natural Resources) for assistance with the funding application process. Generous financial support of this research was provided by the Illinois Wildlife Preservation Fund (Illinois Department of Natural Resources, Contract RC06L21W) and the Western Illinois University Graduate Research Council.

References Cited

Allen, R.T. and R.G. Thompson. 1977. Faunal composition and seasonal activity of Carabidae (Insecta: Coleoptera) in three different woodland communities in Arkansas. Ann. Entomol. Soc. Am. 70: 31–34.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26: 32–46.

Barber, N.A., K.A. LaMagdeleine-Dent, J.E. Willand, H.P. Jones and K.W. McCravy. 2017. Species and functional trait re-assembly of ground beetle communities in restored grasslands. Biodivers. Conserv. 26: 3481–3498.

Butterfield, J. 1996. Carabid life-cycle strategies and climate change: A study on an altitude transect. Ecol. Entomol. 21: 9–16.

Carter, M.R. 1989. The biology and ecology of the tiger beetles (Coleoptera: Cicindelidae) of Nebraska. Trans. Nebr. Acad. Sci. 17: 1–18.

Coope, G.R. 1978. Constancy of insect species versus inconstancy of Quaternary environments, Pp. 176–187. *In* Mound, L.A. and N. Waloff (eds.), Diversity of Insect Faunas. Royal Entomological Society of London Symposium 9. Blackwell Scientific Publications, Oxford, U.K.

Coope, G.R. 1987. The response of late Quaternary insect communities to sudden climatic changes, Pp. 421–438. *In* Gee, J.H.R. and P.S. Giller (eds.), Organization of Communities Past and Present. British Ecological Society Symposium 27. Blackwell Scientific Publications, Oxford, U.K.

Epstein, M.E. and H.M. Kulman. 1990. Habitat distribution and seasonal occurrence of carabid beetles in east-central Minnesota. Am. Midl. Nat. 123: 209–225.

Gilbert, O. 1957. Notes on the breeding seasons of some Illinois carabid beetles. Pan-Pac. Entomol. 33: 53–58.

Hamilton, F.B., R.N. Wiedenmann, M.J. Skvarla, R. Sathyamurthy, D.M. Fisher, J.R. Fisher and A.P.G. Dowling. 2018. Litter-dwelling ground beetles (Coleoptera: Carabidae) and ground spiders (Araneae: Gnaphosidae) of the Ozark Highlands, USA. Southeast. Nat. 17: 55–73.

Holm, S. 1979. A simple sequentially selective multiple test procedure. Scand. J. Stat. 6: 65–70.

Honek, A., Z. Martinkova and V. Jarosik. 2003. Ground beetles (Carabidae) as seed predators. Eur. J. Entomol. 100: 531–544.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. J. Theor. Biol. 29: 151–154.

Iverson, L.R. 1988. Land-use changes in Illinois, USA: The influence of landscape attributes on current and historic land use. Landsc. Ecol. 2: 45–61.

Johnson, N.E. and R.S. Cameron. 1969. Phytophagous ground beetles. Ann. Entomol. Soc. Am. 62: 909–914.

Jones, M.G. 1979. The abundance and reproductive activity of common Carabidae in a winter wheat crop. Ecol. Entomol. 4: 31–43.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439.

Knisley, C.B. and T.D. Schultz. 1997. The Biology of Tiger Beetles and a Guide to the Species of the South Atlantic States. Virginia Museum of Natural History, Martinsville, VA.

Larochelle, A. 1972. Collecting hibernating ground beetles in stumps (Coleoptera: Carabidae). Coleopt. Bull. 26: 30.

Larochelle, A. 1975a. A list of mammals as predators of Carabidae. Carabologia 3: 95–98.

Larochelle, A. 1975b. A list of amphibians and reptiles as predators of Carabidae. Carabologia 3: 99–103.

Larochelle, A. 1980. A list of birds of Europe and Asia as predators of carabid beetles including Cicindelini (Coleoptera: Carabidae). Cordulia 6: 1–19.

Larochelle, A. and M-C Larivière. 2003. Natural History of the Ground-Beetles (Coleoptera: Carabidae) of America North of Mexico. Pensoft, Sofia, Bulgaria.

Lindroth, C.H. 1961–1969. The ground beetles (Carabidae, excl. Cicindelidae) of Canada and Alaska, parts 1–6. Opuscula Entomological Supplementa 20, 24, 29, 33, 34, 35. Lund, Sweden.

Lövei, G.L. and K.D. Sunderland. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Ann. Rev. Entomol. 41: 231–256.

Maelfait, J.P. and L. Baert. 1975. Contributions to the knowledge of the arachno- and entomo-fauna of different wood habitats. Part I. Sampled habitats, theoretical study of the pitfall method, survey of the captured taxa. Biol. Jb. Dodonaea 43: 179–196.

McCravy, K.W. 2018. A review of sampling and monitoring methods for beneficial arthropods in agroecosystems. Insects 9: 170. doi:10.3390/insects9040170.

McCravy, K.W. and J.G. Lundgren. 2011. Carabid beetles (Coleoptera: Carabidae) of the Midwestern United States: A review and synthesis of recent research. Terr. Arthropod Rev. 4: 63–94.

Niemelä, J., J.R. Spence and H. Cárcamo. 1997. Establishment and interactions of carabid populations: An experiment with native and introduced species. Ecography 20: 643–652.

Niemelä, J., J.R. Spence and D.H. Spence. 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. Can. Entomol. 124: 521–540.

Peck, J.E. 2016. Multivariate Analysis for Ecologists: Step-by-Step. 2nd ed. MjM Software Design, Gleneden Beach, OR.

Shannon, C.E. 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27: 379–423, 623–656.

Shelford, V.E. 1908. Life histories and larval habits of the tiger beetles (Cicindelidae). J. Linn. Soc. Lond. Zool. 30: 157–184.

Spomer, S.M., M.L. Brust, D.C. Backlund and S. Weins. 2008. Tiger beetles of South Dakota and Nebraska. Special Publication, University of Nebraska Press, Lincoln.

Suenaga, H. and T. Hamamura. 2001. Occurrence of carabid beetles (Coleoptera: Carabidae) in cabbage fields and their possible impact on lepidopteran pests. Appl. Entomol. Zool. 36: 151–160.

Thiele, H.-U. 1977. Carabid Beetles in Their Environments. Springer, Berlin, Germany.

Werner, S.M. and K.F. Raffa. 2003. Seasonal activity of adult, ground-occurring beetles (Coleoptera) in forests of northeastern Wisconsin and the Upper Peninsula of Michigan. Am. Midl. Nat. 149: 121–133.

Willand, J.E. and K.W. McCravy. 2006. Variation in diel activity of ground beetles (Coleoptera: Carabidae) associated with a soybean field and coal mine remnant. Great Lakes Entomol. 39: 141–148.

Willand, J.E., B.R. Wodika, J. Palmer, S.E. Jenkins and K.W. McCravy. 2011. Diversity of ground beetles (Coleoptera: Carabidae) in relation to habitat type in west-central Illinois. Am. Midl. Nat. 166: 266–282.