

POSSIBLE EXTINCTIONS OF DUNG BEETLES (COLEOPTERA: SCARABAEIDAE) IN BUKIT TIMAH NATURE RESERVE, SINGAPORE

Janice S. H. Lee, Yat Ka Cheung and Lan Qie

Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore

Email: janice.jlsh@gmail.com (Corresponding author); g0600449@nus.edu.sg (LQ)

Johannes Huijbregts

National Museum of Natural History Naturalis, Postbus 9517, 2300 RA Leiden, the Netherlands

Email: huijbregts@naturalis.nl (JH)

ABSTRACT. – Bukit Timah Nature Reserve (BTNR) contains the largest patch (71 ha) of primary rainforest left in Singapore after approximately 95% deforestation by humans over the last century. Floral and faunal diversity have been monitored by the colonial British natural historians and local nature enthusiasts. This information can be used to determine biotic turnover due to deforestation as there is little information available on this subject. We examined dung beetle species collected in the Bukit Timah Nature Reserve from the 1960s to 1970s and compared them with species collected from the same forest patch today. We employed two trapping methods – baited pitfall traps and flight interception traps for our survey. Out of the nine species collected from the past, three species – *Cartharsius molossus*, *Onthophagus deliensis* and *Ont. cf. mentaveiensis* may be extinct. One of these species, *Cartharsius molossus*, a large-bodied dung beetle, plays an important role in nutrient recycling in the forest ecosystem. The possible extinctions of dung beetles within a span of 30 years in BTNR highlights the recurring events of species loss in Southeast Asian forests today and the need to preserve whatever remaining refuges of biodiversity.

KEY WORDS. – Tropical forest, insect, Southeast Asia, species survival, dung.

INTRODUCTION

Tropical forest loss and degradation by human activities continue to threaten earth's biodiversity (Brooks et al., 2002; Brook et al., 2003; Sodhi et al., 2007). This loss of forest habitats may lead to an unprecedented level of species extinctions as forest loss continues to accelerate in the most biodiverse regions (Myers et al., 2000; Pimm & Raven, 2000). The extinction of forest dwelling fauna has been better studied for more charismatic and larger mammal and bird species compared to insects (Dunn, 2005) despite the fact that more than 57% of described living species are insects (Stork, 1997; IUCN, 2008) and that insects perform critical roles in the ecosystem (Didham et al., 1996). The lack of assessment of insect survivability has led to broad estimations of the percentages of threatened insects between 0.07% and 50% (IUCN, 2008). Hence the lack of insect knowledge especially in highly threatened tropical forests may contribute to misleading levels of insect extinctions occurring (McKinney, 1993). Previous assessments of insect extinctions were often carried out at a local scale, in island systems or isolated forest reserves with a history of biodiversity inventories (Brook et al., 2003; Thomas et al., 2004; Hanski et al., 2007; Sodhi et al., 2009). An example

is the fauna of Singapore, which has been well studied since 1819 by British natural historians. In Brook et al. (2003), insects such as butterflies have a similar extinction rate of 38% as compared to commonly studied taxa such as mammals (43%), birds (34%) and vascular plants (26%).

Here, we aim to determine the possible extinctions of dung beetles (Coleoptera: Scarabaeinae) from a small isolated forest fragment, Bukit Timah Nature Reserve (hereafter BTNR), Singapore, by comparing historical documentation of dung beetles from the 1960s to 1970s with an intensive collection carried out in present day. The reduction of forest size and its isolation from a larger tract of forest can result in the decrease in middle to large sized mammal populations (Corlett, 1992; Laidlaw, 2000). This decline in mammalian populations may have cascading effects on animals such as dung beetles, which are generally reliant on mammalian dung for nutrition and nesting (Cambefort & Hanski, 1991). Hence, dung beetle species richness and abundance can be used as a possible indicator of mammal populations in a forest habitat (Andresen & Laurance, 2007; Nichols et al., 2009). A review by Nichols et al. (2008) also show that dung beetles perform a myriad of ecological processes such as nutrient recycling (Yokoyama et al., 1991), controlling

pest populations (Bornemissza, 1970) and secondary seed dispersal (Andresen & Feer, 2005), emphasizing the usefulness and importance of dung beetles in ecosystems. Based on the list of beetles from the 1960s to 1970s, we aim to determine the absence or presence of each individual species and find out if there has been any apparent extinction of dung beetles in BTNR over the last 40 years.

MATERIALS AND METHODS

Study site. – The Republic of Singapore is a highly urbanized city-state at the southern tip of the Malay Peninsula (1°14'N 103°55'E). Rapid deforestation in Singapore occurred in two phases, firstly the cultivation of cash crops which was completed by the end of the nineteenth century and secondly, urbanization which led to rapid development and economic success to the country (Corlett, 1992). Much of Singapore's original vegetation has been cleared and the largest remnant of primary hill dipterocarp rainforest lies in the Bukit Timah Nature Reserve (Corlett, 1992). The total size of BTNR is 163 ha, of which approximately 71 ha consists of primary forests disturbed to varying extents. Records of isolation of the forest on Bukit Timah stretch back to 1843, with accounts of gambier and pepper plantations separating Bukit Timah from other forests (for more details, see Corlett, 1988). Legal protection was more strictly enforced in 1939 where Bukit Timah was gazetted to be a nature reserve under the British colonial law (Corlett, 1988). Several legislations were passed to protect both flora and fauna in the early 20th century, though these were not sufficient to prevent illegal hunting and logging (Corlett, 1988). At present, BTNR is surrounded by a matrix of urban housing and a major expressway, which separates BTNR from a larger forest fragment (ca. 3,043 ha), the Central Catchment Nature Reserve (Fig. 1). A total of 843 forest angiosperm species have been recorded in BTNR, with the most species coming from the following plant families: Euphorbiaceae, Orchidaceae, Rubiaceae and Moraceae (Corlett, 1990).

The fauna history of BTNR has also been recorded albeit not as well studied than the flora. The primary forests in BTNR are different from the rest of Southeast Asia namely because all its large mammals, e.g. the Tiger (*Panthera tigris corbetti*), Leopard (*Panthera pardus*), Sambar (*Rusa unicolor*), have gone extinct between 1930 and 1940s (Yang et al. 1990; Tan et al., 2007). Mammals that are extant in BTNR include small to medium sized mammals such as the Long-tailed Macaques (*Macaca fascicularis*), Common Treeshrews (*Tupaia glis*), and Slender Squirrels (*Sundasciurus tenuis*). The last published survey of mammals found in BTNR was conducted from 1993 to 1997 as part of a larger survey of fauna diversity in the nature reserves of Singapore (Teo & Rajathurai, 1997).

Historical collection of dung beetles. – We searched the Raffles Museum of Biodiversity Research (RMBR) in the National University of Singapore (NUS) for any past collections of dung beetles made in the forest interior of

BTNR. Dennis H. Murphy, a retired NUS entomology professor, made most of the dung beetle collection during the period of 1960s to 1970s. We interviewed D. H. Murphy regarding the methods used for collection of the dung beetles and the exact locations where he made his collections. The beetles were collected with a variety of techniques, such as glycol pitfall traps, light traps and malaise traps. All the beetles were collected opportunistically and there was no systematic sampling design, which could be replicated.

Dung beetle survey. – Since past collections of dung beetles were carried out opportunistically using a variety of methods, we decided to carry out an intensive dung beetle survey using well-used sampling techniques for dung beetles such as dung baited pitfall traps and flight interception traps (Davis et al., 2001). We identified the five valleys of BTNR (Lasia Valley, Taban Valley, Jungle Fall Valley, Fern Valley and Seraya Valley) as forest interiors of BTNR and placed our traps in all these valleys. This study was conducted between January 2008 and March 2008.

Our baited pitfall trap consist of a 500 ml plastic cup (diameter = 8.5 cm and height = 12 cm) buried flushed with the ground. A 15 cm by 15 cm corrugated plastic board served as a rain cover and was supported 10 cm above the surface of the cup by iron wires. We used cow dung collected from the Singapore Zoological Gardens as bait for our traps. The cow dung was kept in an airtight container for at least 4 days at room temperature so as to obtain a more pungent smell of the decomposing dung. We used approximately 100 g of cow dung and wrapped it in a 2 mm by 2 mm green mesh, secured with rubber bands and suspended from the surface of the trap by 5 cm with cotton twine. Each pitfall trap contained formalin, filled to a depth of 3 cm, to kill and preserve trapped dung beetles. Traps were organized in quadrants where one trap was 10 m away from the other and the distance between each quadrant was 50 m. The number of quadrants in each valley differed according to the size of the valley (Table 1). Traps were set up during the morning and left in the field for two nights before collection. Beetles were collected and stored in 100 % ethanol and brought back to the laboratory for species identification.

Flight interception traps collect dung beetles based on their flight activity and is therefore a more unbiased way of catching dung beetles, especially beetles which may specialize on rotting fruits or other types of dung (Davis, 2000). Our flight interception traps were constructed using a black fabric 2 m wide by 1.3 m long and suspended tautly across a forest trail using raffia strings. The black fabric intercepts beetles flying along forest trails and these beetles fall into collecting trays half-filled with a saturated salt solution with a small amount of detergent. A large ground sheet secured with raffia strings above each flight interception trap acted as a rain cover and prevented the collecting containers from being flooded. One flight interception trap was set up in each valley, except for Fern Valley, which had two such traps set up (Table 1). All traps were visited every 7 days and left in the forest

Table 1. Number of quadrants and flight interception traps in each valley of Bukit Timah Nature Reserve.

Site	Number of Quadrants	Number of Flight Interception Traps
Seraya Valley	2	1
Jungle Fall Valley	2	1
Fern Valley	6	2
Lasia Valley	3	1
Taban Valley	4	1

for a period of 21 days. Captured dung beetle individuals were preserved in 100% ethanol, and were processed and identified in the laboratory. Where individuals could not be identified, a series of morphospecies numbers were assigned to the genus. The dung beetle specimens collected from the intensive survey are held in the Raffles Museum of Biodiversity Research, National University of Singapore.

RESULTS

Dung beetles that were not found in our survey could not be labeled as “extinct” since our study was conducted approximately 30 years later. Conventional definition of

extinct species requires that species should not have been reported or seen in the last 50 years (IUCN, 2008). Hence, we shall classify dung beetles, which were not found in our 2008 survey as “possibly extinct”. Based on the historical collection in RMBR, we collated a list of nine dung beetle species and 30 individuals collected from the forest interior of BTNR between 1960s and 1970s. We checked for the presence of any of these species in our pitfall and flight interception traps conducted in February and March 2008. Out of the nine species from the historical records, three (33%) were absent and possibly extinct in BTNR (Table 2). Species not caught in our traps and possibly extinct include *Cartharsius molossus*, *Onthophagus deliensis* and *Onthophagus cf. mentaveiensis* (Table 2).

Using both baited pitfall traps and flight interception traps, we collected a total of 17 species and 867 individuals (Table 3). We recorded 11 species of dung beetles not collected by D. H. Murphy from BTNR in 2008 viz. *Ochicanthon peninsularis*, *Onthophagus angustatus*, *Ont. deflexicollis*, *Ont. pedator*, *Ont. rutilans*, *Ont. sp. 4*, *Ont. sp. 5*, *Ont. sp. 6*, *Ont. sp. 7*, *Ont. sp. 8*, and *Ont. sp. 9*. The number of species sampled using flight interception traps was higher, 16 species compared to 7 species which were found in our baited pitfall traps (Table 3). Similarly, the number of individuals from flight interception traps exceeded the number of individuals from baited pitfall traps, 764 beetles compared to 103 beetles. The majority of dung beetle individuals consisted these three dung beetle species *Onthophagus sp. 1*, *Ont. sp. 2* and *Ont. sp. 3*, which made up 68% of the total number of individuals caught in flight interception traps. There was also a great disparity in the catch of dung beetle species *Onthophagus sp. 1* and *Ont. sp. 2*, where more than a hundred beetles were caught in flight intercept traps and only one or no beetles caught using baited pitfall traps (Table 3).

DISCUSSION

Deforestation and alteration of natural habitats have been shown to cause insect population decline and extinction in studies from tropical (e.g. Brook et al., 2003; Hanski et al., 2007; Sodhi et al., 2008) as well as temperate regions (Lobo, 2000; Brandmayr et al., 2008). The loss of forests can lead to a deterioration of habitat conditions (e.g. greater predation risks and microhabitat changes), which are less conducive for certain insect species (Sodhi et al., 2007).

In the case for dung beetles, larger bodied beetles may be more prone to microclimatic changes as they dissipate heat slower (Bartholomew & Heinrich, 1978) and may find themselves vulnerable to over-heating or desiccation in a hotter and drier forest habitat (Chown, 2001). The drier forest can also lead to lower soil humidity that correlates with increased desiccation of large dung beetle larvae in the soil (Anduaga, 2004). Effects of deforestation are also associated with a decline in middle and large mammals, important dung producers in the tropical forests (Laidlaw, 2000) and this has ramifications on the availability of

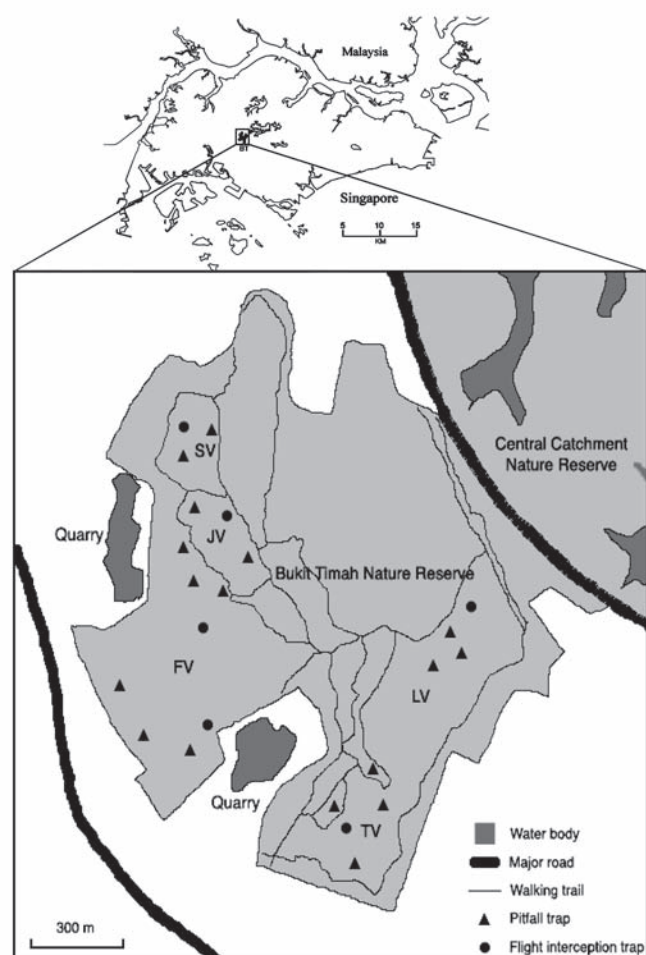


Fig. 1. Map showing geographical location of Bukit Timah Nature Reserve in Singapore and location of traps used in the 2008 dung beetle survey.

Possible dung beetles extinction in Singapore

Table 2. List of nine dung beetles which were collected between 1965 and 1976 and their presence or absence in the pitfall traps (PFT) or flight interception traps (FIT) set up between January and March 2008. Functional guild refers to the size and mode of dung removal based on Cambefort (1991). Biomass data was obtained from a separate study conducted by Lee et al. (in preparation).

Species	Functional Guild*	Biomass (g)	PFT	FIT	Present/Absent (+/-)
<i>Catharsius molossus</i>	LT	0.5719 ± 0.0670	0	0	-
<i>Onthophagus deliensis</i>	ST	0.003	0	0	-
<i>Onthophagus</i> sp. 1	ST	0.0037 ± 0.0019	1	1	+
<i>Onthophagus</i> sp. 2	ST	0.0027 ± 0.0002	0	1	+
<i>Onthophagus</i> sp. 3	ST	0.0110 ± 0.0010	1	1	+
<i>Onthophagus mentawaiensis</i>	ST	0.0040 ± 0.0020	0	0	-
<i>Onthophagus semicupreus</i>	ST	0.005	1	1	+
<i>Onthophagus semifex</i>	ST	0.0393 ± 0.0040	1	1	+
<i>Paragymnopleurus maurus</i>	LR	0.0840 ± 0.0241	1	1	+

* Functional guild of dung beetles include size (L = large, S = small) and mode of dung removal (T = tunneller, R = roller).

Table 3. List of dung beetle species found in pitfall traps (PFT) and flight interception traps (FIT).

Species	PFT	FIT
<i>Ochicanthon peninsularis</i>	0	4
<i>Onthophagus angustatus</i>	0	11
<i>Onthophagus deflexicollis</i>	0	16
<i>Onthophagus pedator</i>	0	30
<i>Onthophagus rutilans</i>	3	0
<i>Onthophagus semicupreus</i>	7	6
<i>Onthophagus semifex</i>	41	86
<i>Onthophagus</i> sp. 1	1	198
<i>Onthophagus</i> sp. 2	0	140
<i>Onthophagus</i> sp. 3	40	186
<i>Onthophagus</i> sp. 4	7	25
<i>Onthophagus</i> sp. 5	0	1
<i>Onthophagus</i> sp. 6	0	6
<i>Onthophagus</i> sp. 7	0	2
<i>Onthophagus</i> sp. 8	0	24
<i>Onthophagus</i> sp. 9	0	27
<i>Paragymnopleurus maurus</i>	4	2
Total species	7	16
Total individuals	103	764

sufficient dung resources for beetles with higher biomass (Larsen et al., 2005). The study by Hanski et al. (2007) on dung beetle extinctions in Madagascar cited the reduction in the population of lemurs as a possible reason for the dramatic decline of *Helictopleurus undatus*, a relatively large dung beetle that was common in the past. In our study, we identified a single large dung beetle *Cartharsius molossus* (ca. 0.572 g in dry mass), a nocturnal tunneller to be possibly extinct in BTNR. *Cartharsius molossus* is a widespread species in Southeast Asia and is commonly found in the interior of primary lowland forests in Johor but not present in the forest fragments of Singapore (Lee et al., in preparation). According to Slade et al. (2007),

the presence of large, nocturnal tunnellers account for approximately 75% of dung removal and the loss of these beetles may have serious consequences on nutrient recycling and secondary seed dispersal processes in BTNR and forests of Singapore. Other dung beetle species that were absent from our 2008 survey included *Onthophagus deliensis* and *Ont. cf mentawaiensis*. Both are small tunnellers (ca. 4–6 mm in length) and have very low biomass. *Ont. deliensis* is a specialist canopy dung beetle with adaptations such as curved and elongated hind metatarsus which is used to carry dung from the canopy, such as monkey dung, to the forest floor (Davis et al., 1997).

Dung beetle species richness in BTNR is much lower in comparison to a similar study by Davis (2000) in Ulu Segama Reserve, Sabah, Malaysia. Flight interception traps set up over 7 days in reduced impact logging and conventionally logged lowland dipterocarp forests collected 57 species and 48 species respectively. In contrast, only 18 species of dung beetles were collected using the same methods but three times the trapping period in BTNR. The eleven new species recorded from our 2008 survey together with the six previously recorded species from BTNR brings the total number of dung beetle species in BTNR to 17 species. Newly recorded species were most likely missed out due to the opportunistic nature of sampling between 1960s and 1970s. It is unclear if their presence may be due to colonization of the forest fragment after 1970s. Out of the collected 17 species, only one species was not found in flight interception traps and the other 16 species found in either flight intercept traps exclusively or in both trap types. Since flight interception traps are passive in nature and collect dung beetles that have a more diversified diet, they serve as an important complementary trap type to survey dung beetle species diversity in a locality. Some dung beetle species such as *Onthophagus* sp. 1, *Ont.* sp. 2 and *Ont.* sp. 3 are found in much higher abundance in flight intercept traps than in baited pitfall traps (Table 3). Considering that flight intercept traps are left in the field for three consecutive weeks and baited pitfall traps are set out only three days for each sampling period, this disparity in abundance may be

a result of the difference in effective trapping period rather than the efficiency or appropriateness of the trap itself. The use of cattle dung instead of human dung as bait for our pitfall traps might also be another reason for the disparity in species and number of individuals between the two trap types. Since human dung is representative of an omnivorous diet, using human dung as bait may have been able to attract a wider range of dung beetle species and a larger number of individuals.

Since the early 19th century, the forest of BTNR has undergone several anthropogenic disturbances ranging from the clearance of land for agriculture and plantation to the modern day influences of human developments for recreation, housing and transport (Corlett, 1988). Between the time of our sampling and the time of collection of dung beetles from the museum, one major disturbance to BTNR was the construction of the six-lane Bukit Timah Expressway (1983 to 1986) that provides an effective barrier between BTNR and the Central Catchment Nature Reserve, restricting the movement of most terrestrial animals especially mammals between the two forests. Furthermore, walking trails that allow access to all parts of BTNR subdivide the forests into smaller areas and expose the forests to increased drying effects from the external environment (Corlett, 1988). All these human disturbances could have resulted in possible extinctions of the three dung beetle species from BTNR since the 1970s. However, we are cautious not to rule out any possible extinction from faunal relaxation due to earlier disturbance events in the early 19th century.

Our study focuses on BTNR, a small, isolated forest fragment in Singapore and hence, its results may not be widely applicable. However, this localized example can still serve as an illustration of the ongoing effects of human disturbance on Southeast Asian forest species (Sodhi et al., 2004) and especially less well-documented insect groups. The preservation of forests in BTNR and conservation of mammals therein has important consequences for the continued survival of dung beetles in the forests.

ACKNOWLEDGMENTS

We thank the National Parks Board for providing the research permits to the Bukit Timah Nature Reserve. We also thank Dr. D. H. Murphy for his time and explanations as well as the Raffles Museum of Biodiversity Research for materials and equipment provided. This study was supported by the National University of Singapore (Grant no. R-154-000-331-112).

LITERATURE CITED

- Andresen, E. & F. Feer, 2005. The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. In: Forget, P. M., J. E. Hulme, P. E. Vander Wall (eds.), *Seed Fate: Predation, Dispersal and Seedling Establishment*. CABI International, Wallingford, Oxfordshire, UK. Pp. 331–349.
- Andresen, E. & S.G.W. Laurance, 2007. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. *Biotropica*, **39**: 141–146.
- Anduaga, S., 2004. Impact of the activity of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) inhabiting pasture land in Durango, Mexico. *Environmental Entomology*, **33**: 1306–1312.
- Bartholomew, G. A. & B. Heinrich, 1978. Endothermy in African dung beetles during flight, ball making and ball rolling. *Journal of Experimental Biology*, **73**: 65–83.
- Bornemissza, G. F., 1970. Insectary studies on the control of the dung breeding flies by the activity of the dung beetle, *Onthophagus gazella* F. (Coleoptera, Scarabaeidae). *Journal of the Australian Entomological Society*, **9**: 31–41.
- Brandmayr, P., R. Pizzolotto, G. Colombetta & T. Zetto, 2008. In situ extinction of carabid beetles and community changes in a protected suburban forest during the past century: the “Bosco Farneto” near Trieste (Italy). *Journal of Insect Conservation*, **13**: 231–243.
- Brook, B. W., N. S. Sodhi, P. K. L. Ng, 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature*, **424**: 420–426.
- Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin & C. Hilton-Taylor, 2002. Habitat loss and extinctions in the hotspots of biodiversity. *Conservation Biology*, **16**: 909–923.
- Chown, S. L., 2001. Physiological variation in insects: hierarchical levels and implications. *Journal of Insect Physiology*, **47**: 649–660.
- Corlett, R. T., 1988. Bukit Timah: the history and significance of a small rain-forest reserve. *Environmental Conservation*, **15**: 37–44.
- Corlett, R. T., 1990. Flora and reproductive phenology of the rain forest at Bukit Timah, Singapore. *Journal of Tropical Ecology*, **6**: 55–63.
- Corlett, R. T., 1992. The ecological transformation of Singapore, 1819–1990. *Journal of Biogeography*, **19**: 411–420.
- Davis, A. J., J. Huijbregts, A. H. Kirk-Spriggs, J. Krikken & S. L. Sutton, 1997. The ecology and behaviour of arboreal dung beetles in Borneo. In: Stork, N. E., J. Adis & R. K. Didham (eds.), *Canopy Arthropods*. Chapman & Hall, London, UK. Pp. 415–430.
- Davis, A. J., 2000. Does reduced-impact logging help preserve biodiversity in tropical rainforests? A case study from Borneo using dung beetles (Coleoptera: Scarabaeoidea) as indicators. *Environmental Entomology*, **29**: 467–475.
- Davis, A. J., J. D. Holloway, H. Huijbregts, J. Krikken, A. Kirk-Spriggs & S. L. Sutton, 2001. Dung beetles as indicators of change in the forests of northern Borneo. *The Journal of Applied Ecology*, **38**: 593–616.
- Didham, R., J. Ghazoul, N. E. Stork & A. J. Davis, 1996. Insects in fragmented forests: A functional approach. *Trends in Ecology and Evolution*, **11**(6): 255–260.
- Dunn, R. R., 2005. Modern insect extinctions, the neglected majority. *Conservation Biology*, **19**: 1030–1036.
- Cambefort, Y. & I. Hanski, 1991. Dung Beetle Population Biology. In: Hanski, I. & Y. Cambefort (eds.), *Dung Beetle Ecology*. Princeton University Press, New Jersey, US. Pp. 36–50.

- Cambefort, Y., 1991. Biogeography and Evolution. In: Hanski, I. & Y. Cambefort (eds.), *Dung Beetle Ecology*. Princeton University Press, New Jersey, US. Pp. 51–67.
- Hanski, I., H. Koivulehto, A. Cameron & P. Raghagala, 2007. Deforestation and apparent extinctions of endemic forest beetles in Madagascar. *Biology Letters*, **3**: 344–347.
- IUCN (World Conservation Union), 2008. Red list of threatened species. IUCN, Gland, Switzerland. Available from <http://www.iucnredlist.org/> (accessed November 2008).
- Laidlaw, K. R., 2000. Effects of habitat disturbance and protected areas on mammals of peninsular Malaysia. *Conservation Biology*, **14**: 1639–1648.
- Larsen, T. H., N. M. Williams & C. Kremen, 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, **8**: 538–547.
- Lobo, J. M., 2001. Decline of roller dung beetle (Scarabaeinae) populations in the Iberian peninsula during the 20th century. *Biological Conservation*, **97**: 43–50.
- McKinney, M. L., 1999. High rates of extinction and threat in poorly studied taxa. *Conservation biology*, **13**: 1273–1281.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca & J. Kent, 2000. Biodiversity hotspots for conservation priorities. *Nature*, **403**: 853–858.
- Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezcuita, M. E. Favila & The Scarabaeinae Research Network, 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, **141**: 1461–1474.
- Nichols, E., T. A. Gardner, C. A. Peres & S. Spector, 2009. Co-declines in large mammals and dung beetles: an impending ecological cascade. *Oikos*, **118**: 481–487.
- Pimm, S. L. & P. Raven, 2000. Biodiversity: Extinction by numbers. *Nature*, **403**: 843–845.
- Slade, E. M., D. J. Mann, J. F. Villanueva & O. T. Lewis, 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*, **76**: 1094–1104.
- Stork, N. E., 1997. Measuring global biodiversity and its decline. In: Reaka-Kudla, M. L., D. E. Wilson & E. O. Wilson (eds.), *Biodiversity II*. Joseph Henry Press, Washington DC. Pp. 41–68.
- Sodhi, N. S., L. P. Koh, B. W. Brook & P. K. L. Ng, 2004. Southeast Asian biodiversity: An impending disaster. *Trends in Ecology and Evolution*, **19**: 654–660.
- Sodhi, N.S., B.W. Brook & C. J. A. Bradshaw, 2007. *Tropical Conservation Biology*. Blackwell Publishers Limited, Oxford, UK.
- Sodhi, N. S., D. S. Wilcove, R. Subaraj, D. L. Yong, T. M. Lee, H. Bernard & S. L. H. Lim, 2009. Insect extinctions on a small denuded Bornean island. *Biodiversity and Conservation* (accepted).
- Tan, H. T. W., L. M. Chou, D. C. J. Yeo & P. K. L. Ng. 2007. *The Natural Heritage of Singapore*. Prentice Hall, Pearson, Singapore. vii + 271 pp.
- Teo, R. C. H. & S. Rajathurai, 1997. Mammals, reptiles and amphibians in the nature reserves of Singapore – Diversity, abundance and distribution. *Gardens' Bulletin Singapore*, **49**: 353–425.
- Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher, R. Fox, R. T. Clarke & J. H. Lawton, 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**: 1879–1881.
- Yang, C. M., K. Yong, K. K. P. Lim. 1990. Wild mammals of Singapore. In: Chou, L. M. & P. K. L. Ng (eds.), *Essays in Zoology*. Department of Zoology. National University of Singapore. Pp. 1–23.
- Yokoyama, K., H. Kai, T. Koga & T. Aibe. 1991. Nitrogen mineralization and microbial populations in cow dung, dung balls and underlying soil affected by paracoprid dung beetles. *Soil Biology and Biochemistry*, **23**: 649–653.