

Insects Associated With Droppings of Moose, *Alces alces* (L), in Isle Royale National Park, Michigan

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Abstract

Moose (*Alces alces* [L]) droppings were sampled in June-August, 2007, in Isle Royale National Park, a remote wilderness island in Lake Superior, to characterize biodiversity of the park's moose dung fauna. Twelve Diptera and nine Coleoptera species were obtained, for a total of 21 insect taxa. Twenty of the taxa are newly recorded colonists or visitors to moose dung. The Diptera were Psychodidae, Anthomyiidae, Muscidae and representatives of three other families, and Coleoptera consisted of three species in each of Scarabaeidae, Staphylinidae and Histeridae. Species per sample ranged from two in early June to nine in mid-July, and a species accumulation curve indicated a total of six more species remain to be detected. The relatively depauperate nature of the island's dung insect fauna may be attributed to absence of other large herbivores, to geographic isolation from source populations on adjacent mainland, or to distinct physical or biological properties of moose dung. Among reared specimens, *Hylemyza partita* (Meigen) (Anthomyiidae) and moose fly, *Haematobosca alcis* (Snow) (Muscidae) required approximately 3 weeks to complete development from egg to adult. Projections from weather records on the island indicated the two species could have completed as many as five generations between dates of last spring frost in May and first autumn frost in November.

Adults and immatures of many arthropods use dung of large herbivores for habitat and nutrition. Faunas associated with many large North American herbivores are well characterized, including cattle (*Bos primigenius* Bojanus), bison (*Bison bison* L.), sheep (*Ovis aires* L.) and horses (*Equus ferus caballus* L.) (see Hammer 1941, Mohr 1943, Blume 1985, Stevenson and Dindal 1987, Cambefort 1991). With notable exceptions, these faunas share many of the same generalist species (Dormont et al. 2007, Tilberg and Floate 2011), and many of the species are naturally Holarctic or have been introduced from Europe through human commerce (Gordon 1983, Hanski and Cambefort 1991). Relatively less is known about the insects associated with droppings of Cervidae, including deer (*Odocoileus* spp.; although see Brousseau et al. 2010), caribou (*Rangifer tarandus* [L.]), elk (*Cervus canadensis* Erxleben), and moose (*Alces alces* L.).

Isle Royale in Lake Superior has a relatively austere community of large herbivorous mammals, largely due to geographic isolation in the lake. Different cervids and cattle have occurred on the island in recent history, but only moose have persisted since the 1930s. Cochrane (1996) reviewed many historic reports and oral histories regarding large mammals on the island. Caribou were common in the 1700-1800s, but the population declined in the late 1800s and was likely extirpated through hunting by 1928. The Island Mine community on the west end of Isle Royale was known to have about 300 cattle for food in 1875. In addition, white-tailed deer (*O. virginianus* Zimmermann) were released in 1910 and may have persisted as late as the 1930s. Moose apparently were absent through the 1800s, but arrived from a Minnesota or Ontario population

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around 1904 (Peterson 1999). The method of arrival is unknown, although the most likely options include swimming or purposeful introduction. In order of decreasing body size, other herbivorous mammals on the island are beaver (*Castor canadensis* Kuhl), snowshoe hare (*Lepus americanus* Erxleben), muskrat (*Ondatra zibethicus* L.), red squirrel (*Tamiasciurus hudsonicus regalis* Howell) and deer mouse (*Peromyscus maniculatus* Wagner).

The present study was undertaken to document the insect fauna associated with moose droppings on the island, with particular interest in species that may be unique to moose, endemic on the island, or potential pests or vectors of parasites or pathogens among moose and other animal populations.

Materials and Methods

Study Area. Isle Royale National Park, Michigan, is an archipelago in northwestern Lake Superior, approximately 46 km SE of Thunder Bay, Ontario, 100 km north of Houghton, Michigan, and 57 km east of Grand Portage, Minnesota (Fig. 1). The park consists of one main island surrounded by hundreds of smaller islands, for a total of 544 km² of land, 99 percent of which is federally designated wilderness. Forest-dominated ecosystems consist of northern hardwoods in western portions of the park, and boreal forest in the east. Access to the park is generally limited to coastal docks and interior foot trails.

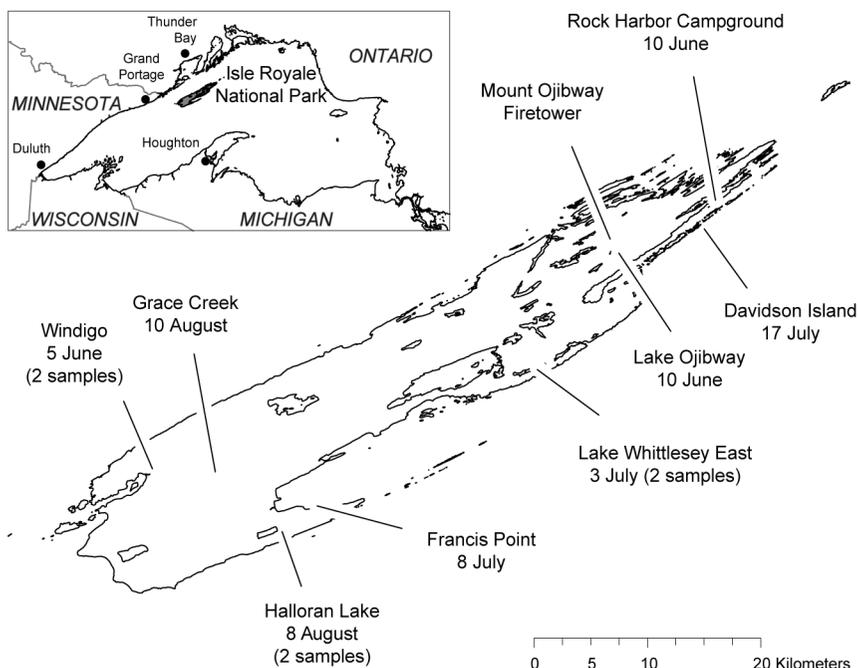


Figure 1. Map of Isle Royale, showing locations and dates of moose dropping collections, and locations of weather station and Davidson Island where droppings were incubated, 2007.

Samples and Rearing Records. Natural fecal droppings from free ranging moose were collected as encountered at scattered locations in the park between 10 June and 10 August 2007 (Fig. 1). Moose droppings in summer consist of somewhat amorphous piles of varying size (Rice 2010), and samples consisted of about 50-100% of encountered piles, depending on pile size. Most of the droppings were near lakes in mature forest settings, except for one at Francis Point, which was between the Lake Superior shoreline and a semi-flooded meadow. Two defecating moose were observed on 15 June and their dung was collected about 8 h later. In all other cases, droppings from unobserved moose were estimated to be within 1-3 d, as judged from surface moisture and apparent insect activity. Intent was to select droppings that had been exposed long enough to be colonized by flies and beetles, yet retrieved before wandering stage larvae of muscoid flies could have dispersed into the surrounding soil substrate.

Each dropping was placed in a plastic bag and transported to a small, unheated outbuilding on Davidson Island (Fig. 1) to rear out insect inhabitants. Each sample was placed on 2.5 cm of sifted sand in a clear plastic tray (30 × 20 × 7.5 cm) and covered with thin linen that allowed ventilation but prevented insect entry and escape. Samples were inspected and intermittently misted with lake water to mimic natural rain and dew. After 2 wk, samples were rechecked almost daily and then disassembled to extract individual insects by hand when most larvae of muscoid flies had pupated in the dung or sand. Mature beetle larvae and fly puparia were transferred to small, perforated Eppendorf tubes and set aside to rear out adults. Free roaming adult beetles were killed directly by freezing, as were representative specimens of small Diptera that were too numerous to extract and count. Free-living mites were noted roaming on the dung and sand, and attached to adult beetles and flies, but none were deliberately collected. Adult beetles and flies with associated puparia were mounted on points or pins, identified using keys in Arnett and Thomas (2001), Bousquet and Leplante (2006), Gordon (1983), Griffiths (2001), McAlpine et al. (1981), and Pratt and Pratt (1980), and compared with determined reference specimens. Although several subgenera of *Aphodius* (Scarabaeidae) have recently been elevated to genus by Gordon and Skelley (2007); we retain previous names for compatibility with earlier literature on the fauna of mammal dung, but include subgenus names in parentheses. Specimens have been deposited in the University of Minnesota St. Paul Insect Museum.

Faunal Diversity. The fauna was characterized initially by the list of species or higher taxonomic units encountered, and then by a species accumulation curve. An accumulation curve shows the cumulative number of species encountered with increasing number of sample units (droppings), and was calculated with EstimateS v. 9beta4, using the Mau Tau estimator. This estimator provides a mean and 95% confidence limits for numbers of taxa actually present, given the number of species encountered in the initial reference sample (Colwell et al. 2012), and has performed well in studies of insect communities elsewhere (e.g., Basset et al. 2012). The difference between number of taxa observed and extrapolated number was interpreted as the number of taxa that remain to be detected.

Development Times. Time required to develop from egg to adult was estimated for two species of muscoid Diptera that were frequent and abundant enough for analysis. Median development times (D_{50}) for cohorts of specimens from individual droppings were calculated as the difference between presumed oviposition date and median emergence date, and then examined for seasonal variation. To test the hypothesis that any seasonal pattern was a result of varying temperatures, concurrent records of daily minimum and maximum air temperatures were obtained from a ground-level weather station at Mount Ojibway, 2 km west of Davidson Island (Fig. 1). Mean temperature for each cohort was calculated by averaging daily minima and maxima from afternoon of oviposition date to afternoon of median emergence date. Analysis of covariance

was used to assess differences in median development times among species and dates or temperatures, as

$$D_{50} = \alpha + b_1S + b_2X + b_3S \times X + e,$$

where α was overall mean, S was a dummy variable for species, X was a covariate, either oviposition day of year or mean temperature, $S \times X$ was an interaction term for unequal slopes, and e was for errors, presumed normal. Significance of b_3 was first checked with F -test ($\alpha = 0.05$), and if insignificant, the interaction term was omitted and the simpler model fit to examine b_2 and b_1 for the covariate and species, respectively. Models were fit with lm in R (R Development Core Team 2012), and F -tests were done with ANOVA in the package *car* (Fox and Weisberg 2011). To estimate possible numbers of generations per yr on the island, development times were expressed as degree-days (DDs) above arbitrary bases of 0, 5 and 10°C (Pruess 1983). Degree-days were calculated from the weather station's daily records with the half-day sine wave method (Allen 1976) without adjustment for latitude. Sums from afternoons of oviposition to median emergence were averaged to estimate mean DD requirement for each species, and then the means of cohorts of the two species were compared with Student's t -test. Number of possible egg-adult intervals was computed by dividing DD accumulations between last to first frost date by mean DDs required.

Results

Samples and Rearing Records. A total of 11 droppings were obtained from eight remote locations on Isle Royale, four on two dates in June, four on three dates in July, and three on two dates in August (Fig. 1). Numbers of associated insects per dropping ranged from 38 on 10 June to 1,040 on 8 Aug (Table 1). The specimens consisted of 12 taxa in six families of Diptera, and nine taxa in three families of Coleoptera, for a total of 21 different taxa (Table 1). Thirteen of the taxa were identified to species, five only to genus, and three only to subfamily. Specimens identified only to genus or to subfamily appeared to be individual species, so we will hereafter refer to each taxon as a separate species.

Numbers of Diptera species ranged from two per dropping in June to six in August (Table 1), and all developed as larvae within the droppings. One species of unidentified moth fly (Psychodinae) was detected in nine of the 11 droppings, and on six of the seven collection dates, and was numerically the most abundant of all insect species. Many samples yielded more than 500 individuals, but many additional specimens escaped uncounted while rearing trays were being processed. The anthomyiid *Hylemyza partita* (Meigen) was present in eight droppings and on every sampling date. The remaining ten species of Diptera were encountered less frequently. They included the moose fly, *Haematobosca alcis* (Snow) and six other muscid flies, and three other species, each in separate families.

Coleoptera in the island's moose dung fauna were fewer and less frequent than Diptera (Table 1). Numbers of species per dropping ranged from zero to three in each month. Only the scarabid *Aphodius (Oscarinus) rusicola* (Melsheimer) and the staphylinid *Ontholestes cingulatus* (Gravenhorst) were reared from larvae; the remaining species were obtained as adults, and were present in the samples when the droppings were originally collected.

Faunal Diversity. Average numbers of insect species per dropping increased from 3.8 in June to 6.5 in July and 6.3 in August. Cumulative number of species detected from first to last sample increased from 6 to 21 (Table 1, Fig. 2). Extrapolation using the Mau Tau estimator led to the prediction that examination of another 19 droppings (bringing the total to 30) would reveal a total of 26 taxa (95% confidence interval: 17-34), while another 89 droppings (bringing total to 100) would reveal a total of 27 taxa (95% confidence interval: 16-37).

Table 1. Presence and relative abundance of 21 insect taxa extracted or reared from moose droppings, Isle Royale, 2007.

Order	Family	Taxon ^a	Collection date								Total ^b	
			6/10	6/15	7/3	7/8	7/17	8/8	8/10			
Diptera	Psychodidae	Psychodinae	●	▲	▲	▲	▲	▲	▲	▲	> 3,560	
	Anthomyiidae	<i>Hylemyza partita</i> (Meigen)	●	○	●	○	●	○	○	○	72	
	Sciaridae	<i>Scatopsiara</i> sp.	●	○	○	○	●	○	○	○	6	
	Muscidae		<i>Brontaea</i> sp.1	○	○	●	○	○	○	○	○	13
			<i>Myospila mediotabunda</i> (F.)	○	○	○	▲	○	○	○	○	26
			<i>Haematobosca alcis</i> (Snow) [†]	○	○	○	○	○	○	○	○	19
			<i>Morellia micans</i> (Macquart) [†]	○	○	○	○	○	○	○	○	2
			<i>Hydrotaea</i> sp.	○	○	○	○	○	○	○	○	1
			<i>Morellia podagrica</i> (Loew) [†]	○	○	○	○	○	○	○	○	2
		<i>Brontaea</i> sp.2	○	○	○	○	○	○	○	○	1	
	<i>Sepsis</i> sp.	○	○	○	○	○	○	○	○	9		
Coleoptera	Sepsidae	<i>Sylveicola marginatus</i> (Say) [†]	○	○	○	○	○	○	○	○	9	
	Anisopodidae	<i>Aphodius (Acrossus) rubripennis</i> Horn [†]	○	○	○	○	○	○	○	○	1 ^c	
	Scarabaeidae		<i>A. (Oscarinus) rusicola</i> (Melsheimer) [†]	○	○	○	○	●	○	○	○	18 ^d
			<i>A. (Chilothorax) distinctus</i> (Müller)	○	○	○	○	○	○	○	○	29 ^c
			<i>Ontholestes cingulatus</i> (Grav.) [†]	○	○	○	○	○	○	○	○	3
			Aleocharinae 1	○	○	○	○	○	○	○	○	1 ^c
	Staphylinidae		Aleocharinae 2	○	○	○	○	○	○	○	○	> 10 ^c
			<i>Margarinotus faedatus</i> (LeConte)	○	○	○	○	○	○	○	○	9 ^c
			<i>Hister furtivus</i> LeConte	○	○	○	○	○	○	○	○	3 ^c
			<i>H. paykullii</i> Kirby	○	○	○	○	○	○	○	○	2 ^c
Total specimens			38	56	1,030	1,034	58	1,040	549	> 3,805		

Families within orders and taxa within families are arranged by date of first collection; ○ = 1-5, ● = 6-20, ▲ = 20 or more individuals per dropping.

^a Taxa with a dagger (†) are native to North America; others Holarctic, introduced from Europe, or of unknown origin.

^b No. adults reared from immatures that developed in the dung, unless noted otherwise.

^c Adults observed, no larvae.

^d Eight specimens reared from larvae.

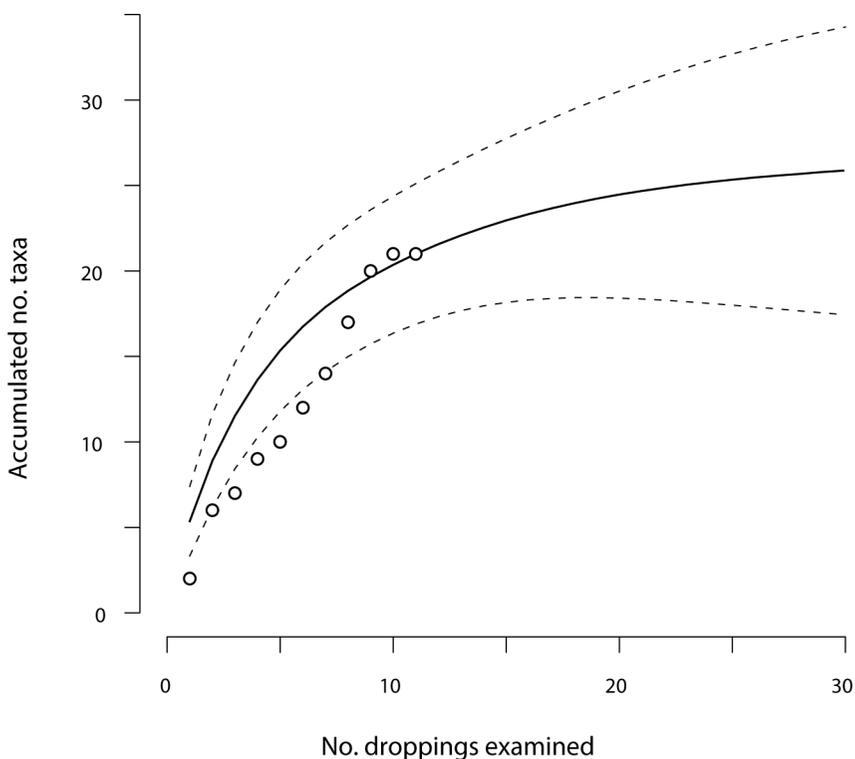


Figure 2. Mau Tau species accumulation curve (solid line) with upper and lower 95% confidence intervals (dashed) for number of insects in moose dung in Isle Royale National Park for a sample size up to 30 droppings. Open circles depict actual numbers of taxa observed in samples accumulated in summer, 2007.

Development Times. Median times from egg to adult for eight cohorts of the abundant anthomyiid, *H. partita*, ranged from 35 d in the first dropping from 10 June down to 19 d in the last dropping from 8 August (Fig. 3A). Similarly, times for four cohorts of moose fly ranged from 24–25 d from 3 July down to 19 d from 10 August. Development times for the remaining muscid flies were comparable to those of *H. partita* and moose fly, but numbers of cohorts were too few for formal analysis.

Analysis of covariance indicated development times of the two species declined similarly ($H_0: b_3 = 0; F < 0.1; df = 1, 8; P > 0.9$), which was by $b_2 = 0.13 \pm 0.02$ (SE) d per calendar d of oviposition between 10 June and 10 August ($H_0: b_2 = 0; F = 25.0; df = 1, 9; P < 0.01$). After adjusting for variable oviposition dates, mean times for the two species were not significantly different from each other ($H_0: b_1 = 0; F = 0.03; df = 1, 9; P = 0.86$). Both moose flies and the anthomyiid would have required about three weeks (22.6 ± 1.8 d) to develop from droppings if they had been obtained on the average of the collection dates, 7 July.

Temperature records from the Mt. Ojibway weather station indicated the last spring frost occurred on 20 May 2007, and the first autumn frost occurred on 1 November. Between those dates, daily extremes ranged in 0.6–31.7 °C, daily averages were in 1.7–26.2 °C, and the overall mean temperature was 14.7 °C. Derived

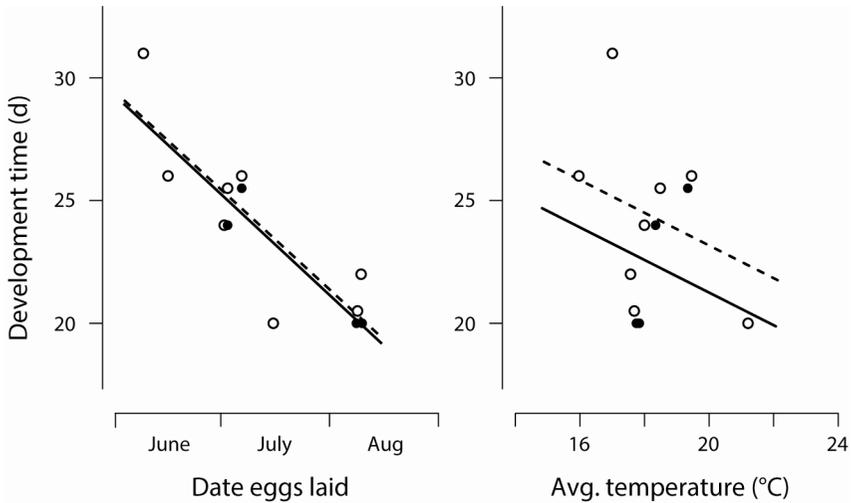


Figure 3. Median development times of *Hylemyza partita* (open circles, dashed lines) and *Haematobosca alcis* (filled circles, solid lines) reared from individual moose droppings, in relation to (A) dates when eggs were presumed to have been laid, or (B) average temperatures between oviposition dates and d of median emergence. Lines in each panel show results of analysis of covariance with common slopes, but different intercepts for the two species.

mean temperatures for the eight anthomyiid cohorts and the four moose fly cohorts ranged narrowly from 16.0 to 21.2°C, and averaged 18.2°C (Fig. 3B). Graphical inspection suggested development times of the two species shortened with increasing incubation temperatures, but analysis of covariance indicated times of the two species were statistically independent of temperature (Ho: $b_2 = 0$; $F = 0.73$; $df = 1, 9$; $P = 0.41$). Thus, the observed seasonal variation in development times (Fig. 3A) was only weakly related to variation in estimated rearing temperatures (Fig. 3B), most likely due to the narrow range in estimated temperatures.

Assuming development times were determined by temperature, DD requirements for the eight cohorts of the anthomyiid fly were calculated to require 436 (\pm SE = 29) DDs $> 0^\circ\text{C}$, 315 (\pm 22) DDs $> 5^\circ\text{C}$ and 195 (\pm 17) DDs $> 10^\circ\text{C}$. Corresponding requirements for the four cohorts of moose fly were slightly lower, 405 (\pm 32) DDs $> 0^\circ\text{C}$, 294 (\pm 25) DDs $> 5^\circ\text{C}$, and 183 (\pm 19) DDs $> 10^\circ\text{C}$. Mean DD requirements for the two species were not significantly different when calculated with any of the different base temperatures (2-sided t -tests, unequal variances: $t \geq -0.82$, $p \geq 0.44$), so estimates for the two species were combined to yield 426 (\pm 17) DDs $> 0^\circ\text{C}$, 308 (\pm 13) DDs $> 5^\circ\text{C}$, and 191 (\pm 10) DDs $> 10^\circ\text{C}$. Estimated number of egg-adult intervals between 20 May and 1 November was 2,416 DDs/426 DDs = 5.6 intervals, using 0 °C base, 1,611/308 = 5.2 using 5 °C base, and 896/191 = 4.7.

Discussion

Most of the 21 insect taxa recorded from moose dung on Isle Royale (Table 1) have been recorded from the dung of cattle, horses, pigs and sheep elsewhere in North America (Mohr 1943, Sanders and Dobson 1966, Kessler et al. 1974,

Valiela 1974, Blume 1985, Skidmore 1985, Cervenka and Moon 1991, Downie and Arnett 1996, Price 2004, Bousquet and Lepante 2006). The one exception is the host-specific moose fly. This *Stomoxys* native of North America is an obligate ectoparasite of moose, and its larvae are only known to develop in moose droppings (Snow 1891, Peterson 1955, Burger and Anderson 1974, Lankester and Samuel 1998). Descriptions of adult moose flies can be found in an early monograph on the biology and ecology of moose on Isle Royale (Murie 1934), and the present results confirm the persistence of the species on the island. The seasonal timing of the initial arrival of moose to Isle Royale, either by dispersal or purposeful introduction, would have influenced the method of arrival of the moose fly. In summer, flies would have arrived with moose; otherwise a separate immigration event would have been necessary.

The remaining insects in moose dung, like those in the dung of other large herbivores, are a mix of detritivores, coprophages and carnivores. Based on what is known about the food habits of taxonomically related species (McAlpine et al. 1981), the detritivores are represented by the small, dung feeding psychodid, sciardid, and anisopodid flies. Populations of these species may be sustained elsewhere on the island by substrates other than moose dung, including aquatic or subaquatic habitats, accumulations of decaying vegetation, rotting wood, fungi, droppings from smaller mammals or colony-nesting birds, and outhouses in campgrounds and remote park housing (McAlpine et al. 1981).

The coprophagous species included moose fly, *H. partita*, the two *Morellia* spp. (Diptera: Muscidae), *Sepsis* sp. (Diptera: Sepsidae), and the three *Aphodius* spp. (Coleoptera: Scarabaeidae). Our records of *Aphodius (Acrossus) rubripennis* (Horn) and *A. rusicola* confirm Gordon's (1983) speculation that the host range of those two endocoprid beetles, previously known from deer dung only, could extend to moose. Carnivorous flies in the fauna were the muscids *Brontaea* spp., *Myospila mediatubunda* (F.), and *Hydrotaea* sp., whose third instar larvae prey on fly larvae (Skidmore 1985). Carnivorous beetles were represented by the six species of Staphylinidae and Histeridae.

In comparison with other surveys of bovine dung in the Great Lakes Region (Sanders and Dobson 1966, Kessler et al. 1974, Valiela 1974, Cervenka and Moon 1991, Rounds and Floate 2012), seven taxa that were prominent elsewhere were not detected on Isle Royale. Absent were large dung feeding Diptera such as *Neomyia cornicina* (F.) (Muscidae), *Ravinia* spp. (Sarcophagidae) and *Scathophaga* spp. (Scathophagidae). Also absent were many large burrowing scarab dung beetles in *Aphodius* and *Onthophagus* and several large burrowing hydrophilid beetles in *Sphaeridium*. Finally, no parasitic *Aleochara* (Staphylinidae) or Hymenoptera were reared from any of the 136 anthomyiid and muscid fly puparia. It seems probable that flies, beetles and wasps recorded from bovine dung elsewhere in the region will be among the six additional taxa predicted to occur based on the species accumulation curve (Fig. 2).

Absence of the noted taxa on Isle Royale may be a result of insufficient sampling, of geographic isolation from mainland source populations, or of fundamental differences in the composition of the feces of moose, caribou and cattle. Moose on a winter and spring diet of twigs, bark and conifer needles pass relatively dry, spheroid pellets that are similar to but larger than those of other North American Cervidae. In contrast, moose on a summer diet of leaves and aquatic plants pass moister, amorphous masses (Peterson 1955, Schwartz and Renecker 1998, Rice 2010) that are similar to dung pats from cattle on dry summer range, but drier than dung from cattle on lush pasture. It would be informative to compare the insect faunas in neighboring localities with moose and cattle to assess the extent of possible intermingling of their respective faunas, and the potential for spread of fecally transmitted pathogens and gastrointestinal parasites between the two hosts.

From a conservation perspective, the present faunal description will serve as a reference for management of insect communities in Isle Royale National Park. Moose populations at Isle Royale are regulated by many factors, both biotic (e.g., predation and forage supply) and abiotic (e.g., temperature, precipitation, and snow depth), with abiotic factors potentially more important (Vucetich and Peterson 2003). Moose become heat stressed at relatively moderate temperatures, which has led to speculation that the range of moose may shift north if regional temperatures continue to warm (Lenarz et al. 2009). With a lack of other ungulate species at Isle Royale, coprophagous insects requiring herbivore dung could collapse if the island's moose population were to decline. Mohr (1943) speculated that loss of extensive buffalo populations in North America may have dramatically changed the fauna of dung-breeding insects associated with buffalo, forcing them to adapt to less advantageous dung of other herbivores or go locally extinct, although herbivore diet may be more important than inherent dung differences (Tiberg and Floate 2011). Alternative sources of dung on the island are few; a much lower invertebrate diversity and richness has been reported for rabbit dung when compared to cattle dung (Galante and Cartagena 1999), and presumably there are fewer species in feces of snowshoe hares than in moose.

In addition to moose, moose fly should be recognized as a species of concern on Isle Royale, due to its specific association with moose. Moose flies are blood sucking ectoparasites that irritate moose and contribute to skin lesions on their hosts' hind hocks (Lankester and Sein 1986). However, moose fly larvae are members of a dung inhabiting community that contribute to dung decomposition and nutrient cycling on the island. Development times of moose flies from Isle Royale were comparable to observations made in Yellowstone National Park (Burger and Anderson 1974). The period of activity on Isle Royale, based on rearings from droppings, was July–August, considerably shorter than May–September period when adult flies were active on hosts near Thunder Bay (Lankester and Sein 1986) and June–September in Yellowstone National Park (Burger and Anderson 1974).

The actual number of generations of moose flies on Isle Royale and elsewhere are likely to be less than the 4.7–5.6 egg-adult intervals estimated from our rearing records. Those estimates do not consider time required by emerged adults to find hosts, mate and lay eggs, and the estimates do not consider pupal diapause, which may constrain population development in spring and autumn. To the extent that the island's climate becomes warmer in the future, the spring-summer period of activity by adult moose flies and numbers of generations per year may increase. More knowledge is needed about the effects of temperature on moose fly development before effects of climate change on moose fly abundance on Isle Royale and elsewhere can be predicted with much confidence.

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