

## SEASONAL OCCURRENCE (PHENOLOGY) OF COPROPHILOUS BEETLES (COLEOPTERA: SCARABAEIDAE AND HYDROPHILIDAE) FROM CATTLE AND SHEEP FARMS IN SOUTHEASTERN MICHIGAN, USA

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### ABSTRACT

A total of 17 species of Scarabaeidae (1,288 individuals) and nine species of Hydrophilidae (482 individuals) were sampled from a cattle and sheep farm in southeastern Michigan between March 2012 and May 2013. Seven of these species are native, while 19 species are of European origin. Despite the closeness of the farms (730 m), *Otophorus haemorrhoidalis* (L.), *Sphaeridium lunatum* F., and *Sphaeridium scarabaeoides* (L.) were found significantly more frequently on the cattle farm, whereas *Labarrus pseudolividus* (Balthasar), *Oscarinus rusicola* (Melsheimer), and *Blackburneus stercorosus* (Melsheimer) were found significantly more frequently on the sheep farm. The highest abundances of beetles were encountered between May and November and correlated with temperatures above 10°C. Eleven species occurred only from spring to summer, eight species occurred from summer until autumn, and six species showed a split pattern of spring to early summer, absence during summer, and a second occurrence in autumn. No beetles were found between 4 January and 16 April 2013. To further understand the invasive potential of adventive dung beetle species, seasonal patterns of species within the three groups were compared to seasonal patterns of the same species at more northern, more southern, and European locations and to predictions arising from climatic differences between these latitudes.

Key Words: seasonality, Aphodiinae, Scarabaeinae, *Cercyon*, *Sphaeridium*, *Onthophagus*, dung

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Dung is one of the fundamental returns of animal matter and energy into the nutrient and energy cycles of the planet and supports a bio-diverse community, especially arthropods that contribute to decomposition (Bornemissza 1960; Waterhouse 1974; Fincher 1981; Slade *et al.* 2007; Nichols *et al.* 2008; O’Hea *et al.* 2010; Wu *et al.* 2010; Beynon *et al.* 2012; Kudavidanage *et al.* 2012). Coprophilous beetles are mainly comprised of larvae and adult beetles from the families Scarabaeidae (subfamilies Scarabaeinae and Aphodiinae) and Geotrupidae (Pakaluk *et al.* 1995; Ratcliffe and Jameson 2005) and adult Hydrophilidae (subfamily Sphaeridiinae) (Smetana 1978) whose larvae are predacious. Coprophilous adult and larval beetles compete with dung-inhabiting Diptera larvae for food, whereas the larvae of hydrophilid beetles are important predators on dipteran larvae. Both competition and predation by coprophilous beetles reduce the fitness of many pest species that develop within dung (Valiela 1974; Fay and Doube 1983; Kirk 1992). Another benefit of dung beetles is the enhancement of soil fertility (Brown *et al.* 2010; Ishikawa 2011). Dung beetles increase the rate of dung decomposition by tunneling through dung pads and mixing dung with soil when provisioning for their offspring (Fincher *et al.* 1981;

Miranda *et al.* 1998; Nichols *et al.* 2008; Brown *et al.* 2010; Liu *et al.* 2012).

Previous research focused on dung beetle communities in southern North America include studies in Texas (Nealis 1977; Fincher *et al.* 1986; Howden and Scholtz 1986; Howden and Howden 2001), Georgia (Fincher 1975; Fincher and Woodruff 1979), Florida (Woodruff 1973), South Carolina (Harpoottlian 2001), Louisiana (Radtke *et al.* 2008), Arkansas (Fiene *et al.* 2011), and North Carolina (Bertone *et al.* 2005). Dung beetle studies from northern North America that provide distributional and phenological information include studies in New York (Valiela 1969; Pimsler 2007), South Dakota (Kessler *et al.* 1974), North Dakota (Helgesen and Post 1967), Minnesota (Cervenka and Moon 1991), southern Alberta (Floate and Gill 1998; Kadiri *et al.* 2014), southern Québec (Matheson 1987; Levesque and Levesque 1995), New Jersey and Maryland (Price 2004; Price *et al.* 2012) and just recently the first study from Michigan (Rounds and Floate 2012). Only five of the above mentioned studies examined Hydrophilidae (Kessler *et al.* 1974; Matheson 1987; Cervenka and Moon 1991; Levesque and Levesque 1995; Rounds and Floate 2012). Furthermore, Matheson (1987) and Levesque and Levesque (1995) were the only

studies to provide data on the phenology of hydrophilid dung beetles. Many areas either lack information on local species assemblages, their relative abundance, or their seasonal composition. The only study from Michigan so far provides data only for cattle pastures but not other types of dung, *e.g.*, sheep dung. Studies that provide natural history data are essential to understand beetle biodiversity (Braga *et al.* 2013; Korasaki *et al.* 2013), the monitoring and advancement of adventive species (Floate and Gill 1998; Gollan *et al.* 2011; Kaufman and Wood 2012; Rounds and Floate 2012; Floate and Kadiri 2013), for providing essential ecological information on local pasture ecosystems (Qie *et al.* 2011; Agoglitta *et al.* 2012; Liu *et al.* 2012; Numa *et al.* 2012; Campos and Hernandez 2013), and as a proxy to monitor global climate change (Menendez and Gutierrez 2004; Wu and Sun 2012).

My goals in the current study were to determine the species of Scarabaeidae and Hydrophilidae on two pastures in southeastern Michigan throughout an entire year, identify community differences between sheep and cattle farms, and to record and compare the seasonality/phenology of each species sampled. Year-round surveys of insects allow us to document the species richness, abundance, and seasonal occurrence of species in local areas throughout North America. These data provide historical records for researchers and policy makers to compare their own data to and document changes in species diversity.

## MATERIAL AND METHODS

I sampled coprophagous beetles from two farms located approximately 16 km NW of Adrian Michigan, in Rome Township, Lenawee County, Michigan at an elevation of ~270 m above sea level. Warrick Sheep (41°55.351' N, 84°9.626' W) – referred herein as “sheep farm” – possesses about 60 adult sheep of two breeds (Lincoln wool sheep and Suffolk meat sheep), and after the lambing season, up to 80 lambs roam the 25-hectare sheep farm. The sheep farm is on well-drained Morley loam (SoilWeb-Earth 2013). Ryan’s Farm (41°55.703' N, 84°9.359' W) – herein referred to as “cattle farm” – is home to 40 Holstein steers, which can also freely move around the 12-hectare farm. The generic label “cattle farm” for Ryan’s steer farm is used despite the fact that steers are bred, castrated, and fed for meat production and therefore defecate qualitatively different pats than dairy cows. Steers are generally fed a diet higher in grains than dairy cows are, so they put on weight faster. Dairy cows, in contrast, are fed more roughage and grasses because a lot of grain would cut into milk production. This differ-

ence causes steer pats to have different physical and chemical characteristics compared to dairy cow pats, such as higher fiber content, which might lead to differences in their attractiveness for coprophilous beetle species (unpublished data). The cattle farm sits on poorly drained Blount loam (SoilWeb-Earth 2013). Both farms have been grazed year-round for at least the last 30 years and are 730 m apart.

Forage plants found on the sheep farm are mainly Kentucky blue grass (*Poa pratensis* L.; Poaceae) and Dutch white clover (*Trifolium repens* L.; Fabaceae). The diet was supplemented by corn and white Japanese radishes (*Raphanus sativus* var. *longipinnatus* L. H. Bailey; Brassicaceae) in October. The cattle farm used a pasture mix of various grasses, white clover, and alfalfa (*Medicago sativa* L.; Fabaceae), supplemented by corn and sorghum to substitute for low forage productivity growth periods. Neither farm used growth promoters, antibiotics, or parasiticides on a regular basis.

Long-term climate data (Weatherbase 2013) for Adrian, Michigan (16 km SE of the sampling sites) reported the average high and low temperatures in the coldest months (January and February) of 0 and –8 °C, respectively. Average high and low temperatures in the hottest month (July) are 29 and 15 °C, respectively. Average annual precipitation is 863 mm. Weather conditions during the sampling days were recorded by the Weather Underground station at Adrian airport (KADG) (WeatherUnderground 2013) and are shown in Fig. 1.

Biweekly sampling started on 26 March 2012 on the sheep farm only. From 29 May 2012 until 16 May 2013, both farms were sampled every other week, except on 15 January, 1 February, 1 April, and 1 May 2013 (Fig. 1). I sampled both farms between 10:00 am and 5:00 pm depending on the season and weather. Beetles were obtained by hand-picking through dung pats using a pair of feather tweezers and a trowel and spatula to open up and scoop through the dung pats as well as digging up and sampling the dung – soil interface. To get a representative sample of all successional groups, I sampled dung pats of various ages (freshly deposited to several weeks old), judged by the presence or absence of a crust and the overall dung texture, *e.g.*, the ratio between fiber and fine-grained matrix. In addition, I sampled dung pats deposited in all microclimates on each pasture, *e.g.*, shaded vs. non-shaded areas in proportion of their occurrence on the pasture to include specialist species of all microhabitat types (Wassmer 1995). On each sampling day, I spent approximately one hour on each farm sampling between 20–40 steer pats (1,631±872 g per pat, mean±SD) and 40–80 sheep lumps (41±13 g per lump, median± median absolute

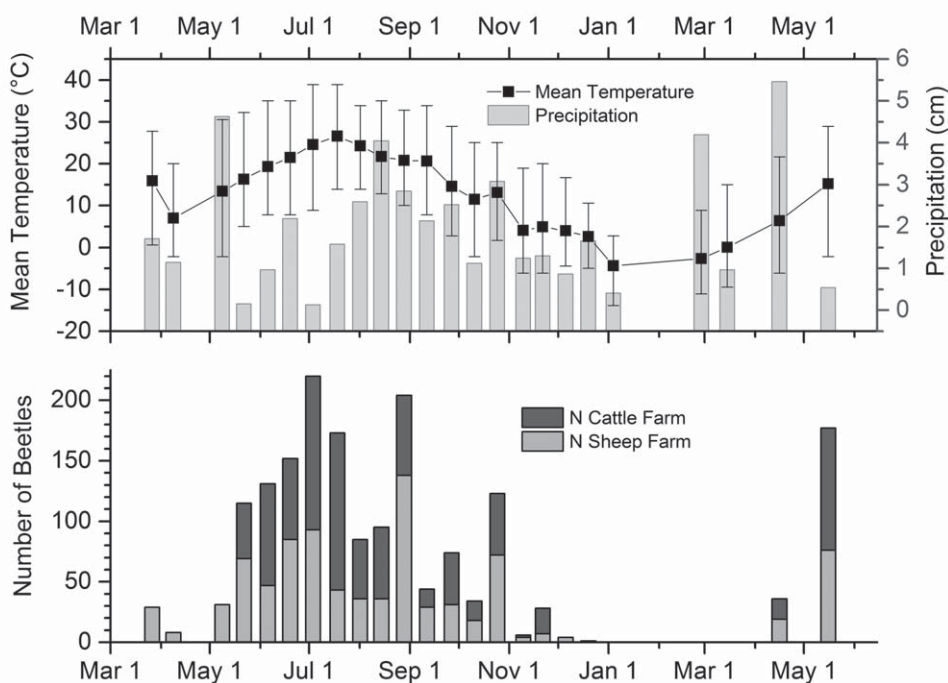


Fig. 1. Mean temperature (with maximum and minimum bars) and accumulated precipitation between sampling dates for Adrian, MI from March 2012 to June 2013 and number of beetles (N) sampled on those dates.

deviation) depending on how densely dung pats were populated. To compensate for the natural bias of hand-picking rare and new species, I intentionally collected common species more often than rare species relative to their abundance in each dung pat. However, as this method is not properly quantifiable, I based my phenological analyses solely on the incidence (presence or absence) of each species in a sample rather than abundance (Gotelli *et al.* 2011). As I used a standardized sampling technique and identified every species that occurred in each sample, limiting my analyses to incidence compensates the problem of not having counted the abundance of every species in my samples (Nicholas J. Gotelli, personal communication). Bias against paracoprid (tunneling) species was compensated by sampling the dung-soil interface and digging at least 0.1 m deep into the soil to retrieve beetles if tunnels were visible.

Scarabaeidae were identified using the keys in Howden and Cartwright (1963), Freude *et al.* (1969), Wegner and Niemczyk (1979), Ratcliffe (1991), Lohse and Lucht (1992), Stebnicka and Lago (2005), Gordon and Skelley (2007), and Skelley (2007a–c). Hydrophilidae were determined with the help of Freude *et al.* (1971), Smetana (1978), and Lohse and Lucht (1989).

Voucher specimens were placed in the insect collection of Siena Heights University, Department of Biology, Adrian, Michigan.

Data visualization was done with the help of Origin Pro 8.0 (OriginLab Corporation, Northampton, MA). Data analyses were performed using Statistica 10 (StatSoft Inc., Tulsa, OK).

## RESULTS

**Species Composition.** A total of 1,770 beetles were sampled, representing 17 species of Scarabaeidae and nine species of Hydrophilidae (Table 1). I could not quantitatively distinguish between *Ataenius strigatus* (Say) and *Ataenius spretulus* (Haldeman) and therefore address them as *A. strigatus sensu lato* (a grouping commonly used for these difficult species (Stebnicka and Lago 2005)). Paul K. Lago from the University of Mississippi determined that almost all of the individuals that I collected were *A. spretulus*, with a few individuals of *A. strigatus*. Ten of the 17 scarabaeid species are adventive Palearctic species, whereas seven are indigenous to the Nearctic region. Of the nine species of Hydrophilidae, only one species, *Ceryon praetextatus* (Say), is indigenous to North America.

**Table 1.** Numbers of dung beetles sampled from two farms near Adrian, Michigan between March 2012 and June 2013. n/a = native (n) or adventive (a) species; N = number of individuals collected; Species Totals: % = relative abundance of species on either farm as percentage of total number sampled from both farms.

Species	n/a	Sheep Farm	Cattle Farm	Species Totals	
		N	N	Sheep%	Cattle%
<b>Scarabaeidae</b>					
<b>Aphodiinae</b>					
<i>Aphodius fimetarius</i> (L.)	a	14	25	35.9	64.1
<i>Ataenius strigatus sensu lato</i> *	n	114	172	39.9	60.1
<i>Blackburneus stercorosus</i> (Melsheimer)	n	20	3	87.0	13.0
<i>Calamosternus granarius</i> (L.)	a	166	105	61.3	38.7
<i>Chilo thorax distinctus</i> Müller	a	16	24	40.0	60.0
<i>Colobopterus erraticus</i> (L.)	a	39	55	41.5	58.5
<i>Labarrus pseudolividus</i> (Balthasar)	a	175	12	93.6	6.4
<i>Melinopterus prodromus</i> (Brahm)	a	0	6	0	100
<i>Oscarinus rusicola</i> (Melsheimer)	n	82	8	91.1	8.9
<i>Otophorus haemorrhoidalis</i> (L.)	a	5	144	3.4	96.6
<i>Pseudagolius bicolor</i> (Say)	n	3	6	33.3	66.7
<i>Teuchestes fossor</i> (L.)	a	0	1	0	100
<b>Scarabaeinae</b>					
<i>Onthophagus hecate</i> (Panzer)	n	7	0	100	0
<i>Onthophagus nuchicornis</i> (L.)	a	2	1	66.7	33.3
<i>Onthophagus pennsylvanicus</i> Harold	n	5	0	100	0
<i>Onthophagus taurus</i> (Schreber)	a	27	51	34.6	65.4
<b>Hydrophilidae</b>					
<b>Sphaeridiinae</b>					
<i>Cercyon haemorrhoidalis</i> (F.)	a	52	20	72.2	27.8
<i>Cercyon praetextatus</i> (Say)	n	0	1	0	100
<i>Cercyon pygmaeus</i> (Illiger)	a	3	1	75.0	25.0
<i>Cercyon quisquilius</i> (L.)	a	138	207	40.0	60.0
<i>Cryptopleurum</i> c.f. <i>crenatum</i> (Kugelann)	a	1	1	50.0	50.0
<i>Cryptopleurum minutum</i> (F.)	a	1	1	50.0	50.0
<i>Sphaeridium bipustulatum</i> F.	a	2	5	28.6	71.4
<i>Sphaeridium lunatum</i> F.	a	2	31	6.1	93.9
<i>Sphaeridium scarabaeoides</i> (L.)	a	1	15	6.3	93.7
<b>Total</b>		<b>875</b>	<b>895</b>		

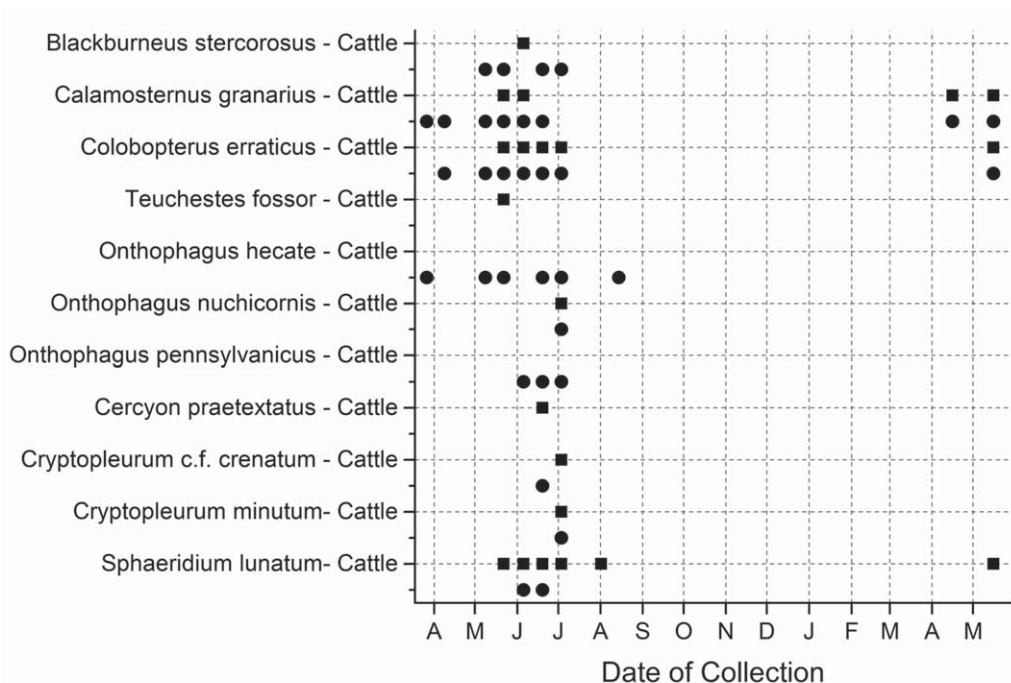
\* Includes *Ataenius spretulus* (Haldeman) and *Ataenius strigatus* (Say).

**Species Occurrence.** Approximately the same numbers of beetles were sampled from the sheep and cattle farms (Table 1). However, two species, *Onthophagus hecate* (Panzer) and *Onthophagus pennsylvanicus* Harold, were only sampled on the sheep farm, while three species (*Teuchestes fossor* (L.), *Melinopterus prodromus* (Brahm), and *C. praetextatus*) were only sampled on the cattle farm. All five of these species were very rare – thus their absence on one of the farms could be a random event. Conversely, several abundant species were significantly more frequently observed on one of the farms (Chi square test,  $p < 0.05$ ). *Otophorus haemorrhoidalis* (L.), *Sphaeridium lunatum* F., and *Sphaeridium scarabaeoides* (L.) were found more frequently on the cattle farm (96.6%, 93.9%, and 93.8%, respectively, of all individuals of each species collected on both farms), whereas *Labarrus pseudolividus* (Balthasar), *Oscarinus rusicola* (Melsheimer), and *Blackburneus*

*stercorosus* (Melsheimer) occurred more frequently on the sheep farm (93.6%, 91.1%, and 87.0%, respectively, of all individuals of each species collected on both farms).

**Seasonal Occurrence and Phenology.** Based on the number of sampled specimens, the period of greatest beetle productivity occurred from late spring (May) through late autumn (November). Low precipitation during this period did not seem to have a great effect on beetle numbers, even if coupled with maximum temperatures above 30 °C. Beetle activity greatly diminished when temperatures fell below 10 °C (Fig. 1).

Eleven species occurred only in spring and early summer (Fig. 2), including the aphodiines *Calamosternus granarius* (L.), *Colobopterus erraticus* (L.), and *B. stercorosus*, and the large hydrophilidae *S. lunatum*. With the exception of *B. stercorosus*, *T. fossor*, and *O. hecate*, all species could be found again in spring 2013 after being



**Fig. 2.** Phenology of dung beetle species that occurred only in spring and early summer. Symbols indicate the presence of a species in each sample. Sampling started 26 March 2012 (before the first A on the date of collection axis) and ended 16 May 2013 (after the last M on the same axis). Circles show the presence of a beetle species on the sheep farm on the respective collection date, while squares show the presence of a beetle species on the cattle farm on the respective collection date. Presence of a species at the sheep farm is indicated below the labeled presence of the species at the cattle farm.

absent from the dung since July or August 2012. *Onthophagus hecate* was found between early spring and late summer 2012, extending beyond the temporal range of the other species in the spring-summer group by about a month.

Another group of eight species occurred from summer until late autumn (Fig. 3). This group included the aphodiines *O. haemorrhoidalis*, *O. rusicola*, *L. pseudolividus*, and *A. strigatus sensu lato*, the only abundant scarabaeine, *Onthophagus taurus* (Schreber), and the small hydrophilid *Cercyon quisquilius* (L.), which was by far the most frequently encountered coprophilous beetle in this study.

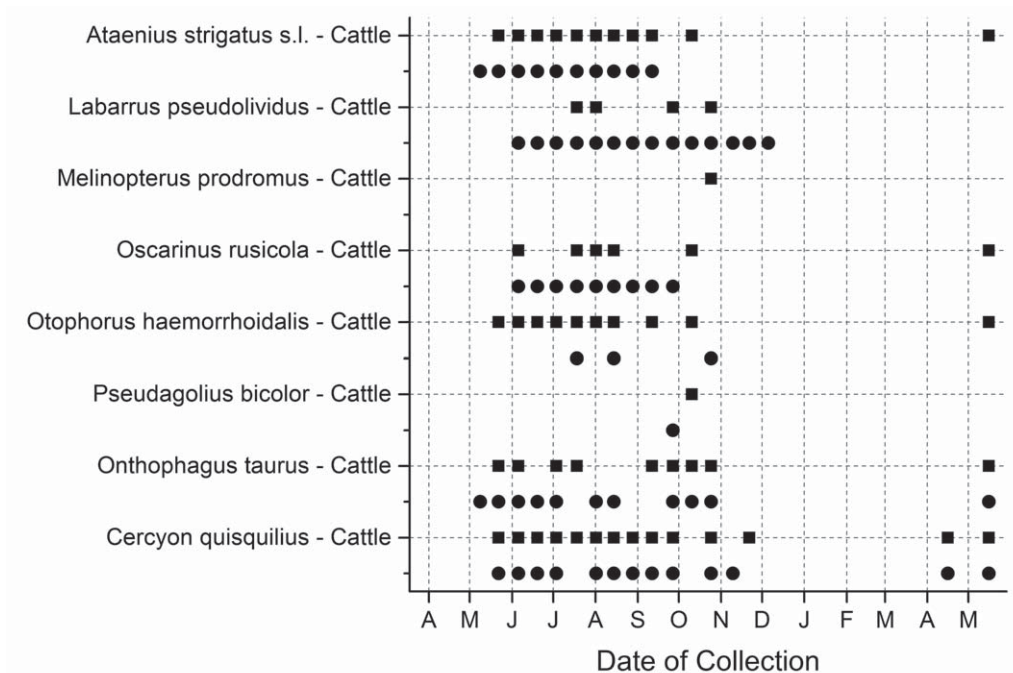
Finally, six other species, including the aphodiinaes *Aphodius fimetarius* (L.) and *Chilo thorax distinctus* Müller, and the small hydrophilidae *Cercyon haemorrhoidalis* (F.) showed a split pattern of a spring to early summer occurrence, absence during summer, and a second occurrence in autumn to early winter (Fig. 4). These species were accompanied by the less frequently encountered, small hydrophilid *Cercyon pygmaeus* (Illiger) and the larger hydrophilids *Sphaeridium bipustulatum* F. and *S. scarabaeoides*.

Despite these similarities, the seasonal patterns of these species are all slightly different.

No beetles were found between 4 January and 16 April 2013 despite intensive attempts to localize any – thus there might not be any true winter species on these Michigan pastures. However, some species occurred early in early spring 2012 (16 March): *C. distinctus*, *C. granarius*, *O. hecate*, and *C. haemorrhoidalis*. *Cercyon haemorrhoidalis* was the last species found alive before winter (on 12 December 2012).

## DISCUSSION

**Species Composition.** The species composition of the two dung beetle communities on a sheep farm and a cattle farm in southeastern Michigan is similar to that of North Carolina, Maryland, and New Jersey (Bertone *et al.* 2005; Price 2004; Price *et al.* 2012) and more northern locations such as, Minnesota, South Dakota, and southern Alberta (Kessler *et al.* 1974; Cervenka and Moon 1991; Floate and Gill 1998; Kadiri *et al.* 2014). They are also comparable to the study by Round and Floates (2012) on dung beetles



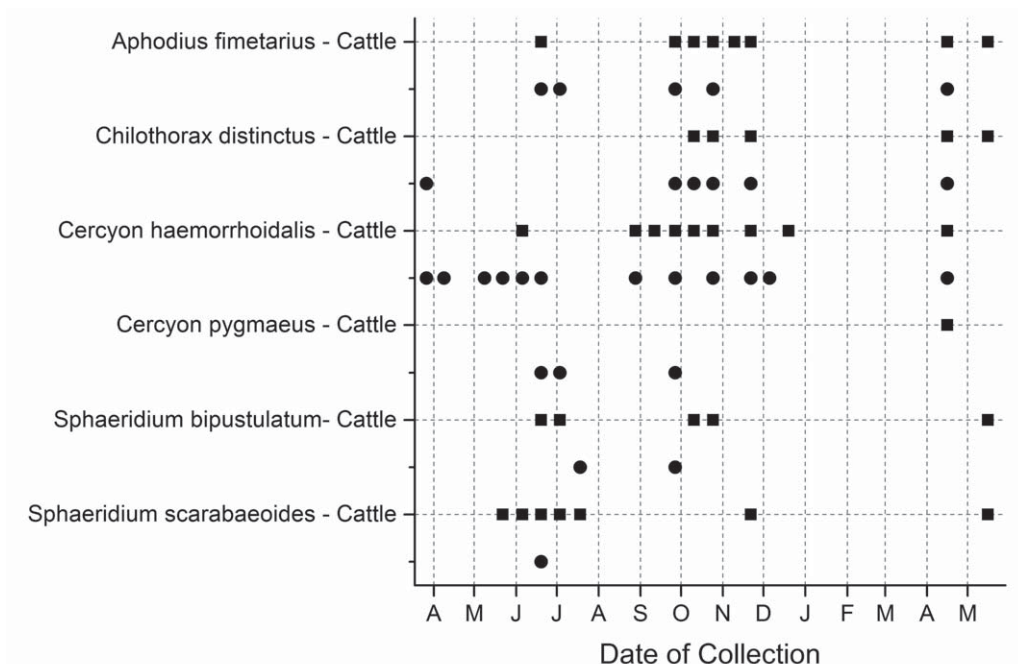
**Fig. 3.** Phenology of dung beetle species that occurred from summer until late autumn. Symbols indicate the presence of a species in each sample. Sampling started 26 March 2012 (before the first A on the date of collection axis) and ended 16 May 2013 (after the last M on the same axis). Circles show the presence of a beetle species on the sheep farm on the respective collection date, while squares show the presence of a beetle species on the cattle farm on the respective collection date. Presence of a species at the sheep farm is indicated below the labeled presence of the species at the cattle farm.

near Lake City, Michigan. The species community of the current study is clearly dominated by adventive species. Only one of the abundant species, *L. pseudolividus*, is indigenous. This dominance of non-native species, however, is not specific to this study alone but is a common theme in the dung beetle communities of most reference studies (e.g., Kessler *et al.* 1974; Cervenka and Moon 1991; Floate and Gill 1998; Bertone *et al.* 2005; Pimslar 2007; Rounds and Floate 2012; Kadiri *et al.* 2014), with the remarkable exception of New Jersey and eastern Maryland, where mostly indigenous species dominated (Price 2004; Price *et al.* 2012). This might be due to the study design that sampled nature preserves not used as farmland and forested areas thus probably showing the original indigenous fauna of northeastern North American coprophilous beetles.

This study confirms the presence of the invasive species *O. taurus* in Michigan, which was previously reported by Rounds and Floate (2012). In fact, this species was the most common scarabaeine in the current study, encountered much more frequently than the likewise adventive *Onthophagus nuchicornis* (L.), which dominated the study at

Lake City (Rounds and Floate 2012), which is about 280 km NNW of Adrian (250 km farther north) and about 100 m higher in elevation. In addition, *C. distinctus* was less frequently encountered in this study, while *C. granarius* dominated at the Lake City site. The lack of *O. haemorrhoidalis*, *A. spretulus*, and *A. strigatus* in the Lake City study (Rounds and Floate 2012) is striking. One reason might be the different collection methods used in both studies. Baited pitfall traps used in the study by Rounds and Floate (2012) might not be attractive to species that prefer the interface between dung, vegetation, and soil where I found most specimens of the two *Ataenius* species and *O. haemorrhoidalis* in this study. However, it is questionable whether beetles could differentiate between dung located in pitfall traps and dung lying on the ground.

Another remarkable difference between the two Michigan sites is the lack of Geotrupidae in Adrian compared to three species collected at Lake City (Rounds and Floate 2012). One reason might be the dense soils rich in clay at the site of my study in southeastern Michigan compared to the sandy loam at the Lake City site. Dense



**Fig. 4.** Phenology of dung beetle species with a split temporal distribution pattern in spring/summer and late autumn. Symbols indicate the presence of a species in each sample. Sampling started 26 March 2012 (before the first A on the date of collection axis) and ended 16 May 2013 (after the last M on the same axis). Circles show the presence of a beetle species on the sheep farm on the respective collection date, while squares show the presence of a beetle species on the cattle farm on the respective collection date. Presence of a species at the sheep farm is indicated below the labeled presence of the species at the cattle farm.

clay-rich soils are more resistant to tunneling and keep the groundwater table higher than sandy soils, which could both interfere with tunneling. However, all Geotrupidae found by Rounds and Floate (2012) were quite rare and might have been missed in the current study, as Geotrupidae are known to construct very deep tunnels (Paulian 1959; Brussaard 1983; Turner 1997).

Only a few studies have included Hydrophilidae to species level in their species list. In their Minnesota study, Cervenka and Moon (1991) found similar species composition, and *C. quisquilius* was by far the most abundant small *Cercyon* species, whereas *S. lunatum* was by far the most abundant large *Sphaeridium* species. Rounds and Floate (2012) also reported finding the two large *Sphaeridium* species but only two unidentified specimens of *Cercyon*. In their study, *S. scarabaeoides* was more frequent than *S. lunatum*.

**Species Occurrence on Both Farms.** The sheep and cattle farms were only about 730 m apart from each other - no apparent dispersal obstacles were observed. Differences in the species composition and incidence of the two coprophilous beetle communities can most likely be attributed to the different kind of dung on both

farms in terms of food and habitat preferences (Gordon 1983; Wassmer 1995; Finn and Giller 2002; Errouissi *et al.* 2004; Holter and Scholtz 2007; Whipple and Hoback 2012). While the absence of some rare species from either farm is difficult to interpret, the significantly biased distribution of a few common species may hint to species preferences for a certain type of dung. In the present study, *O. haemorrhoidalis*, *S. lunatum*, and *S. scarabaeoides* were found much more frequently on the cattle farm, whereas *L. pseudolividus*, *O. rusicola*, and *B. stercorosus* were encountered much more frequently on the sheep farm (Table 1). In a previous study on a mixed sheep and cow farm in Germany, I found a clear preference for cow dung in all three species mentioned above (Wassmer 1995). None of the indigenous Nearctic species found significantly more often on the sheep farm occurred on the mixed farm studied in Germany. In that earlier study, however, *C. distinctus* and *C. granarius* were found significantly more often in sheep dung, a result that does not agree with the present study. Only one other study in North America compared the occurrence of dung beetles in sheep and cow dung (Kessler *et al.* 1974). The authors mention

a preference of *C. granarius* for sheep dung, which cannot be verified by the results of the present study. According to Gordon and Skelley (2007) and BugGuide (2013), *L. pseudolividus* occurs in a variety of dung with a preference for bovine dung but showed a clear preference for the sheep farm in the present study (94% of all *L. pseudolividus* taken on both farms). *Oscarinus rusicola* is believed to have a preference for deer dung but is also found to feed and reproduce on sheep and cattle dung (Gordon and Skelley 2007). In the present study, this species preferred the sheep farm (91% of all *O. rusicola* taken on both farms). Gordon and Skelley (2007) list *B. stercorosus* as a detritivore found on small mammal and cow dung. In this study, it preferred the sheep dung over the cattle dung (87% of all *B. stercorosus* taken on both farms) and was usually found in older droppings, which supports the assumption of a more detritivorous nutrition in this species.

**Seasonal Occurrence/Phenology.** Like most other climatically comparable studies in the New World, the period of greatest beetle activity occurred from late spring (May) through late autumn (November) (Fig. 1). This corresponds with mean temperatures above 10 °C, as previously reported by (Bertone *et al.* 2005) for the Piedmont region of North Carolina. In contrast to their observations, low precipitation at maximum temperatures of more than 30 °C did not lead to reduced beetle counts in my study (Fig. 1). This, however, might be attributed to different sampling methods, *i.e.*, proportional hand-picking of species in this study compared to quantitative pitfall trapping in the study by Bertone *et al.* (2005).

A pattern of high beetle activity between late spring and late autumn also relates to the seasonality of beetle activity found on pastures in cold-temperate Europe (Wassmer 1994). However, it seems that while the beginning of the productive season coincides quite well, the end of the season on the Michigan pastures is extended into November. The ability of introduced Eurasian beetles to extend their phenology into the “autumn niche” like it was found for several invasive plant species (Fridley 2012) might provide them with a selective advantage over native new world species that enter the “winter mode” earlier, and might partially explain their invasive potential and increasing spread into northern latitudes.

Seasonality is common among insect species since it corresponds with climate and the availability of food. Many species are able to adjust to various climate conditions, and the differences in their phenology are most probably due to genetic polymorphism (Kivelä *et al.* 2013). Sea-

sonality or phenology is therefore a key adaptive trait that determines the distribution of species (Chuine 2010) and may provide clues to the actual and potential spreading of invasive species (Kollmann and Bañuelos 2004; Clements and DiTommaso 2012), especially if the degree of heritability and polymorphism of the phenological traits in the populations are known (Dirlewanger *et al.* 2012). In addition, phenological traits are valuable markers to monitor the progress of local and global climate change (Menendez and Gutierrez 2004; Wu *et al.* 2010; Wu and Sun 2012).

Figures 2–4 show the seasonal occurrence of adult beetles of the 26 coprophilous beetle species but do not necessarily indicate the number of egg-to-adult generations per year. Many species overwinter as adults; they develop from egg to adult in the latter half of one year (autumn peak), disappear during winter, and reappear as a new peak in spring thus not indicating two generations. Other species overwinter in the egg or one of their larval stages, and their late spring/summer peak of adult activity indicates a new generation. To complicate things more, some species, *e.g.*, *A. fimetarius* may overwinter in several developmental stages and are thus capable of multiple overlapping generations per year (Landin 1961).

**Spring to Early Summer Species.** The aphodiines *B. stercorosus*, *C. granarius*, *C. erraticus*, and *T. fossor*, the scarabaeines *O. hecate*, *O. nuchicornis*, and *O. pennsylvanicus*, and the hydrophilids *C. praetextatus*, *Cryptopleurum* c.f. *crenatum* Kugelann, *Cryptopleurum minutum* (F.), and *S. lunatum* occurred only in spring and early summer (Fig. 2).

**Predictions:** If these species are truly adapted to the climatic conditions of a single time period from spring to summer at middle latitudes, it can be predicted that more northern populations should emerge from winter later and extend their seasonal range into the more mild summer months, whereas southern populations should appear earlier in spring and disappear earlier in summer.

*Calamosternus granarius* showed an almost uninterrupted unimodal pattern from March until July but did not reappear in the second spring until May. In southwestern Germany, this species occurred from mid-March until the beginning of August, with two very close peaks in mid-April and mid-June, indicating a single generation (Wassmer 1994). The potential for a later, prolonged, and clearly bimodal distribution was found in the Lake City site by Rounds and Floate (2012). However, the overall range of the pattern is still too narrow to indicate two yearly generations.



In southern Alberta, the same predicted trend was found (Floate and Gill 1998; Kadiri *et al.* 2014), though less pronounced than at the northern Michigan location. In contrast, *C. granarius* appeared as predicted already in February or even January in Arkansas (Fiene *et al.* 2011) and North Carolina (Bertone *et al.* 2005) and disappeared in June or even in May. Overall, this species seems to be univoltine and fits the prediction of a fixed seasonal pattern that is flexible enough to adapt to latitudinal climatic variation.

In the present study, the adventive *C. erraticus* also showed a unimodal appearance from April to July but did not reappear until May in the second spring. In Denmark, the species appeared in late May and disappeared in late August (Holter 1982). This corresponds to the pattern observed in Adrian; however, as predicted, *C. erraticus* occurred four weeks later at Lake City than in Adrian and extended even later into October (Rounds and Floate 2012). In southern Alberta, the species appeared also as predicted, later and longer from May throughout October, showing a clearly bimodal pattern with distinct peaks in May and August (Kadiri *et al.* 2014). This might indicate a bivoltine pattern of two generations in a year unless the first peak in spring is adult beetles from the previous year. In Arkansas and North Carolina, the species appeared as early as in Adrian, disappearing also in July - in some years, however, indicating a dense bimodal pattern of two close peaks (Bertone *et al.* 2005; Fiene *et al.* 2011). In the current study, *C. erraticus* followed the predictions for a fixed seasonal pattern, however, the species might be flexible in its overwintering stage and able to generate one or two generations per year.

The large, non-native hydrophilid *S. lunatum* appeared in mid-May and disappeared in August, showing a unimodal distribution. Matheson (1987) found the species in southern Québec from the end of May until mid-September with peaks in early June (most prominent peak), July and September. In southwestern Germany, *S. lunatum* was recovered from mid-May through mid-September with a clear single peak in August (Wassmer 1994). The shorter summer occurrence in Adrian might be due to more extreme summer temperatures in Michigan as compared to Germany and southern Québec. Otronen and Hanski (1983) identify all *Sphaeridium* species as univoltine in Finland, whereas Hansen (1987) describes the members of the genus as bivoltine in Fennoscandia and Denmark. Anlas *et al.* (2008) consider all coprophilous *Sphaeridiinae* in Turkey to have 2–3 generations per year. *Sphaeridium lunatum* seems to be quite flexible

in its phenology but apparently has only one or possibly two generations throughout its distribution. The species is very successfully extending its range worldwide, which coincides with a widely flexible phenology.

No other study reported the seasonal occurrence of the indigenous *B. stercorosus* for any other location so far. In the present study, the species is clearly unimodal, appearing from May until July, indicating a single generation. Gordon and Skelley (2007) reported its temporal range as being from April to October.

**Summer to Late Autumn Species.** Species that occurred from summer until late autumn include the aphodiines *A. strigatus sensu lato*, *L. pseudolividus*, *M. prodromus*, *O. rusicola*, *O. haemorrhoidalis*, and *Pseudagolius bicolor* (Say), the scarabaeine *O. taurus*, and the hydrophilid *C. quisquilius* (Fig. 3).

**Predictions:** If these species are truly adapted to a single time period from late spring/summer to autumn in the middle latitudes, it can be predicted that more northern populations should emerge slightly later but might not extend their range into late autumn due to the possibility of early frost. In contrast, southern populations should appear earlier in spring and disappear earlier in summer.

The species complex *A. strigatus sensu lato* in this study contained the two indigenous taxa *A. spretulus* and *A. strigatus* that were found from May until October. No *Ataenius* species were found in the Lake City study (Rounds and Floate 2012) or any of the two studies from southern Alberta (Floate and Gill 1998; Kadiri *et al.* 2014). In Arkansas, *A. spretulus* occurred from May to August, indicating two peaks, one in June and again in August (Fiene *et al.* 2011). The species is known to have two generations in southern Ohio, the first in late June and the second in August, and it is known to only have one generation in northern locations such as Minnesota (Wegner and Niemczyk 1981). The lack of the species in the two studies from southern Alberta and northern Michigan does not indicate that the genus *Ataenius* is at its latitudinal climatic limits in southeastern Michigan, as *A. spretulus* is an important pest of golf turfgrass and was found to cause damage first in Minnesota (1932), then New York (1969) and Ohio (1973), with most damage done in Michigan and western states such as Colorado, Iowa, and California (Shetlar and Niemczyk 1999). The currently available data indicate, therefore, a seasonal range expansion towards the south facilitated by increasing numbers of yearly generations.

*Labarrus pseudolivinus* is most probably a South American species introduced or invading North America (BugGuide 2013). It was found in high numbers in almost all southern reference studies. In Adrian, the species showed a broad distribution from June until December. *Labarrus pseudolivinus* was not found at Lake City by Rounds and Floate (2012) nor in southern Alberta (Floate and Gill 1998; Kadiri *et al.* 2014). In Arkansas, *L. pseudolivinus* was the single eudominant species of the community, comprising 91–99% of all beetles occurring from May to August and showing two peaks in June and August (Fiene *et al.* 2011). This meets both initial predictions. In North Carolina, *L. pseudolivinus* occurred even earlier in March and extended its range almost as late into autumn as in the current study, showing two or more peaks indicating at least two overlapping generations (Bertone *et al.* 2005). The species is obviously able to extend its temporal range by two months in more southern latitudes. The lack of *L. pseudolivinus* from more northern latitudes may indicate that southeastern Michigan might be the latitudinal climatic limit of its range. However, *L. pseudolivinus* occurred in high numbers over seven months and well into December. This does not seem to be indicative for a borderline edge habitat. In comparison, the seasonal occurrence of *L. pseudolivinus* suggests wide seasonal amplitude, at least to the middle latitudes, which might be one reason for its success in conquering the North American continent.

*Oscarinus rusicola* is an indigenous dung beetle that occurred quite abruptly in mid-May and disappeared in mid-September, showing a broad unimodal pattern. The species was not found at Lake City (Rounds and Floate 2012) but was a subdominant species in southern Alberta, where it occurred slightly earlier than in Adrian but disappeared much earlier in mid-July, which is in disagreement with the predictions (Floate and Gill 1998; Kadiri *et al.* 2014). *Oscarinus rusicola* was not reported in any studies in southern sites.

*Otophorus haemorrhoidalis* was found on all sampling dates from May until October, with two exceptions on 28 August and 26 September 2012. This species was missing in the Lake City study (Rounds and Floate 2012) but was a subdominant species in southern Alberta, where it showed the same seasonal range but a clearer separation into two or even three peaks (Floate and Gill 1998; Kadiri *et al.* 2014). In Arkansas, the species did appear, as predicted, slightly earlier and disappeared, as predicted, earlier in mid-August (Fiene *et al.* 2011). In its original home range in Europe, *O. haemorrhoidalis* occurred also from mid-May until October but showed two distinct peaks in mid-May and August

(Wassmer 1994). It needs to be verified if this indicates two distinct generations. Yoshida and Katakura (1995) categorize the species as univoltine in Hokkaido, Japan, hibernating as adults that feed before hibernation. Overall, this species follows the predictions of a single phenological pattern able to adjust to latitudinal climate changes.

*Onthophagus taurus* was detected from May until late October. From its first reported location in Florida, this non-native species has spread north and west (Hoebeke and Beucke 1997), with this study providing only the second record of this species for Michigan. In the more northern Lake City site, *O. taurus* occurred from May until September, with a clear peak in August (Rounds and Floate 2012). The species was not reported from southern Alberta (Floate and Gill 1998; Kadiri *et al.* 2014) but was found in Arkansas from mid-April until November, showing a multimodal pattern with 4–5 peaks probably indicating overlapping generations (Fiene *et al.* 2011). In North Carolina, *O. taurus* was the most common species (45–73%) and was caught from late March until November, also showing 4–5 peaks probably indicating partially overlapping generations (Bertone *et al.* 2005). Both southern locations showed the expected expansion of the seasonal niche. In Germany, *O. taurus* occurred from mid-May until mid-October, showing a clear maximum in September but no clearly separated peaks that might indicate overlapping generations (Wassmer 1994). The development from egg to adult takes 6–8 weeks in summer but much longer in winter, allowing *O. taurus* to establish at least two generations per year (Edwards and Pavri 2007). The long activity range in all locations identifies this species as highly opportunistic and explains its fast spreading into different climate zones.

*Cercyon quisquilius* was found from mid-May until the end of November, with the exception of only a single collection date (10 October 2012). There are no other North American studies that report on the seasonal occurrence of this species. In Germany, *C. quisquilius* was found from mid-March until December, showing three distinct peaks indicating probably three generations with little overlap (Wassmer 1994). This corresponds well to the observed distribution in the present study but indicates that the species is not cold-adapted enough to extend its seasonal range into early spring and winter in Michigan. However, this would need to be verified in a second winter.

**Seasonally Bimodal Species.** The aphodiines *A. fimetarius* and *C. distinctus* and the hydrophilids *C. haemorrhoidalis*, *C. pygmaeus*, *S. bipustulatum*, and *S. scarabaeoides* exhibit a split pattern of spring to early summer occurrence, absence

during summer, and a second period of occurrence in autumn (Fig. 4).

Prediction: If the observed phenology of the above species at middle latitudes is flexible or if the species are phenologically polymorphic, beetles at more northern latitudes should occur later in spring or at about the same time in summer, and extend their seasonal range into the less extreme summer months, eventually into autumn, and disappear earlier in autumn due to the chance of earlier winter storms. At more southern locations, these species should in contrast occur earlier in spring, disappear earlier in summer, reappear later in autumn, and stay around until late autumn or even throughout winter, connecting to the spring without interruption.

In Adrian, the non-native *A. fimetarius* was found in late June and early July, was absent until the end of September, and disappeared from December until mid-April next year, indicating two distinct generations in July and October. The Lake City (Rounds and Floate 2012), and southern Alberta (Floate and Gill 1998; Kadiri *et al.* 2014) sites saw the species against the prediction earlier from April/May on. Following the prediction, *A. fimetarius* did not completely disappear during the summer but disappeared in most cases earlier in autumn – clearly indicating two distinct generations per year. In Arkansas, the species was very rare and occurred as single individuals from May until July, disappeared until late November and occurred off and on throughout the winter (Fiene *et al.* 2011). It was also found in North Carolina, but no phenology was provided, however, the species also occurred in winter (Bertone *et al.* 2005). Thus, these southern sites follow the general predictions. In Germany, *A. fimetarius* occurred throughout the year with only two short interruptions in January and late August, showing a clear trimodal pattern, indicating at least two overlapping generations per year. The seasonal flexibility, overlapping generations, and cold hardiness of *A. fimetarius* could be caused by the ability of the species to overwinter in various life stages, *i.e.*, as egg, larva, and adult as it was reported for Urbana, Illinois by Mohr (1943) and Anderson (1975) for various altitudes in the Sierra Nevada Mountains of the western United States. *Aphodius fimetarius* is one of the most opportunistic and consequently worldwide almost ubiquitously distributed coprophilous beetles described so far.

The non-native *C. distinctus* appeared as just three specimens on the sheep farm in late March 2012, was not found again until the end of Sep-

tember, and disappeared in late November, reappearing in mid-April and May 2013. This species was the second most abundant species at Lake City, only occurring in October (Rounds and Floate 2012). In southern Alberta, it occurred in small numbers in March, disappeared from May until mid-September, peaking in mid-October, and disappearing in November, thus showing almost the same pattern as in Adrian (Floate and Gill 1998; Kadiri *et al.* 2014). *Chilo thorax distinctus* was missing from the dung beetle community in Arkansas (Fiene *et al.* 2011) but was found as a subdominant species in North Carolina, where it appeared as early as in Adrian, disappeared longer until November when it was found again until the end of December or even mid-January (Bertone *et al.* 2005). This pattern indicates flexibility to extend into the winter months at mild southern locations. In Germany, *C. distinctus* showed principally the same pattern, with a small appearance in early spring and a major peak in December, indicating most probably one overwintering generation then laying eggs in early spring that undergo summer dormancy (Wassmer 1994). This might be the reason why the species is not able to extend into the summer niche at northern latitudes.

*Chilo thorax distinctus* is not known to breed in dung, but rather in soil (Christensen and Dobson 1976). Overwintering adults show little attraction to fresh dung, whereas F<sub>1</sub> progeny swarm to dung to feed prior to overwintering. Rather than summer dormancy of eggs, another hypothesis is that F<sub>1</sub> adults may remain underground in pupal cells until weather conditions trigger their emergence in the fall (Seamans 1934). *Chilo thorax distinctus* seems to have limited ability to expand its northern to mid-latitude range into the south.

The small hydrophilid *C. haemorrhoidalis* appeared first in spring, then disappeared in July and August, and reappeared in a broad second period of occurrence from mid-August until mid-December, allowing at least for two or more likely three overlapping generations. In southern Québec, the species was found to peak in May and fade out until August, being absent in September and October (Levesque and Levesque 1995), which might indicate an extension into the milder summer and suspension of the climatically risky autumn niche. In accordance to this, the species showed a spring to early summer abundance, absence during August and September, and a second low abundance from October until December in Germany (Wassmer 1994).

*Cercyon quisquilius* and *C. haemorrhoidalis* showed a wide multimodal distribution, which could account for 2–3 yearly generations as proposed by Anlas *et al.* (2008). While *C. quisquilius* did not expand into late autumn and winter,

indicating lesser cold hardiness, *C. haemorrhoidalis* showed a clear gap through the summer months, suggesting lower drought tolerance, which is expected to be the major limiting factor for the distribution of coprophilous Sphaeriidae in the mountains of Turkey (Anlas *et al.* 2008).

In conclusion, most non-native species show a capacity to adjust their seasonal range to the latitudinal climate of the locations in which they were found and thus optimize their abundance at those locations. This flexibility relates in most cases to the potential that can be seen in their Old World seasonal ranges (*e.g.*, Hanski 1980; Wassmer 1994) and allows them to continuously invade further into North American pasture systems. It is especially the utilization of the “autumn niche” that is discussed as a major reason why Eurasian understory trees are so successful in North America (Fridley 2012), that transforms some non-native species into invasive species with the potential to displace and eventually eradicate native species and cause massive ecological and economical damage. It is widely discussed whether invasive species directly replace native species (*e.g.*, by hybridization, Huxel 1999) or if they invade due to anthropogenic habitat modification (*e.g.*, Didham *et al.* 2005). In Finland, it was concluded that conversion of agricultural lands likely explained the decline in native coprophilous beetles (Bistrom *et al.* 1991). Tiberg and Floate (2011) came to the same conclusion for grasslands in northern North America. The dominance of exotic species in northern latitudes of North America may reflect the historical presence of native communities lacking large herbivore herds and consequently having low species richness in coprophilous beetles (Lobo 2000). Another important factor that may contribute to the success of invasive dung beetle species is global climate change (Dortel *et al.* 2013). More field studies of the seasonal occurrence of native and adventives species under comparable climatic conditions, as well as laboratory studies examining the correlation of seasonal patterns with the number of yearly generations and the degree of heritability of these traits, are needed to better understand the progressing changes in pasture communities and the success of invasive species. However, it might also be the time to think about counter measures against the extinction of native species, such as breeding programs, whether the decline is caused by competition with invasive species, hybridization, habitat modification, or global climate change.

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