SPECIES DIVERSITY AND SEASONAL ABUNDANCE OF SCARABAEOID DUNG BEETLES (COLEOPTERA: SCARABAEIDAE, GEOTRUPIDAE AND TROGIDAE) ATTRACTED TO COW DUNG IN CENTRAL NEW JERSEY

DANA L. PRICE

14 College Farm Road, Department of Ecology, Evolution, Natural Resources, Rutgers University, New Brunswick, New Jersey 08901

Abstract.—Species diversity and abundance of scarabaeoid dung beetles (Coleoptera) attracted to fresh cow dung were studied in three habitats of New Jersey: Hutcheson Memorial Forest (HMF) disturbed field, HMF old growth forest, and Rutgers University Bovine Farm. Over a one year period, baited pitfall traps yielded a total of 15,206 beetles representing at least 26 species. *Onthophagus hecate* was a dominant species in all three sites, accounting for 55.1% of all individuals collected. *Onthophagus pennsylvanicus* and *Copris minutus* were present in high numbers in the field, comprising 25.1% and 3.8%, respectively, of specimens collected in that habitat, while *O. orpheus* and *C. minutus* were numerous in the forest (20.8% and 13.3%, respectively). Two introduced species, *Aphodius lividus* (68.5%) and *O. taurus* (9.6%), were the most numerous species on the farm. Nine species accounted for more than 96% of all scarabaeoid dung beetles collected during the year-long study. The majority of the beetles were collected during the warmer months (May–September), with general peaks appearing to be correlated with temperature. A total of five introduced species were collected: five in the farm site, two in the field site, but none in the forest; 80% of the individuals collected on the farm were introduced.

Key words: dung beetles, New Jersey, *Onthophagus, Aphodius*, species diversity, species abundance, introduced species.

A variety of factors may influence the presence and distribution of coprophagous beetles in a given area, including fauna, flora, solar radiation, temperature, soil type, soil pH, rainfall and, most importantly, the supply of excrement for food (Fincher et al., 1970). Dung is patchy and ephemeral; desiccation and some of the stiffest competition among arthropods often limits its period of availability to only a few hours. In tropical and temperate localities, thousands of individuals and dozens of species may be attracted to a single dropping (Hanski and Cambefort, 1991). One of the best known examples of this was demonstrated by Anderson and Coe (1974) when they observed 16,000 dung beetles arriving at a 1.5 kg heap of elephant dung in East Africa. These beetles found, fought over, ate, buried, pushed and rolled this "minor habitat" away in two hours.

Human impact on landscape, with the attendance of cattle, horses, and other domesticated mammals, has been significant in Europe for thousands of years (Birks, 1986). In contrast, Native Americans had no domesticated mammals except dogs (Delcourt, 1987), and large-scale clearing of forests did not take place before the westward expansion of the American frontier between 1790 and 1880 (Delcourt and Delcourt, 1987). The cumulative Native American impact on the landscape in North America over millennia increased the size of old fields and early successional forests, which led to an increase in the populations of white-tailed deer, a major food source for Indians (Delcourt, 1987). In forested North America,

environmental conditions have long been favorable for *Aphodius* specializing on deer-dung. In turn, these species have been unable to colonize recent pasture ecosystems, probably because of their general ecophysiological adaptations to forest habitats. Currently, dung beetle communities in pastures in North America are dominated by intentionally or accidentally introduced dung beetles (Hanski and Cambefort, 1991). Thus these introduced species may be important for nutrient cycling in disturbed habitats but might also adversely impact native dung beetle communities if and when they spread into other habitats.

Studies conducted in Hutcheson Memorial Forest and The Great Swamp National Wildlife Refuge have demonstrated a high diversity of necrophagous beetles in Central New Jersey including 10 species of scarab beetles (Shubeck et al., 1977; Shubeck et al., 1981). However, there have been no studies in this region to examine the composition of coprophagous beetle assemblages. The purpose of this study was to determine species diversity and abundance of scarabaeoid dung beetles (Scarabaeidae, Geotrupidae, and Trogidae) attracted to cow dung in three habitats of central New Jersey: Hutcheson Memorial Forest (HMF) disturbed field; HMF old growth forest; and Rutgers University Bovine Farm (RUBF). The main objectives were 1) to compare species diversity among the three different habitats; 2) to determine seasonal variation in the abundance of scarabaeoid dung beetles; and 3) provide baseline data to document the presence of introduced dung beetles in the disturbed field and forest habitat.

MATERIALS AND METHODS

Field sites

A survey of coprophagous Scarabaeoidea was conducted in Middlesex County, New Brunswick (RUBF) and Somerset County, Franklin Township (HMF), New Jersey, USA. The RUBF consists of a 2-hectare farm which, on average, holds approximately 45 cows. During the year, the cows were herded from one arena to another within this area. These cows are fed a combination of corn silage, Timothy hay and wet brewer's grain. Pilot studies conducted at the University farm suggested that the abundance of beetles found in pitfalls by the open pasture was equivalent to the number of individuals collected by the barn (Price, unpubl. obs., 2002). The Hutcheson Memorial Forest (HMF), owned by Rutgers University, is a 26-ha oldgrowth mixed-oak stand believed to be relatively undisturbed since 1702 (Buell et al., 1954; Buell, 1957). The tract includes a number of adjoining 1-ha abandoned fields of known-age (Robertson and Vitousek, 1981). The soils at HMF belong to the Penn soil series, derived from the Triassic red shale of the Brunswick Formation and there are only slight variations in soil texture, drainage, and depth among the sites (Ugolini, 1964). In addition, there are no significant differences in chemical composition, mineralization potential, soil structure, soil texture, or organic matter between the fields of different ages (Robertson and Vitousek, 1981; Robertson, 1982). The climate of the area includes mild winters with subtropical summers (Biel, 1958) and about 124 cm of annual rainfall. Average annual temperature is 11.4°C with monthly means ranging from -1.3° C to 24° C (New Jersey monthly climate maps, 2003).

Collection of beetles

Dung baited pitfall traps were used according to Steyskal et al. (1986). Each trap consisted of a 2.5 qt. plastic container, 15 cm in diameter and 16 cm deep, buried to its rim in the soil. Insects falling into the traps were killed by water during the warmer months (June–November, and March–May), and a 1:4 ratio of antifreeze/water during the colder months (December–February). The bait consisted of 225–250 g of cow dung wrapped in cheesecloth, tied with a 20 cm piece of polypropylene twine, and hung from a 13 mm square piece of hardware cloth

placed on the top of the bucket. Plywood tiles were nailed into the ground above each trap in order to discourage rainwater flooding. Five traps were put at intervals of 18 m on each transect line that ran for 72 m (15 to 16 m intervals were used in the forest due to natural barriers and accessibility) in each of the three locations: 1) HMF disturbed field ($40^{\circ}30.028'$ N, 74°33.835'W), 2) HMF old growth forest ($40^{\circ}29.753'$ N, 74°33.852'W), and 3) RUBF ($40^{\circ}28.542'$ N, 74°26.263'W). Although similar studies have used ~9 m (Jameson, 1989), and 20 m intervals (Galante et al., 1995), 18 m intervals were chosen in this study due to the size of the disturbed field (~110 m in length). Field and forest pitfall traps were positioned in their sites parallel to each other, with forest pitfall #3 positioned next to a trail. Farm traps were placed along the fence of the bovine farm and a maintenance road. Trap–1 was closest to the barn and trap–5 was adjacent to a ~100 year old forest containing red and white oak as well as sweetgum (Ehrenfeld, pers. comm., 2003).

Collections were made once a week from May, 2002 to May, 2003. Beetles were collected in 15 Ziploc bags labeled forest 1–5, field 1–5, and farm 1–5, and were brought back to the lab for preservation in vials containing 80% alcohol. Specimens collected during June and July were pinned. All specimens were counted and identified at a later date. Voucher specimens are in Prices' personal reference collection, and have been deposited at the Rutgers University Insect Museum and the National Museum of Natural History, Washington, DC. Books and papers that were helpful in identifying the species were: Howden (1955), Vaurie (1955), Matthews (1962), Howden and Cartwright (1963), Dillon and Dillon (1961), Cartwright (1974), Gordon (1983), Edmonds (1994), Downie and Arnett (1996).

Alpha diversity

In the absence of general agreement on the most appropriate matrices of biodiversity, several non-parametric indices were selected to measure species richness and diversity. The following are explained in detail in Magurran (1988) where formulas for each appear. Species richness was determined using Margalef's and Menhinick's indices. Both indices use a combination of S (the number of species recorded) and N (the total number of individuals summed over all S species). One advantage of these indices is the simplicity of the calculation, in addition to providing an instantly comprehensible expression of diversity. Other indices used include the Shannon index (an information theory index), Simpson's index, McIntosh's index, and Berger-Parker index, of which the last three are generally referred to as dominance measures. Shannon index takes into account the evenness of the abundance of species and assumes that individuals are randomly sampled from an 'infinitely large' population, while Simpson's index is less sensitive to species richness and more sensitive to the most abundant species. McIntosh's index is a dominance measure where accuracy is strongly influenced by sample size, but that is numerically independent of N. The Berger-Parker dominance index expresses the proportion of the total catch that is due to the dominant species. Though there is little consensus on the best diversity measure to use, the most widely used index is species richness (S), or, if species abundances are taken into consideration, the Shannon and the Simpson's indices (Magurran, 1988).

Correlation statistics

Correlations of the total monthly abundance of beetles collected in each site, with temperature or precipitation were determined with SAS (1990), using Proc GLM.

RESULTS

A total of 15,206 beetles were collected from the HMF disturbed field, HMF old-growth forest and RUBF (Table 1). Approximately twice as many individuals were collected in the

		ſ∕vſ		ł	A/S^		0	vN/O		Д	D/J		F/M^	<		A/M			Totals		Overall	% of
Species	Fld	For	Fm	Fld	For	Fm	Fld I	For I	Fm I	FId F	For Fm	n Fld	1 For	· Fm	Fld	For	- Fm	Fld	For	Fm	Total	Individuals
hecate	2,206	231	17	1,649 1,934	1,934	13	173	1	1	*	*	6	*	*	2,00;	2,005 140	*	6,042	2,306	31	8,379	55.10%
Unthophagus pagaschications	1 173	-	*	1 207	27	~	Ŧ	*	*	*	*	*	*	*	20	*	*	1771 2	55	~	2 500	16 440%
Duthonhagus ornhaus	c/1,1 *	1 282	. 5	107,1 *	355	m t	*	· *	· ~	· *	· *	· *	*	· *	R *	84	*	, * *	ربر 1901	+ %	1 047	10. 44 .%
Copris minutis	L	6	i *	140	455) *	91	05	1 *	*	*	53	43	*	82	48	*	373	653	*	1.026	6.75%
Aphodius terminalls	*	*	*	*	*	*	153	54	*	39 1	* 0	Ē	5 30	*	76	42	*	384	136	*	520	3.42%
Aphodius lividis	*	*	116	*	*	232	*	*	32	*	*	*	*	*	*	*	*	*	*	380	380	2.50%
Trox hamatus	219	80	*	13	10	*	-	*	*	*	*	*	*	*	23	8	*	256	98	*	354	2.33%
Aphodius ruricola	35	74	9	0	30	*	*	1	*	*	*	*	*	-	71	12	4	108	117	11	236	1.55%
Aphodius manitobensis	*	*	*	б	173	*	*	*	*	*	*	*	*	*	*	*	*	ŝ	173	*	176	1.16%
Trox spp.	*	17	1	4	57	*	S	14	*	*	1	0	٢	*	4	62	*	15	158	1	174	1.14%
Aphodius bicolor	*	*	*	9	50	*	12	20	-	*	*	*	*	*	*	*	*	18	120	1	139	0.91%
Ataenius strigatus	23	19	6	0	11	11	1	0	*	*	*	*	*	*	1	*	*	27	32	20	79	0.52%
Onthophagus taurus	0	*	S	9	*	46	*	*	0	*	*	*	*	*	*	*	*	8	*	53	61	0.40%
Copris fricator	4	*	*	0	9	*	-	1	*	*	*	-	*	*	ŝ	10	*	13	17	*	30	0.20%
Phanaeus vindex	12	*	*	12	*	*	1	*	*	*	*	*	*	*	*	*	*	25	*	*	25	0.16%
Aphodius rubripennis	1	8	*	*	*	*	*	*	*	*	*	*	*	*	*	10	*	-	18	*	19	0.12%
Onthphagus tuberculifrons	*	*	*	*	*	*	*	*	*	*	*	-	*	*	13	-	*	14	1	*	15	0.10%
Ataenius spretulus	*	*	6	*	1	ŝ	*	*	*	*	*	*	*	*	*	*	*	*	1	14	15	0.10%
Aphodius granarius	*	*	S	*	*	*	*	*	*	*	*	*	*	-	*	*	4	*	*	10	10	0.07%
Geotrupes semiopacus	*	*	*	*	4	*	*	1	*	*	*	*	*	*	*	*	*	*	S	*	S	0.03%
Aphodius sp.	1	1	1	*	-	*	*	*	*	*	*	*	*	*	*	*	*	-	0	1	4	0.03%
Dialytes striatulus	*	*	*	*	4	*	*	*	*	*	*	*	*	*	*	*	*	*	4	*	4	0.03%
Aphodius distinctus	*	*	*	*	*	*	1	*	*	*	*	-	*	*	*	*	-	0	*	1	33	0.02%
Aphodius fimetarius	*	*	0	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0	2	0.01%
Aphodius rubeolus	0	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	0	*	*	7	0.01%
Onthophagus striatulus	*	1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	-	*	1	0.01%
TOTALS	3,685	1,016	192	3,685 1,016 192 3,046 3,135 314 448	3,135	314	48	245	40	39 1	1 0	183	3 80	ы	2,33(2,330 417	6	9,733	4,918	555	15,206	15,206 100.00%

337

field site as in the forest site, with many fewer still collected from the farm site. *Onthophagus hecate*, accounting for 55.1% of the total individuals collected, was a dominant species in all three sites. *Onthophagus pennsylvanicus* and *Copris minutis* were the second and third most abundant species collected in the field site (Fig. 1A; Table 1), while *O. orpheus* and *Copris minutis* were the second and third most abundant species collected in the forest site (Fig. 1B; Table 1). *Aphodius lividus*, an imported species, was found to be the most abundant species collected in the farm site, accounting for 68.47% of the total individuals caught on the farm (Fig. 1C; Table 1).

The general diversity of each site is shown in Table 2. With the exception of Menhinick's index, which estimates the farm to have the highest diversity, all of the diversity indices estimate the forest to have the highest diversity over all. All indices are in agreement that the field site has the lowest diversity. In addition, all of the dominance indices estimate the forest to have the lowest degree of dominance, and therefore the highest evenness of scarabs (Table 2).

Ninety-three percent of the total individuals in all three sites were collected during the months of June–September 2002 and, April and May 2003 (Table 1). *Aphodius terminalis*, a winter species, was collected from October to May; it was the main species collected during the winter months, and the only one collected in December and January (with the exception of one *Trox* specimen). *Aphodius* species in the forest site demonstrated a clear seasonal pattern as follows: *A. rubripennis* collected in May and June, *A. ruricola* collected from May to October, *A. manitobensis* collected in August and September, *A. bicolor* collected from September to November, and *A. terminalis* collected from October to May (Fig. 2).

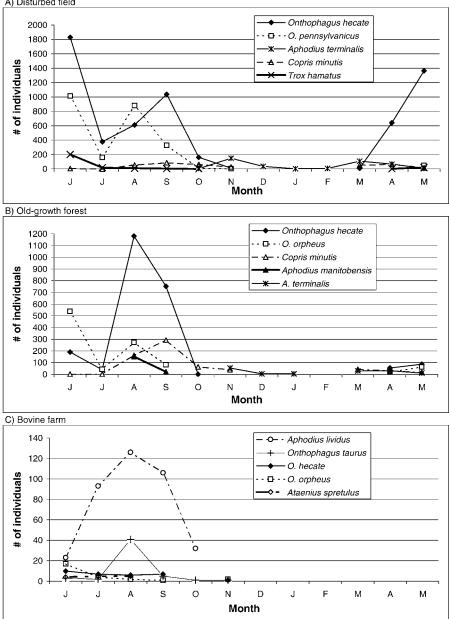
Abiotic factors examined in this study include temperature and precipitation over the entire year (Fig. 3A and B). The total annual precipitation for June 2002 to June 2003 was 134.8 cm verses an average of 123.9 cm for the previous 30 years (1971–2000). Temperature had a significant effect on the abundance of beetles collected each month in the farm site (Table 3). None of the sites showed a significant correlation with precipitation.

A total of five introduced species were collected among the three sites; five in the farm site, two in the field site and none in the forest (indicated in Table 1). In the farm site, 80% of the total individuals collected were introduced species. Introduced species in the field only accounted for 0.10% of the individuals collected.

Additional families of Coleoptera collected included; Staphylinidae, Carabidae, Silphidae, Coccinellidae, Chrysomelidae, Curculionidae, Elateridae, Histeridae, Lampyridae, Byrrhidae, Hydrophilidae, and Mordellidae. Individuals of the family Silphidae (Coleoptera) were collected throughout the summer, with high abundances in July and August.

DISCUSSION

Coprophagous beetles are of ecological and economic importance as well as of general interest for several reasons. In communities where they are common, coprophagous beetles play an important role in the cyclic breakdown of organic wastes and in the redistribution of biologically useful substances (Lindquist, 1933; Holter, 1979; Fincher et al., 1981), in addition to helping to reduce densities of manure-breeding dipterans, many of which are pests (Bornemissza, 1970; Fincher, 1990). Coprophagous beetles exhibit the instincts of maternity and progeny protection (Lindquist, 1935; Halffter and Edmonds, 1982) making them useful for studies dealing with sexual selection and intraspecific competition (Emlen, 1997; Rasmussen, 1994; Moczek and Emlen, 2000; Kotiaho, 2001). They have also been used extensively to



A) Disturbed field

Fig. 1. Five most abundant dung beetle species collected at each site. A. Disturbed field site. Scale: 0 to 2,000. B. Old-growth forest site. Scale: 0 to 1,200. C. Bovine farm site. Scale: 0 to 140. Collection started 30 May 2002 and was complete 30 May 2003.

	Field	Forest	Farm
Number of species	18	19	14
Totals scarabs collected	9,733	4,918	555
Species richness indices			
Margalef's diversity index (DMg)	1.851	2.117	2.057
Menhinick's diversity index (DMn)	0.182	0.271	0.594
Information statistic index			
Shannon index (H')	1.126	1.679	1.252
Evenness (E)	0.390	0.570	0.474
Dominance measures			
Simpson's index (D)	0.452	0.285	0.490
Simpson's index reciprocal (1/D)	2.212	3.504	2.058
McIntosh's index	0.331	0.473	0.316
Evenness (E)	0.429	0.604	0.413
Berger-Parker index (d)	0.621	0.469	0.685
1/d	1.610	2.132	1.460

Table 2. Diversity parameters for each site.

understand the nature of tropical rainforest diversity (e.g., Brown, 1991; Brown, 1997; Sutton and Collins, 1991; Davis, 2000). This study examined three different habitats of scarabaeoid dung beetles in order to determine species diversity and seasonal abundance, and to provide data on the presence of introduced dung beetles in a disturbed field and old growth forest habitat.

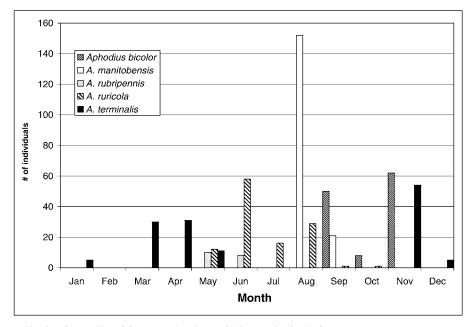
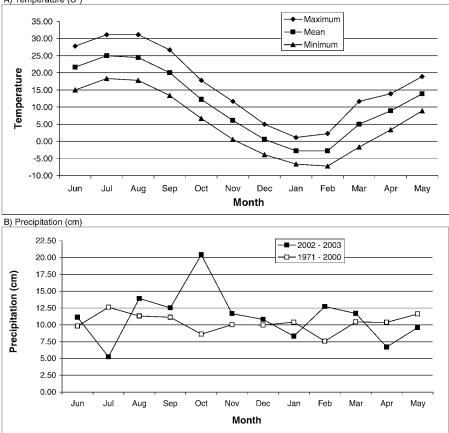


Fig. 2. Seasonality of five most abundant Aphodius species in the forest.



A) Temperature (Cº)

Fig. 3. Weather data collected from Office of the New Jersey State Climatologist. (http://www.climate.rutgers.edu/stateclim/njclimdata.html). A. Average minimum monthly temperature, average temperature, and average maximum monthly temperature. B. Total monthly precipitation during study and monthly average for 1971–2000.

Species diversity

Overall, the forest site had the highest diversity and evenness of all three sites with 19 species collected, a Shannon index of 1.679 and a Shannon evenness index of 0.570. Eighteen species were collected in the field site and 14 on the farm. Only six species were found in all three sites: *Onthophagus hecate*, *O. pennsylvanicus*, *Aphodius ruricola*, *A. bicolor*, *Aphodius sp.*, and *Ataenius strigatus*. In the forest site *O. hecate* and *O. orpheus* accounted for 47 and 21%, of the beetles collected, respectively. In the field, *Onthophagus hecate* accounted for 62% of the beetles collected. *Onthophagus pennsylvanicus* was the second most abundant species in the field accounting for 26% of the beetles collected. *Onthophagus hecate* appears to be a strong flier and was always the first to appear at the dung. Upon numerous collection trips to HMF, *O. hecate* was found in high abundances between the hours of 11:00 a.m.–4:00 p.m. on

	Field	Forest	Farm
Temperature			
r	0.65	0.63	0.81
F	5.05	4.68	11.63
Р	0.0594	0.0672	0.0143
Precipitation			
r	0.06	0.18	0.01
F	0.02	0.21	0.00
Р	0.8873	0.67	0.9732

Table 3. Correlation coefficients of the total monthly abundance of beetles collected in each site, with temperature or precipitation.

sunny days. Though Shubeck (1983) reported similar findings on *O. hecate* in a study dealing with carrion beetle habitat preference (79% of the specimens were collected in the field), Walker (1957) found that *O. hecate* prefer the forest habitats in Tennessee.

One factor that might explain a higher overall diversity of dung beetles in the forest site is mammal diversity. Hanski and Cambefort (1991) and Davis (2000) suggest that areas which are rich in mammals and in particular that have a significant biomass of large herbivores will contain more species of dung beetles than those that have comparatively poor mammal faunas. Another contributing factor might be the more moderate climate conditions in the forest, as explained below. Two other factors may actually have reduced the abundance of individuals collected in the forest pitfalls relative to those in other sites: the shorter distance between the pitfall traps, and the number of times these pitfalls were pulled out of the ground by various animals (most likely skunks and raccoons).

Aphodius lividus, an introduced beetle, was the dominant species found on the farm, accounting for 68% of the total individuals collected. Native species that were collected on the farm include *O. hecate* and *O. orpheus. Onthophagus orpheus*, a woodland species (Howden and Cartwright, 1963) was only collected in the pitfall located next to the forest (#5). The low abundance of beetles collected on the farm could be attributed to several factors: several to many dung pads were produced each day on the farm site in addition to the bait that was used for this study, the position of the pitfalls located next to a maintenance road, and several additional farms located in the vicinity (e.g., goat farm). With the exception of adult yellow dung flies (Diptera: Scatophagidae), which were present in all three sites during April, only a few fly larvae (additional families of Diptera) were observed in the field and forest, while several to many larvae were observed each week in the farm pitfalls during the summer months.

Hanski and Cambefort (1991) give two possible reasons why the colonization of a new resource in open grasslands (in this case an open pasture) by native forest species may be hindered: 1) the type of resource; and 2) the difference in climate between forests and open grasslands. The former is unlikely to be of great significance, because cattle dung in forests is readily colonized by native species (Hanski and Cambefort, 1991; see results). However, the microclimate conditions in droppings on open pastures are probably so different from the conditions in forests that species are unable to make the shift even after hundreds of generations (Hanski and Cambefort, 1991). Landins' (1961) measurements from southern Sweden indicate that even in northern temperate regions, temperatures in droppings may reach levels that are lethal to forest species, and he concluded that the distribution of

Aphodius "in different habitats does not depend on the kind of dung, but on the climatic factors." Additional authors have also drawn the same conclusion about other species of dung beetle (Halffter and Matthews, 1966; Gordon and Cartwright, 1974; Fincher et al., 1970; Oppenheimer, 1977).

Dung beetles display pronounced latitudinal patterns, and as one proceeds from subtropical and tropical areas to grassland habitats in temperate areas, there is a large decrease in species of the family Scarabaeidae (Hanski, 1986). While scarabaeoid dung beetle assemblages in southern Africa may contain over 100 species (Doube, 1990), studies conducted in north temperate regions typically have found only a small number of species (11 species, Jameson, 1989; 17 species, Galante et al., 1995). This was also demonstrated in this study with 26 species collected. According to Davis (2000), pitfall traps collect $10 \times$ more beetles than other methods of collection. However, they may only capture 80% of the total species present in one particular site. Though the same method of collection was used in each of the three above mentioned north temperate studies, the addition of a third site and the duration of the study both appear to have increased the number of species collected in the present case.

Seasonality

Dung beetles were collected during all months of the year and there were only five weeks during that period when no beetles were collected. The discrete phenological patterns seen in the forest *Aphodius* spp. were not surprising, as other studies have reported similar findings in *Aphodius* (Hanski, 1980; Gittings and Giller, 1997; Gordon, 1983). According to Gordon (1983), the eastern species of *Aphodius* can be divided into five categories based on food and habitat preference, and Category I (species associated with deer dung) is the most important in terms of numbers of species and biological significance. Several factors that restrict the beetles to a certain habitat include moisture content and exposure to deer dung, latitude, thermal factors, wind, and vagility (Gordon, 1983). Though Landin (1961) argued that fluctuations in natural populations of dung-beetles depend on abiotic factors rather than on competition, competition may also be a factor when food resources are limited, which is often the case with deer dung (Gordon, 1983).

Temperature appears to have had a pronounced effect on the abundance of scarabs collected in the farm site and may also have had a significant effect on the field and forest sites, though not linear. There was a large abundance of beetles collected in all the sites from June to September when temperatures were reaching 20°C and above. However, there was a considerable drop in species abundance in the field and forest site during July. Jameson (1989) reported similar results in Western Nebraska, where beetle abundance in traps during this period (when temperatures were exceedingly high) dropped from a high of 3,387 to a low of 268 individuals. Precipitation, though not significant, was low (5.3 cm) for the month of July and species abundance during this period decreased considerably. However, these two factors do not discount the idea that the decrease in species abundance in July may have been due to developmental phenology.

Introduced dung beetles

A total of five introduced species were collected in the farm and field site, while none were collected in the forest. Two imported species collected in the field site were *Onthophagus taurus*, and *Aphodius distinctus*. Field observations showed that *O. taurus* is present in the field site in low numbers all summer (Price, unpubl. obs., 2002), though it was only collected in field pitfalls when the abundance of individuals collected at the farm was high. In 1987, *O. taurus* was released by the Department of Agriculture (Biological Control Group) at several sites in

two counties of New Jersey and has since been reported in Burlington County, NJ and Suffolk County, NY (Hoebeke and Beucke, 1997). In addition to the above introduced species three additional species were collected in the farm site, including *Aphodius lividus*, *A. fimetarius*, *A. granarius*.

Elton (1958) suggested that newly arrived species (introduced in this case) are opposed by an array of competitors, predators, parasites, and diseases, termed an "ecological resistance." This resistance is lowered in the simplified setting of disturbed habitats. Additionally, Elton argued that most of the really successful invaders were ones that, for a variety of reasons, were able to cross major barriers because of their relationship with *Homo sapiens*. These assumptions are supported by the present study.

Implications for conservation efforts

Biodiversity surveys provide fundamental information needed for conservation planning, protected area justification and design, and development of management plans (Spector and Forsyth, 1998). Recent studies have shown that dung beetles may be excellent biodiversity indicator taxa (Spector and Forsyth, 1998; Davis et al., 2001; Goldstein and Simmons, 2002). Their high degree of habitat specialization and unambiguous response to deforestation makes them useful for predicting the outcome of habitat alteration as a result of factors such as fire management, road construction, logging (Spector and Forsyth, 1998), and agriculture. In Goldstein and Simmons' (2002) study on the scarabaeid fauna of the Massachusetts offshore islands, it was reported that structurally complex communities such as shrubby heathlands and grassy shrublands support a greater species richness as well as greater richness of uncommon species than homogenous agriculturally derived areas and other "pure grasslands." The present study is also consistent with previous data on the importance of structurally complex habitats to preserving insect diversity.

In conclusion, species collected in this study demonstrate patterns of habitat preference as well as distribution throughout the year. Using several diversity measures, the forest was estimated to have the highest diversity over all. Though five species of introduced dung beetles were collected in this study, they were not collected in high numbers and none were collected in the forest habitat. Future studies should include additional methods of collection (e.g., flight intercept traps), as well as several different types of animal dung and malt as bait.

ACKNOWLEDGMENTS

My thanks go to my advisor, Michael May, for his comments and suggestions on the manuscript. I also thank John LaPolla for numerous discussions about this research and I thank the individuals of the Rutgers University bovine farm for allowing me to use their facilities. This research was supported by the William Hutcheson Memorial Forest Summer Research Grant.

LITERATURE CITED

- Anderson, J. M. and M. J. Coe. 1974. Decomposition of elephant dung in an arid, tropical environment. Oecologia (Berl.) 14: 111–125.
- Biel, E. R. 1958. The climate of New Jersey, pp. 58–98 in The Economy of New Jersey. Rutgers University Press, New Brunswick.
- Birks, H. J. B. 1986. Late-Quarternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe, pp. 39–56 in B. E. Berglund (ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley, New York.

- Bornemissza, G. F. 1970. Insectary studies on the control of dung breeding flies by the activity of the dung beetle, *Onthophagus gazella* F. (Coleoptera: Scarabaeidae). Journal of the Australian Entomological Society 9: 31–41.
- Brown, K. S., Jr. 1991. Conservation of neotropical environments: insects as indicators. *In:* N. M. Collins and J. A. Thomas (eds.), The Conservation of Insects and Their Habitats. Academic Press, London, 450 pp.
- Brown, K. S., Jr. 1997. Diversity, disturbance, and sustainable use of neotropical forest: insects as indicators for conservation monitoring. Journal of Insect Conservation 1: 25–42.
- Buell, M. F., H. F. Buell and J. A. Small. 1954. Fire in the history of Mettler's Woods. Bulletin of the Torrey Botanical Club 81: 253–255.
- Buell, M. F. 1957. The mature oak forest of Mettler's Woods. William Hutcheson L. Memorial Forest Bulletin 1: 16–19.
- Cartwright, O. L. 1974. Ataenius, Aphotaenius, and Pseudataenius of the United States and Canada (Coleoptera: Scarabaeidae: Aphodiinae). Smithsonian Contributions to Zoology 154: 1–106.
- Davis, A. J. 2000. Species richness of dung-feeding beetles (Coleoptera: Aphodiidae, Scarabaeidae, Hybosoridae) in tropical rainforest at Danum Valley, Sabah, Malaysia. Coleopterists Bulletin 54: 221–231.
- Davis, A. J., J. D. Holloway, H. Huijbregts, J. Krikken, A. H. Kirk-Spriggs and S. L. Sutton. 2001. Dung beetles as indicators of change in the forests of Northern Borneo. Journal of Applied Ecology 38: 593–616.
- Delcourt, H. R. 1987. The impact of prehistoric agriculture and land occupation on natural vegetation. Trends in Ecology and Evolution 2: 39–44.
- Delcourt, P. A. and H. R. Delcourt. 1987. Long-term Forest Dynamics of the Temperate Zone. (Ecological Studies 63). Springer-Verlag, New York.
- Dillon, E. S. and L. S. Dillon. 1961. A Manual of Common Beetles of Eastern North America. Row, Peterson and Company, Evanston, Illinois and Elmsford, New York.
- Doube, B. M. 1990. A functional classification of the structure of dung beetle assemblages. Ecological Entomology 15: 371–383.
- Downie, N. M. and R. H. Arnett, Jr. 1996. The Beetles of Northeastern North America, Vol. II. Polyphaga: Series Bostrichiformia through Curculionoidea. The Sandhill Crane Press, Gainsville.
- Edmonds, W. D. 1994. Revision of *Phanaeus* MacLeay, a new world genus of Scarabaeinae dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). Contributions in Science, Natural History Museum of Los Angeles County 443: 1–105.
- Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen and Co Ltd., London, John Wiley and Sons Inc., New York, 181 pp.
- Emlen, D. J. 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle Onthophagus acuminatus (Coleoptera: Scarabaeidae). Behavioral Ecology and Sociobiology 41: 335–341.
- Fincher, G. T. 1990. Biological control of dung-breeding flies: pests of pastured cattle in the United States, pp. 137–151 in D. Rutz and R. Patterson (eds.), Biocontrol of Arthropods Affecting Livestock and Poultry. Westview Press, Boulder, San Francisco, and Oxford.
- Fincher, G. T., T. B. Stewart and R. Davis. 1970. Attraction of coprophagus beetles to feces of various animals. Journal of Parasitology 56: 378–383.
- Fincher, G. T., W. G. Monson and G. W. Burton. 1981. Effects of cattle feces rapidly buried by dung beetles on yield and quality of coastal bermudagrass. Agronomy Journal 73: 775–779.
- Galante, E., J. Mena and C. Lumbreras. 1995. Dung beetles (Coleoptera: Scarabaeidae, Geotrupidae) attracted to fresh cattle dung in wooded and open pasture. Environmental Entomology 24: 1063–1068.
- Gittings, T. and P. S. Giller. 1997. Life history traits and resource utilization in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera, Scarabaeidae). Ecography 20: 55–66.
- Goldstein, P. Z. and T. Simmons. 2002. A checklist and commentary on the scarabaeid fauna of the Massachusetts offshore islands (Coleoptera: Scarabaeidae). Journal of the New York Entomological Society 110: 389–401.

- Gordon, R. D. 1983. Studies on the genus *Aphodius* of the United States and Canada (Coleoptera: Scarabaeidae). VII. Food and habitat; distribution; key to eastern species. Proceedings of the Entomological Society of Washington 85: 633–652.
- Gordon, R. D. and O. L. Cartwright. 1974. Survey of food preferences of some North American Canthonini (Coleoptera: Scarabaeidae). Entomological News 85: 181–185.
- Halffter, G. and E. G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). Folia Entomologica Mexicana 12–14: 1–313.
- Halffter, G. and W. D. Edmonds. 1982. The Nesting Behavior of Dung Beetles: An Ecological and Evolutive Approach. Instituto de Ecologia, Mexico.
- Hanski, I. 1980. Spatial variation in the timing of the seasonal occurrence in coprophagous beetles. Oikos 34: 311–321.
- Hanski, I. 1986. Individual behavior, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. Acta OEcologia, OEcologia Generalis 7: 171–187.
- Hanski, I. and Y. Cambefort. 1991. Competition in dung beetles, pp. 305–329 in I. Hanski and Y. Cambefort (eds.), Dung Beetle Ecology. Princeton University Press, Princeton, New Jersey.
- Hoebeke, R. E. and K. Beucke. 1997. Adventive *Onthophagus* (Coleoptera: Scarabaeidae) in North America: geographic ranges, diagnoses and new distributional records. Entomological News 108: 345–362.
- Holter, P. 1979. Effect of dung-beetles (*Aphodius* spp.) and earth worms on the disappearance of cattle dung. Oikos 32: 393–402.
- Howden, H. F. 1955. Biology and taxonomy of North American beetles of the subfamily Geotrupinae, with revisions of the genera *Bolbocerosoma*, *Eucanthus*, *Geotrupes*, and *Peltotrupes* (Scarabaeidae). Proceedings of the United States National Museum. Smithsonian Institute, Washington, D.C. 104: 151–319.
- Howden, H. F. and O. L. Cartwright. 1963. Scarab beetles of the genus Onthophagus Latreille north of Mexico (Coleoptera: Scarabaeidae). Proceedings of the United States National Museum. Smithsonian Institution, Washington, D.C. 114: 1–135.
- Jameson, M. L. 1989. Diversity of coprophagous Scarabaeidae (Coleoptera) in grazed versus ungrazed sandhills prairie in western Nebraska. Transactions of the Nebraska Academy of Sciences 17: 29–35.
- Kotiaho, J. S., L. W. Simmons and J. L. Tomkins. 2001. Towards a resolution of the lek paradox. Nature 410: 684–686.
- Landin, J. 1961. Ecological studies on dung beetles (Col. Scarabaeidae). Opuscula. Entomologica Supplement 19: 1–228.
- Lindquist, A. W. 1933. Amounts of dung buried and soil excavated by certain Coprini (Scarabaeidae). Kansas Entomological Society 6: 109–124.
- Lindquist, A. W. 1935. Notes on the habits of certain coprophagous beetles and methods of rearing them. United States Department of Agriculture circular no. 351: 9.
- Magurran, A. E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, New Jersey.
- Matthews, E. G. 1962. A revision of the genus *Copris* Muller of the Western Hemisphere (Coleoptera, Scarabaeidae). Entomologica Americana 41: 1–139.
- Moczek, A. P. and D. J. Emlen. 2000. Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favor alternative phenotypes? Animal Behavior 59: 459–466.
- New Jersey Monthly Climate Maps. 2003. (http://www.climate.rutgers.edu/state/cmli/njclimdata.html), viewed June 2003.
- Oppenheimer, J. R. 1977. Ecology of dung beetles (Scarabaeidae: Coprinae) in two villages of West Bengal. Records of the Zoological Survey of India 72: 389–398.
- Rasmussen, J. L. 1994. The influence of horn and body size on the reproductive behavior of the horned Rainbow Scarab Beetle *Phanaeus difformis* (Coleoptera: Scarabaeidae). Journal of Insect Behavior 7: 67–82.

- Robertson, G. P. 1982. Factors regulating nitrification in primary and secondary succession. Ecology 63: 1561–1573.
- Robertson, G. P. and P. M. Vitousek. 1981. Nitrification in primary and secondary succession. Ecology 62: 376–386.
- SAS Institute Inc. 1990. SAS/STAT User's Guide, Version 6, 4th edition, Vol. 2. Cary, SAS Institute Inc., North Carolina.
- Shubeck, P. P. 1983. Habitat preferences of carrion beetles in the Great Swamp National Wildlife Refuge, New Jersey (Coleoptera: Silphidae, Dermestidae, Nitidulidae, Histeridae, Scarabaeidae). New York Entomological Society 91: 333–341.
- Shubeck, P. P., N. M. Downie, R. L. Wenzel and S. B. Peck. 1977. Species composition of carrion beetles in a Mixed-Oak forest. William Hutcheson Memorial Forest Bulletin 4: 12–17.
- Shubeck, P. P., N. M. Downie, R. L. Wenzel and S. B. Peck. 1981. Species composition and seasonal abundance of carrion beetles in an Oak-Beech Forest in the Great Swamp National Wildlife Refuge, N.J. Entomological New 92: 7–16.
- Spector, S. and A. B. Forsyth. 1998. Indicator taxa in the vanishing tropics, pp. 181–210 in A. Balmford and G. Mace (eds.), Conservation in a Changing World. Zoological Society of London, London.
- Steyskal, G. C., W. F. Murphy and E. M. Hoover. 1986. Insects and mites: techniques for collection and preservation. United States Department of Agriculture 1443: 1–16.
- Sutton, S. L. and N. M. Collins. 1991. Insects and tropical forest conservation. *In:* M. Collins and J. A. Thomas (eds.), The Conservation of Insects and Their Habitats. Academic Press, London, 450 pp.
- Ugolini, F. C. 1964. Soil development on the red beds of New Jersey. William L. Hutcheson Memorial Forest Bulletin 2: 1–34.
- Vaurie, P. 1955. A revision of the genus *Trox* in North America (Coleoptera, Scarabaeidae). Bulletin of the American Museum of Natural History 106: 1–371.
- Walker, T. J. 1957. Ecological studies of the arthropods associated with certain decaying materials in four habitats. Ecology 38: 262–276.

Received 22 October 2003; accepted 30 October 2004.