

Insect Diversity During Different Stages of Asiatic Elephant Dung Deterioration in Eastern Thailand

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ABSTRACT

A determination was conducted in eastern Thailand of the family composition of dung-utilizing insects in relation to various elephant dung pad stages: A (dung intact with odor and moisture), B (dung intact, no odor, no moisture), C₁ (less than 50% degraded), C₂ (50% or more degraded) and stage D (flat mass). A total of 4,857 individuals representing 30 families of insects utilized the sampled elephant dung; these included beetles from three prominent families: Ptiliidae, Staphylinidae and Scarabaeidae. Scarab beetles could be found throughout all stages of dung disintegration. The Shannon-Wiener index (H') for all insects in all elephant dung piles was considered relatively high. In addition, H' obtained by calculating the pooled data set of this study was 2.09, with high evenness ($E = 0.615$), and dominance by the Simpson index was high for all dung-utilizing insects ($D = 0.723$). Stage B showed the highest family diversity index ($H' = 2.274$), whereas stage C₁ had the lowest levels of diversity ($H' = 1.401$). Significant differences in the family diversity indices of five Asian elephant dung stages were detected ($P < 0.05$) in all comparisons. The results show that such biodiversity parameters as the richness, diversity and composition of these insect communities differ during the various stages of elephant dung decay. The relevance of these findings to the interpretation of what constitutes a dung stage preference is discussed.

Keywords: dung-utilizing insects, insect decomposer, diversity, asian elephant

INTRODUCTION

Insects are the earth's most varied organisms (Daly *et al.*, 1998). Almost three-quarters of all described animal species are insects (Borror *et al.*, 1989; Gullan and Cranstan, 1994; Daly *et al.*, 1998). Their numbers far exceed all other terrestrial animal species, and are found in almost every terrestrial habitat on the Earth's surface, having diversified to fill almost every environmental niche imaginable (Putman, 1983;

Gullan and Cranstan, 1994), which makes them one of the most crucial components of most terrestrial ecosystems. Considered to be the dominant detritivores in terrestrial systems (Matherson, 1960), they play an important role in the recycling of nitrogen and other nutrients, herbivory, pollination and seed dispersal (Triplehorn and Johnson, 2005; Nichols *et al.*, 2008).

Dung provides a temporary, changing habitat which can support a large community of organisms and an arthropod community

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(Scholtz and Holm, 1985; Hanski and Cambefort, 1991; Voss *et al.*, 2008; Scholz *et al.*, 2009). Dung-consuming insects play an important role in tropical ecosystems (Nichols *et al.*, 2008; Louzada *et al.*, 2009) by providing important functions including mechanically breaking down excrement into smaller-sized particles, mixing of organic matter in the soil, soil aeration (Brussaard and Slager, 1986) and nutrient cycling (Bang *et al.*, 2005). They also serve to remove unhealthy materials from their surroundings (Borror *et al.*, 1989). Among the major hexapod groups (wingless arthropods and insects) involved in decomposition are springtails (Collembolla), beetles (especially Scarabaeidae, Geotrupidae, Silphidae), and fly larvae (especially Calliphoridae, Sarcophagidae, Muscidae, and Fanniidae) (Capinera, 2010).

Coprophilous (dung-loving) organisms include insects that use dung as their food source and breeding habitat (Hanski and Cambefort, 1991). A succession of insect species can be found in dung, from those that have adapted to very fresh dung, which arrive within seconds of a new dropping, to those which are more adapted to drier dung and arrive several days later (Mohr, 1943). Although insects associated with dung have been widely studied, typical studies conducted have focused on a few species. The economically important pest fly (Muscidae) and the scarab (dung) beetle (Scarabaeidae) are the most extensively researched dung insect fauna (Floate, 2011).

Little is known about the diversity of coprophagous insects in Thailand, the natural breakdown of animal dung or how insects contribute to this process. The present study investigated the diversity of dung-utilizing insects associated with the different stages of decaying elephant dung along an ecotone between the dry evergreen forest and agricultural areas in eastern Thailand.

MATERIALS AND METHODS

Study area and collection of insects

An analysis of the diversity of dung-utilizing insects relating to different decaying elephant dung stages was carried out along an ecotone between dry evergreen forest (the main low-land forest occupied and used by the Asian elephant, *Elephas maximus* Linnaeus), and agricultural areas of cassava (*Manihot esculenta* Crantz) cultivation in Chachoengsao province, eastern Thailand from May to October 2009. One permanent transect line of 1 km was set out for dung surveys, following conventional methods described by Dawson and Dekker (1992). The richness of insect families was estimated from different elephant dung stages—namely, stages A, B, C₁, C₂ and D, with a total of 150 dung piles for all stages (30 dung piles per stage). Examples of each stage, suggested by Dawson and Dekker (1992), are given in Figure 1.

All insect samples from elephant dung were extracted with a Berlese funnel (modified from Martin, 1977) for 2–3 d, using 60 W incandescent lights. Specimens were then preserved in 70% ethyl alcohol for further sorting and identification. All specimens were classified to the family level using the identification key of Triplehorn and Johnson (2005) and Ross *et al.* (1944).

Data analysis

The dung-utilizing insect assemblages were determined by separating the assemblage data (family diversity and family composition) from the elephant dung into five main stage groups (A, B, C₁, C₂ and D). All assemblage parameters in this study were calculated based on the average density of each insect family in each stage group. The Shannon-Wiener function (H') (Ludwig and Reynolds, 1988; Margurran, 1988) and Simpson's diversity index (1-D; Simpson, 1949) were used to determine the diversity among dung-utilizing



Figure 1 Stages of decaying elephant dung: A (dung is intact with odor and moisture), B (dung is intact, no odor, no moisture), C₁ (less than 50% degraded), C₂ (50% or more degraded) and D (flat mass).

insects in each dung stage. To determine the family composition or relative abundance of different insects using elephant dung, the similarity in family composition among elephant dung stage groups was determined by a cluster analysis using Sorensen (Bray-Curtis) distance measurement (Sorensen, 1948; Bray and Curtis, 1957).

The percentage occurrence and the percentage frequency (McAney *et al.*, 1991) were determined using Equations 1 and 2, respectively:

$$PO_A = (n_A/N) \times 100 \quad (1)$$

where, PO_A is the percentage occurrence of insect family A, n_A is the number of dung piles in which insect family A was found and N is the total dung piles examined.

$$PF_A = (n_A \sum_{i=1}^N I_i) \times 100 \quad (2)$$

where PF_A is the percentage frequency of insect family A, n_A is the number of dung piles in which insect family A was found and I_i is the total number of insects found.

Statistical tests were conducted using the Statistical Package for Social Sciences (SPSS) software program version 16.0 (Statistical Package for Social Sciences, 2007). Cluster analysis was carried out using the PC-ORD 5.10 software (McCune and Mefford, 2006). A rarefaction model was also used to compare the insect diversity among the stages of decay in the elephant dung. The rarefaction value and its 95% confidence intervals were computed by the EcoSim version 7.72 software (Gotelli and Entsminger, 2004). Afterwards, the values of every stage group were plotted as a function of the sampling effort. With this plot, a significant difference in family diversity is indicated by an absence of overlap in the confidence interval of rarefaction curves among the five different decaying dung stages at the maximum sampling effort (Colwell *et al.*, 2004).

RESULTS

In total, 4,857 individual insects from

30 families were extracted from 150 elephant dung piles. The total number of insect families in each elephant dung stage, from the highest to the lowest, was: Stage B (29 families); Stage C₁ (20 families); Stage A (17 families); Stage C₂ (13 families) and Stage D (10 families), respectively, as shown in Table 1. The five most common insect groups found in the elephant dung were: Ptiliidae (31.17%), Staphylinidae (26.85%), Scarabaeidae

(10.50%), Termitidae (8.85%) and Carabidae (7.08%).

The insect (alpha) diversity related to the elephant dung stage is shown in Table 2. The Shannon-Wiener index (H') for all insects in all elephant dung piles was considered relatively high, with a range from 1.401 to 2.274. The H' value obtained by calculating the pooled data set of this study was 2.09, with high evenness ($E = 0.615$),

Table 1 Family composition, total number recovered, percentage occurrence (PO_A) and percentage frequency (PF_A) of insect group presented in each stage of decay in elephant dung (A, B, C₁, C₂ and D).

Family composition	Total number recovered	Total (PO_A , PF_A)				
		Stage A	Stage B	Stage C ₁	Stage C ₂	Stage D
O. Coleoptera						
F. Anobiidae	5	0 (0, 0)	4 (13.33, 0.26)	0 (0, 0)	1 (3.33, 0.30)	0 (0, 0)
F. Anthicidae	7	3 (6.67, 0.13)	3 (10, 0.20)	1 (3.33, 0.19)	0 (0, 0)	0 (0, 0)
F. Bostrichidae	27	2 (3.33, 0.09)	14 (43.33, 0.92)	3 (10, 0.56)	7 (16.67, 2.12)	1 (3.33, 0.68)
F. Carabidae	344	131 (93.33 [*] , 5.59)	49 (90 [*] , 3.23)	134(63.33, 25.09)	13(13.33, 3.94)	17 (10, 11.64)
F. Coccinellidae	74	37 (46.67, 1.58)	19 (50, 1.25)	18 (20, 3.37)	0 (0, 0)	0 (0, 0)
F. Cucujidae	11	0 (0, 0)	8 (26.64, 0.53)	2 (6.67, 0.37)	0 (0, 0)	1 (3.33, 0.68)
F. Curculionidae	3	0 (0, 0)	3 (10, 0.20)	0 (0, 0)	0 (0, 0)	0 (0, 0)
F. Dytiscidae	9	0 (0, 0)	7 (23.33, 0.46)	2 (6.67, 0.37)	0 (0, 0)	0 (0, 0)
F. Elateridae	2	0 (0, 0)	0 (0, 0)	0 (0, 0)	2 (6.67, 0.61)	0 (0, 0)
F. Endomychidae	43	8 (26.67, 0.34)	21 (56.67, 1.39)	3 (10, 0.56)	11 (20, 3.33)	0 (0, 0)
F. Histeridae	76	31 (43.33, 1.32)	42 (50, 2.77)	2 (6.67, 0.37)	0 (0, 0)	1 (3.33, 0.68)
F. Hydrophilidae	3	0 (0, 0)	2 (6.67, 0.13)	0 (0, 0)	1 (3.33, 0.30)	0 (0, 0)
F. Lymexylidae	29	0 (0, 0)	21 (46.67, 1.39)	8 (26.67, 1.50)	0 (0, 0)	0 (0, 0)
F. Mordellidae	90	28 (40, 1.20)	46 (50, 3.04)	12 (33.33, 2.25)	4 (13.33, 1.21)	0 (0, 0)
F. Nitidulidae	83	48 (93.33 [*] , 2.05)	32 (70, 2.11)	3 (10, 0.56)	0 (0, 0)	0 (0, 0)
F. Phalacridae	30	19 (40, 0.81)	11 (26.67, 0.73)	0 (0, 0)	0 (0, 0)	0 (0, 0)
F. Platypodidae	5	0 (0, 0)	4 (13.33, 0.26)	1 (3.33, 0.19)	0 (0, 0)	0 (0, 0)
F. Ptiliidae	1,514	1,038 (100 [*] , 44.32 [†])	457 (100 [*] , 30.17 [†])	19 (10, 3.56)	0 (0, 0)	0 (0, 0)
F. Scarabaeidae	510	158 (100 [*] , 6.67)	136 (100 [*] , 8.98)	129 (100 [*] , 24.16)	39 (100 [*] , 11.82)	48 (100 [*] , 32.88)
F. Silvanidae	11	0 (0, 0)	10 (33.33, 0.66)	0 (0, 0)	0 (0, 0)	1 (3.33, 0.68)
F. Staphylinidae	1,304	749 (100 [*] , 31.98)	383 (96.67 [*] , 25.28)	141 (90 [*] , 26.40 [†])	18 (20, 5.45)	13 (16.67, 8.90)
F. Tenebrionidae	84	26 (50, 1.11)	37 (50, 2.44)	2 (6.67, 0.37)	12 (13.33, 3.64)	7 (6.67, 4.79)
F. Trogidae	5	0 (0, 0)	3 (10, 0.20)	0 (0, 0)	1 (3.33, 0.30)	1 (3.33, 0.68)
O. Collembola						
F. Entomobryidae	30	0 (0, 0)	18 (50, 1.19)	0 (0, 0)	12 (16.67, 3.64)	0 (0, 0)
O. Diptera						
F. Muscidae	36	25 (26.67, 1.49)	11 (6.67, 0.73)	0 (0, 0)	0 (0, 0)	0 (0, 0)
F. Sarcophagidae	10	8 (10, 0.34)	2 (3.33, 0.13)	0 (0, 0)	0 (0, 0)	0 (0, 0)
O. Hemiptera						
F. Cydnidae	29	17 (16.67, 0.73)	10 (16.67, 0.66)	2 (3.33, 0.37)	0 (0, 0)	0 (0, 0)
F. Lygaeidae	24	4 (10, 0.17)	12 (20, 0.79)	8 (16.67, 1.50)	0 (0, 0)	0 (0, 0)
O. Hymenoptera						
F. Formicidae	29	0 (0, 0)	27 (50, 1.78)	2 (6.67, 0.37)	0 (0, 0)	0 (0, 0)
O. Isoptera						
F.Termitidae	430	0 (0, 0)	123 (6.67, 8.12)	42(16.67, 7.87)	209 (10, 63.33 [†])	56 (10, 38.36 [†])
Total	4,857	2,332	1,515	534	330	146

O. = Order; F. = Family; A, B, C₁, C₂ and D refer to each stage of decay in the elephant dung.

* = $PO_A \geq 90\%$, † = the highest % PF_A of the insect group in each stage of decay in the elephant dung.

and dominance by the Simpson index was high for all dung-utilizing insects ($D = 0.723$). The highest H' value was in stage B ($H' = 2.274$), followed by stage C_1 ($H' = 1.922$), stage A ($H' = 1.576$), stage D ($H' = 1.515$) and stage C_2 ($H' = 1.401$), respectively. Sets of individual t -tests of index values among the five different stages of decay in the elephant dung were compared (Table 3). The results of the comparison in each set of family diversity indices were significantly different and the data were: stage A : B ($t = -9.04$; $df = 1869$; $P < 0.05$); stage A : C_1 ($t = -6.44$; $df = 836$; $P < 0.05$); stage A : C_2 ($t = 2.24$; $df = 405$; $P < 0.05$); stage B : C_1 ($t = 3.95$; $df = 2027$; $P < 0.05$); stage B : C_2 ($t = 8.35$; $df = 1045$; $P < 0.05$); stage B : D ($t = 7.05$; $df = 468$; $P < 0.05$); stage C_1 : C_2 ($t = 5.90$; $df = 599$; $P < 0.05$); stage C_1 : D ($t = 4.44$; $df = 267$; $P < 0.05$). On the other hand, the results of stage A : D ($t = -0.74$; $df = 176$; $P > 0.05$) and stage C_2 : D ($t = -1.06$; $df = 388$; $P > 0.05$) indicated that there were no statistically significant differences in these set comparisons.

On the basis of the coefficient of community indices (beta diversity) calculated for all possible combinations of the five elephant dung decay stages, no stage had an index value higher than 0.5 (Table 4). Among the combinations of pair comparisons, the index between stages B and C_1 was the highest (0.45), whereas stage A had the lowest value (0.29) when compared with stage C_2 . Based upon the dendrogram obtained by the cluster analysis, it is clear that the communities of insect families that utilize the various stages of decaying elephant dung are significantly different (Figure 2). The two stages A and B formed a sister group in which the communities of families at these stages were more similar to each other than those found in the various other habitats. In addition, the rarefaction curves in the various stages of decay in the elephant dung (A, B, C_1 , C_2 and D) as shown in Figure 3 indicate a divergence between the 95% confidence intervals of these curves, indicating that the dung-utilizing insect diversity was significantly different among these different dung stages.

Table 2 Insect diversity in different stages of decay in elephant dung (A, B, C_1 , C_2 and D).

Stage	Number of individuals	Number of families	H_{\max}	H'	E	1-D
A	2332	17	2.83	1.58	0.556	0.6921
B	1515	29	3.37	2.27	0.675	0.8252
C_1	534	20	3.00	1.92	0.642	0.7992
C_2	330	13	2.56	1.40	0.546	0.5760
D	146	10	2.30	1.52	0.658	0.7208

H_{\max} = Maximum value of Shannon Wiener index of diversity, H' = Shannon Wiener index of diversity; E = Evenness (H'/H_{\max}); 1-D = Simpson's diversity index.

Table 3 Comparison in each set of individual t -tests of family diversity index (H') among the various elephant dung pad stages (A, B, C_1 , C_2 and D).

	$H'A$	$H'B$	$H'C_1$	$H'C_2$	$H'D$
$H'A$	---	-0.69*	-0.35*	0.17*	0.06 ^{ns}
$H'B$	-0.69*	---	0.34*	0.86*	0.75*
$H'C_1$	-0.35*	0.34*	---	0.52*	0.41*
$H'C_2$	0.17*	0.86*	0.52*	---	-0.11 ^{ns}
$H'D$	0.06 ^{ns}	0.75*	0.41*	-0.11 ^{ns}	---

* = Significantly different ($P < 0.05$), ns = Non-significant ($P > 0.05$).

Table 4 Pair-wise combinations of the assemblage of insects recorded in each elephant dung stage (A, B, C₁, C₂ and D). Values shown are the coefficient of community indices (upper right) and the number of insect families shared in common (lower left).

	Stage A	Stage B	Stage C ₁	Stage C ₂	Stage D
Stage A	---	0.43	0.41	0.29	0.31
Stage B	17	---	0.45	0.36	0.34
Stage C ₁	13	20	---	0.33	0.35
Stage C ₂	6	12	8	---	0.38
Stage D	6	10	8	7	---

DISCUSSION

The diversity and family richness of dung-utilizing insects were considerably different at the different stages of deterioration in elephant dung, with moderate coefficients of community index and relatively high evenness. Some diversity values (H') were relatively different, especially between stages B and C₂ (Table 2 and Figure 3). The colonization of dung depends on a series of sequential dung stages (Laurence, 1954; Floate, 2011). The present study showed that the first stage (stage A) in dung piles contains large numbers of insects. Interestingly, dung stage B seemed to be more attractive to coprophilous insects than the dung of other stages among the 29 insect families (96.67% of total). These results suggest that these two stages appear the most attractive for insects utilizing fresh dung. Lee (2004) reported that adults of most species are attracted to very fresh pats during the first few days following deposition, where they feed on dung fluids before ovipositing. Lee and Wall, (2006) also showed that dung remains attractive to adults of *Aphodius* (Coleoptera: Scarabaeidae) for 3–4 d after deposition. The dendrogram produced from the cluster analysis appears to indicate that the communities of insect families from the five different deterioration stages of elephant dung were somewhat different. However, the insect family communities between stages A and B were more similar to each other than to the other stages of elephant dung decomposition

(Figure 2). This similarity can be explained by the presence of dipterous flies, especially house flies (Muscidae) and flesh flies (Sarcophagidae) in both decomposition stages. Floate (2011) reported that the earliest colonists are mainly adult flies. These flies begin to arrive within minutes of dung deposition to oviposit, thereafter adult fly colonization usually declines. This decline coincides with the formation of a crust on the pat surface that slows the release of volatile chemicals used by the flies and other insects to locate the pat (Floate, 2011).

Of all the dung-utilizing insects found, approximately 80% (24 out of 30 families) were Coleoptera; consisting of bostrichid, carabaid, scarabaeid, staphylinid and tenebrionid beetles. Each of these beetle types was represented at every stage in the decaying dung. According to Payne (1965), coleopterans are considered to be one of the most diverse components of dung and carrion communities. Some coprophagous insect groups (such as anthicid, nitidulid, phalacrid, platypodid and ptiliid beetles) are attracted to fresh dung by its odor, which is absent when the dung crusts over (Finn and Giller, 2002; Lee, 2004; Floate, 2011). The numerically dominant coleopterans, mainly Ptiliidae (31.17% of individuals), were found to feed on elephant dung piles in the present study. These beetles also appear to primarily exploit fungi and rotting wood litter (Borror *et al.*, 1989) as well as carrion (Kelly *et al.*, 2008; Francis Dupont *et al.*, 2011). Other frequently encountered adult insects included Staphylinidae

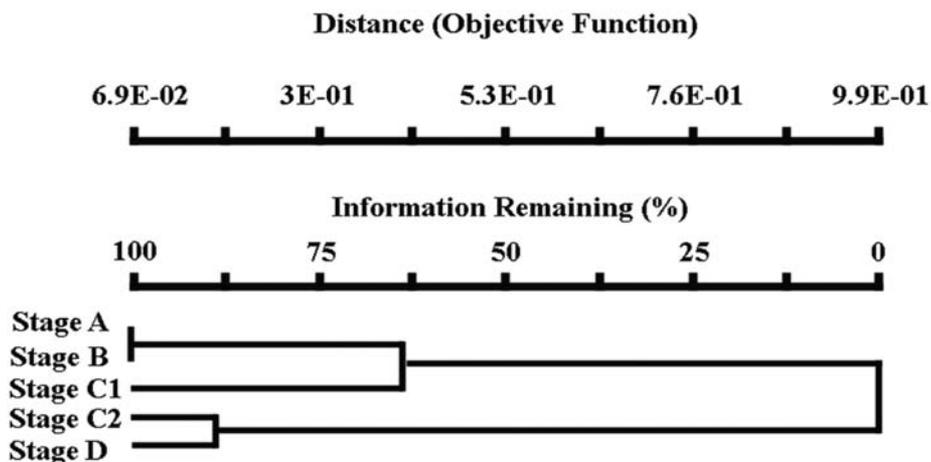


Figure 2 Dendrogram of the communities of insects in the various stages of deterioration of elephant dung, obtained by cluster analysis (Bray-Curtis index).

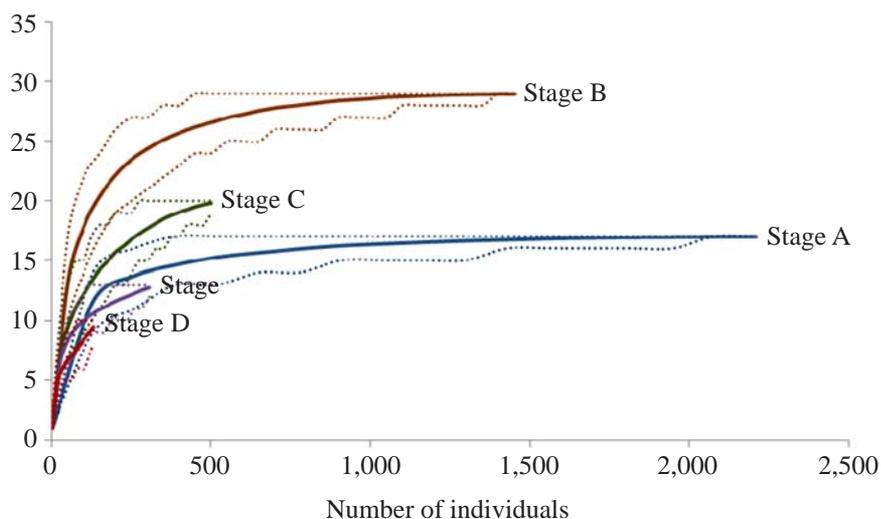


Figure 3 Comparison of family richness in the different stages of deterioration in elephant dung by rarefaction curve with $\pm 95\%$ confidence intervals shown as dotted lines.

(26.85%) and Scarabaeidae (10.50%), which corresponded to the report of Caballero and Leon-Cortes (2012). Most rove beetle (Staphylinidae) species appear to be predaceous, playing an important role in the soil ecosystem (Hanski, 1987; Newton and Chandler, 1989). They are probably most often seen in decaying material, especially dung and carcasses (Triplehorn and Johnson,

2005; Capinera, 2010). Moreover, scarabaeid beetles, particularly *Heliocopris dominus*, the predominantly coprophagous species of elephant dung, was the largest dung beetle that during the bi-annual rainy seasons comprises the most important agency of elephant dung removal (Hanboonsong and Masumoto, 2000). Giant dung beetles also acted as dung feeders and secondary

seed dispersers, thus protecting against seed predation (Shepherd and Chapman, 1988; Floate, 1998; Boonrotpong *et al.*, 2004; Capinera, 2010). Even during the last stage of decay, elephant dung piles still retain sufficient moisture to be used by insects for breeding, feeding and completing their offspring's life cycle from within a week (flies) to as long as a year (beetles) (Bailey and Ridsdill-Smith, 1993).

Many insect fauna occurring in elephant dung were not typically regarded to be members of the dung- insect community. According to Floate (2011), some insect fauna are best considered accidental visitors or wanderers from adjacent habitats looking for prey or hosts, or species related to carrion and the like. In his report, which corresponded with the findings of this survey, he speculated that incidental insect groups found in cattle dung, include Collembola (springtails: Entomobryidae), Coleoptera (ground beetle: Carabidae and click beetles: Elateridae), Hymenoptera (ants: Formicidae) and Heteroptera (seed bugs: Lygaeidae) as shown in Table 1. Furthermore, other common insects found in elephant dung that are beneficial include hister beetles (Histeridae) and water scavenger beetles (Hydrophilidae); the former act as predators and dung feeders (Macqueen and Beirne, 1974; Bousquet and Laplante, 2006), and the latter are considered predators feeding on pestiferous fly eggs (Macqueen and Beirne, 1974; Smetana, 1978; Floate 1998, 2011).

CONCLUSION

Prior to the present study, there was no publication specifically regarding the diversity of dung-utilizing insects in the different stages of elephant dung decomposition other than the work of Wanghongsa *et al.* (2004). The present research demonstrates the potential richness of insect fauna using elephant dung in eastern Thailand. The results seem to indicate that such

biodiversity parameters as the richness, diversity and composition of these insect communities differ during various elephant dung decay stages because of the conditions during each stage. Therefore, it appears they may be affected by the physiographical nature of this patchy and ephemeral resource. It would be interesting to expand this study to include the insect fauna in the dung of other animals in both natural and human-altered (livestock farming) habitats, thereby applying this research to aspects such as dung beetles as bio-indicators for environmental risk assessment. In addition, monitoring of dung beetle insect habitat change, determining their suitability as a biological pest control agent and determining their chemical and physical impacts on the soil are potential areas for future research.

ACKNOWLEDGEMENTS

The authors would like to thank: Mr. Yu Senatham, superintendent of the Khao Ang Rue Nai Wildlife Sanctuary; Dr. Swai Wanghongsa, chief of the Khao Ang Rue Nai Wildlife Research Station; Colonel Liab Chunsukkho, Agricultural and Cooperation Deputy Director, Chachoengsao province; and all their staff for their kind support and for assistance with accommodation during the field work. The authors are grateful to Dr. Catherine Sole, Scarab Research Group, Department of Zoology and Entomology, Faculty of Natural and Agricultural Sciences, University of Pretoria, Republic of South Africa and to Mr. James Makinson, Behaviour and Genetics of Social Insects Lab, School of Biological Sciences, University of Sydney who provided valuable comments on earlier drafts of the manuscript.

LITERATURE CITED

- Bailey, W.J. and T.J. Ridsdill-Smith. 1993. Reproductive behavior of insects. Individuals and populations. **J. N. Y. Entomol. Soc.** 101(4): 585–587.

- Bang, H.S., J.H. Lee, O.S. Kwon, Y.E. Na, Y.S. Jang and W.H. Kim. 2005. Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. **Appl. Soil Ecol.** 29: 165–171.
- Boonrotpong, S., S. Sotthibandhu and C. Pholpunthin. 2004. Species composition of dung beetles in the primary and secondary forests at Ton Nga Chang Wildlife Sanctuary. **Science Asia** 30: 59–65.
- Borror, D.J., C.A. Triplehorn and N.F. Johnson. 1989. **An Introduction to the Study of Insects.** Harcourt Brace College Publishing. New York, NY, USA. 873 pp.
- Bousquet, Y. and S. Laplante. 2006. **The Insects and Arachnids of Canada, part 24. Coleoptera Histeridae.** NRC Research Press. Ottawa, Ontario, Canada. 486 pp.
- Bray, J.R. and J.T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. **Ecol. Monogr.** 27: 325–349.
- Brussaard, L. and S. Slager. 1986. The influence of soil bulk density and soil moisture on the habitat selection of the dung beetle *Typhaeus typhoeus* in the Netherlands. **Biol. Fert. Soils.** 2: 50–58.
- Caballero, U. and J.L. Leon-Cortes. 2012. High diversity beetle assemblages attracted to carrion and dung in threatened tropical oak forests in Southern Mexico. **J. Insect Conserv.** 16(4): 537–547.
- Capinera, J. L. 2010. **Insect and Wildlife.** Wiley-Blackwell. Chichester, West Sussex, UK. 487 pp.
- Colwell, R.K., C.X. Mao and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. **Ecol.** 85(10): 2717–2727.
- Daly, H.V., J.T. Doyen and A.H. Purcell III. 1998. Continuity of the generations: development and reproduction, pp. 66–68. *In* H.V. Daly, J.T. Doyen and A.H. Purcell III, (eds.). **Introduction to Insect Biology and Diversity.** 2nd ed. Oxford University Press. New York, NY, USA.
- Dawson, S. and A.J.F.M. Dekker. 1992. **Counting Asian Elephants in Forests.** A techniques manual for methods endorsed at the International Workshop on Censusing Elephants in Forest. Mudumalai Wildlife Sanctuary. South India.
- Finn, J.A. and P.S. Giller. 2002. Experimental investigations of colonisation by north temperate dung beetles of different types of domestic herbivore dung. **Appl. Soil Ecol.** 20: 1–13.
- Floate, K.D. 1998. Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada. **Bull. Entomol. Res.** 88: 25–35.
- _____. 2011. Arthropods in cattle dung on Canada's grasslands, pp. 71–88. *In* K.D. Floate, (ed.). **Arthropods of Canadian Grasslands (Vol. 2): Inhabitants of a Changing Landscape.** Biological Survey of Canada, Ottawa, ON, Canada.
- Francis Dupont, F.Y., D-L. Champlain, A.A. Jean Cyrille and B.B. Charles Félix. 2011. A preliminary study of arthropod associated with carrion in Yaounde, Cameroon: A first step in forensic entomology in Central Africa. **J. Ecol. Nat. Environ.** 3(6): 215–220.
- Gotelli, N.J. and G.L. Entsminger. 2004. **EcoSim: Null models software for ecology Version 7.** Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. [Available from: <http://garyentsminger.com/ecosim/index.htm>]. [Sourced: 15 November 2012].
- Gullan, D.J. and P.S. Cranston. 1994. **The Insect: An Outline of Entomology.** Chapman and Hall. London, UK. 491 pp.
- Hanboonsong, Y. and K. Masumoto. 2000. Dung beetles (Coleoptera, Scarabaeidae) of Thailand (part 2 genus *Onitis*). **Elytra Tokyo.** 28(1): 101–114.

- Hanski, I. 1987. Colonization of ephemeral habitats, pp. 155–185. *In* A.J. Gray, M.J. Crawley and P.J. Edwards, (eds.). **Colonization, Succession and Stability**. Blackwell. Oxford, UK.
- 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, NJ, USA.
- Kelly, J.A., T.C. Van Linde and G.S. Anderson. 2008. The influence of clothing and wrapping on carcass decomposition and arthropod succession: A winter study in central South Africa. **Can. Soc. Forensic Sci. J.** 41: 135–147.
- Laurence, B.R. 1954. The larval inhabitants of cow pats. **J. Anim. Ecol.** 23: 234–260.
- Lee, C.M. 2004. **The Ecology of the Insect Cow-dung Community in South West England**. Ph.D. thesis, University of Bristol. Bristol, UK.
- Lee, C.M. and R. Wall. 2006. Cow-dung colonization and decomposition following insect exclusion. **Bull. Entomol. Res.** 96: 315–322.
- Louzada, J.N.C., C.E. Silva and R. Paulo. 2009. Utilisation of introduced Brazilian pastures ecosystems by native dung beetles: diversity patterns and resource use. **Insect Conserv. Diver.** 2(1): 45–52.
- Ludwig, J.A. and J.F. Reynolds. 1988. **Statistical Ecology**. New York, NY, USA: John Wiley and Sons. 337 pp.
- MacAney, C.N., C.B. Shiel, C.M. Sullivan and J.S. Fairley. 1991. **The Analysis of bat droppings. No.14**. An Occasional Publication of the Mammal Society. London, UK. 48 pp.
- Macqueen, A. and B.P. Beirne. 1974. Insects and mites associated with fresh cattle dung in the southern interior of British Columbia. **J. Entomol. Soc. B. C.** 71: 5–9.
- Margurran, A.E. 1988. **Ecological Diversity and Its Measurement**. Princeton University Press. Princeton, NJ, USA. 179 pp.
- Martin, J.E.H. 1977. **The Insects and Arachnids of Canada, Part 1: Collecting, Preparing and Preserving Insects, Mites and Spiders**. Canada Department of Agriculture, Research Branch. Ottawa, Ontario, Canada. 182 pp.
- Matheson, R. 1960. **Entomology: For Introductory Courses**. Vail-Ballou Press, Inc. New York, NY, USA. 629 pp.
- McCune, B. and M.J. Mefford. 2006. **PC-ORD**. Multivariate Analysis of Ecological Data. Version 5. MjM Software. Gleneden Beach, OR, USA.
- Mohr, C.O. 1943. Cattle droppings as ecological units. **Ecol. Monogr.** 131: 275–298.
- Nichols, E., S. Spector, J. Louzada, T.H. Larsen, S. Amezcua and M.E. Favila. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. **Biol. Conserv.** 141: 1461–1474.
- Newton, A.F. and D.S. Chandler. 1989. World catalog of the genera of Pselaphidae (Coleoptera). **Fieldiana Zool.** 53(1–4): 1–93
- Payne, J.A. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. **Ecol.** 46: 592–602.
- Putman, R.J. 1983. **Carrion and Dung: The Decomposition of Animal Wastes**. Edward Arnold. London, UK. 62 pp.
- Ross H.A., N.M. Downie and H.E. Jaques. 1944. **How to Know the Beetles**. 2nd ed. Wm. C. Brown Company Publishers. Dubuque, IA, USA. 416 pp.
- Scholtz, C.H. and E. Holm. 1985. **Insects of Southern Africa**. Butterworths. Durban, South Africa. 502 pp.
- Scholz, J., M.C. Klein, T.E. Behrens, H. Johansen-Berg. 2009. Training induces changes in white-matter architecture. **Nat. Neurosci.** 12(11): 1370–1371.
- Shepherd, V.E. and C.A. Chapman. 1988. Dung beetles as secondary seed dispersers: Impact on seed predation and germination. **J. Trop. Ecol.** 14(2): 199–215.

- Simpson, E.H. 1949. Measurement of diversity. **Nature** 163: 688.
- Smetana, A. 1978. Revision of the subfamily Sphaeridiinae of America north of Mexico (Coleoptera: Hydrophilidae). **Mem. Ent. Soc. Can.** 105: 292.
- Sorensen, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. **Kon. Dan. Vid. Sel. Biol. Skr.** 5: 1–34.
- Statistical Package for Social Sciences. 2007. **SPSS for Windows. User's guide: Statistics version 16.** SPSS Inc. Cary, NC, USA.
- Triplehorn, C.A. and N.F. Johnson. 2005. **Borror and Delong's Introduction of the Study of Insect.** 7th ed. Peter Marshall Publishing. Belmont, CA, USA. 864 pp.
- Voss, C.S., S.L. Forbes and I.R. Dadour. 2008. Decomposition and insect succession on cadavers inside a vehicle Environment. **Forensic Sci. Med. Pat.** 4: 22–32.
- Wanghongsa, S., K. Boonkerd, D. Saengsen and S. Bua-Ngam. 2004. Composition of wild elephant dung and insects that use those elephant dung at Khao Ang Rue Nai Wildlife Sanctuary. **Wildlife Yearbook** 5: 101–112. [in Thai]