POST-DISPERSAL OF SEEDS IN FECES OF WHITE-HANDED GIBBONS (*HYLOBATES LAR*) BY DUNG BEETLES (COLEOPTERA: SCARABAEIDAE)

JANYA JADEJAROEN

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR
THE DEGREE OF MASTER OF SCIENCE
(ENVIRONMENTAL BIOLOGY)
FACULTY OF GRADUATE STUDIES
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ISBN 974-04-3663-3

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was submitted to the Faculty of Graduate Studies, Mahidol University
for the degree of Master of Science (Environmental Biology)

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ACKNOWLEDGEMENTS

I would like to express my grateful thank to my major- and co-advisors; Dr. Warren Y. Brockelman, Dr. Sompoad Srikosamatara, Dr. Vacharobon Thirakhupt, and Dr. Yupa Hanboonsong for their kind supervision, instruction, advice, helpful comments for thesis proposal and manuscript, and their other assistance and supports.

I indebted Dr. Yupa Hanboonsong and Mr. Sura Pimpasalee for their help in identification of dung beetles and for providing several useful papers.

I thank Dr. J. F. Maxwell, Ms. Panarat Charoenchai, Ms. Onuma Petchmitr and other related persons for help with seed identification. Many thanks also go to all friends from Center for Conservation Biology who have helped and shared a lot of good experiences particularly in Mo Singto Plot, Khao Yai National Park and at Mahidol University, Salaya Campus.

I am grateful to all teachers, staffs, and friends from the Department of Biology especially Dr. Udomlux Suwanvecho, Ms. Chuti-on Kanwattanakid, Ms. Anchana Thancharoen, and Ms. Bantika Areekul for their moral support, suggestions, and other help. All of them have fulfilled my student life here.

This study was mainly supported by the TRF/BIOTEC Special Program for Biodiversity Research and Training Grant (BRT 543017). Kind assistance of Prof. Dr. Visut Baimai, BRT Director and all BRT staffs are very appreciated.

I wish to extend my sincere thanks to Mr. Philip D. Round, Dr. Samaisukh Sophasan, Ms. Dararat Sirisingkarn, Mr. Akira Koiwai and many other persons including old teachers, friends, and colleagues who always give me good advice and encouragement.

I thank Mr. Arnuparp Yhamdee for all his help, friendship, and every good moment we have shared.

Finally, I thank my parents, brothers, and sisters for their eternal love, care, and understanding. They and their love are always in my heart wherever I am.

Janya Jadejaroen

POST-DISPERSAL OF SEEDS IN FECES OF WHITE-HANDED GIBBONS (*HYLOBATES LAR*) BY DUNG BEETLES (COLEOPTERA: SCARABAEIDAE)

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ABSTRACT

Seeds dispersed by fruigivorous mammals like gibbons were found to be positively affected by dung beetles (Coleoptera: Scarabaeidae). They incidentally remove seeds while feeding and removing feces, to be used for brooding. The study was done between Jan.-Dec., 2000, in a primary rain forest at Khao Yai National Park, Thailand, to provide a basic knowledge of ecological interactions between these beetles and the seeds dispersed in feces of white-handed gibbons (*Hylobates lar*). A total of 3,809 seeds of 42 species (27 families) were recovered from 157 samples of gibbon feces. These seeds ranged 0.5-30 mm in length. From 288 pitfall traps and 49 direct observations of post-seed dispersal, 2,194 beetles of 53 species (9 genera) were collected. Beetles were caught more from night traps than day traps and more during the beginning of the rainy season (Apr.-Jun.) than in other seasons. However, beetles were equally abundant in valley and hill habitats. According to their dung processing and nest constructing methods, dung beetles are classified into three functional groups; tunnelers (86% of 1,818 beetles from traps), rollers (3%), and dwellers (11%). All tunnelers and rollers removed small seeds from their original positions while dwellers did not. From 49 observations, 10% (range 0-100%) of large seeds were removed by 9% (0-75%) of dung beetles that visited dung. Tunnelers of eight species (5-26 mm in length) moved those seeds into their tunnels under or short distances from dung piles with an average of 14.9 cm (range 0-105, N=32) and buried them 2.7 cm (range 0-7, N=32) under the soil. Each tunneler transported a single or two seeds during each observation. Large rollers (26 mm) removed 4-8 large seeds (mean 6.3, N=3) in their balls while dung balls of two small roller species (4 and 7 mm) contained only small seeds. These rollers rolled their balls an average of 62.8 cm away (range 5-150 cm, N=24) and buried them an average of 5.2 cm (range 0-7, N=21). Considering these removal distances and burial depths, seeds are most likely to be given the advantages of escaping from clumping and avoiding predator attraction and have a greater possibility of germinating.

KEY WORDS: SEED POST-DISPERSAL / DUNG BEETLE / WHITE-HANDED GIBBON / KHAO YAI NATIONAL PARK

88 P. ISBN 974-04-3663-3

บทบาทของด้วงมูลสัตว์ในการกระจายเมล็ดพืชจากกองมูลของชะนีมือขาว (POST-DISPERSAL OF SEEDS IN FECES OF WHITE-HANDED GIBBONS (*HYLOBATES LAR*) BY DUNG BEETLES (COLEOPTERA: SCARABAEIDAE))

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บทคัดย่อ

เมล็ดพืชในกองมูลของสัตว์ที่กินผลไม้เป็นอาหารมักได้ประโยชน์จากด้วงมูลสัตว์หรือแมงกุดจี่ในการเคลื่อนย้ายไปพร้อมกับมูลที่ด้วงนำไปฝังใต้พื้นดินเพื่อใช้ในการวางไข่และเป็นที่อยู่ของตัวอ่อน จากการศึกษาปฏิสัมพันธ์เชิงนิเวศวิทยาของด้วงมูลสัตว์ในการช่วยกระจายเมล็ดพืชจากกองมูลของชะนีมือขาว ณ อุทยานแห่งชาติเขาใหญ่ ระหว่าง ม.ค.–ธ.ค. พ. ศ. 2543 พบเมล็ดพืช 3,809 เมล็ด จาก 42 ชนิด ใน 27 วงศ์ จากมูลชะนี 157 กอง เมล็ดพืชมีความยาว 0.5–30 มม. จากการวางกับดักหลุมตกที่ใช้มูลชะนีเป็นเหยื่อล่อ 288 กับดัก และการสังเกตการกระจายเมล็ดพืชจากกองมูลจำนวน 49 ครั้ง พบด้วง 2,194 ตัว จาก 53 ชนิด ใน 9 สกุล จำนวนด้วงจากกับดักกลางคืนมีมากกว่ากลางวัน และจากต้นฤดูฝน (เม.ย.–มิ.ย.) มากกว่าฤดูอื่นๆ แต่ด้วงจากกับดักบริเวณหุบเขาและเนินเขามีจำนวนไม่แตกต่างกันอย่างมีนัยสำคัญ ด้วงเหล่านี้แบ่งตามลักษณะการนำมูลเพื่อสร้างรังได้ 3 ประเภท คือ พวกขุดอุโมงค์ (86% ของด้วงจากกับดัก 1,818 ตัว) พวกกลิ้งมูลเป็นรูปทรงกลม (3%) และพวกที่อาศัยในกองมูล (11%) ด้วงที่ขุดอุโมงค์และกลิ้งมูลทุกชนิดสามารถกระจายเมล็ดขนาดเล็กจากกองมูล แต่พวกที่อาศัยในกองมูลไม่ช่วยกระจายเมล็ด จากการสังเกต 49 ครั้ง ด้วง 9% (0–75%) จาก 376 ตัว พาเมล็ดขนาดใหญ่ 10% (0–100%) ของทั้งหมด 502 เมล็ด จากกองมูล โดยด้วงที่ขุดอุโมงค์จำนวน 8 ชนิด (ขนาด 5–26 มม.) พาเมล็ด 1–2 เมล็ด ลงใต้ดินและห่างจากกองมูล 14.9 ซม. (0–105 ซม., N=32) และลึก 2.7 ซม. (0–7 ซม., N=32) โดยเฉลี่ย ส่วนพวกกลิ้งมูลตัวใหญ่ (ขนาด 26 มม.) พาเมล็ดครั้งละ 4–8 เมล็ด (เฉลี่ย 6.3, N=3) ไปพร้อมกับมูลทรงกลม ในขณะที่พวกกลิ้งมูลขนาดเล็ก 2 ชนิด (4 และ 7 มม.) ช่วยกระจายเพียงเมล็ดขนาดเล็ก ๆ ด้วงเหล่านี้เคลื่อนย้ายเมล็ดเป็นระยะเฉลี่ย 62.8 ซม. (5–150 ซม., N=24) และฝังเมล็ดลึก 5.2 ซม. โดยเฉลี่ย (0–7 ซม., N=21) การที่ด้วงเคลื่อนย้ายเมล็ดพืชจากกองมูลของชะนีมือขาว เมล็ดพืชน่าจะได้ประโยชน์โดยพ้นจากการรวมเป็นกลุ่มในกองมูลและลดการเป็นจุดสนใจของสัตว์ที่ทำลายและกินเมล็ดที่กองมูล และจากระยะและความลึกดังกล่าว เมล็ดพืชน่าจะมีโอกาสในการงอกเพิ่มขึ้น

88 หน้า. ISBN 974-04-3663-3

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CHAPTER I

INTRODUCTION

Seed dispersal by primates in their forest habitats has been studied in many parts of the world. Frugivorous primates such as white-handed gibbons (*Hylobates lar*) have been known to swallow, transport seeds away from the parent plants, and defecate them in viable condition (Whitington, 1990, Vimuktayon, 2001). Further seed dispersal by dung beetles (Coleoptera: Scarabaeidae) attracted to the feces is possible when the insects remove dung for food and oviposition sites and accidentally took seeds away together with their food from the original locations without damaging them. The removal of dung is because of nesting behavior of these insects. The beetles that process dung balls before transporting them away to bury are called rollers. The species that usually make burrows under dung piles and pull dung down into that are burrowers or tunnelers. The other group of dung beetles that live within dung piles without moving them away are called dwellers. Post-dispersal of seeds from the dung piles by these beetles might reduce lethal risks according to density and seed predation but increase germination and survival rates when being relocated into more suitable microsites (Estrada & Coates-Estrada, 1991; Shepherd & Chapman, 1998; Andresen, 1999; Feer, 1999; Andresen, 2001). Not only frugivores but also these insects were then thought to be important in determining the future of their forest habitat composition.

White-handed gibbons in a tropical forest in Khao Yai National Park, Thailand, have been known as one of the major seed-dispersing animals. A group of them has been habituated and studied in Mo Singto long-term forest dynamics plot in this park for more than 20 years. Their home range covered about 25 hectares and the gibbons traveled, on average, 1,160 m per day (range 724-1,655 m) throughout the area (Reichard, 1996; Bartlett, 1999). The gibbons of the group spent about 32% of their daily activity feeding. They fed mainly on fruit (47%) and figs (19%) other than leaves, flowers, vines, and insects (Bartlett, 1999). These gibbons dispersed seeds of trees and woody climbers of at least 58 species through their feces (Whitington & Treesucon, 1991; Brockelman & Charoenchai, 1999; Kanwattanakid, 2000). Various seeds from small figs to large ones such as that of wild rambutan (*Nephelium melliferum*) and mangosteen (*Garcinia benthamii*) were found in gibbon feces. During April to June 1989, each gibbon of this group defecated approximately 200 seeds/day (including rambutan seeds) or about 25 seeds/pile. The gibbons defecated every 1-1.5 hours, therefore four members (during that year) of the group dispersed about 72,000 seeds during that season with an average of 3,000 seeds/hectare (Whitington, 1990). However, little is known about post-dispersal of seeds from feces of these gibbons including by dung beetles. The study of these ecological interactions among seeds and their animal dispersers might lead to the understanding of regeneration of plants in the area and beneficial to forest conservation and management as well.

This study was attempted to provide ecological knowledge of dung beetles that feed on gibbon feces and their effects on dispersal of seeds from gibbon feces throughout the period of one year. The questions of the study were:

1. How many species of seeds are dispersed by whited-handed gibbons in Mo Singto study area?
2. What dung beetles are attracted to gibbon feces? How many functional groups were they in?
3. Do numbers of dung beetles differ in habitat preference, daily activity or seasonal activity?
4. What groups or species of dung beetles are involved with post-dispersal of seeds?
5. What are the patterns of seed removal of each group or species?
6. How many species of seeds are removed by the beetles?
7. What are the distances and depths of seed burial after being removed?

CHAPTER II
LITERATURE REVIEW

2.1 Gibbons and seed dispersal in Khao Yai National Park, Thailand

Two species of gibbons occurr in Khao Yai National Park. They are white-handed or lar gibbon (*Hylobates lar*) and crowned or pileated gibbon (*H. pileatus*) (Marshall *et al.,* 1972). This makes the park the only place in the world in which these two species of gibbons occur together (Brockelman & Gittins, 1984). The park, with 2,168 sq. km in total area, is the habitat of about 3,000 white-handed gibbons and 4,300 of pileated gibbons (Srikosamatara & Hansel, 1996). They live in families averaging 4 animals in territories of about 20 ha, or 125 *rai* (Brockelman *et al.,* 1998). Both species are diurnal and feed on similar diet in which fruits are their main food item (70-75%) and leaves, young shoots, buds, flowers and insects are the remaining (Ellefson, 1974; Srikosamatara, 1984).

Among the gibbons in this park, a family of white-handed gibbons (called group A) living in Mo Singto area has been habituated and studied for more than 20 years. Studies related to feeding behavior, fruit consumption, and seed dispersal by the group have been done by several researchers as well. It was found in the study of Whitington and Treesucon (1991) that the gibbons fed on fruits of 61 species including 23 different *Ficus* species in their territory and surrounding areas. This gibbon group consumed at least 100 plant species and defecated seeds of 58 species in their feces. Most of the fruits eaten by the gibbons were berries and drupes that they swallowed whole without removing the seeds. The large fruits with tough covers such as *Sandoricum koetjape, Nephelium melliferum,* and *Garcinia benthamii* were also consumed by the gibbons. They did this by removing the fruit skins by their canines and swallowing the flesh-covered seeds (Whitington & Treesucon, 1991; Kanwatanakid, 2000). It was also reported by Bartlett (1999) that the gibbons feed on non-fig fruit (47%), fig (19%), and leaves, flowers, vine shoots, and insects. Their fruit diet comprises at least 50 species including many fig species. In each day, gibbons spent 36% of their time feeding (Suwanvecho, 1997). They spent 80% of the feeding time eating fruits during June and July when fruits were abundant but during November and February when ripe fruits were scarce, they reduced some of their activities and fed increasingly on other diets such as fig fruit (Bartlett, 1999). Kanwatanakid (2000) found that the gibbon group consumed 50 fruit species (77% of their plant diet). Of those, 69% of the species were wholly swallowed and 25.5% were swallowed after the fruit skins were removed. The dispersal distance of seeds of a tree species, *Aphananthe cuspidata,* was studied by Touranont (2000). A single individual of the species fruited during August and October 1999. The seeds were found in 16 fecal samples on average of 194 m from the parent tree with the maximum distance of 420 m.

Large (18-25 mm) seeds, including those of *Nephelium melliferum* or wild rambutan, were swallowed and passed in feces of this gibbon group (Vimuktayon, 2001). During April and June 1997, 365 fecal samples contained 1,847 rambutan seeds. After their dispersal, it was found that 71% of the 1,847 rambutan seeds from the fecal samples were lost but 90% of the remaining germinated. The others died from seed-eating by insects and fungi, gnawing by invertebrates, and desiccation. Fifty percent of 2 year-old seedlings survived while the others were eaten or damaged by insects and herbivores.

Seeds of some species, e.g. *N. melliferum* and *Sapium baccatum* processed by the gibbons, had higher percentage of germination (Whitington, 1990). Whitington estimated that the gibbons defecated every 1-1.5 hours. They were active about 10 hours from early morning to the afternoon. Therefore, there were about 5-8 defecations per animal per day (Whitington, 1990; Touranont, 2000; Vimuktayon, 2001). Whitington (1990) collected 52 samples during April and June 1989 containing 1,370 seeds of 10 species including rambutan (25 seeds/fecal sample), and estimated that 200 seeds were dispersed daily by a gibbon. During that three-month period in their 25-ha home range, 72,000 seeds were then dispersed by the four gibbons with an average of 3,000 seeds per hectare.

Because the gibbons feed mainly on fruits and disperse various viable seeds in large amounts in their feces and they defecate every 1–1.5 hours during the day, white-handed gibbons are considered to be good seed dispersers of the area.

2.2 Dung beetles

2.2.1 General information

Dung beetles (Coleoptera: Scarabaeidae) are insects in which both adults and larvae feed mainly on dung of vertebrates, particularly mammals. Those that feed on dung are called coprophagous dung beetles and those that feed on rotting vegetable matter, carrion, and dung are necro-coprophagous (Hanski & Cambefort, 1991, Hanboonsong *et al.*, 1999).

Dung beetles can detect and reach their food sources by using their olfactory organs in their antennae. After reaching a dung pile, they cut the dung into pieces by using their head parts and front legs, and relocate it quickly to construct their underground nests. Therefore, they play an important role in recycling organic nutrients and contribute to the aeration of the soil, and improve soil structure and water circulation. By disposing of the wastes, dung beetles help reduce a number of dung-breeding flies because their dung processing makes the resources less suitable for the development of flies' eggs and larvae (Hanski & Cambefort, 1991).

Dung beetles relocate dung of frugivorous mammals without feeding on seeds but they accidentally help disperse the seeds when relocating them together with dung (Estrada & Coates-Estrada, 1991; Shepherd and Chapman, 1998). Their quick dung processing reduces seed predation by rodents and ants by decreasing the olfactory cues for those predators. The rapid movements also reduce mortality of seeds by reducing clumping, fungal attack, and desiccation as well (Estrada & Coates-Estrada, 1991, Hanski & Cambefort, 1991, Shepherd & Chapman, 1998).

Dung beetles are of various colors and sizes. Most of them are black or dark brown, some are coppery, and some have metallic patterns (White, 1983; Hanski & Cambefort, 1991). The adults range from 2 to 20 mm in length but the largest dung beetles are up to 50 mm. Horns are present in many species, usually in males. The horns vary in size, shape and location on the beetles' body: on the thorax, at the center of the head, and sometimes on both (Harvey & Godfray, 2001). Like other insects of the family Scarabaeidae, dung beetles have distinctive antennae. Each antenna is composed of 8–11 segments expanded laterally into oval or elongate lobes that can be closed tightly. The last 3–4 segments of each antenna are lamellate (White, 1983).

2.2.2 Dung beetle communities

Dung beetles usually co-exist and compete with the same and other species in the same dung pile. Each species or each group has its particular morphology and size. Dung beetles with thick and strong legs are better at burrowing while some with thinner but longer legs are good at making and rolling dung balls and can move larger distances away from competitive sites. These beetles usually build their nests and have lower fecundity; thus they pay higher costs in nest guarding. Some dung beetles with relatively small sizes are poorer competitors. These have higher fecundity and generally do not make nests. Dung beetles in a community utilizing the same resource may reduce competition by the separation of activity period as nocturnal and diurnal species. Many other factors influence the composition of the dung beetle community, including food source, season, time of day and habitat (particular altitude, latitude, soil structure). Other than dung beetles, dung flies and predatory beetles are also found in dung piles (Hanski & Cambefort, 1991).

2.2.3 Functional groups of dung beetles

Dung beetles are classified into three main groups based on their nesting behavior: the dwellers, the tunnelers, and the rollers. The dwellers (endocoprids) are relatively small dung beetles that feed and live directly in the dung and most species deposit their eggs in dung pats without constructing nests or chambers. Because there is less competition for food, the fecundity of this group is relatively higher than that of other nest-building groups. All dweller dung beetles are in the single genus *Aphodius* (Hanski & Cambefort, 1991).

The tunnelers or burrowers (paracoprids) dig vertical burrows using their front legs and head, construct nests below dung piles and transport dung into them before laying eggs in the dung. Their front legs are relatively short and thick, and are modified for digging or constructing tunnels (Hanski & Cambefort, 1991, Gullan & Cranston, 1994). Genera of tunnelers include *Caccobius*, *Catharsius*, *Copris*, *Digitonthophagus* and *Onthophagus*.

The last group is the rollers (telecoprids) which make dung balls, roll them some distance away from the food source usually using their hind legs, and bury them in suitable sites, and oviposit in the dung balls. The legs of rollers are narrow and elongate, adapted for ball construction and rolling. They are capable of roll dung balls that weigh up to 79 times their own weight (Hanski & Cambefort, 1991). Because of their leg structure, rollers are not good at digging soil. Most of them can only put their balls shallowly in the soil while some species attach the balls to grass stems or simply leave them on the soil after laying eggs in them. Roller genera include *Cassolus, Phacosoma,* and *Sisyphus* (Hanski & Cambefort, 1991).

Besides the three functional groups, there is a group of kleptoparasites, which are tunneler and roller dung beetles that do not make their own nests but steal or simply use a part of the food or nesting resources of other beetles (Hanski & Cambefort, 1991).

However, Vulinec (2002) categorized dung beetles into 6 guilds based on their seed burial effectiveness ranking beetles with poor seed burial to beetles that bury a high proportion of seeds at depths with high germination rates.

2.2.4 Life cycle of dung beetles

All developmental stages of coprophagus dung beetles feed on dung. Females lay their eggs in it, and make use of it as food for their larvae. Eggs of dung beetles are about 1–4 mm long and relatively large, up to 5% of the female body weight. Larvae of dung beetles are of scarabaeiform type having a cylindrical body typically curled into a C-shape, a well-developed head, and thoracic legs. Larvae of many species consume dung from inside the dung ball and construct a pupation chamber. The pupae are of the exarate category with the appendages free and not covered by a cocoon (Romoser & Stoffolano, 1994). The pupae are similar to their adults in general form (Daly *et al.*, 1981), and finally emerge as new adults. Sometimes, the emergence cannot occur until the balls and pupation chambers have been softened by increased soil moisture during the rainy season (Hanski & Cambefort, 1991).

2.2.5 Species richness of dung beetles

More than 5,000 species of dung beetles are recorded worldwide, with 1,650 species of genus *Aphodius* (dwellers) dominating the North temperate regions while there are 3,500 species of tunnelers and 350 species of rollers dominating the tropical regions. The tunnelers and rollers in the tropical communities depend on season, soil type, soil moisture, and dung types. For example, rollers are often most abundant after the beginning of rains on soil making it easy to dig (Hanski & Cambefort, 1991).

The species richness of dung beetles is related to latitude, altitude and mammalian species richness. Like the pattern of nearly all taxa, the species number of dung beetles increases with decreasing latitude and altitude. The species richness is highest in the tropical region while relatively low in the South and North temperate regions and relatively low on higher areas, especially on isolated mountain peaks with smaller area (Hanski & Cambefort, 1991).

The evolution of coprophagus dung beetles which feed on dung is closely associated with the evolution of mammals as they are the most significant dung producers from past to present. Therefore, the species richness of dung beetles is greater in areas of rich mammalian fauna. In addition, the abundance, range, and size of mammals in different habitats determine the range, abundance, and species number of dung beetles. The tropical savannas with elephants, with cattle, and those without large mammals have about 50, 47, and 30 dung beetle species, respectively, while tropical primary forest rich in mammals has 49 species, tropical secondary forest rich in mammals has 40 species, and tropical secondary forest poor in mammals has 27 species (Hanski & Cambefort, 1991).

2.2.6 Dung beetles in Thailand

Although a number of dung beetles have been recorded from many countries in Asia including Indonesia and Malaysia, very little has been known about dung beetles in Thailand. There has been a limited number of researches on dung beetles conducted.

One hundred and fifty-four species of 15 genera of dung beetles have been recorded from forest and agricultural areas of the 19 northeastern provinces. The Northeast covers 170,000 km^2, or about 1/3 of the country, and ranges from 150 to 1,000 m above sea level (Hanboonsong *et al.*, 1999). The beetles were collected by hand searching from dung pads, pitfall trapping baited with pig dung, light trapping for nocturnal and positively phototactic species, and extracting from forest leaf litter for small litter dwelling species. The 15 genera were *Gymnopleurus, Sisyphus, Panelus, Phacosoma, Cassolus, Synapsis, Heliocopris, Catharsius, Copris, Onitis, Drepanocerus, Oniticellus, Liatongus, Caccobius,* and *Onthophagus.* Of those beetles, 103 species are of genus *Onthophagous.* The species richness of the beetles is greater in forest than in cultivated or cleared lowland areas. Some genera such as *Catharsius, Onitis,* and *Oniticellus* are dominant in lowland areas, while most *Caccobius, Cassolus, Panelus, Phacosoma,* and *Sisyphus* occur in forest habitats.

A total of 33 species of 13 genera have also been collected in northeastern Thailand during a single year (Pimpasalee, 2000). Twenty-one species of 10 genera were collected from agricultural areas in Khon Kaen and 18 species of 9 genera were collected from a natural forest in Chaiyaphum. The forest areas were a mixture of many habitat types including evergreen, dipterocarp, and bamboo forest and grasslands, while agricultural areas consisted of livestock pasture and paddy fields. The collected specimens were obtained by hand searching, light traps, and pitfall traps baited with pig, cow, and buffalo dung. All the genera obtained were *Caccobius, Catharsius, Copris, Digitonthophagus, Drepanocerus, Garreta, Heliocopris, Liatongus, Oniticellus, Onitis, Onthophagus, Paragymnopleurus,* and *Sisyphus.* The genera *Drepanocerus* and *Sisyphus* were restricted to forest habitats while *Onitis, Garreta* and *Heliocopris* were found only in lowland or agricultural areas (Pimpasalee, 2000).

Twenty-nine species of 8 genera of dung beetles were recorded during a single year from primary and secondary forests in the southern province of Songkhla (Boonrotpong, 2001). The most abundant genus from the study was *Onthophagus* (18 species). There were 29 species (8 genera) and 22 species (6 genera) found in the primary and secondary forest, respectively. Species diversity and evenness were higher in the primary forest.

A study on carrion insect succession and diversity in grassland and forested areas of Khao Yai National Park was done during the year 1999 (Areekul, 2000). Insects from many families were attracted to mouse and chicken carcasses. The two dominant groups in the carcasses were Diptera (flies) and Coleoptera (beetles) comprising 34 and 12%, respectively. Flies initially arrived at the food followed by other insects. Dung beetles attracted to the carcasses included *Catharsius molossus, Copris reflexus, Synapsis* sp., *Onthophagus apilularius, O. lindaae, O. penicillatus, O. phanaeiformis, O. proletarius, O. rudis, O. tricornis,* and *O. vividus.* The species diversity of Coleoptera was greater in forest area than in grassland. The species richness of Coleopteran insects from forest areas was highest during the rainy season while in grassland it was highest during summer.

2.3 Previous studies on seed dispersal by primates and dung beetles

A number of dung beetle species have been captured in feces of primary seed dispersers, including primates, mostly in tropical habitats relatively rich in plants and animals. Effects of the beetles on post-dispersal of seeds from feces of frugivorous primates have been studied in many countries as many primates swallow fruits and seeds of many species and disperse undestroyed seeds in their feces (Estrada & Coates-Estrada, 1991; Shepherd & Chapman, 1998; Andresen, 1999; Feer, 1999; Andresen, 2001, Andresen, 2002).

Howler monkeys (*Alouatta palliata*), in Mexico, defecated viable seeds of 28 plant species (Estrada & Coates-Estrada, 1991). Pitfall traps baited with their feces attracted 20 species of dung beetles with 10 species of tunnelers and 7 of ball-rollers. Fecal samples, 10 diurnal and 10 nocturnal, were removed within 1–3 hours. In the forest, dung beetles buried 4–79% of seeds at 1–10 cm beneath the soil. Rollers transported balls 0.1–5 m away (mean = 1.2 m). In PVC cylinders (40 cm high x 20 cm diameter), selected burrowers buried 60% of their processed seeds of all the 20 species while rollers buried 22% their processed seeds of 11 seed species. From the study, seed sizes correlated with burying percentage by dung beetles and bimodal peaks of fruiting were matched by the two peaks of dung beetle abundance (Estrada & Coates-Estrada, 1991).

From a study of Andresen (1999), 21 species of tunneler dung beetles and 6 species of ball-rollers were captured in pitfall traps, and observation on seed dispersal by dung beetles were made in an evergreen floodplain forest in Peru. The pitfall traps baited with feces of howler monkeys were left for about 24 hours in the forest. The observations were done by placing feces of spider monkeys (*Ateles paniscus*) with a single species of seed in plastic cylinders and checking them after 24 hours. Some of the dung piles were observed on the forest floor up to 7 hours during the day. The first beetles seen to arrive within an average of 7 ± 7 minutes (N = 9) and, within 45 minutes, the dung piles were visited by 9 ± 4 beetles. From the observations, 5–64 % (mean = 41%) of the seed were removed by dung beetles by relocating seed with the feces and burying them, or by firstly removed fecal material and seeds together and then discarding the seeds.

Andresen (2001) captured 61 species of dung beetles from Central Amazonia by using pitfall traps baited with dung of howler monkeys. A study on burial depth of the seeds buried by dung beetles and seedling establishment showed that after 2 days, 55% of 117 seeds were buried at ≤ 5 cm depth while 45% were at > 5 cm depths. Twenty-two percent of the seeds were moved horizontally and 92% of these were found within 15 cm of the original location. The median horizontal distance of the seeds moved was 7.5 cm and the maximum distance was 80 cm. A germination study showed that at depths of 5 and 10 cm, 49 and 11% of the seeds were able to emerge, respectively.

Red howler monkeys (*Alouatta seniculus*) defecated different numbers of seed species, in different study areas for example, 137 in Amazonia (Andresen, 2002), 47 in French Guiana (Feer, 1999), and 14 in Peru (Andresen, 1999). In French Guiana, their feces attracted 57 species of dung beetles (Feer, 1999) with the first beetle arriving at dung piles within 1 minute. A ball-roller pushed a dung ball away from the source after 7 minutes of processing. In a plastic cylinder, burial depths of seeds by the beetles varied from 2 to 28 cm. The rate of seed burial was negatively correlated with seed size and positively correlated with dung beetle size (Shepherd & Chapman, 1998; Feer, 1999; Andresen, 1999).

Shepherd & Chapman (1998) conducted research on secondary seed dispersal by dung beetles in feces of baboons (*Papio anubis*) in Uganda. The seeds used in the experiment were chosen from the feces of chimpanzees (*Pan troglodytes*). The feces and seeds were placed in buckets and were left in the forest for 22–24 hours to study seed burial depths. It was found that almost all the seeds remained at shallow depths of 1–9 cm. From a germination study, they found that the germination rate was higher in seeds buried at 1–3 cm than those buried more deeply.

Vulinec (2002) collected 133 species of dung beetles from primary forest and disturbed land in Amazonia using pitfall traps baited with human dung. In captivity, the ability to bury large (> 10 mm) and small (<0.5 mm) seeds for 72 hours were observed in 20 selected species. Only a few species of beetles buried many large seeds while 19 species buried small seeds. Beetles that buried large seeds were capable of burying many small seeds as well. The burial depths of small seeds ranged from 0 to 9 cm while that for large seeds was 0 to 8 cm; many seeds were left at the ground surface. A single species of the beetle, *Dichotomius boreus,* buried many small and some large seeds too deep for germination.

This research was attempted to study secondary seed dispersal from the feces of the white-handed gibbons in Khao Yai National Park, Thailand.

CHAPTER III
STUDY SITE AND METHODS

3.1 Study Site

3.1.1 Khao Yai National Park

This study was conducted in the Mo Singto Area in Khao Yai National Park. It is the oldest national park of Thailand, established in 1962. It is situated in the central, eastern, and lower northeastern parts of the country and covers an area of approximately 2,169 km^2 in four provinces; Prachinburi, Nakhon Ratchasima, Nakhon Nayok, and Saraburi. It is about 160 km northeast of Bangkok.

There are various forest types in the park including hill evergreen forest, seasonal evergreen forest, dry evergreen forest, mixed deciduous forest, and grassland and secondary growth. Evergreen forest covers 86% of the park area. The elevation of this park ranges from 250 to 1,400 m above sea level. Evergreen forest and secondary growth occur from 400 to 1,000 m above sea level (Smitinand, 1977).

The average temperature of the park is 23°C but usually decreases to 6°C during winter (November-February) and increases to 30°C during summer (March-May). The average rainfall during the rainy season (June-October) is about 3,000 mm (Smitinand, 1977).

Khao Yai National Park is very rich in wildlife. It contains about 2,500 plant species (Smitinand, 1977), 71 mammal species including white-handed and pileated gibbons, and 333 bird species (Srikosamatara & Hansel, 1996) including 4 species of hornbills (Poonsawad & Kemp, 1993), and many other faunas.

3.1.2 Mo Singto Study Area

The study area in Mo Singto is located at 14°26′ N and 101°22′ E and is about 0.5 km west of the park headquarters and visitor center. Many studies on ecology and behavior of a family of white-handed gibbons (group A) in this area have been initiated from 1979 by Dr. Brockelman and his colleagues.

Since 1994, a 28.6-ha (178 *rai*) plot in the Mo Singto area has been established and developed into a permanent forest dynamics research plot by Dr. Warren Brockelman and his team from the Center for Conservation Biology, Mahidol University. The survey of this plot was completed in 1998 with a total size of 714 20x20 m numbered quadrats. The plot area is in primary tropical forest with several ridges, valleys, and brook ranging from 725 to 860 m above sea level (Brockelman & Charoenchai, 1999) (Figures 3-1 to 3-2). It includes the 25-ha (156 *rai*) home range of the gibbon family (Group A) surrounding by about 5 other neighboring groups.

About 200 species of trees and 114 species of woody climbers have been identified on the plot. About 16,000 trees ≥ 10-cm dbh were tagged, identified, mapped for the census. The data of censused trees were then input to the database. The most abundant families of trees are Lauraceae, Elaeocarpaceae, Aquifoliaceae, Meliaceae, and Icacinaceae. About 100 species of the plants are eaten by the gibbons including at least 60 fruit species (Whitington & Treesucon, 1991; Brockelman & Charoenchai, 1999). The fruits include 7 species of Annonaceae and 15 species of Moraceae (*Ficus* spp.) which were consumed by the gibbons in all months of the year (Bartlett, 1999; Kanwatanakid, 2000).

3.1.3 White-handed gibbons in the study area

This study focused on a family of white-handed gibbons group A, in the Mo Singto plot. Their home range covered about 25 hactares. The group structure of the gibbons group has been recorded from 1980 and it has changed by birth, emigration (e.g. to form the new group) and disappearance, and displacement by other (males) (Brockelman *et. al.*, 1998). During January and October 2000, the group consisted of three gibbons: an adult female (Andromeda, brown, > 32 years old), an adult male (Fearless, black, 26), and a subadult female (Akira, brown, 7). The other subadult male offspring (Amadeus, black, 13), had left the group to form his new group, but sometimes joined group A during the beginning of the year 2000. In October, a subadult male (Christopher, black, 14) of the neighboring group C west of group A invaded the group. The first few weeks, they aggressively fought and chased each other until they once fell from 6-7 m onto the ground and both of them very quickly ran and climbed up back in the trees (Janya & Arnuparp pers. obs.). After that, all four of them lived together and Christopher has become Andromeda's new partner. Fearless, who usually stayed some distance away from the other two members of the group when foraging and traveling, seemed to keep farther away from the three other gibbons. Finally, it was reported that in early 2001, Fearless left the group and moved to join with the group of Amadeus living in the south (Brockelman *et. al*, 2001).

Therefore, there were three gibbons in the group during January and October and after being joined by the new adult male, there were four gibbons until the end of this fieldwork in December 2000. A picture of a white-handed gibbon is shown in Figure 3-3.

3.1.4 Dung beetles in Khao Yai National Park

Khao Yai National Park is in central-northeast part of Thailand and, in the region, there are reports of 154 species of dung beetles from 19 provinces studied by Hanboonsong (1999) and 33 species from Khao Kaen and Chaiyaphum provinces from a study of Pimpasalee (2000). However, very little data of dung beetles has been reported from Khao Yai National Park. Some species documented in the study of carrion-feeding insects conducted in this park by Areekul (2000) were *Catharsius molossus, Copris reflexus, Synapsis sp., Onthophagus apilularius, O. lindaae, O. penicillatus, O. phanaeiformis, O. proletarius, O. rudis, O. tricornis,* and *O. vividus.*

3.2 Methods

The field work was conducted monthly in Mo Singto from January to December, 2000. The feces of the gibbon group was collected for voucher seed specimens, for baits in pitfall traps, and for the studies of post-dispersal of seeds by dung beetles. Before use in the pitfall traps and studies of post seed dispersal, the feces was kept in plastic bags to maintain its odor and to prevent drying.

3.2.1 Seeds from feces of white-handed gibbons

After collection, seeds in feces were counted and some were removed as voucher specimens. The seeds were then preserved in 70% ethanol and dried at about 40°C for 24-48 hours. They were compared with seed specimens in the reference collection, identified, and stored at the plant herbarium of the Center for Conservation Biology, Mahidol University at Salaya Campus. Seed length was measured and recorded.

3.2.2 Dung beetles

All the dung beetle species were collected monthly from direct studies on post-dispersal of seeds and from baited pitfall traps. In each month, 24 pitfall traps baited with c. 30 g of gibbon feces were set within the home range of the gibbons of group A. This amount of feces was used for each trap since it represents the amount that gibbons defecate naturally defecate each time. All feces collection of the same day was homogenized before use to reduce heterogeneity. Pitfall traps used in this study were made from 0.96-litre plastic bottles (c. 9 cm in diameter and 12 cm tall) with small holes at the bottom for water drainage. Each trap was covered with 1-mm mesh screen, allowing the odor to disperse. A 2.5 cm-diameter hole was made in the middle of the screen to serve as the entrance for dung beetles. The screen and trap height helped prevent escape of the beetles, especially those rolling or moving feces. The screen also helped protect against other animals attracted to the feces for meals such as rodents, amphibians, fowl, and other birds from entering. A plastic roof (15 cm x 15 cm), supported at the corners by four bamboo sticks at each corner, was used to cover the trap for rain protection (Figure 3-4).

A total of 24 pitfall traps are set in each month for the different habitats (valley and hill) and time of day (night and day). The 24 traps were divided in four groups: 6 valley-night, 6 valley-day, 6 hill-night, and 6 hill-day. Therefore, there were 72 traps of each treatment that made up a total of 288 traps throughout the 12-month period.

Locations of the 12 stations in valley and hill or ridge areas were randomly selected within the home range of the gibbons. Each station was at least about 45 m from all others. Valley stations ranged from 725 to 737 m above sea level (asl) and most of them were on slopes or near small streams, while hill stations varied from 762 to 793 m asl and most of them were on hill slopes or ridges with relatively lower soil moisture. Valley and hill areas were in the upper and lower parts of the Mo Singto area, respectively, with their positions shown in Figure 3-5. Day traps were set from approximately 10 to 12 hours between 6:00 h and 18:00 h and night traps from 18:00 h to 6:00 h.

Each trap was checked about 10-12 hours after baiting. Used bait was discarded and the dung beetles were separated by hand from the pitfall traps. Then the specimen were preserved in 70% ethanol, pinned, dried at about 40°C for 24-48 hours, and kept in plastic boxes with napthalene. Dung beetle specimens were identified to species at Department of Entomology, Faculty of Agriculture, Khon Kaen University and the Division of Entomology and Zoology, Ministry of Agriculture and Cooperatives.

Two nonparametric statistics were used to test for differences in mean dung beetle numbers from pitfall traps at different times of day, habitats, and seasons. The Mann-Whitney U test was for comparing the dung beetles from two different habitats (144 of valley-night and day & 144 of hill-night and day traps) and time of day (144 of valley-night and valley-day & 144 of hill-night and hill-day traps). The Kruskal-Wallis test for the comparison of more than two groups was used to test for differences of numbers of dung beetles among the 4 sets of different habitats and time of day (72 valley-night, 72 valley-day, 72 hill-night, and 72 hill-day traps) and among

4 seasons. The 4 seasons were the warming dry period (Jan-Mar), the early rainy season (Apr-Jun), the late rainy season (Jul-Sep) and the cool dry period after the rainy season (Oct-Dec). The tests were run in SPSS program (version 10.0).

3.2.3 Post-dispersal of seeds by dung beetles

To study post-dispersal of seeds by dung beetles, direct observations were conducted at least three times per month; ; twice during daytime (between 6:00 h and 18:00 h) and once during night (between 18:00 h and 6:00 h). Day observations were done throughout the study area but night observations were made only at the camp. The observations were made, with the aid of a pair of binoculars, at 1.5 m away the dung piles in order to avoid disturbance of the beetle activities. Some observations were done at the sites where gibbons defecated.

Approximately 30 g of fresh gibbon feces was put on the forest ground and observed for visits by dung beetles. The morphological characteristics of the beetles including estimated body length, especially dominant dung beetles that remove seeds, and their specific dung processing methods were recorded. The number and kinds of removed seeds, removal distances, and burying depths were also recorded at the end of each observation. The observations were done until the end of a predetermined time period or until no dung beetles were seen for many hours. After finishing each observation, dung beetles were collected for comparison with beetles from pitfall traps.

Figure 3-1. Primary forest in Mo Singto forest dynamics research plot. Photo by A. Yhamdee.

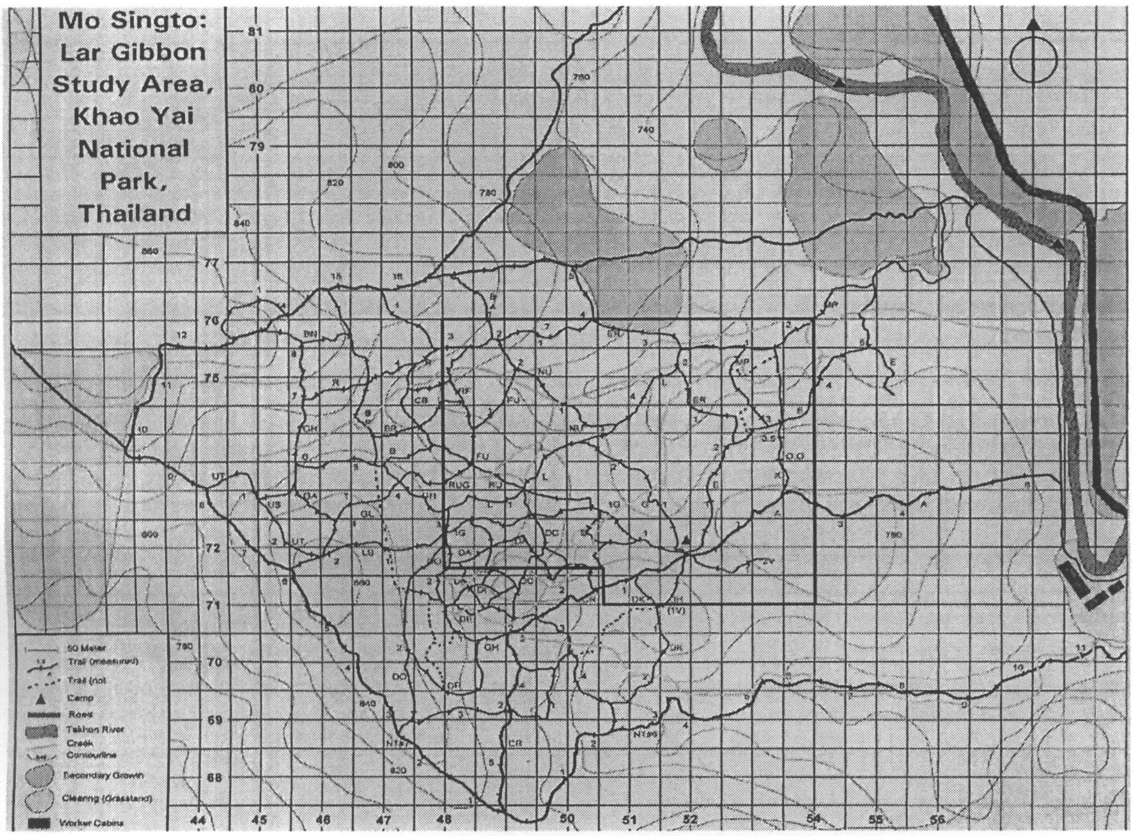


Figure 3-2. Map of the Mo Singto plot (outlined in the middle of the map), Khao Yai National Park. Each block in the map represents each 20x20m quadrat.

Figure 3-3. A white-handed gibbon feeding in a fig tree. Photo by Dr. Warren Brockelman.

Figure 3-4. A baited pitfall trap used to capture dung beetles in Mo Singto plot. Photo by A. Yhamdee.

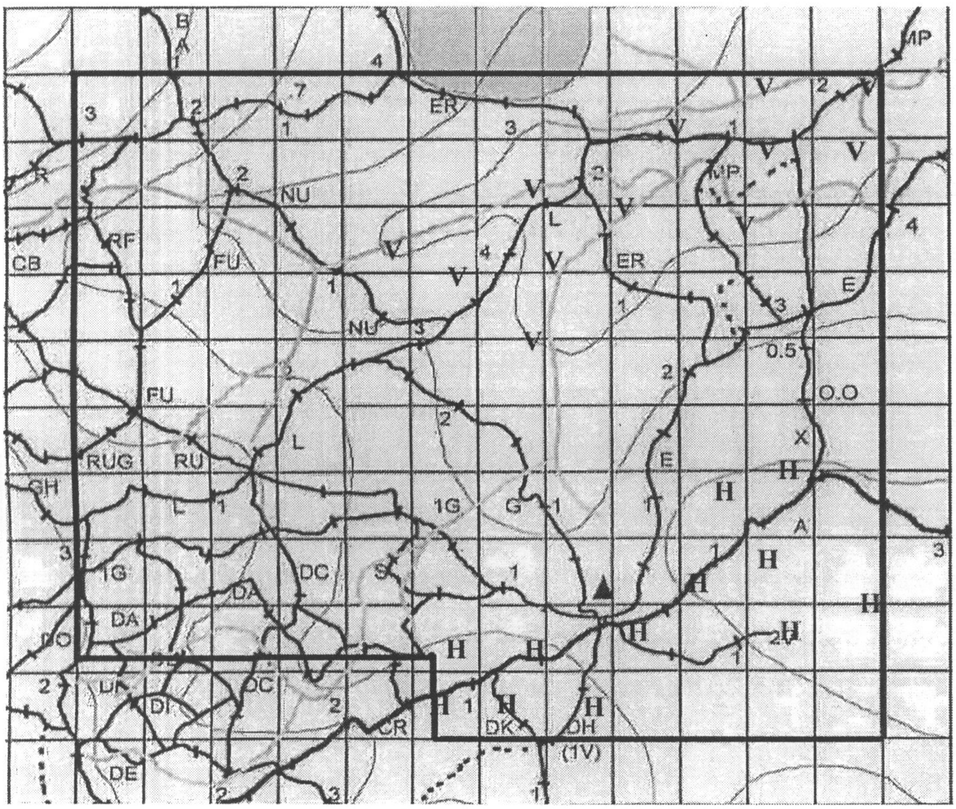


Figure 3-5. Positions of pitfall traps in Mo Singto plot. Twelve in valley (V, upper part of the map) and 12 in hill (H, lower part) areas. Each block represents each 20x20m quadrat.

CHAPTER IV
RESULTS

4.1 Seeds from feces of white-handed gibbons

Seeds of 42 species of 27 families were recovered from 157 samples of gibbon feces (9,550 g, about 800 g/month) collected on 85 days scattered throughout the year 2000 (Table 4-1, Appendix 1). A total of 3,809 seeds were of 40 species excluding the large numbers of small seeds of *Ficus* spp. which were found in the feces in all the months and *Diplectria barbata* that were collected from June to September (Appendix 1). Those seeds were of 21 tree, 16 liana and 4 unknown species not including figs or *Ficus* spp. (In the Mo Singto Plot, there were 20 *Ficus* species; 8 tree, 7 hemiepiphyte, and 5 liana species but seeds of genus *Ficus* contained in gibbon feces were counted here as a single species.) The fecal samples ranged from 20 to 120 g and averaged 60 g. There were no samples without seeds. A single sample contained 1–210 seeds (mean = 24 seeds/sample) of 1–11 species (mean = 4 species/sample).

Seeds from feces of white-handed gibbons were very diverse and varied in length from < 1.0 mm to > 29 mm (mean = 11.4 mm). Of the 40 species, large seeds (>20 mm in length) of 5 species made up 14% (of 3,809 seeds), medium-sized seeds (10.0–19.9 mm) of 17 species made up 16%, and smaller seeds (< 9.9 mm) of 18 species made up the highest proportion (70%) (Appendix 2–5). Seeds larger than 20 mm in mean length were of *Sandoricum koetjape* (29.5±3.2 mm), *Elaeagnus conferta* (25.8±4.6 mm), *Garcinia benthamii* (23.0±5.3 mm) or wild mangosteen, *Nephelium melliferum* or wild rambutan (20.4±4.4 mm) and *Knema elegans* (20.2±1.8 mm). Medium-sized seeds 8.0–8.9 mm in length made up 20% (758 seeds) of the total number (Figure 4-1). Among these, 668 seeds (18% of all seeds) were of a single species, *Tetrastigma pyriforme* (8.2±1.2 mm) which were found in fecal samples during February and April before the start of the rainy period of that year. The four smallest seeds were of *Diplectria barbata* (< 1.0 mm), *Aidia densiflora* (1.8±0.3 mm), *Anthocephalus chinensis* (2.0±0.1 mm), and seeds of *Ficus* spp. (2.9±0.3 mm). Seeds of *Ilex chevalieri* (3.8 mm) was an inseparable species that attached together with each other and with fecal matter. From Figure 4-1, those seeds < 3 mm made up 27% or 1,044 of 3,809 seeds which were 599 seeds of *Aidia densiflora* and 445 of *Anthophalus chinensis*.

Table 4-1. List of seeds from 9.550 g (157 samples) of feces of white-handed gibbons collected during the year 2000.

No.	Family	Scientific name	Thai name	Life form	Av. length ± SD (mm)	Total
1	Anacardiaceae	*Choerospondias axillaris* Roxb.	สีเสียดเทศ มะกอกหนัง	T	17.6 ± 2.1	175
2	Annonaceae	*Alphonsea boniana* Fin. & Gagnep.	กล้วยค่าง	T	12.5 ± 2.1	2
3	Annonaceae	*Desmos dumosus* (Roxb.) Saff. var. *glabrior* Craib	ตีนตั่ง	L	6.8 ± 0.8	188
4	Annonaceae	*Fissistigma oblongum* (Craib) Merr.		L	11.0 ± 1.3	34
5	Annonaceae	*Uvaria fauveliana* (Pierre ex Fin. & Gagnep.) Ast	เงาะพวงผลกลม	L	14.0 ± 2.2	4
6	Annonaceae	*Uvaria hirsuta* Jack		L	11.8 ± 1.1	5
7	Annonaceae	*Uvaria* sp.		L	11.6 ± 1.7	38
8	Apocynaceae	*Melodinus cambodiensis* Pierre ex Spire	เครือขางปุก	L	10.8 ± 0.9	15
9	Aquifoliaceae	*Ilex chevalieri* Tard.		T	3.8 ± 0.4	101
10	Araliaceae	*Schefflera elliptica* (Bl.) Harms	นิ้วมือพระนารายณ์	L	3.8 ± 0.5	34
11	Celastraceae	*Salacia chinensis* L.	กำแพงเจ็ดชั้น	L	16.9 ± 3.1	8
12	Daphniphyllaceae	*Daphniphyllum cambodianum* Gagnep.		T	11.1 ± 1.1	7
13	Elaeagnaceae	*Elaeagnus conferta* Roxb.	สลอดเถา	L	25.8 ± 4.6	105
14	Elaeocarpaceae	*Elaeocarpus* sp. 1		T	13.8 ± 1.1	49
15	Elaeocarpaceae	*Elaeocarpus* sp. 2		T	15	1
16	Escalloniaceae	*Polyosma elongata* Gedd.	เหมือดโลน	T	6.2 ± 1.5	145
17	Euphorbiaceae	*Balakata baccata* (Roxb.) Ess.	โพบาย ข้าวเย็น	T	7.1 ± 0.4	8
18	Euphorbiaceae	*Bridelia insulana* Hance	มะกาต้น	T	7.3 ± 1.0	40
19	Euphorbiaceae	*Bridelia stipularis* Bl.	มะกาเครือ	T	8	1
20	Gnetaceae	*Gnetum montanum* Markgr.	เมื่อย	L	16.8 ± 3.7	42
21	Guttiferae	*Garcinia benthamii* Pierre	มังคุด ชะมวง	T	23.0 ± 5.3	161
22	Melastomataceae	*Diplectria barbata* (Bl.) Franken & Roos		L	< 0.5	***
23	Meliaceae	*Aglaia elaeagnoidea* (A. Juss) Benth	กระดูกเขียด	T	10.9 ± 0.9	4
24	Meliaceae	*Sandoricum koetjape* (Burm. f.) Merr.	กระท้อน มะต้อง	T	29.5 ± 3.2	101
25	Menispermaceae	*Diploclisia glaucescens* (Bl.) Diels	เครือไส้ไก่ เครือตะบัว	L	16.4 ± 1.3	16
26	Moraceae	*Ficus* spp.	ไทร มะเดื่อ	T. H. L*	2.9 ± 0.3	***
27	Myristicaceae	*Knema elegans* Warb.	เลือดใหญ่	T	20.2 ± 1.8	63
28	Myrtaceae	*Cleistocalyx operculata* Roxb.	หว้าเขา	T	7.0 ± 1.2	182
29	Palmae	*Daemonorops jenkinsiana* (Griff.) Mart.	หวาย	L	13.4 ± 1.2	13
30	Rubiaceae	*Aidia densiflora* (Wall.) Masam.		T	1.8 ± 0.3	599
31	Rubiaceae	*Anthocephalus chinensis* (Lmk.) A. Rich. ex Walp.	กระทุ่ม ตะโกใหญ่	T	2.0 ± 0.1	445
32	Rutaceae	*Toddalia asiatica* (L.) Lmk.	เครืองูเห่า ผักแปมป่า	L	4.2 ± 0.7	17
33	Sapindaceae	*Nephelium melliferum* Gagnep.	เงาะป่า คอแลน	T	20.4 ± 4.4	114
34	Simaroubaceae	*Picrasma javanica* Bl.	กอมขม ดีงูต้น	T	7.5 ± 0.7	9
35	Tiliaceae	*Grewia laevigata* Vahl	ปอขี้ไก่ ย่านเลือด	L	8.6 ± 0.7	30
36	Ulmaceae	*Aphananthe cuspidata* (Bl.) Pl.	กรวยเหลม	T	10.3 ± 0.7	170
37	Ulmaceae	*Gironniera nervosa* Pl.	ขี้หนอนควาย	T	5.7 ± 0.9	6
38	Vitaceae	*Ampelopis cantoniensis* Pl.	เถากวางดุ้ง	L	4.72 ± 0.34	40
39	Vitaceae	*Tetrastigma pyriforme* Gagnep.		L	8.2 ± 1.2	668
40		Unknown 1			17.4 ± 3.1	7
41		Unknown 2			8.8 ± 1.6	59
42		Unknown 3			5.3 ± 0.7	103
					Total	**3,809**

Note: T = tree. L = liana. H = hemiepiphyte. * There were 20 *Ficus* species (8 tree. 7 hemiepiphyte. and 5 liana species) in the Mo Singto Plot.. *** = large number of small-seeded species

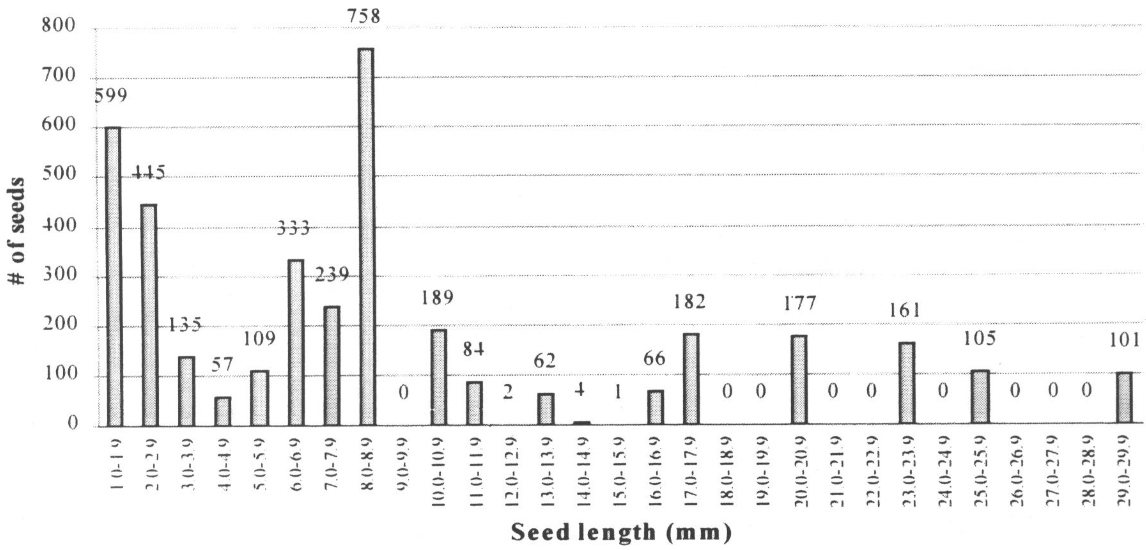


Figure 4-1. Abundance of seeds of different lengths (range 1.8–29.5 mm. N = 3.809. mean = 11.4 mm. not including large numbers of small seeds of *Ficus* spp. and *Diplectria barbata*). Small seeds (< 10 mm in length) of 18 species (Table 4-1) made up 70% of 3.809 seeds. medium-sized seeds (< 20 mm) of 17 species made up 16%. and larger seeds (> 20 mm) of 5 species made up 14%. Of all. the two smallest species with high numbers were 599 seeds (< 2 mm) of *Aidia densiflora* and 445 (2.0–2.9 mm) of *Anthocephalus chinensis*. The peak with the highest number (758 seeds) of 8.0–8.9 mm seeds were belong to four species with 668 seeds of *Tetrastigma pyriforme*. Larger seeds (> 20 mm in length) were 63 seeds of *Knema elegans* and 114 of *Nephelium melliferum* (20.0–20.9 mm). 161 of *Garcinia benthamii* (23.0–23.9 mm). 105 of *Elaeagnus conferta* (25.0–25.9 mm). and 101 of *Sandoricum koetjape*.

4.2 Dung beetles from Mo Singto

4.2.1 All dung beetles

A total of 2,194 dung beetles of 53 species (9 genera) were collected from 288 pitfall traps and 49 observations of seed removal by dung beetles throughout the year 2000 (Table 4-2, Appendices 6-9). The 288 pitfall traps baited with feces of the white-handed gibbons (24 traps/month) captured 1,818 dung beetles of 51 species (9 genera). There were 376 individuals of 24 species (7 genera) collected from the 49 observation times (12 valley-day, 21 hill-day, and 16 hill-night).

Dung beetles from traps and observations were classified into 3 functional groups: tunnelers, rollers, and dwellers. Tunnelers usually make tunnels or burrows under or near dung piles and transport pieces of dung into them for making their brood balls and for food of their offspring. Rollers always make dung balls before rolling them farther distances away before burying their balls. Dwellers use dung piles directly as food, oviposition sites, and usually complete their relatively short life cycle in dung piles. Of all the 53 species, 46 species (5 genera) were tunnelers: 40 *Onthophagus*, 3 *Copris*, a *Catharsius*, a *Caccobius* and a *Cassolus*. Dung beetles of genera *Onthophagus*, *Catharsius*, *Caccobius*, and *Cassolus* have oval bodies but those of *Copris* are elongated (Appendix 10). The ball-rollers included 5 species in 3 genera: 2 *Sisyphus*, 2 *Phacosoma*, and a *Synapsis*. Rollers have relatively long legs, particularly those of genera *Sisyphus* and *Synapsis*, while tunnelers have thicker and shorter legs (Appendix 11). Some of both tunnelers and rollers have horns on head and/or pronotum parts. The last two species of the genus *Aphodius* are dweller types with relatively small and elongated bodies (2-3 mm in length) (Appendix 12). Most dung beetles from Mo Singto plot were brown and black. Some tunneler species were coppery and some had different patterns such as metallic or non-metallic reflections, and dotted or plain-colored wings.

Among 1,818 beetles from pitfall traps, 1,555 tunnelers made up 86%, rollers 3%, and dwellers 11% (Table 4-3). Of the 86% of tunnelers, 77% were of 1,393 individuals from genus *Onthophagus* and 8% were of 146 individuals of *Copris*.

Catharsius, *Copris*, *Caccobius* and *Cassolus* made up only 1% of all the beetles. In 3% of rollers, 40 individuals of *Sisyphus* made up 2%, 12 individuals of *Synapsis* 0.7%, and the left were of the genera *Phacosoma*. The 206 individuals of small *Aphodius* dung beetles made up 11% of all the beetles. From 33 day and 19 night observations, 89% (336 individuals) of 376 beetles were tunnelers, 8% (30 individuals) were dwellers, and 3% (11 individuals) were rollers.

The average sizes of dung beetles of different species ranged from 2.4 to 26.9 mm in length (mean = 8.4 mm) (Table 4-2). The smallest dung beetles were the dwellers *Aphodius lewisii* (2.6 mm) and *Aphodius* sp. (2.4 mm) while the largest beetles were the tunneler *Catharsius molossus* (26.9 mm) and the roller *Synapsis boonlongi* (25.9 mm). The other four roller species; *Phacosoma fallacilaetum*, *P. laetum*, *Sisyphus maniti*, and *S. thoracicus*, averaged 5.0, 4.0, 4.2, and 7.1 mm in length, respectively. Tunnelers of genus *Onthophagus* were from 3.4 mm (*Onthophagus naaroon*) to 18.3 mm (*O. balthasari*). The other three genera of tunnelers, *Caccobius, Cassolus* and *Copris* were, 3.7, 5.5, and 10.0-15.2 mm, respectively. The abundance of dung beetles of different sizes is shown in Figure 4-2.

Table 4-2. List of dung beetles attracted to gibbon feces in 288 pitfall traps and 49 observations of post dispersal of seeds during the year 2000.

No.	Scientific name	Functional group	Av. length ± SD (mm)	# from 288 traps	# from 49 observations	Total
1	*Aphodius lewisii* Waterhouse	D	2.6 ± 0.3	206	26	232
2	*A.* sp.	D	2.4 ± 0.1		4	4
3	*Caccobius bidentatus* Boucomont	T	3.7 ± 0.2	14	5	19
4	*Cassolus pongchaii* Masumoto	T	5.5	1		1
5	*Catharsius molossus* Linne	T	26.9 ± 0.1	1	1	2
6	*Copris cariniceps* Felsche	T	12.8 ± 0.6	20	9	29
7	*Copris carinicus* Gillet	T	15.2 ± 1.4	62	4	66
8	*Copris reflexus* Felsche	T	10.0 ± 0.8	64	27	91
9	*Onthophagus anguliceps* Boucomont	T	8.2 ± 0.8	10		10
10	*O. apilularius* Masumoto	T	15.5	1		1
11	*O. avocetta* Arrow	T	5.6	1		1
12	*O. balthasari* Vsetetka	T	18.3	1		1
13	*O. bonorae* Zonino	T	7.1 ± 0.9	2		2
14	*O. brutus* Arrow	T	5.2	1		1
15	*O. coracinus* Boucomont	T	8.3 ± 0.4	8	2	10
16	*O. dapcauensis* Boucomont	T	5.5 ± 0.4	7		7
17	*O. deemaak* Masumoto	T	8.2 ± 0.1	2		2
18	*O. diabolicus* Harold	T	17.0 ± 1.5	6		6
19	*O. doiinthanonensis* Masumoto	T	6.0	1		1
20	*O. doisuthepensis* Masumoto	T	4.7 ± 0.4	7	21	28
21	*O. falsivigilans* Masumoto	T	5.6	1	1	2
22	*O. gracilipes* Boucomont	T	7.3 ± 0.5	103	15	118
23	*O. kanyaayonus* Masumoto	T	6.2 ± 0.3	53	4	57
24	*O. laevis* Harold	T	7.2 ± 1.3	2		2
25	*O. lindaae* Masumoto	T	6.7 ± 0.7	567	46	613
26	*O. luridipennis* Boheman	T	5.4	1		1
27	*O. manipurensis* Arrow	T	15.7 ± 0.1	2		2
28	*O. naaroon* Masumoto	T	3.4 ± 0.3	27	1	28
29	*O. ochii* Masumoto	T	6.6 ± 0.4	54	1	55
30	*O. orientalis* Harold	T	12.4 ± 1.1	41	47	88
31	*O. pacificus* Lansberge	T	6.7 ± 0.6	161	67	228
32	*O. penicillatus* Harold	T	7.1	1		1
33	*O. phanaeiformis* Boucomont	T	7.2 ± 0.8	4		4
34	*O. punnaae* Masumoto	T	6.4 ± 0.5	151	21	172
35	*O. rudis* Sharp	T	7.2	1		1
36	*O. rugulosus* Harold	T	11.1 ± 0.8	126	57	183
37	*O. singhaakhomus* Masumoto	T	5.3 ± 0.5	33	6	39
38	*O. taurinus* White	T	7.6 ± 0.6	6		6
39	*O. thanwaakhomus* Masumoto	T	5.0	1		1
40	*O. tricornis* Wiedmaan	T	15.0	1		1
41	*O. vividus* Arrow	T	10.5	1		1
42	*O.* sp. 1	T	4.5 ± 0.3	4		4
43	*O.* sp. 2	T	7.2	1		1
44	*O.* sp. 3	T	5.5		1	1
45	*O.* sp. 4	T	4.5	1		1
46	*O.* sp. 5	T	6.7	1		1
47	*O.* sp. 6	T	9.5	1		1
48	*O.* sp. 7	T	6.7	1		1
49	*Phacosoma fallacilaetum* Masumoto	R	5.0	1		1
50	*P. laetum* Arrow	R	4.0 ± 0.3	4		4
51	*Sisyphus maniti* Masumoto	R	4.2 ± 0.1	33	5	38
52	*S. thoracicus* Sharp	R	7.1 ± 0.5	7	2	9
53	*Synapsis boonlongi* Hanboonsong & Masumoto	R	25.9 ± 1.5	12	3	15
			Total	**1,818**	**376**	**2,194**

Note: D = dweller. T = Tunneler. R = Roller. 288 traps were of 24 traps (6 valley-night. 6 hill-night. 6 valley-day. and 6 hill-day) x 12 months. 49 observations = 33-day and 16-night observations

Table 4-3. Number and percentage of each functional group of dung beetles from traps and observations. All the nine genera of dung beetles caught from the Mo Singto Study Area were classified into 3 groups of tunneler. roller. and dweller. Five genera (*Onthophagus*. *Catharsius*. *Copris*. *Caccobius*. and *Cassolus*) were tunneler species. three genera (*Synapsis*. *Sisyphus*. and *Phacosoma*) were rollers. while the only genus *Aphodius* was dweller. Most (> 80%) of these beetles were tunnelers and almost 80% of them were of genus *Onthophagus*.

Functional group	Genus	# of dung beetles		% # of dung beetles	
		288 traps	49 observations	288 traps	49 observations
Tunneler	*Onthophagus*	1.393	290	76.6	77.1
	Catharsius	1	1	0.1	0.3
	Copris	146	40	8.0	10.6
	Caccobius	14	5	0.8	1.3
	Cassolus	1	0	0.1	0.0
	Sub-total	**1,555**	**336**	**85.5**	**89.4**
Roller	*Synapsis*	12	3	0.7	0.8
	Sisyphus	40	7	2.2	1.9
	Phacosoma	5	0	0.3	0.0
	Sub-total	**57**	**10**	**3.1**	**2.7**
Dweller	*Aphodius*	**206**	**30**	**11.3**	**8.0**
	Total	**1,818**	**376**	**100.0**	**100.0**

Note: 288 traps were of 24 traps (6 valley-night. 6 hill-night. 6 valley-day. and 6 hill-day) x 12 months.
49 obs. = 33-day and 16-night observations

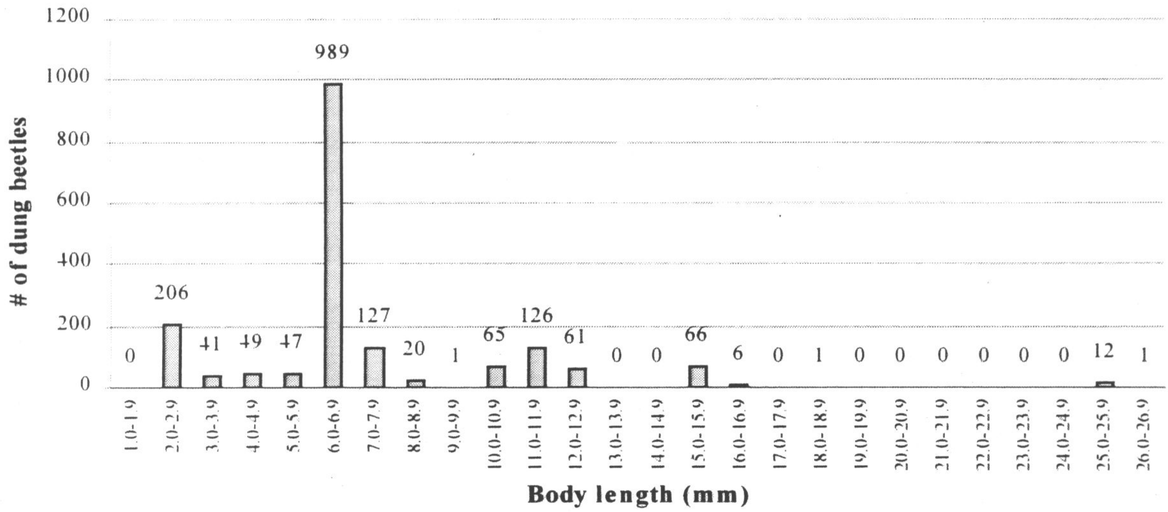


Figure 4-2. Abundance of dung beetles of different body lengths (2.6–26.9 mm, N 1,818, mean = 8.4 mm) collected from 288 pitfall. Two hundred and six individuals (11%) of *Aphodius lewisii* fell into the smallest size class of 2.6±0.3 mm. Among all, 88% were of tunnelers (genera *Onthophagus*, *Caccobius*, *Cassolus*, and *Copris*) and small rollers (*Sisyphus* and *Phacosoma*) of 3.7–18.3 in length. In these length classes, 989 individuals of 8 species (*Onthophagus lindaae*, *O. pacificus*, *O. punnaae*, *O. ochii*, *O. kanyaayonus*, *O. doiinthanonensis*, *O.* sp. 5, and *O.* sp. 7) of 6.0–6.9 mm made up 54%. Most of the 989 dung beetles were 567 individuals (57% of 989 beetles) were *O. lindaae*, 161 (16%) were *O. pacificus*, and 151 (15%) were *O. punnaae*. Thirteen large beetles (12 roller *Synapsis boonlongi* and a tunneler *Catharsius molossus*) larger than 25 mm made up 1% of all dung beetles attracted to gibbon feces in pitfall traps.

4.2.2 Dung beetles from traps of different times of day, habitats, and seasons

In each month, 24 pitfall traps baited with gibbon feces were placed in different times of day and habitats (6 valley-night; VN, hill-night; HN, valley-day; VD, and hill-day; HD traps). According to the rainfall data of the study area (Appendix 15), the 12 months during this study were grouped into 4 3-month periods (seasons) from the warming dry period (Jan–Mar), early rainy season (Apr–Jun), late rainy season (Jul–Sep), and the cool dry period after the rainy season (Oct–Dec). Therefore there were 72 traps (18 VN, 18 HN, 18 VD, and 18 HD) in each season and 288 traps in the whole year (Table 4-4).

The number of dung beetles caught in pitfall traps ranged from 0 to 43 individuals (mean ± SD = 6.3±6.9) (Figure 4-3, Appendix 6). Of 288 traps, 31 captured no dung beetle; 11 in Jan–Mar, 4 in Apr–Jun, 10 in Jul–Sep, and 6 during the last three months. Sixty-three percent (182 traps) captured ≤ 5 individuals. A valley-night trap in June caught the highest number (43 individuals) of dung beetles. Number of dung beetle species from traps ranged from 0 to 10 (mean ± SD = 2.7±1.9) (Appendix 6). Most traps (86% or 218 traps) captured 1–4 species. The four traps with the highest number (10) of dung beetle species were night traps set in May during the beginning of the rainy season.

Each set of 144 traps of different habitats caught 50% of 1,818 dung beetles (905 individuals in 144 V & 913 in 144 H traps) (Figures 4-3 to 4-4, Appendix 6). But each set of 144 traps of different times of day caught different numbers of dung beetles (60% or 1,080 individuals in 144 N and 40% or 738 individuals in 144 D traps). On average, V traps caught 6.3±7.2, H 6.3±6.5, N 7.5±7.6 and D 5.1±5.9 individuals. Many species of dung beetles were found in both night and day traps and sometimes both valley and hill. Most beetles genus *Copris* were found in night traps while both species of *Sisyphus* especially *S. maniti* were found more in day traps of both valley and hill habitats (Appendix 7). Dung beetles species found in hill in both night and day traps included all (7 individuals) of *O. doisuthepensis*. For species number, 144 V traps captured a total of 36 species (from 51 species caught in all traps), 144 H traps caught 42 species, 144 N 41 species, and 144 D 37 species

(Appendix 7). Mean number of species in each trap of V was 2.7±1.9, of H 2.6±1.9, N 3.1±2.2, and D 2.3±1.5 (Figures 4-3, 4-5).

The mean numbers of dung beetles in each set of 72 traps (VN, HN, VD, and HD) were higher in night traps than in day traps. Mean number of 72 traps of VN, HN, VD, and HD were 7.7±8.1, 7.3±7.1, 4.9±6.0, and 5.3±5.8, respectively (Figure 4-6). Numbers of dung beetles caught during the same time of day were approximately the same namely both sets of 72 traps of VN and HN caught 30% of 1,818 beetles while both sets of 72 traps of VD and HD captured 20%. Like their mean individual numbers, mean species numbers were higher in night traps of both habitats (3.2±2.1 in valley and 2.9±2.3 in hill areas) but lower in day traps (2.2±1.6 in valley and 2.3±1.5 in hill areas) (Figure 4-7). But when considering each of the four sets of 72 traps, total species number of dung beetles were similar with the highest (31 species of 51 species or 61%) in valley-night and lowest (29 species or 57%) in valley-day. Proportions of dung beetles from each set of traps from different time of day and habitats are shown in Figure 4-8.

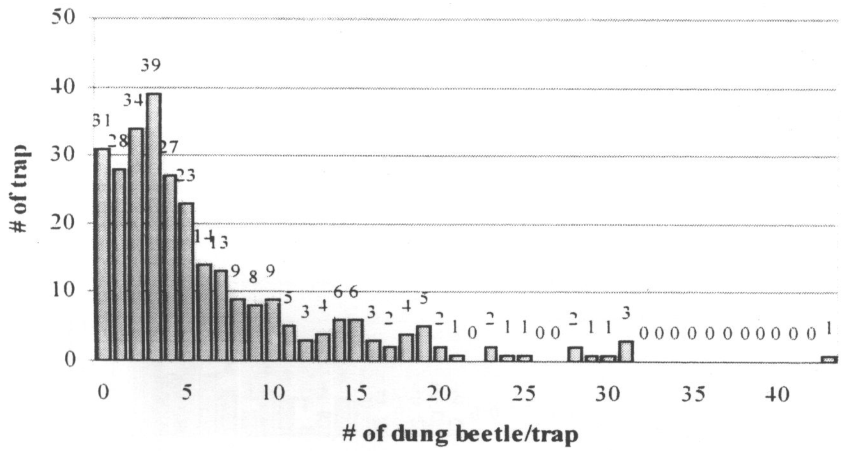
Considering dung beetles captured in each period or season of the year, average numbers of individuals and species were highest during April and June while lower in other periods. Traps set in valley and hill habitats (VN and HN) captured more individuals and species at night than during day (VD and HD) in every period (season) but night and day traps captured similar numbers during the rainy season from July to September (Figure 4-9, Appendices 7 to 9, Appendix 15). From all pitfall traps, 802 individuals (44% of 1,818 beetles) of 34 species (67 % of 51 species) were caught during the early rainy season. Common species such as *Onthophagus lindaae*, *O. pacificus*, and *O. punnaae* which were found in all the months were also found in higher number during this season but some species were found more during the dry periods (Jan–Mar and/or Oct–Dec) such as *Sisyphus maniti* and *O. gracilipes*. *O. gracilipes* was the species which were not found during rainy period but were found in warming and cool dry period (Jan–Mar and/or Oct–Dec). This species have curved and longer front legs when comparing with other species of the same genus (Appendix 10). There were approximately the same numbers of dung beetles from other seasons. Among all, 330 individuals (18%) of 20 species of dung beetles captured in warming dry period (Jan–Mar), 346 (19%) of 28 species in traps of rainy period (Jul–Sep), and

340 (19%) of 31 species in cool dry period (Oct-Dec). The relationship between number of dung beetle and rainfall is shown in Figure 4-10. Numbers of dung beetles increased at the start of the rainy season and declined during the middle of the rainy period. Less than 200 dung beetles occurred in each of the first three months with less than 50 mm precipitation. In April, the numbers of the beetles began to increase with increasing rainfall. They were highest (405 individuals, 22.3 % of 1,818 beetles) in May and started to decrease in June although the rainy season, with about 300 mm of rainfall per month, lasted until October.

The numbers of dung beetle individuals and species were tested for differences between habitats, time of day, and seasons (Table 4-5). In all 288 traps, the mean numbers were very significantly different both individual (P-value = 0.002) and species (P-value = 0.001) between different time of day. In contrast, they were not significantly different between different habitats; P-value of number of individuals was 0.816 and that of species was 0.813. In both tests of number of dung beetles among 4 different habitats and time of day (VN, HN, VD, and HD) and among 4 seasons, both numbers of individual and species were significantly different. The P-value shows that in the beginning of rainy period (Apr-Jun) with relatively high number of dung beetles were very much different when compared with number of those in different seasons.

Table 4-4. Number of pitfall traps in each month, season, and in the whole year.

Trap	# of trap/month	# of trap/season (3 months)	# of trap/year
Valley-night (VN)	6	18	72
Hill-night (HN)	6	18	72
Valley-day (VD)	6	18	72
Hill-day (HD)	6	18	72
Total	**24**	**72**	**288**



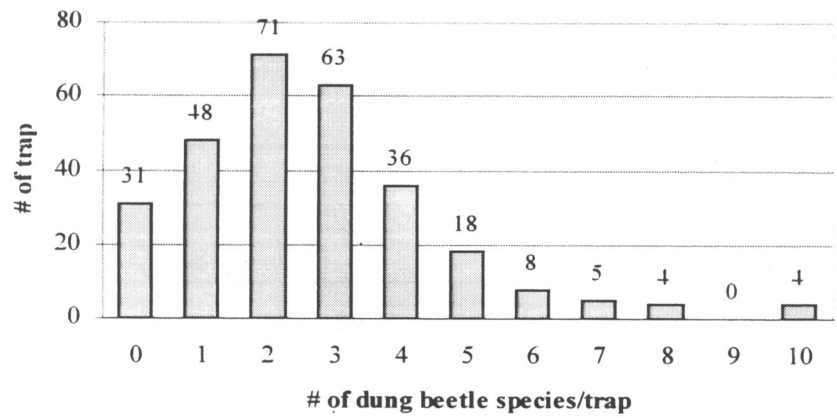


Figure 4-3. Frequency of traps with different numbers of individual (upper) and species (lower) of dung beetles caught in 288 pitfall traps. Number of individual/trap ranged from 0 to 43 (mean ± SD = 6.3±6.9, total number of individuals = 1,818). Of all traps, 63% or 182 of 288 traps captured ≤ 5 individuals. Number of species/trap ranged 0–10 (mean ± SD = 2.7±1.9, total number of species = 51). Most traps (86% or 218 traps) captured 1–4 species.

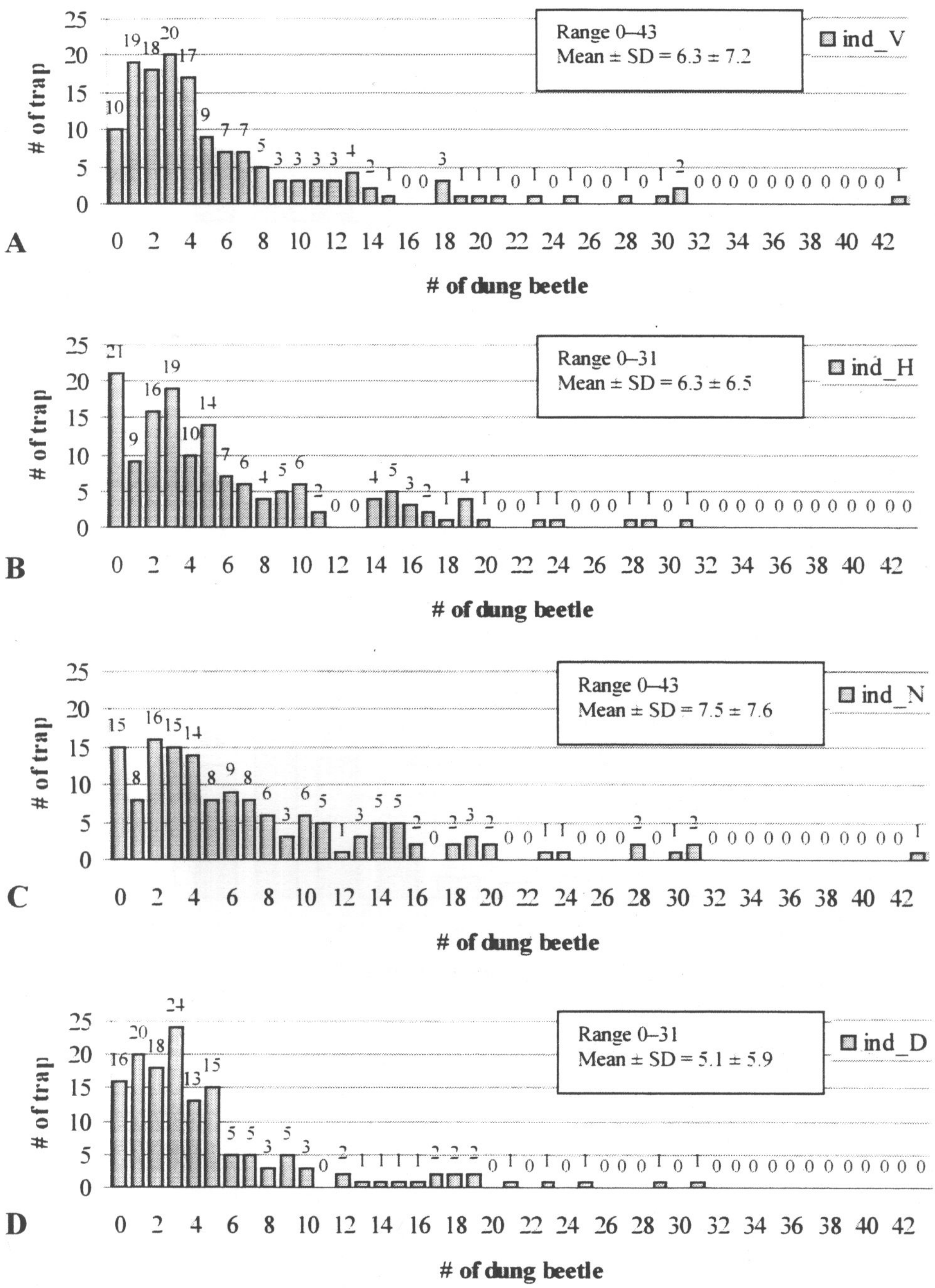


Figure 4-4. Number of traps with different numbers of dung beetles. Graphs A and B are of sets of 144 traps from different habitats (V & H) and C and D from different time of day (N & D). Each graph is with average numbers of beetles caught per trap. Most traps captured ≤ 5 beetles. Mean numbers of the beetles caught per trap were similar between V & H (6.3±7.2 & 6.3±6.5) but different between N & D (7.5±7.6 & 5.1±5.9).

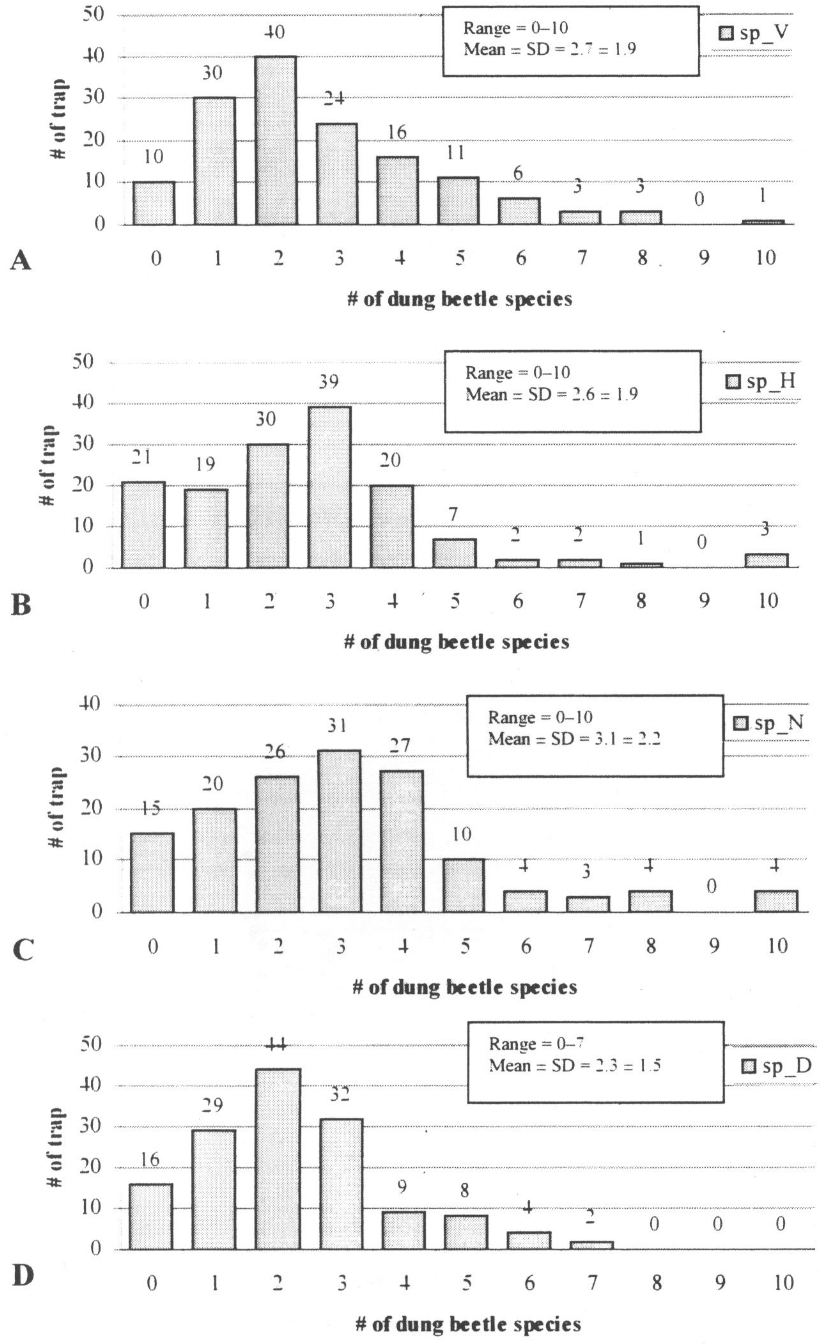


Figure 4-5. Number of traps with different species numbers of dung beetles. Graphs A and B are of sets of 144 traps from different habitats (V & H) and C and D from different time of day (N & D). Each graph is with average species numbers of beetles caught per trap. Like number of individuals, mean numbers of dung beetle species were similar from traps of different habitats (2.7±1.9 in V & 2.6±1.9 in H traps) but more species were caught in night than day traps (3.1±2.2 in V & 2.3±1.5 in H traps).

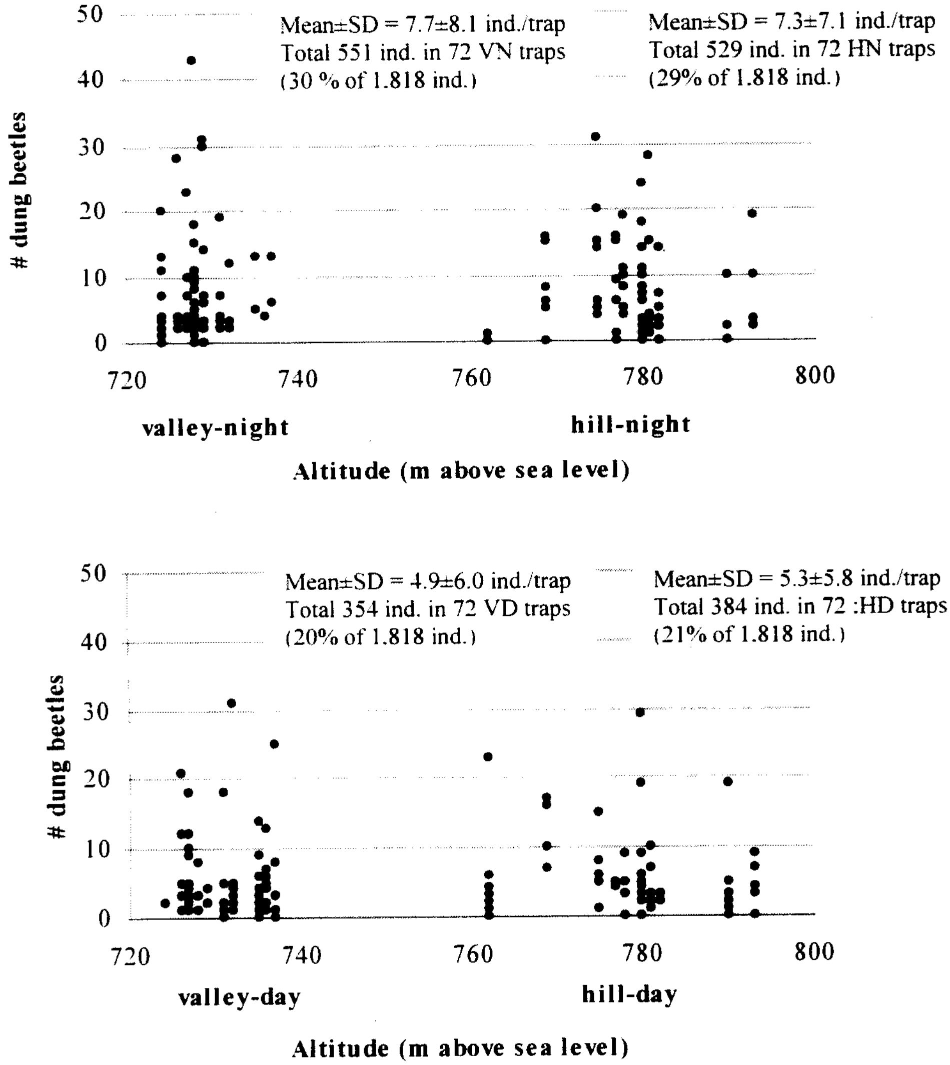


Figure 4-6. Number of dung beetles in each of 288 traps in valley (725–737 m above sea level) and hill (762–793 m asl) during nighttime (upper) and daytime (lower). Each dot represents number of dung beetle from each trap. Many traps caught same numbers of individuals and yielded same dots on graphs.

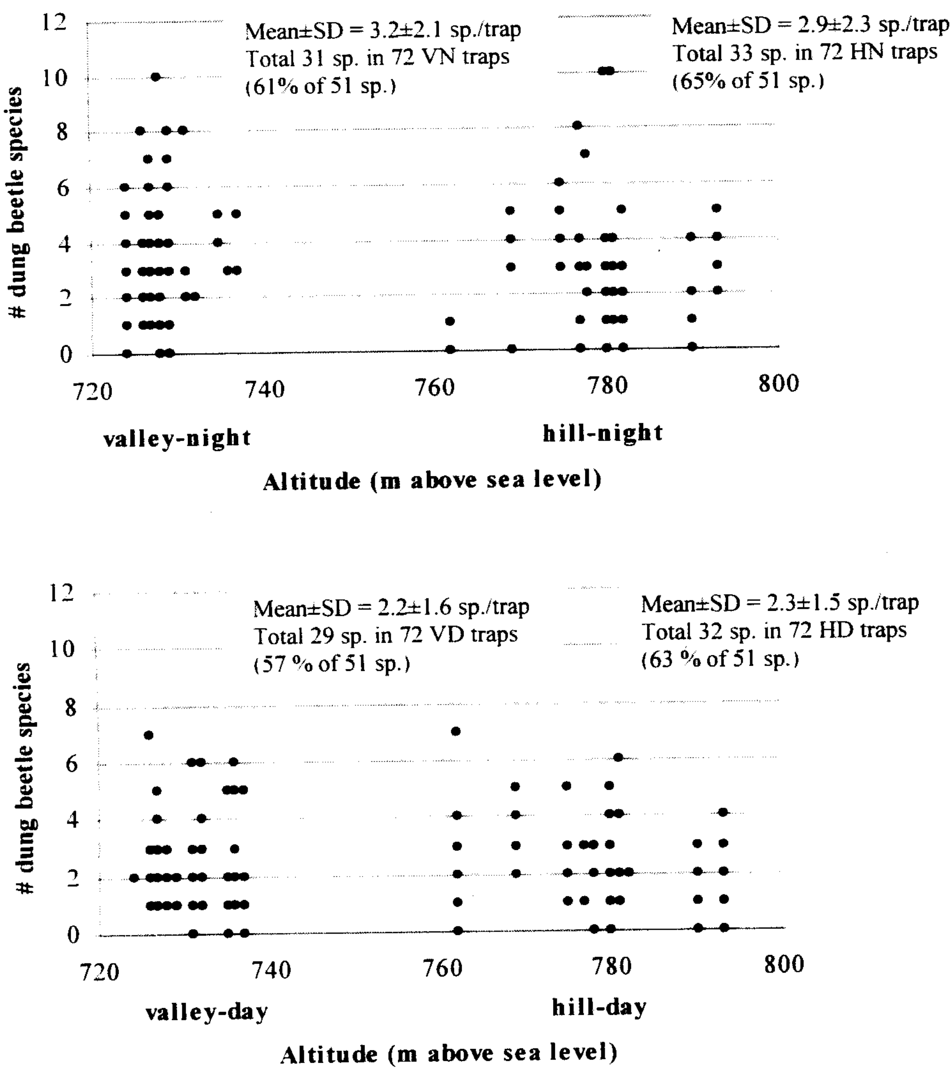


Figure 4-7. Number of dung beetle species in each of 288 traps in valley (725–737 m asl) and hill (762–793 m asl) during nighttime (upper) and daytime (lower). Each dot represents number of dung beetle from each trap. Many traps caught same numbers of individuals and yielded same dots on graphs.

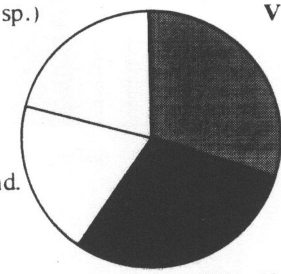
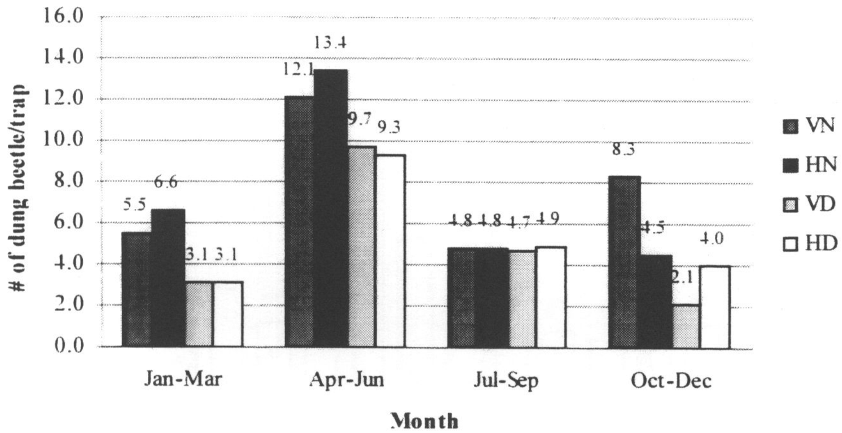


Figure 4-8. Number of individuals and species of dung beetles from each set of 72 traps in different times of day (night and day) and habitats (valley and hill). For all 288 traps with a total of 1.818 individual, there were 30% in 72 VN, 29% in 72 HN, 20% in 72 VD, and 21% in 72 HD traps. Approximately the same percentages of dung beetles species were from each set of 72 traps (60% of 51 species). (ind. = individuals, sp. = species)



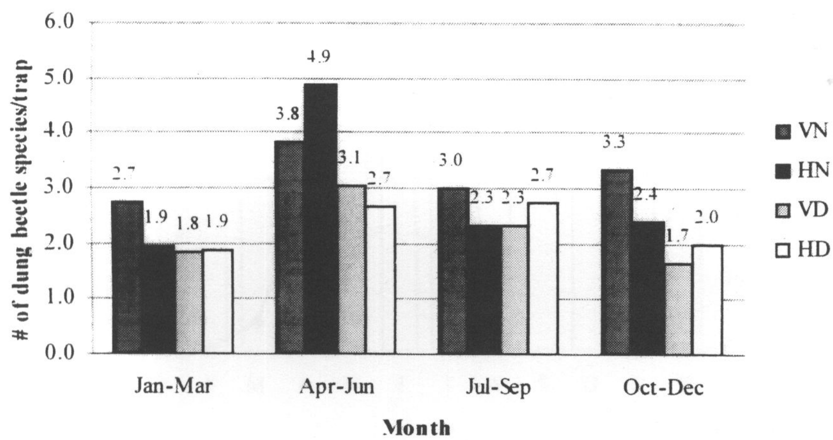


Figure 4-9. Mean number of dung beetle individuals (upper) and species (lower) per trap of different times of day (night and day or N and D) and habitats (valley and hill or V and H) in each period (season) of the year. Both numbers of individuals and species were highest in night traps (VN and HN. the first two columns of each series) set from April to June and relatively high in other periods except from July to September. Numbers of dung beetle individual and species from traps of the same time of day in different habitats of each series (the first two columns of VN & HN and the last two columns of VD & HD) were similar (Appendix 9).

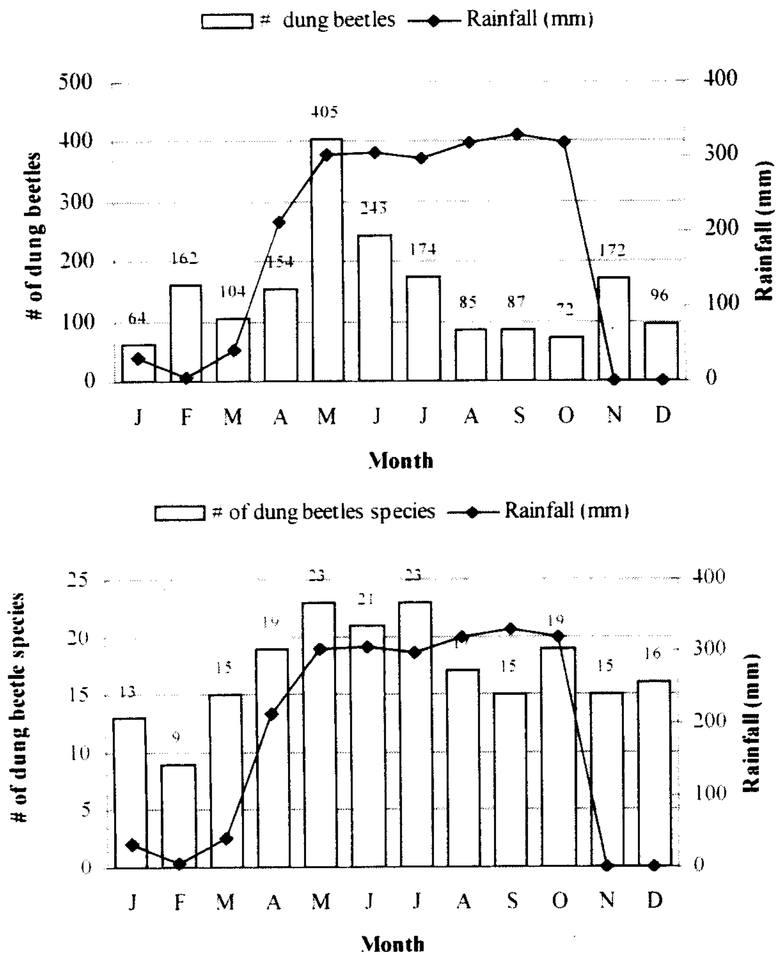


Figure 4-10. Rainfall and number (upper) and species (lower) of dung beetles caught in 24 pitfall traps in each month (1,818 individuals and 51 species in total). Number of individuals and species of dung beetles from pitfall traps in each month were not in the same way. Number of dung beetles was highest in March (405 individuals of 23 species) when it was the start of the rainy season and lower in other months. Their species numbers were relatively low during the warm dry period during the first few months and became higher with increasing average rainfall from March on. The species numbers became highest from May to July with approximately 300 mm average rainfall and were slightly lower from August before the end of the rainy season. During the cool dry period at the end of the year. their species numbers were not very much decreased although the average rainfall were equal to zero.

Table 4-5. P-value of Mann-Whitney U and Kruskal-Wallis tests of dung beetles from traps in different times of day, habitats, seasons. (* indicate that that number of dung beetles was significantly different in that comparison; P-value < 0.05, ** high significantly different; P-value < 0.01, *** very high significantly different; P-value < 0.001)

Comparison of dung beetles	traps compared	# of traps compared	P-value from	
			# of individuals	# of species
Between habitats[1]	V & H	288	0.816	0.813
Between time of day[1]	N & D	288	0.002**	0.001**
Among 4 treatments of habitat & time of day[2]	VN, HN, VD, & HD	288	0.015*	0.006**
Among 4 seasons[2]	S1, S2, S3, & S4	288	0.000***	0.000***
Between 2 seasons[1]	S1 & S2	144	0.000***	0.000***
	S1 & S3	144	0.543	0.159
	S1 & S4	144	0.684	0.617
	S2 & S3	144	0.000***	0.011*
	S2 & S4	144	0.000***	0.000***
	S3 & S4	144	0.323	0.381

Note: 1 = tested by Mann-Whitney U test. 2 = by Kruskal-Wallis test: V = valley. H = hill. N = night. D = day. 4 seasons: S1 = warming dry period (Jan–Mar). S2 = early rainy season (Apr–Jun). S3 = late rainy season (Jul–Sep).and S4 = cool dry peirod (Oct–Dec)

4.3 Post-dispersal of seeds by dung beetles

4.3.1 Seeds in seed removal observations

Depending on fruits eaten by the gibbons, each of the fecal samples collected for each observation contained 1 to 6 species of seeds including small-seeded species (< 3 mm in length) such as *Ficus* spp., *Diplectria barbata*, *Aidia densiflora*, *Anthocephalus chinensis* and an inseparable species, *Ilex chevalieri* (3.8 mm) (Appendix 5). The seeds of *I. chevalieri* aggregated tightly and were difficult to separate from each other and from other fecal materials. Seeds of some small-seeded and inseparable species were in the 29 fecal samples used in observations of post-dispersal of seeds by dung beetles. Not counting these small-seeded and inseparable species, each of 49 samples used in 49 observation times contained 3-30 (larger) seeds (mean=10.2) (Table 4-6).

4.3.2 Dung beetles and their patterns of seed removal

During the 49 observation times, 376 individuals of 24 species (7 genera) were sighted (Table 4-2). According to their nesting behavior, some tunneler dung beetles (genera *Onthophagus* and *Copris*) and ball-rollers (*Synapsis*, *Sisyphus*, and *Catharsius*) removed seeds away from original positions in dung piles (Appendices 10 to 12). The tunnelers, in this study, dug tunnels under or near dung piles and removed pieces of feces into them (Appendix 13). *O. doisuthepensis* was a tunneler species that pushed large seeds (one at each time) or large pieces of dung away immediately after reaching the piles, before finding their burying sites. Other tunnelers with ability of moving large seeds away from dung piles were *Catharsius molossus*, *O. rugulosus*, *O. orientalis*, *O. coracinus*, *Copris cariniceps*, *C. carinicus* and *C. reflexus*. The rollers *Synapsis boonlongi*, *Sisyphus maniti* and *Sisyphus thoracicus* made balls approximately twice their body lengths and rolled them away to bury (Appendix 14). The rollers and tunnelers usually removed seeds together with the feces particularly small and/or inseparable seeds while the small dwellers

(*Aphodius lewisii* and *Aphodius* sp.) did not move seeds and were inside or in the ground (1–2 cm deep) under dung piles.

4.3.3 Seed dispersed by dung beetles

Seeds of small-seeded and larger seeds of other species in gibbon feces were relocated by dung beetles in 33 (or 67%) of 49 observation times (Table 4-6). Of the 33 times. 15 involved removal of small-seeded species. 8 involved removal of large seeds. and 10 both small and large seeds. (Because small-seeded and inseparable species were seen to be removed by tunnelers and rollers by being included in their pieces of dung or dung balls. every observed dung pile that contained these seeds was counted if any beetles relocated fecal matter.) Dung beetles removed 8.3–100% (1–7 of 1–30 seeds in each dung pile. mean = 10.2%) of large seeds in a total of 18 observation times. An average of 12.3 tunnelers and rollers (range 1–43) were observed at each pile. On average. 9% (1–4 individuals) of dung beetles that visited at each dung pile helped in the removal of large seeds. The 16 out of 49 observation times with no seeds removed were with no involved few or no visits by dung beetles (0–6 individual. mean = 1.9). Details of seeds included and removed from each observed dung pile and dung beetles are shown in Table 4-6.

Removal of seeds by dung beetles in different habitats. times of day. and season are summarized in Table 4-7. Seeds in 92 % (12 of 13) the dung piles observed during early rainy season (Apr–Jun) and 100% (12 of 12) during late rainy season (Jul–Sep). in all habitats and times of day were dispersed by dung beetles. There were few (62%. 8 of 13) observations of seed removal during the cool dry season (Oct–Dec) and only 9% (1 of 11 times) during the warm dry period (Jan–Mar). The only observation of removal during the warm dry period was of a *Sisyphus maniti* that rolled a ball of dung containing small fig seeds away. and an *Onthophagus punnaae* that relocated feces with small seeds down under that dung pile.

Of all the large seeds present in 49 observed dung piles. 51 (10.2 % of 502 seeds. 12 of 26 species) were removed by 9% (34 of 376 individuals. 9 of 24 species) of dung beetles attracted to dung piles (Table 4-6. 4-8). Of the all removed seeds. 60% (30 seeds) were removed by 30 individuals (7 species) of tunnelers and

40% (21 seeds) by 4 rollers of 2 species Table 4-8. The three individuals of *Synapsis boonlongi* (26 mm in length) removed the total of 19 seeds (6 species) including large (> 20 mm) *Nephelium melliferum* and *Garcinia benthamii* seeds within their balls during the night in May, September, and November. The one individual of *Catharsius molossus* buried 2 seeds under a dung pile during a night in August. The 14 individuals of *Onthophagus rugulosus* relocated 13 seeds of 7 species: 11 seeds were removed in 7 observation times during the day in May–June and September–November. The remaining 2 seeds (1 *Nephelium melliferum* and 1 *Knema elegans*) were removed at night in April. The 4 individuals of *Onthophagus doisuthepensis* removed 4 seeds of 4 species including 6 mm *Polyosma elongata* and 29 mm *Sandoricum koetjape* seeds. Two seeds were removed from dung piles during daytime in May and August and the other two during the night in December. The 4 individuals of *Copris cariniceps* removed 4 seeds of 3 different species: *Choerospondias axillaris*, *Nephelium melliferum* and *Garcinia benthamii*, all during the night in the late rainy season.

Seeds removed by other dung beetles are shown in Table 4-8. The average number of seeds in each ball of *S. boonlongi* (mean diameter = 57.7 mm, range 55–61) was 6.3 while other dung beetle species transported on average 1 seed/individual. Of the 9 dung beetle species that removed large seeds, tunnelers *Onthophagus doisuthepensis* (4.7mm in length) and *Copris cariniceps* (13 mm), and roller *Catharsius molossus* (27 mm), could take seeds of up to about 30 mm in length (Table 4-8, Figure 4-11). *O. coracinus* (8 mm), *O rugulosus* (11 mm), *O. orientalis* (12 mm), and S*ynapsis boonlongi* could disperse seeds 20–25 mm in length while *Copris carinicus* and *C. reflexus* were seen removing seeds no greater than 10 mm in length.

Besides these beetles, small rollers *Sisyphus maniti* and *S. thoracicus* were seen to remove their dung balls with small seeds (< 3 mm in length) (Table 4-9). Mean ball size of the four *S. maniti* was 8.5 mm diameter (range 8.5–9.4, N = 4) and a dung ball of *S. thoracicus* was 14.5 mm in diameter. *S. maniti* removed many seeds of *Ficus* spp. and *Anthocephalus chinensis* in two observation times during the day of dry season (Jan and Nov), while a *S. thoracicus* relocated a dung ball with fig seeds away from a dung pile during an observation during the day in May.

4.3.4 Dispersal distances and burial depths of the removed seeds

Of all 51 seeds removed by the 9 species of dung beetles, average removal distance was 32.9 cm (range 0–120 cm) and average burial depth was 3.8 cm (range 0–7 cm) (Table 4-8). *Synapsis boonlongi*, *Onthophagus doisuthepensis*, and *Copris reflexus* were the dung beetles that relocated seeds the farthest distances. Three individuals of *Synapsis boonlongi* removed 19 seeds an average of 63.2 cm (range 15–120 cm) away and buried them an average 5.5 cm (range 4–7 cm) under the ground. Four individuals of *O. doisuthepensis* dispersed seeds to an average distance of 53.8 cm (range 30–105 cm) and an average depth of 2.0 cm (range 0–4 cm). Four *C. reflexus* took 4 seeds away 30.5 cm on average (range 5–47 cm) and buried them 2.3 cm on average (range 2–3 cm). The two species of small rollers, *Sisyphus maniti* and *S. thoracicus*, removed seeds of small-seeded species away with their dung balls. Four dung balls of *S. maniti* were removed an average of 38.8 cm (range 5–90, N = 4) and buried at 2.5 cm (range 2–3, N = 2) under the soil. A *S. thoracicus* removed its dung ball 150 cm away from original dung pile but its ball was not seen buried. Figure 4-12 shows distance and burial depths of removed seeds by each dung beetle species.

Considering all tunnelers (8 species) and rollers (3 species) that removed seeds, their average dispersal distance was 35.4 cm (range 0–150, N = 56) and burial depth was 3.7 cm (range 0–7, N = 53) (Tables 4-8 to 4-10). For tunnelers, average removal distance was only 14.9 cm (range 0–105, N = 32), but that of rollers was 62.8 cm (range 0–150, N = 24). Burial depth of all tunnelers (average 2.7 cm, range 0–7, N = 32) was shallower than that of rollers (5.4, range 0–7, N = 23). Mean burial depth by rollers was deeper than that of rollers because only 2 of 32 seeds buried by tunnelers were at 7 cm depth while 15 of 24 seeds buried by rollers (*Synapsis boonlongi*) were at 5–7 cm.

Table 4-6. The 49 observations with details of seeds in observed dung piles, dung beetles sighted, and seeds removed by dung beeltes.

No.	Date	Habitat-Time	SS-IS in observed dung pile					No. and names of other seeds in observed dung pile	Total Seeds	DB sighted			Total	No. and names of DB (No. seeds removed)	Total no. of DB removing seeds	% of DB removing seeds	No. of seeds removed	% of seeds removed
			Ficus spp.	*Ac*	*Ad*	*Db*	*Ic*			T	R	D						
1	22-Jan	VD						3 *Ec*	3				0			no DB	0	0
2	24-Jan	VD	x					4 *Dd*, 5 *Se*, 3 *E*, 2 *Pj*	14				0			no DB	0	0
3	24-Jan	HN	x					4 *Dd*, 5 *Se*, 3 *E*, 2 *Pj*	14				0			no DB	0	0
4	29-Jan	HD	x					2 *Fo*, 2 *Ec*	4	1	1		2			0	SS-IS	SS-IS
5	21-Feb	VD						10 *Dd*, 2 *Ec*, 10 *Tp*	22	1	1		2			0	0	0
6	21-Feb	HN						10 *Dd*, 1 *Ec*, 10 *Tp*	21	1	1		2			0	0	0
7	24-Feb	HD	x					5 *Dd*, 10 *Ec*, 10 *Tp*	25				0			no DB	0	0
8	19-Mar	HD						5 *Dd*, 10 *Tp*	15	1		3	4			0	0	0
9	29-Mar	HD						4 *Tp*	4	2		4	6			0	0	0
10	29-Mar	HN						4 *Tp*	4	3		3	6			0	0	0
11	31-Mar	HD						3 *Dj*	3	1	1		2			0	0	0
12	13-Apr	HN						7 *Tp*, 2 *Ae*	9	10			10	1 *O. rugulosus* (1)	1	10.0	1	11.1
13	14-Apr	VD						7 *Tp*	7	6			6			0	0	0
14	15-Apr	HN						1 *Ke*, 8 *Tp*	9	9			9	1 *O. rugulosus* (1)	1	11.1	1	11.1
15	17-Apr	VD	x					10 *Ke*, 5 *Tp*	15		1	1	2			0	SS-IS	SS-IS
16	18-Apr	HD	x					10 *Ke*, 5 *Tp*	15	7		3	10			0	SS-IS	SS-IS
17	13-May	HD	x					2 *Mc*, 2 *Dg*, 2 *Ke*, 2 *Nm*	8	7	1		8	4 *O. rugulosus* (3), 2 *O. orientalis* (2)	6	75.0	5	62.5
18	13-May	HN	x					2 *Dg*, 2 *Nm*	4	13	1		14	1 *S. boonlongi* (4)	1	7.1	4	100.0
19	21-May	HD						5 *Nm*	5	17			17	1 *O. doisuthepensis* (1)	1	5.9	1	20.0
20	22-May	HD						5 *Nm*	5	14			14	2 *O. rugulosus* (1)	2	14.3	1	20.0
21	23-May	HN						5 *Nm*	5	18			18	1 *O. rugulosus* (1)	1	5.6	1	20.0
22	16-Jun	HD						2 *U* sp., 2 *Sk*, 5 *Co*, 2 *Nm*	11	18			18	2 *O. rugulosus* (3), 1 *O. orientalis* (1)	3	16.7	4	36.4
23	17-Jun	HD						2 *U* sp., 2 *Sk*, 5 *Co*, 2 *Nm*	11	15		4	19	1 *O. rugulosus* (1)	1	5.3	1	9.1
24	20-Jun	HN				x		10 *Se*, 2 *Nm*, 1 *Sc*	13	43			43	3 *C. reflexus* (4)	3	7.0	4	30.8
25	18-Jul	HN	x				x	5 *Gb*	5	16			16	1 *C. cariniceps* (1), 1 *O. coracinus* (1)	2	12.5	2	40.0

Note: VD = valley-day, HN = hill-night, HD = hill-day, DB = dung beetle, T = Tunneler, R = Roller, D = Dweller, ss-is = small-seeded and/or inseparable species, see seed codes in Appendix I, x indicates presence of SS-IS in observed dung piles

Table 4-6. The 49 observations with details of seeds in observed dung piles, dung beetles sighted, and seeds removed by dung beeltes. Cont.

No.	Date	Habitat-Time	SS-IS in observed dung pile					No. and names of other seeds in observed dung pile	Total Seeds	DB sighted			Total	No. and names of DB (No. seeds removed)	Total no. of DB removing seeds	% of DB removing seeds	No. of seeds removed	% of seeds removed
			Ficus spp.	*Ac*	*Ad*	*Db*	*Ic*			T	R	D						
26	19-Jul	HD	x				x	5 *Gb*	5	4			4			0	SS-IS	SS-IS
27	24-Jul	HD	x	x	x	x		2 *Ca*, 5 *Sk*	7	33			33			0	SS-IS	SS-IS
28	25-Jul	HD	x	x	x	x		2 *Ca*, 5 *Sk*	7	4		2	6			0	SS-IS	SS-IS
29	16-Aug	HD	x					3 *Sk*, 5 *Acu*, 20 Unk3	28	3			3			0	SS-IS	SS-IS
30	16-Aug	HN	x					2 *Gb*, 3 Sk, 5 *Acu*, 20 Unk3	30	4	1		5	2 *C. cariniceps* (2), 1 *C. molossus* (2)	3	60.0	4	13.3
31	18-Aug	HD			x	x		3 *Bi*, 3 *Sk*, 3 *Acu*	9	9			9	1 *O. doisuthepensis* (1)	1	11.1	1	11.1
32	20-Sep	VD	x	x				5 *Acu*	5	9			9	1 *C. carinicus* (1), 1 *O. rugulosus* (1)	2	22.2	2	40.0
33	21-Sep	HD		x		x		5 *Acu*	5	6			6			0	SS-IS	SS-IS
34	21-Sep	HN		x		x		5 *Acu*	5	2			2			0	SS-IS	SS-IS
35	25-Sep	HD			x		x	2 *Ca*, 5 *Gb*, 5 *Acu*, 5 *Aca*	17	2			2			0	SS-IS	SS-IS
36	27-Sep	HN			x			2 *Ca*, 5 *Gb*, 5 *Acu*	12	4	1		5	1 *C. cariniceps* (1), 1 *S. boonlongi* (8)	2	40.0	9	75.0
37	19-Oct	VD						2 *Ca*, 4 *Ec*, 4 *Pe*, 4 *Co*, 4 *Gl*	18	2			2			0	0	0
38	19-Oct	HN						2 *Ca*, 4 *Ec*, 4 *Pe*, 4 *Co*, 4 *Gl*	18	2			2			0	0	0
39	26-Oct	HD						2 *Ca*, 10 *Uf*, 2 *Uh*, 1 *Gb*, 5 *Acu*	20	5			5			0	0	0
40	26-Oct	HN						2 *Ca*, 10 *Uf*, 2 *Uh*, 1 *Gb*, 5 *Acu*	20	3			3			0	0	0
41	16-Nov	HN	x					4 *Ca*, 5 *Pe*	9	5	1		6	1 *S. boonlongi* (7)	1	16.7	7	77.8
42	19-Nov	VD	x					4 *Ca*, 5 *Pe*, 3 *Gl*	12	1		1	2	1 *O. rugulosus* (1)	1	50.0	1	8.3
43	20-Nov	VD						5 *Pe*, 5 *Co*, 3 *Gl*	13	1			1			0	0	0
44	23-Nov	HD		x						3	1	2	6			0	SS-IS	SS-IS
45	24-Nov	VD	x	x						7		4	11			0	SS-IS	SS-IS
46	18-Dec	HN	x					3 *Pe*, 3 *Gl*	6	3			3	2 *O. doisuthepensis* (2)	2	66.7	2	33.3
47	20-Dec	HD	x					2 *Fo*, 3 *Gl*	5	3			3			0	SS-IS	SS-IS
48	25-Dec	HD	x	x						4			4			0	SS-IS	SS-IS
49	28-Dec	VD		x						13		3	16			0	SS-IS	SS-IS
	Total							**26 species**	**502**	**335**	**11**	**30**	**376**	**34 dung beetles (51 seeds)**	**34**	**9.0**	**51**	**10.2**

Note: VD = valley-day, HN = hill-night, HD = hill-day, DB = dung beetle, T = Tunneler, R = Roller, D = Dweller, ss-is = small-seeded and/or inseparable species, see seed codes in Appendix 1, x indicates presence of SS-IS in observed dung piles

Table 4-7. Number of observation times of seed removal by dung beetles in different seasons, habitats, and times of day. Numbers of observations in which seeds (including small-seeded and inseparable species) were relocated by dung beetles are in parentheses. (obs. = observation, HN = hill-night, HD = hill-day, and VD = valley-day).

Month	Season	No. of observation times (No. with seeds removal)			Total no. of observation times	No. of observation times with seed removal
		HN	HD	VD		
Jan–Mar	warming dry	3 (0)	5 (1)	3 (0)	11	1
Apr–Jun	early rainy	5 (5)	6 (6)	2 (1)	13	12
Jul–Sep	late rainy	4 (4)	7 (7)	1 (1)	12	12
Oct–Dec	cool dry	4 (2)	4 (3)	5 (3)	13	8
	Total	**16 (11)**	**22 (17)**	**11 (5)**	**49**	**33**

Table 4-8. The 51 large seeds removed by each of the 9 species of dung beetles. Numbers in parentheses represent distance and depth of each seed relocated and buried by one or a pair of dung beetles. In each column of each dung beetle species, the same series of numbers for example (77,5) (77,5) of the same date indicate locations of seeds removed by the same dung beetle.

Seed	Dung beetle	*Synapsis boonlongi**	*Catharsius molossus**	*Onthophagus rugulosus*	*O. orientalis*
	length±SD (mm)	26.0±1.5	26.9±0.1	11.1±0.8	12.4±1.1
Choerospondias axillaris	17.6±2.1	27 Sep-HN (77.5), (77.5) 16 Nov-HN (15.7), (15.7), (15.7)			
Melodinus cambodiensis	10.8±0.9			13 May-HD, (0,1), (0,4)	
Polyosma elongata	6.2±1.5	16 Nov-HN (15.7), (15.7), (15.7), (15.7)			
Garcinia benthamii	23.0±5.3	27 Sep-HN (77.5), (77.5)			
Sandoricum koetjape	29.5±3.2		16 Aug-HN (0,7), (0,7)		
Diploclisia glaucescens	16.4±1.3	13 May-HN (120,4), (120,4)			
Knema elegans	20.2±1.8			15 Apr-HN (4,3) 13 May-HD 2 ind. (0,5)	
Cleistocalyx operculata	7.0±1.2			16 Jun-HD (0,3), (0,3) 17 Jun-HD (35,2)	
Nephelium melliferum	20.4±4.4	13 May-HN (120,4), (120,4)		22 May-HD 2 ind (8,4) 23 May-HN (6,0) 16 Jun-HD (12,0)	13 May-HD (0,4), (10,0) 16 Jun-HD (12,0)
Grewia laevigata	8.6±0.8			19 Nov-VD (0,4)	
Aphananthe cuspidata	10.3±0.7	27Sep-HN (77.5), (77.5), (77.5), (77.5)		20 Sep-VD (20,2)	
Tetrastigma densiflora	8.2±1.2			13 Apr-HN (8,2)	
	Total dung beetles	**3**	**1**	**14**	**3**
	Total seeds	**19**	**2**	**13**	**3**

Note: * = roller, HN = hill-night, VD = valley-day, HD = hill-day, ind. = individual

Table 4-8. The 51 large seeds removed by each of the 9 species of dung beetles. Numbers in parentheses represent distance and depth of each seed relocated and buried by one or a pair of dung beetles. In each column of each dung beetle species, the same series of numbers for example (77,5) (77,5) of the same date indicate locations of seeds removed by the same dung beetle. (Cont.)

Seed	Dung beetle	*O. doisuthepensis*	*O. coracinus*	*Copris cariniceps*	*C. carinicus*	*C. reflexus*
	length±SD (mm)	**4.7±0.4**	**8.3±0.4**	**12.8±0.6**	**15.2±1.4**	**10.0±0.8**
Choerospondias axillaris	**17.6±2.1**			27 Sep-HN (0,3)		
Melodinus cambodiensis	**10.8±0.9**					
Polyosma elongata	**6.2±1.5**	18 Dec-HN (40,4)				
Garcinia benthamii	**23.0±5.3**		18 Jul-HN (0,1)	18 Jul-HN (26,3) 16 Aug-HN (0,4)		
Sandoricum koetjape	**29.5±3.2**	18 Aug-HD (30,0)		16 Aug-HN (0,3)		
Diploclisia glaucescens	**16.4±1.3**					
Knema elegans	**20.2±1.8**					
Cleistocalyx operculata	**7.0±1.2**					20 Jun-HN (35,2), (35,2), (5,2), (47,3)
Nephelium melliferum	**20.4±4.4**	21 May-HD (40,2)				
Grewia laevigata	**8.6±0.8**	18 Dec-HN (105,3)				
Aphananthe cuspidata	**10.3±0.7**				20 Sep-VD (0,2)	
Tetrastigma densiflora	**8.2±1.2**					
	Total dung beetles	**4**	**1**	**4**	**1**	**3**
	Total seeds	**4**	**1**	**4**	**1**	**4**

Note: * = roller, HN = hill-night, VD = valley-day, HD = hill-day, ind. = individual

Table 4-9. Small roller dung beetles sighted during observations, seeds removed by them, and removal distances and burial depths of their dung balls.

Month	Habitat & Time	Roller	Seeds included in dung ball	Removal distance (cm)	Burial depth (cm)
Jan	HD	Sisyphus maniti	fig	20	not seen*
Feb	VD	S. maniti	none (no dung ball)		
Feb	HN	S. maniti	none (no SS-IS)	40	not seen*
Apr	VD	S. maniti	fig	5	2
Nov	HD	S. maniti	*Anthocephalus chinensis*	90	3
Mar	HD	S. thoracicus	none (no dung ball)		
May	HD	S. thoracicus	fig	150	not seen*

Note: HD = hill-day. VD = valley-day. HN = hill-night. SS-IS = seeds of small-seeded and/or inseparable species.
* = not seen until the end of observation

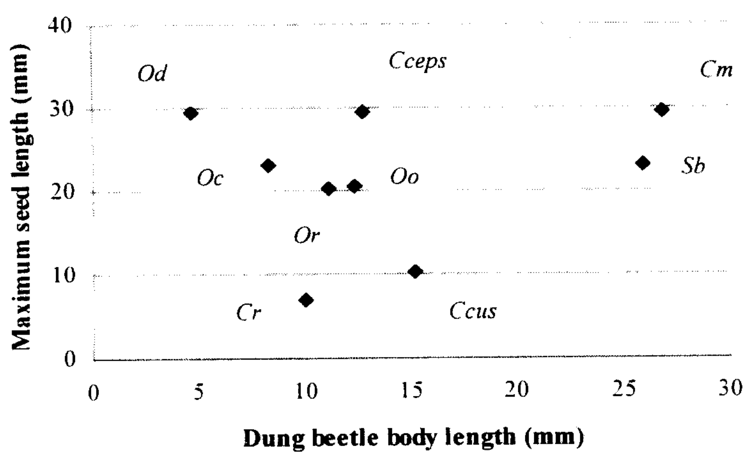


Figure 4-11. Relationship between dung beetle body length and maximum length of seeds removed by those beetles. Of all the 9 species that removed larger seeds, dung beetles from < 5 mm body length could removed seeds > 20 mm in length. The dot at the top corner on the left was of *Onthophagus doisuthepensis* (*Od*) which were seen to push a large seed of *Sandoricum koetjape*. Various sizes of dung beetles (from < 10 to > 25 mm) of *O. coracinus* (*Oc*), *O. rugulosus* (*Or*), *O. orientalis* (*Oo*), and *Synapsis boonlongi* (*Sb*) could remove seeds 20–25 mm in length. The other two lower dots represent the two dung beetle species, *Copris reflexus* (*Cr*) and *C. carinicus* (*Ccus*) that removed seeds ≤ 10 mm in length.

Table 4-10. Seed removal distances and depths of each species of dung beetles with average distance and depth of removed seeds.

Dung beetle	Functional group	Range of seed removal distance (mm)	Range of seed burial depth (mm)	N	Av. distance (cm)	Av. depth (cm)
Onthophagus doisuthepensis	T	30–105	0–4	4	53.8	2.0
O. rugulosus	T	0–35	0–5	13	7.2	2.5
O. orientalis	T	0–12	0–4	3	7.3	1.3
O. coracinus	T	0	1	1	0	1.0
Copris reflexus	T	5–47	2–3	4	30.5	2.3
C. cariniceps	T	0–26	3–4	1	6.5	3.3
C. carinicus	T	0	2	4	0	2.0
Catharsius molossus	R	0	7	2	0	7.0
	All T	**0–105**	**0–7**	**32**	**14.9**	**2.7**
Synapsis boonlongi	R	15–120	4–7	19	63.2	5.5
Sisyphus maniti	R	5–90	2–3	4	38.8	2.5 (N =2)
Sisyphus thoracicus	R	150	–	1	150	–
	All R	**5–150**	**0–7**	**24**	**62.8**	**5.2 (N =21)**
	All T & R	**5–150**	**0–7**	**56**	**35.4**	**3.7 (N = 53)**

Note: T = tunneler. R = roller

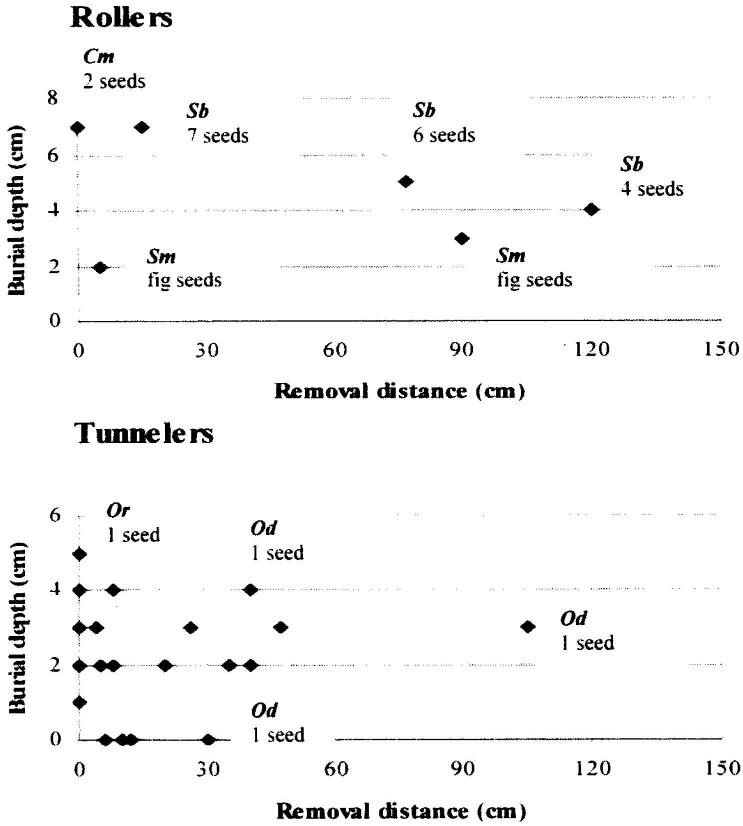


Figure 4-12. Removal distances and burial depths of seeds removed by rollers (upper) and tunnelers (lower). In three different observation times, three individuals of large rollers, *Synapsis boonlongi* (*Sb*) rolled their 60-mm dung balls with, on average, 6.3 seed at up to 120 cm (range 5–120, N = 3, mean = 63.2 cm) away from original position. They buried their balls 4–7 cm under the soil (mean = 5.5 cm). The other large roller, *Catharsius molossus* (*Cm*) was found with 2 seeds at 7 cm under a dung pile. A *Sisyphus maniti* (*Sm*) rolled ball 15 cm away and buried it at 2 cm depth while the other *Sm* took its ball 90 cm away and buried it at 3 cm depth. Dung balls of these *Sm* were with many fig and *Anthocephalus chinensis* seeds. *Sisyphus thoracicus* the other small roller, rolled a ball 150 cm away but was did not bury it. Among tunnelers, the farthest distance (105 cm) of removed seeds was by *Onthophagus doisuthepensis* (*Od*). This seed was buried at 3 cm depth. Other *Od* took seed away 40 cm and buried it at 4 cm depth. The last *Od* pushed a large seed of *Sandoricum koetjape* 30 cm away without burying it. The deepest burial depth (5 cm) made by tunneler was of a pair *O. rugulosus* with a single seed of *Knema elegans* in their tunnel under a dung pile. Other tunnelers dispersed seeds at < 50 cm away from dung piles and buied them ≤ 4 cm under the ground.

CHAPTER V

DISCUSSION

6.1 White-handed gibbons and seed dispersal

The white-handed gibbons in Mo Singto study area had a beneficial effect on dispersal of seeds of many plant species within their home range. In this study, seeds were found in every one of the 157 fecal samples collected during the year 2000. In total, these gibbons dispersed at least 42 seed species (Table 4-1) through those piles (58 species in Brockelman & Charoenchai, 1999), including fig seeds, throughout the year. However, more than 42 species were thought to be dispersed because there were 20 different species of fig fruits within the gibbons' home range which could not be identified to species by observation of the seeds in gibbon dung. Those then were counted as a single collective species if their seeds were seen in dung piles. In equal amounts of dung (approx. 800g) collected within about one week in every month, the number of seeds were relatively high (> 500 seeds) from July to September (during late rainy season) and in February. Bartlett (1999) reported that the peak of feeding time of non-fig fruits by these gibbons, in the year 1994, was during June and July (approx. 80% of the diet, which included non-fig and fig fruits, leaves, buds, flowers, and insects). Figs made up an average of 19% of all species in the diet per month but were highest (approx. 50% of their diet) in November and December due to the scarcity of other fruits. Both non-fig and fig fruits made up, on average, 60% of their diet that year.

The average number of seeds found per fecal sample, excluding figs and other small seeds, was 24 (3,809 seeds/157 samples) and was similar to the 25 seeds from the study of seed dispersal by gibbon group A by Whitington (1990). An individual of white-handed gibbon in Mo Singto defecates 5–8 times/day (Whitington, 1990; Touranont, 2000; Vimuktayon, 2001), then the 3–4 gibbons (during this study) dispersed 360–770 seeds of different species per day throughout their 25-ha home range. Fruit with seeds $\geq$ 30 mm in length were swallowed by these gibbons but those with seeds < 9 mm in length made up 70% of 3,809 seeds recovered from the 157 samples of feces.

6.2 Dung beetles from Mo Singto

Feces of group A gibbons attracted 53 species of 9 genera of dung beetles (45 tunneler, 6 roller and 2 dweller species, Table 4-2). The species richness of these dung beetles was similar to that reported from other habitats of tropical savanna within elephant dung (50.4±3.4 species) and other tropical primary forests rich in mammals (48.7±2.7 species, Hanski & Cambefort, 1991) which were dominated by tunnelers and rollers. The species diversity of dung beetles depends on species and species richness of mammals, dung type, soil moisture and texture, and vegetation cover (Hanski & Cambefort, 1991; Vulinec, 2002) and hence may indicate the quality of their tropical primary forest habitats.

Among the 53 species caught in Mo Singto, many of the same species have also been reported from previous studies in agricultural areas in the Northeast, including *Catharsius molossus*, *Copris reflexus*, *Onthophagus orientalis* and *O. tricornis*. These species that were found in both forest and cultivated area tended have broader niches including feeding on more diverse food types. *C. molossus* fed on feces of many animals, including buffalo and elephant, *C. reflexus* fed on cow, buffalo, pig, gaur and elephant dung, *O. orientalis* on cow, buffalo, monkey and pig dung, and *O. tricornis* was attracted to elephant, wild cat, and pig dung (Hanboonsong *et al.*, 1999; Pimpasalee, 2000). Ten (except *Onthophagus proletarius*) out of eleven species of dung beetles found in carcasses in Khao Yai National Park, studied by Areekul (2000), were also attracted to gibbon dung. They were *Catharsius molossus, Copris reflexus, Synapsis boonlongi, Onthophagus apilularius, O. lindaae, O. penicillatus, O. phanaeiformis, O. rudis, O. tricornis,* and *O. vividus*. However, some species of dung beetles attracted to gibbon feces in this study are still unknown, or are new records for the park including seven species of genus *Onthophagus* and the one of *Aphodius*.

Dung beetles of each guild of functional group have specific strategies for competing for food and space. Relatively high inter- and intraspecific competition among tunnelers beneath each dung pile are mainly for space. Some tunneler species reduce competition by pushing fragments or pieces of dung horizontally on the ground before burying them. *Phanaeus howdeni*, *P. pyrois* and *Sulcophanaeus cupricollis* from Mexico are examples of this type of beetle as they often constructed their burrows 5–20 cm away from dung piles (Hanski & Cambefort, 1991). In Mo Singto, *Onthophagus doisuthepensis*, *O. rugulosus* and *Copris reflexus* might be tunnelers that reduce competition for space by pushing dung short distances away before digging their burrows. Rollers have adapted to avoid or reduce competition with dung beetles of other guilds by making dung into spherical balls which they can more easily transport longer distances away before burying them. However, this process might increase the risk of predation. Most dweller species complete their life cycles in dung piles, so they compete for both food and space in them. These beetles therefore prefer larger dung piles than are needed for their development process. As documented from tropical regions in previous studies, dwellers, in terms of number of species, were less common than tunnelers and rollers at Mo Singto.

The size, numbers, and species of dung beetles can be related to dung size (Peck & Howden, 1984). In Panama, pitfall traps baited with different amounts (2 and 200 ml) of human dung attracted different dung beetles. Traps with larger baits captured 3 times more dung beetles with larger mean body lengths (13.1 mm) than traps using small baits (7.5 mm average, range 3–28 mm). A total of 31 species were caught in those traps (22 species from each type of trap). Six species of those beetles were found only in traps with smaller baits and six different species were found only in traps with larger ones. Dung beetles in Mo Singto, with 8.4 mm mean body length (range 2.4–27.0 mm, might relate to the size of gibbon dung (30 g) baited in each trap. Among 1,818 dung beetles caught in 288 traps, only 13 individuals (one *Catharsius molossus* and twelve *Synapsis boonlongi*) of large beetles (> 25 mm) were found. The other species ranged from 2.4 (*Aphodius* sp.) to 18.3 mm (*Onthophagus balthasari*). When larger size of dung was used, higher numbers of individual and species of dung beetles including large rollers and tunnelers tended to be found.

Numbers of individual and species of dung beetles caught in the traps were significantly different in different times of day and different seasons, but hill top and valley habitats attracted similar numbers (Figure 4-8). From all traps, 60% (1,080 individuals) of all dung beetles was caught in traps set during nighttime while 40% (738 individuals) were caught in traps during daytime. This was approximately the same proportion as caught in tropical forest of Africa (75%) and Panama (60%) (Hanski & Cambefort, 1991). Within the home range of this gibbon group, there are other mammals including nocturnal species (rabbits, porcupines, binturongs, deers, elephants, bears, civets, leopards, and tigers) sharing the habitat. It was possible that these other mammals also attracted high numbers of dung beetles, particularly generalists that have adapted to feed on a variety of dung, carrion and rotten fruit. In addition, during the night with relatively high moisture, the soil tended to be softer for them to dig their burrows and construct their nests. Hence, pitfall traps set during the night attracted more dung beetles. However, dung beetles that are specialists on gibbon dung might appear mostly during daytime.

Dung beetles of many species were caught in both day and night, and in both habitats. This might be because these beetles were the most common species in these areas and have broad niches, while others have specific activity periods. Some beetles species in Africa, for example, were reported to be active during "dusk and dawn", following the activity period of the elephants there (Hanski & Cambefort, 1991). In the Mo Singto plot, wild dogs are an example of mammals that forage during dusk and dawn (Srikosamatara & Hansel, 1996). Therefore, if these dung beetles feed on dung of these animals, they might be caught in both traps set during day and night because their foraging period overlaps during both day and night. In addition, because nighttime was slightly longer than daytime in the cool dry season, traps set during the day in this season might also have caught several nocturnal species. Thus, it is unclear if many species of dung beetles captured in traps at different times of day were nocturnal or diurnal. In previous studies, large tunnelers have been reported to be primarily nocturnal while some species of small tunnelers were diurnal and some were nocturnal. It was reported that dung beetles of genus *Copris* were nocturnal while some species of genus *Onthophagus* were diurnal and some were nocturnal. Most rollers, such as genus *Sisyphus*, have been reported to be diurnal while some species of dweller dung beetles of genus *Aphodius* were diurnal and some were nocturnal (Hanski & Cambefort, 1991). In Mo Singto, some tunnelers, including *Copris cariniceps*, *C. carinicus*, *C. reflexus*, *O. lindaae* and *O. punnaae*, were collected in higher numbers at night in both habitats. The large rollers *Catharsius molossus* and *Synapsis boonlongi* tended to be nocturnal species while *Sisyphus maniti* and *S. thoracicus* tended to be diurnal, as in previous studies (Hanski & Cambefort, 1991). These diurnal species including genus *Sisyphus* might be more specific to gibbon dung than nocturnal or other species with broad niches, but many species, particularly those large beetles of genera *Onthophagus*, *Copris*, and *Synapsis*, were found during day and night in high numbers, and with their ability to move more dung, may play an important roles in dispersing seeds from original sites.

In different habitats, soil moisture was expected to be higher in valley (725–737 m asl) than hill (762–793 m asl) areas because water naturally runs to lower areas and, the valley area in Mo Singto plot contained small brooks. The result that numbers of dung beetles from different areas were not significantly different might have been effected by the locations selected for traps. In addition, it might depend on distribution of mammals there including gibbons. The gibbon group A, the main mammals that defecated daily within the study area, might use the entire area throughout their home range. During the day, they spent about each half of their time in valley and half in hill areas (Touranont, 2000) and they changed their sleeping trees each night. Another possible interpretation is that the altitudes of those areas were not much different (only about 70 m difference) and the soil did not differ sufficiently between hill and valley.

Rainfall is a key factor that influences the seasonality and activity of dung beetles. Many species emerge after the first rain and take advantage of the soft soil for burrowing and constructing their nests. Moreover, in drier periods, dung dries quicker and become less attractive for dung beetles. The numbers of these beetles then is relatively high during the rainy season. Although the activities of most dung beetles depended on the pattern of rainfall, some species were restricted to the dry season (Hanski & Cambefort, 1991). The pitfall traps set in Mo Singto plot captured different numbers of dung beetles in different seasons. Many species occurred throughout the year but increased in the rainy season, especially at the beginning.

After May (the first month, with about 300 mm rainfall) with highest number of dung beetles, rainfall was still high until October (Figure 4-10) but the numbers of those beetles were decreasing and slightly increased again after in November after the late rainy period. This might be because, during the continuous rainy months, dung piles are more quickly washed out by rain and hence release less scent for detection by dung beetles, and feces in rain itself might less suitable for dung beetles to process. However, 85% (28 of 33 individuals) of the small roller *Sisyphus maniti* were captured in the drier seasons (Jan–Mar and Oct–Dec) while 15% (6 individuals) were from the wet season (Apr–Sep) during the year 2000.

6.3 Post-dispersal of seeds by dung beetles

In Mo Singto, tunneler and roller beetles, except the dweller genus *Aphodius*, were capable of dispersing seeds of many different sizes, especially small seeds. From 49 observations of seed dispersal, a total of 376 dung beetles were seen and 10% the seeds (including 12 of 26 species, not including large numbers of those of small-seeded species) were removed by only 9% of those beetles. Even though only 10% of seeds were removed from dung piles, there were no other invertebrates seen to disperse large seeds during those observations except for an ant that picked up and carried a small fig seed away. Many species of ants are known as seed predators but some species that cache seeds (Roberts & Heithaus, 1986) may, the same as dung beetles, accidentally help disperse seeds and reduce mortality from desiccation and predation. Unlike ants, dung beetles do not feed on seeds and their removal of dung might be evolutionarily beneficial to seeds in feces of mammals that they rely on. The 10% of seeds removed by dung beetles were large seeds but of small ones taken by them might be up to 100% if feces was all removed. Andresen (1999) estimated that there were about 100 seeds of *Ficus* spp./g feces, when present in that of spider and howler monkey in a Peruvian forest. Therefore dung beetles possibly transport thousands of seeds of small-seeded species from each 30-g dung pile used in observations.

In addition, because the activities of dung beetles during removal of seeds were observed for only a limited time (each about 8–12 hours), only some parts of seed dispersal were seen. Generally, most gibbon dung piles were defecated during daytime in the forest and were partly used by dung beetles active during that period, and the remaining dung might be used up by the different species active during the night. Further studies of post-dispersal of seeds by dung beetles may be done through longer period of observations to find out how long it will take for most dung piles and seeds to be all removed by dung beetles.

A large roller, *Synapsis boonlongi* (26 mm in length), was an important species that removed large dung balls (60 mm in diameter) containing many small and large seeds. Of all 51 large seeds removed in 49 observations, 19 were included in dung balls moved by only three individuals of this species while 31 other tunnelers of 8 species removed only 1 seed on average each time, directly under the dung pile or only a shorter distance away. Also, *S. boonlongi* were found in all months of the year, in both habitats and during night and day (but most dominant during the night) (Appendices 7 to 9). They were attracted in relatively low numbers to each pile of 30 g feces (12 individuals from 288 traps and 2 individuals from 49 observation times). Because larger dung piles attract higher numbers of different species and large sizes of dung beetles (Peck & Howden, 1984), many gibbon droppings more than 30 g (60–120 g of each pile collected during this study) in the Mo Singto plot should attract higher numbers of this large roller and other species which should remove higher numbers of large seeds.

Some species such as *O. doisuthepensis* and *Copris reflexus* were beneficial to removal of both small and large seeds (Table 4-8). Many other species including tunnelers and small rollers might be important in dispersal of large numbers of small seeds during the whole year. All of the dung beetles including small dwellers reduced the quantity of dung by removing it or feeding directly in it thus positively help decreasing olfactory cue of dung detected by seed predators.

During observations, seeds in dung piles were not all removed including because 1) there were no or few visits by dung beetles (especially during the period of the cool dry season from Jan to Mar and 2) dung piles contained only large seeds particularly in piles with relatively low competition and the dung beetles attracted to them (especially small dung beetles) tended to transport small pieces of dung and discarded large seeds, and 3) dung piles was in the rain and was quickly washed out and no longer attractive and suitable for dung beetles. Anyway, although there were only large seeds and if the piles were visited by dung beetle that were capable of removing them away, post-dispersal of seeds could occur.

The rate of seed burial depended on seed and dung beetle sizes that it was negatively correlated with seed size and positively correlated with dung beetle size (Shepherd & Chapman, 1998; Feer, 1999; Andresen 1999). In Mo Singto, the large roller *Synapsis boonlongi* (26 mm), for example, included on average 6.3 large and many small seeds in its 60-mm diameter ball, which it rolled more than a meter away to bury at 7 cm depth. The small rollers *Sisyphus maniti* (4 mm) and *S. thoracicus* (7 mm) could also roll their balls away > 1 m but with only small seeds in their balls which were < 2-cm diameter, and buried them at shallow depths (1–2 cm) under the ground. Other tunneler beetles species that removed large seeds were no larger than 15 mm and could remove and bury only a single or two seeds at each time but buried at shallower depths when compared with those buried by large *C. molossus*. *Onthophagus doisuthepensis* (5 mm) was the smallest tunneler species that removed largest seeds away > 50 cm on average but an individual of the species left a large seed of *Sandoricum koetjape* on the ground after pushing it 30 cm away from the original position. This might be because it was too large to be buried.

At shallow burial depths, seeds tended to have higher germination rates. Andresen (2001) studied germination of seeds at 5 and 10 cm depths and found that higher percent (49%) of the seeds germinated at the shallower burial depth while fewer seeds (11%) germinated at the deeper position. The burial depths of dung beetles < 15 mm were found no deeper than 3 cm while those of large beetles > 25 mm were found from 5 to 7 cm under the soil. The burial depths made by ball-rollers just allow them to cover their balls in the soil because they have relatively thin forelegs when compared with tunnelers. They were not good at digging deep burrows. These results agreed with Hanski and Cambefort (1991) who found that rollers dig shallow burrows to bury their balls while tunnelers make relatively deep holes. Shepherd & Chapman (1998) suggested that larger seeds are more capable to germinate from greater depth than smaller ones. From this study, 2 seeds of rambutan (*Nephelium melliferum*) buried at 7 cm depth under the soil by a *Synapsis boonlongi* in May were seen germinating in June, 2000. Shepherd & Chapman (1998) also found that seeds buried by dung beetles at 1- and 3-cm depth had high probability of germinating and also escaped from seed predators such as rodents. With the average burial distance of 33 cm (range 0–20) and depth of 3.8 cm (range 0–7), those seeds removed by dung beetles in this study seemed to have the benefit of being less clumped in dung piles and escaping from seed predators. However, further studies for optimum burial depth of each seed species by each dung beetle species are needed.

CHAPTER VI

CONCLUSIONS

1. Through the examination of 159 collected fecal samples, it was found that during the year 2000, the white-handed gibbons in Mo Singto plot, Khao Yai National Park, dispersed seeds of trees and woody climbers. The seeds were of 42 species of 27 families varying in lengths from < 1 mm to 30 mm.

2. A total of 53 species of 9 genera of dung beetles (Scarabaeidae) were attracted to feces of the gibbons. They were classified into 3 functional groups. Forty-six species (86%) of 5 genera were tunnelers, 5 species (3%) of 3 genera were ball-rollers, and 2 species (11%) of a genus were dwellers. Their body lengths ranged from 2 to 27 mm.

3. The numbers of dung beetles caught were significantly different according to time of the day and month or season. They were more abundant at night and during April–June, the early rainy season. With respect to different habitats, valley (762–793 m asl) and hill (725–737 m asl), the numbers of dung beetles caught in pitfall traps were not significantly different.

4. All tunneler and ball-roller dung beetles helped in secondary or post seed dispersal, particularly small-seeded and inseparable species because they removed fecal materials and seeds from original locations. Dwellers did not remove any seeds. The eight species of tunnelers that removed large plant seeds were *Catharsius molossus*, *Onthophagus rugulosus*, *O. orientalis*, *O. doisuthapensis*, *O. coracinus*, *Copris carinicep*, *C. carinicus* and *C. reflexus*. The only species of rollers that could disperse larger seeds were *Synapsis boonlongi*. These beetles were from 5 to 27 mm in length.

5. The patterns of seed removal by dung beetles varied according to their nesting behavior. All tunneler species removed seeds and feces directly beneath or near dung piles. *Onthophagus doisuthepensis*, *O. rugulosus* and *Copris reflexus* always pushed feces and/or seeds for short distances before burying them. The ball-rollers *Synapsis boonlongi*, *Sisyphus thoracicus* and *S. maniti* made dung balls, rolled them away (at longer distances than the tunnelers) and buried them. The dwellers did not relocate dung or seeds.

6. During the direct observations of beetles at feces piles, post-dispersal of seeds from gibbon feces was only by dung beetles. Seeds of various sizes, including large seeds (> 20 mm) of *Sandoricum koetjape*, *Garcinia benthamii*, *Knema elegans* and *Nephelium melliferum*, were relocated by those beetles ≥ 5 mm in length. The possibility of secondary dispersal of seeds in Mo Singto plot depended on number and species of dung beetles, time of day, season and other factors, for example, predation on dung beetles.

7. The dispersed distances by dung beetles ranged from 0 to 150 cm with an average of 35.4 cm (N = 56). The mean burial depth of those seeds at the end of observation was 3.7 cm (range = 1–7 cm, N = 53). Being removed by dung beetles at distances away from original position of dung piles and buried at these shallow distances, seeds tended to have benefit of escaping from predators and clumping with possibility to germinate.

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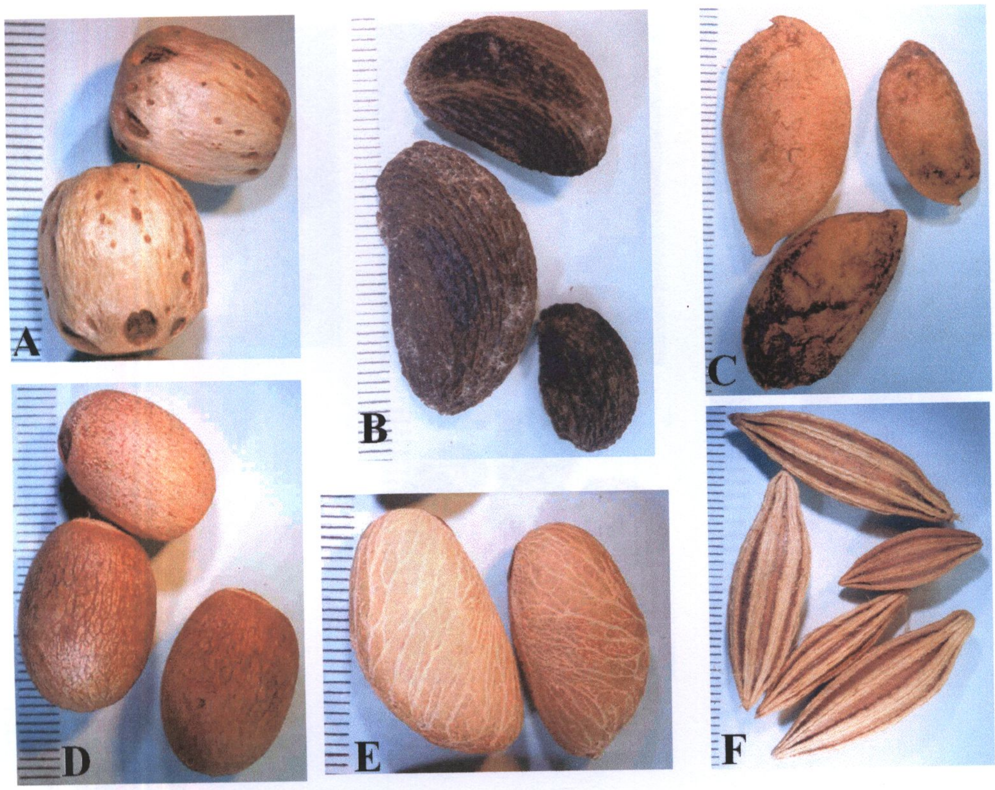
APPENDIX

Appendix 1. Number of each species of seeds recovered from a total of 9,550 g (157 samples) of gibbon feces collected throughout the year 2000.

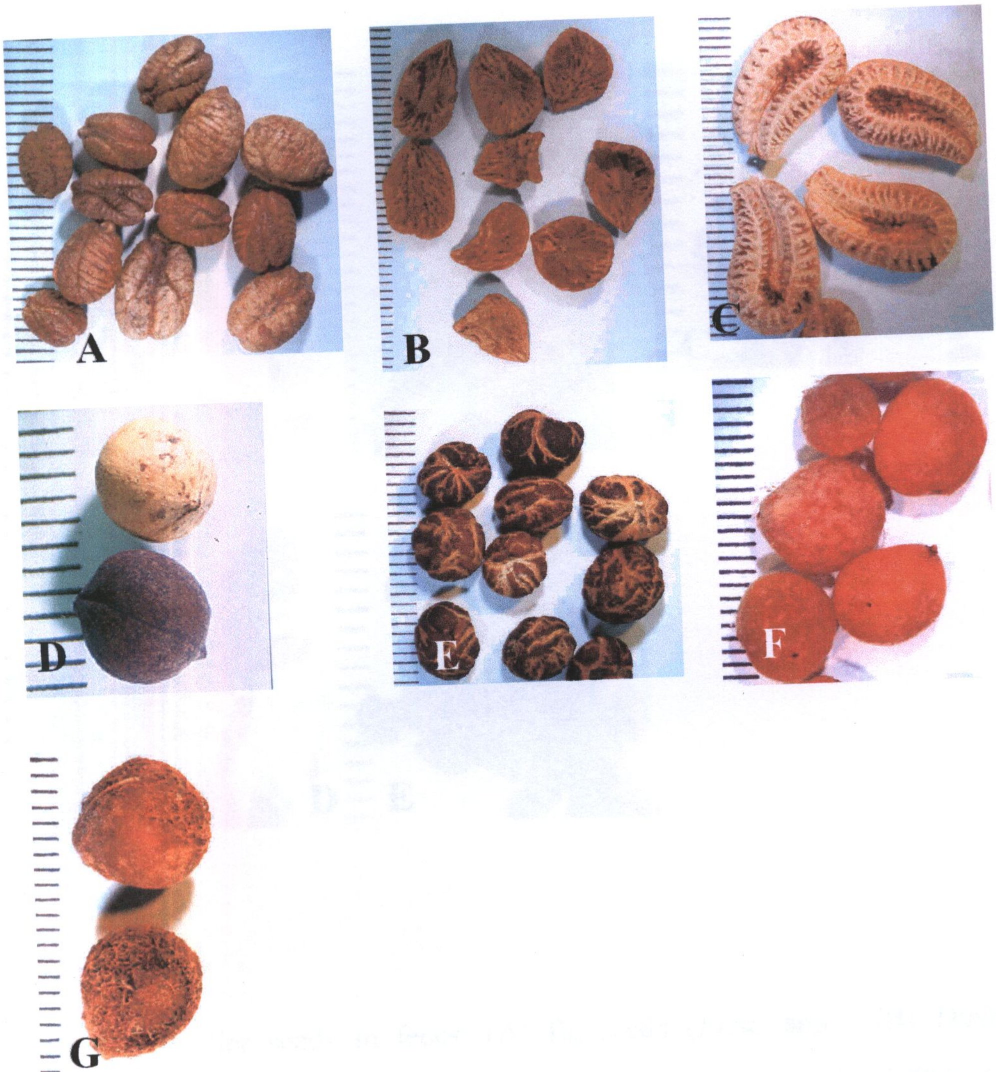
No.	Scientific name	Abbr.	# of seeds in about 800 g gibbon feces/month												Total
			J	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	
1	*Choerospondias axillaris* Roxb.	*Ca*						6	19	5	55	50	40		175
2	*Alphonsea boniana* Fin. & Gagnep.	*Ab*							2						2
3	*Desmos dumosus* (Roxb.) Saff. var. *glabrior* Craib	*Dd*	30	128	26					1	3				188
4	*Fissistigma oblongum* (Craib) Merr.	*Fo*	7	2						6				19	34
5	*Uvaria fauveliana* (Pierre ex Fin. & Gagnep.) Ast	*Uf*							2	2					4
6	*Uvaria hirsuta* Jack	*Uh*										5			5
7	*Uvaria* sp.	*U* sp.					6	8			2	10	6	6	38
8	*Melodinus cambodiensis* Pierre ex Spire	*Mc*	2	6		2	3			2					15
9	*Ilex chevalieri* Tard.	*Ic*							28	33	40				101
10	*Schefflera elliptica* (Bl.) Harms	*Se*	34												34
11	*Salacia chinensis* L.	*Sc*						8							8
12	*Daphniphyllum cambodianum* Gagnep.	*Dc*										2	5		7
13	*Elaeagnus conferta* Roxb.	*Ec*	23	66									16		105
14	*Elaeocarpus* sp. 1	*E* sp1	2						10	37					49
15	*Elaeocarpus* sp. 2	*E* sp2					1								1
16	*Polyosma elongata* Gedd.	*Pe*										2	92	51	145
17	*Balakata baccata* (Roxb.) Ess.	*Bc*						8							8
18	*Bridelia insulana* Hance	*Bi*								28	12				40
19	*Bridelia stipularis* Bl.	*Bs*											1		1
20	*Gnetum montanum* Markgr.	*Gm*					1	30	1	10					42
21	*Garcinia benthamii* Pierre	*Gb*							47	71	40	3			161
22	*Diplectria barbata* (Bl.) Franken & Roos	*Db*						***	***	***	***				***
23	*Aglaia elaeagnoidea* (A. Juss) Benth	*Ae*				4									4
24	*Sandoricum koetjape* (Burm. f.) Merr.	*Sk*						21	56	24					101
25	*Diploclisia glaucescens* (Bl.) Diels	*Dg*				1	15								16
26	*Ficus* spp.	-	***	***	***	***	***	***	***	***	***	***	***	***	***
27	*Knema elegans* Warb.	*Ke*			3	60									63
28	*Cleistocalyx operculata* Roxb.	*Co*						152					30		182
29	*Daemonorops jenkinsiana* (Griff.) Mart.	*Dj*		1	7		3						2		13
30	*Aidia densiflora* (Wall.) Masam.	*Ad*				102	81	42	87	114	116		57		599
31	*Anthocephalus chinensis* (Lmk.) A. Rich. ex Walp.	*Ach*							217		148			80	445
32	*Toddalia asiatica* (L.) Lmk.	*Ta*							15	2					17
33	*Nephelium melliferum* Gagnep.	*Nm*					107	7							114
34	*Picrasma javanica* Bl.	*Pj*	6	3											9
35	*Grewia laevigata* Vahl	*Gl*										2	17	11	30
36	*Aphananthe cuspidata* (Bl.) Pl.	*Acu*							2	56	73	39			170
37	*Gironniera nervosa* Pl.	*Gn*	2						1	3					6
38	*Ampelopis cantoniensis* Pl.	*Aca*								17	23				40
39	*Tetrastigma pyriforme* Gagnep.	*Tp*		331	258	79									668
40	Unknown 1	Unk1					7								7
41	Unknown 2	Unk2							59						59
42	Unknown 3	Unk3								103					103
			106	**537**	**294**	**248**	**224**	**282**	**546**	**514**	**512**	**113**	**266**	**167**	**3,809**

Note: *** = large number of small seeds

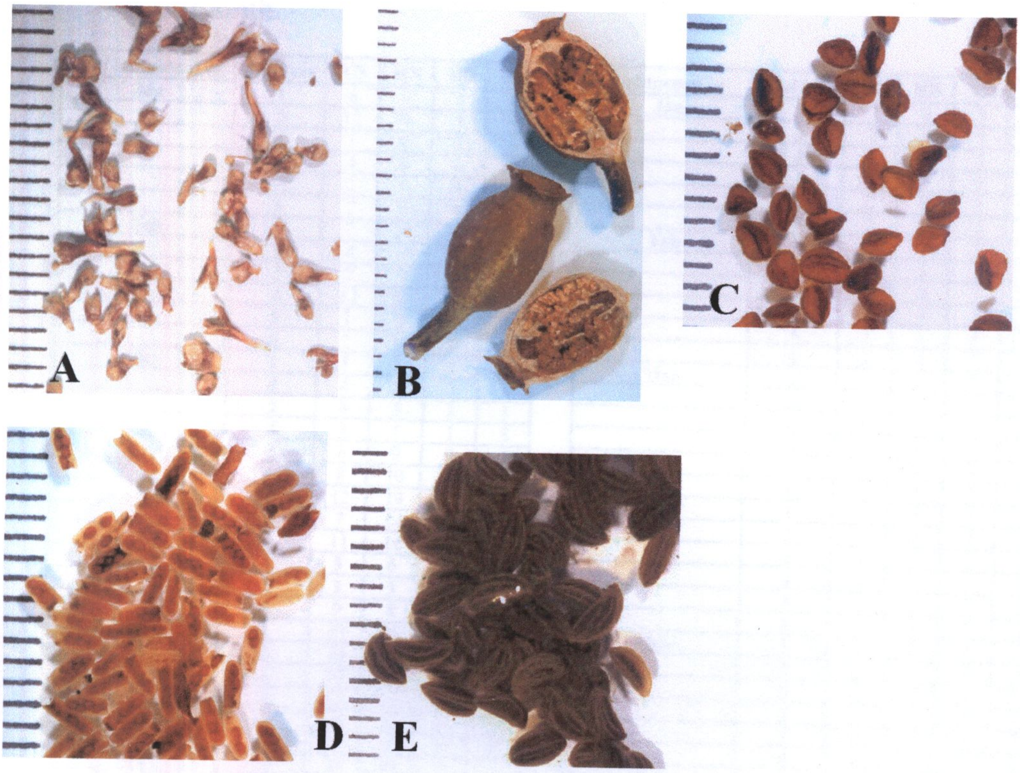
Appendix 2. Gibbon feces with large and small seeds (upper) and with only small fig seeds (lower). Photos by A. Yhamdee.



Appendix 3. Some large seeds from gibbon feces; (A) *Choerospondias axillaris*, (B) *Garcinia benthamii* or wild mangosteen, (C) *Sandoricum koetjape* or wild santol, (D) *Knema elegans*, (E) *Nephelium melliferum* or wild rambutan, and (F) *Elaeagnus conferta*, a woody climber. Seeds of A–E were found during and after March, 2000 and some of them were removed by dung beetles while seeds of F were found during dry period of January–February with relatively low numbers of dung beetles and all of them were not removed from their deposition sites. (Scale = 1 mm) Photos by A. Yhamdee.



Appendix 4. Medium-sized seeds from gibbon feces that were dispersed by dung beetles; (A) *Tetrastigma pyriforme*, (B) *Melodinus cambodiensis*, (C) *Diploclisia glaucescens*, (E) *Cleistocalyx operculata*, (F) *Grewia laevigata*, and (G) *Aphananthe cuspidata*. These seeds tended to be removed in higher numbers particularly during rainy period with higher number of dung beetles. (Scale = 1 mm) Photos by A. Yhamdee.



Appendix 5. Smaller seeds in feces: (A) fig seeds (*Ficus* spp.), (B) *Diplectria barbata* (inside the fruit), (C) *Aidia densiflora*, (D) *Anthocephalus chinensis*, and (E) *Ilex chevalieri*. These seeds were always included in pieces of dung or dung balls taken by any tunneler and ball-rollers dung beetles during seed removal observations. (Scale = 1 mm) Photos by A. Yhamdee.

Appendix 6. Number of dung beetles individuals and species in each trap of each month.

# of individual in	# of trap	VN	HN	VD	HD
Jan	1	6	0	3	0
	2	11	0	3	3
	3	1	0	5	6
	4	4	0	0	3
	5	2	0	3	0
	6	2	0	5	7
Feb	1	7	15	8	4
	2	4	19	6	1
	3	7	7	1	4
	4	13	31	1	0
	5	7	2	1	3
	6	2	15	2	2
Mar	1	8	3	0	3
	2	4	2	3	5
	3	4	5	3	3
	4	3	1	1	5
	5	6	9	9	2
	6	8	10	2	5
Apr	1	12	19	12	2
	2	7	14	6	4
	3	11	16	0	2
	4	8	6	3	1
	5	3	3	7	2
	6	0	8	5	3
May	1	23	11	18	19
	2	13	15	14	19
	3	13	15	18	29
	4	31	11	13	7
	5	18	14	31	23
	6	6	6	21	17
Jun	1	43	18	0	3
	2	10	28	3	0
	3	4	16	2	2
	4	5	10	12	17
	5	6	24	9	15
	6	4	8	1	3
Jul	1	19	10	10	10
	2	14	1	0	8
	3	10	2	25	9
	4	1	1	5	3
	5	3	4	4	7
	6	7	9	8	4
Aug	1	0	6	2	0
	2	3	7	1	2
	3	6	5	5	6
	4	0	5	1	0
	5	4	14	4	0
	6	2	0	2	10
Sep	1	3	3	1	5
	2	7	6	4	3
	3	3	4	3	9
	4	2	10	5	4
	5	2	0	1	7
	6	0	0	4	1
Oct	1	3	2	1	0
	2	2	2	2	6
	3	1	1	2	1
	4	2	8	1	3
	5	4	0	4	2
	6	11	4	5	5
Nov	1	30	5	2	9
	2	3	3	2	5
	3	15	20	0	5
	4	5	4	3	3
	5	28	2	1	0
	6	20	0	4	3
Dec	1	3	2	4	3
	2	4	14	3	0
	3	9	5	1	2
	4	4	5	1	5
	5	2	3	1	4
	6	3	1	1	16
Total		**551**	**529**	**354**	**384**

# of species in	# of trap	VN	HN	VD	HD
Jan	1	3	0	3	0
	2	2	0	3	2
	3	1	0	3	2
	4	3	0	0	1
	5	2	0	1	0
	6	2	0	2	4
Feb	1	3	4	2	3
	2	1	3	2	1
	3	5	3	1	2
	4	5	4	1	0
	5	3	1	1	2
	6	1	4	2	2
Mar	1	4	3	0	3
	2	2	1	2	3
	3	3	3	2	2
	4	2	1	1	3
	5	3	4	5	1
	6	4	4	2	3
Apr	1	2	5	3	2
	2	4	4	2	1
	3	4	5	0	2
	4	4	4	2	1
	5	2	1	1	2
	6	0	3	2	2
May	1	6	2	4	3
	2	2	4	5	3
	3	5	4	6	5
	4	6	7	6	4
	5	5	2	6	7
	6	4	3	3	4
Jun	1	10	10	0	2
	2	4	10	3	0
	3	1	8	1	2
	4	4	4	7	3
	5	3	10	3	3
	6	3	2	1	2
Jul	1	8	4	5	5
	2	7	1	0	5
	3	7	2	5	3
	4	1	1	5	2
	5	1	2	4	3
	6	5	3	2	3
Aug	1	0	4	1	0
	2	2	4	1	2
	3	4	4	3	4
	4	0	1	1	0
	5	4	5	2	0
	6	2	0	2	6
Sep	1	2	2	1	3
	2	4	3	2	3
	3	3	3	2	3
	4	2	3	3	4
	5	2	0	1	2
	6	0	0	2	1
Oct	1	3	2	1	0
	2	2	2	2	3
	3	1	1	2	1
	4	1	3	1	3
	5	3	0	3	2
	6	4	3	4	3
Nov	1	8	3	2	1
	2	2	3	2	3
	3	5	5	0	3
	4	4	3	2	3
	5	8	1	1	0
	6	6	0	2	1
Dec	1	3	2	2	2
	2	1	6	2	0
	3	3	3	1	2
	4	2	2	1	3
	5	1	3	1	2
	6	3	1	1	4
Total		**31**	**33**	**29**	**32**

Note: VN = valley-night, HN = hill-night, VD = valley-day, HD = hill-day

Appendix 7. Number of each species of dung beetles caught in a total of 288 traps from different habitats, time of day, and seasons (18 VN, 18 HN, 18 VD, and 18 HD traps x 4 seasons).

No.	Scientific name	VN				HN				VD				HD				Total
		S1	S2	S3	S4	S1	S2	S3	S4	S1	S2	S3	S4	S1	S2	S3	S4	
1	*Aphodius lewisii* Waterhouse	1	11	16	21		29	19	19		10		6	1	41		32	206
2	*A.* sp.																	
3	*Caccobius bidentatus* Boucomont		2		4		1		2		1	2	1			1		14
4	*Cassolus pongchaii* Masumoto								1									1
5	*Catharsius molossus* Linne								1									1
6	*Copris cariniceps* Felsche	1	7	1			6	1	1		3							20
7	*Copris carinicus* Gillet	6	9	3		21	11	2	1	2	4				2	1		62
8	*Copris reflexus* Felsche	12	12	5	3	13	6	3	2	1	3				3	1		64
9	*Onthophagus anguliceps* Boucomont			4			2	2				1				1		10
10	*O. apilularius* Masumoto						1											1
11	*O. avocetta* Arrow						1											1
12	*O. balthasari* Vsetetka					1												1
13	*O. bonorae* Zonino		1								1							2
14	*O. brutus* Arrow														1			1
15	*O. coracinus* Boucomont			1	1		5						1					8
16	*O. dapcauensis* Boucomont	1						1		1						3	1	7
17	*O. deemaak* Masumoto														1		1	2
18	*O. diabolicus* Harold			1			1					2				2		6
19	*O. doiinthanonensis* Masumoto															1		1
20	*O. doisuthepensis* Masumoto						2	1							1	3		7
21	*O. falsivigilans* Masumoto								1									1
22	*O. gracilipes* Boucomont	12	2		28	12			1	10	1		9	11			17	103
23	*O. kanyaavonus* Masumoto	1	2	3	2		4	4			3	19		5	6	2	2	53
24	*O. laevis* Harold						1						1					2
25	*O. lindaae* Masumoto	26	95	15	14	48	99	32	7	13	72	23	5	12	75	24	7	567
26	*O. luridipennis* Boheman													1				1
27	*O. manipurensis* Arrow										1					1		2
28	*O. naaroon* Masumoto	7	1	1					5	6	1		2	3	1			27
29	*O. ochii* Masumoto	15	4		1	12				7	4	1		6	4			54
30	*O. orientalis* Harold		6	2	2		4				9	10			1	6	1	41
31	*O. pacificus* Lansberge	6	18	19	29	9	19	10	7	5	9	1	2	2	9	15	1	161
32	*O. penicillatus* Harold		1															1
33	*O. phanaeiformis* Boucomont		1	2	1													4
34	*O. punnaae* Masumoto	4	17	6	34	1	29	6	30	2	2		1	5	9	3	2	151
35	*O. rudis* Sharp													1				1
36	*O. rugulosus* Harold		19	5	5	1	12	4			41	18	1		1	18	1	126
37	*O. singhaakhomus* Masumoto		2				1	1			5	6	3		7	3	5	33
38	*O. taurinus* White			1	1		2			1					1			6
39	*O. thanwaakhomus* Masumoto										1							1
40	*O. tricornis* Wiedmaan		1															1
41	*O. vividus* Arrow			1														1
42	*O.* sp. 1												3			1		4
43	*O.* sp. 2	1																1
44	*O.* sp. 3																	
45	*O.* sp. 4																1	1
46	*O.* sp. 5				1													1
47	*O.* sp. 6				1													1
48	*O.* sp. 7								1									1
49	*Phacosoma fallacilaetum* Masumoto															1		1
50	*P. laetum* Arrow								1			2				1		4
51	*Sisyphus maniti* Masumoto	6	2		1		1		1	8	1		3	8	1		1	33
52	*S. thoracicus* Sharp		1				1				3				2			7
53	*Synapsis boonlongi* Hanboonsong & Masumoto		3			1	4	1			1			1	1			12
	Total	99	217	86	149	119	242	87	81	56	176	85	38	56	167	88	72	**1,818**

Note: VN = valley-night, HN = hill-night, VD = valley-day, and HD = hill-day traps; S1 = warming dry season (Jan–Mar), S2 = early rainy season (Apr–Jun), S3 = late rainy season (Jul–Sep), and S4 = cool dry period after rainy season (Oct–Dec)

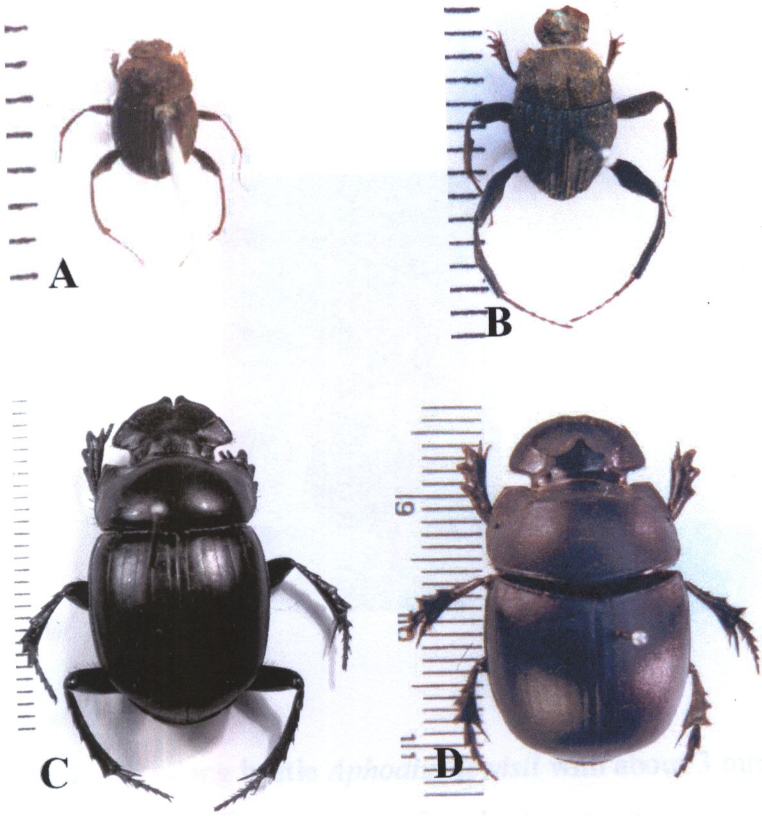
Appendix 8. Number of dung beetles caught in each month in 288 pitfall traps baited with gibbon feces. Dung beetles were in higher numbers of both individuals and species during early rainy period (Apr–Jun) but some species were found more during the dry period (Jan–Mar and/or Oct–Dec) such as *Sisyphus maniti* and *O. gracilipes*.

No.	Scientific name	Dung beetles from pitfall traps in each month												Total
		J	F	M	A	M	J	J	A	S	O	N	D	
1	*Aphodius lewisii* Waterhouse			2	17	27	47	14	9	12	16	36	26	206
2	*A.* sp.													0
3	*Caccobius bidentatus* Boucomont					3	1	2		1	1	2	4	14
4	*Cassolus pongchaii* Masumoto												1	1
5	*Catharsius molossus* Linne												1	1
6	*Copris cariniceps* Felsche	1				1	15	2			1			20
7	*Copris carinicus* Gillet	2	27			4	22	4	2		1			62
8	*Copris reflexus* Felsche		24	2		3	21	6	2	1	1	4		64
9	*Onthophagus anguliceps* Boucomont				1	1		3	4	1				10
10	*O. apilularius* Masumoto				1									1
11	*O. avocetta* Arrow						1							1
12	*O. balthasari* Vsetetka			1										1
13	*O. bonorae* Zonino						2							2
14	*O. brutus* Arrow						1							1
15	*O. coracinus* Boucomont				5				1		2			8
16	*O. dapcauensis* Boucomont	1		1				2		2			1	7
17	*O. deemaak* Masumoto					1					1			2
18	*O. diabolicus* Harold						1	2	2	1				6
19	*O. doiinthanonensis* Masumoto							1						1
20	*O. doisuthepensis* Masumoto				1	1	1	2	2					7
21	*O. falsivigilans* Masumoto											1		1
22	*O. gracilipes* Boucomont	5	20	20	3						6	31	18	103
23	*O. kanyaayonus* Masumoto	5		1	4	6	5	17	7	4	3		1	53
24	*O. laevis* Harold					1					1			2
25	*O. lindaae* Masumoto	13	52	34	79	197	65	34	32	28	13	17	3	567
26	*O. luridipennis* Boheman	1												1
27	*O. manipurensis* Arrow				1			1						2
28	*O. naaroon* Masumoto	9	5	2		3				1	4	3		27
29	*O. ochii* Masumoto	4	8	28		12		1				1		54
30	*O. orientalis* Harold				1	13	6	12		6	1	2		41
31	*O. pacificus* Lansberge	7	9	6	10	25	20	32	6	7	5	28	6	161
32	*O. penicillatus* Harold					1								1
33	*O. phanaeiformis* Boucomont						1	1	1			1		4
34	*O. punnaae* Masumoto	11		1	7	41	9	5	4	6	4	40	23	151
35	*O. rudis* Sharp			1										1
36	*O. rugulosus* Harold			1	13	41	19	27	7	11	5	2		126
37	*O. singhaakhomus* Masumoto				1	13	1	2	3	5	3		5	33
38	*O. taurinus* White			1	2	1				1	1			6
39	*O. thanwaakhomus* Masumoto					1								1
40	*O. tricornis* Wiedmaan				1									1
41	*O. vividus* Arrow							1						1
42	*O.* sp. 1							1					3	4
43	*O.* sp. 2	1												1
44	*O.* sp. 3													0
45	*O.* sp. 4											1		1
46	*O.* sp. 5												1	1
47	*O.* sp. 6												1	1
48	*O.* sp. 7												1	1
49	*Phacosoma fallacilaetum* Masumoto								1					1
50	*P. laetum* Arrow							2	1				1	4
51	*Sisyphus maniti* Masumoto	4	15	3	4		1				3	3		33
52	*S. thoracicus* Sharp				2	4	1							7
53	*Synapsis boonlongi* Hanboonsong & Masumoto		2		1	5	3		1					12
	Total	**64**	**162**	**104**	**154**	**405**	**243**	**174**	**85**	**87**	**72**	**172**	**96**	**1,818**

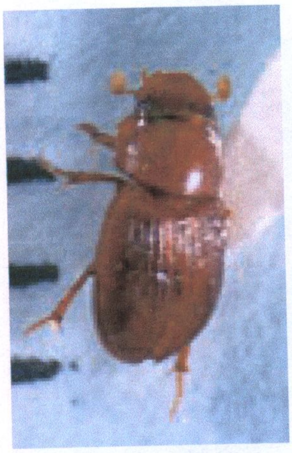
Appendix 9. Number of dung beetles attracted to gibbon feces during all the 49 observation times in each month. Number of individuals and species visited at dung piles were higher during early rainy season from April to June.

No.	Scientific name	Dung beetles from observations in each month												Total
		J	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	
1	*Aphodius lewisii* Waterhouse			10	4		4	2				4	2	26
2	*A.* sp.											3	1	4
3	*Caccobius bidentatus* Boucomont					2			1	2				5
4	*Cassolus pongchaii* Masumoto													0
5	*Catharsius molossus* Linne								1					1
6	*Copris cariniceps* Felsche					2		2	3	1			1	9
7	*Copris carinicus* Gillet					1	2			1				4
8	*Copris reflexus* Felsche				3	3	15	3	2			1		27
9	*Onthophagus anguliceps* Boucomont													0
10	*O. apilularius* Masumoto													0
11	*O. avocetta* Arrow													0
12	*O. balthasari* Vsetetka													0
13	*O. bonorae* Zonino													0
14	*O. brutus* Arrow													0
15	*O. coracinus* Boucomont				1			1						2
16	*O. dapcauensis* Boucomont													0
17	*O. deemaak* Masumoto													0
18	*O. diabolicus* Harold													0
19	*O. doiinthanonensis* Masumoto													0
20	*O. doisuthepensis* Masumoto				1	2	5	5	1		2	1	4	21
21	*O. falsivigilans* Masumoto										1			1
22	*O. gracilipes* Boucomont		2		4						3	1	5	15
23	*O. kanyaavonus* Masumoto					2					1	1		4
24	*O. laevis* Harold													0
25	*O. lindaae* Masumoto			2	3	10	13	4		3	1	6	4	46
26	*O. luridipennis* Boheman													0
27	*O. manipurensis* Arrow													0
28	*O. naaroon* Masumoto							1						1
29	*O. ochii* Masumoto							1						1
30	*O. orientalis* Harold			1	10	12	8	7	6	3				47
31	*O. pacificus* Lansberge			2	4	9	12	24	1	6	3	3	3	67
32	*O. penicillatus* Harold													0
33	*O. phanaeiformis* Boucomont													0
34	*O. punnaae* Masumoto	1		2		6	4			2		1	5	21
35	*O. rudis* Sharp													0
36	*O. rugulosus* Harold				6	19	17	8	2	4	1			57
37	*O. singhaakhomus* Masumoto					1		1		1		3		6
38	*O. taurinus* White													0
39	*O. thanwaakhomus* Masumoto													0
40	*O. tricornis* Wiedmaan													0
41	*O. vividus* Arrow													0
42	*O.* sp. 1													0
43	*O.* sp. 2													0
44	*O.* sp. 3												1	1
45	*O.* sp. 4													0
46	*O.* sp. 5													0
47	*O.* sp. 6													0
48	*O.* sp. 7													0
49	*Phacosoma fallacilaetum* Masumoto													0
50	*P. laetum* Arrow													0
51	*Sisyphus maniti* Masumoto	1	2		1							1		5
52	*S. thoracicus* Sharp			1		1								2
53	*Synapsis boonlongi* Hanboonsong & Masumoto					1				1		1		3
	Total	**2**	**4**	**18**	**37**	**71**	**80**	**59**	**17**	**24**	**12**	**26**	**26**	**376**

ppendix 10. Some of tunneler dung beetles of genera *Onthophagus* (A–F) with oval-shaped bodies and *Copris* (G–I) with elongated bodies. They were (A) *O. rugulosus*, (B) *O. orientalis*, (C) *O. lindaae*, (D) *O. coracinus*, (E) *O. doisuthepensis*, (F) *O. gracilipes* (with curved and long front legs), (G) C. *cariniceps*, (H) *C. carinicus*, and (I) *C. reflexus*. These species were medium-sized beetles (< 15 mm in length). All of the species above removed small-seeded species and all except *O. lindaae* (although found in every month) and *O. gracilipes* removed large seeds from dung piles. *O. doisuthepensis* always pushed large seeds or pieces of dung longer distances than other tunnelers. (Scale = 1 mm) Photos by A. Yhamdee.



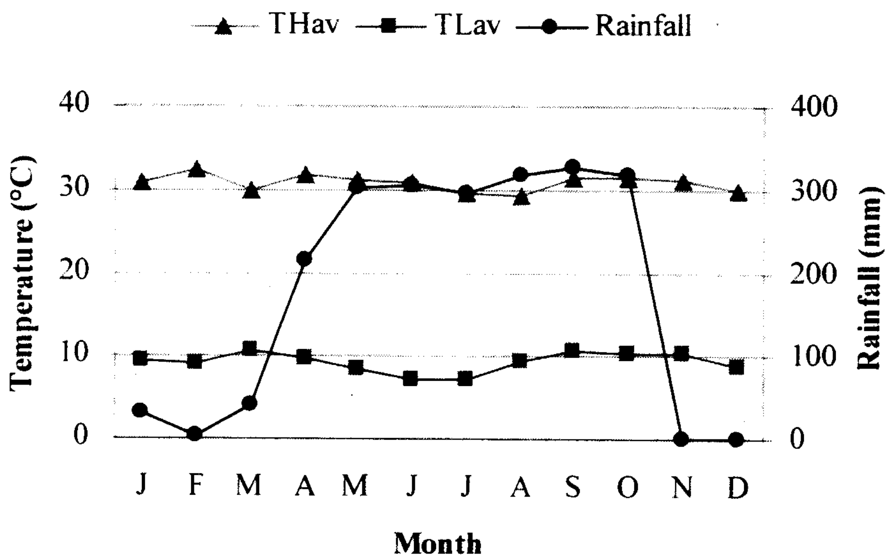
ppendix 11. Two small ball-rollers, *Sisyphus maniti* (A) and *S. thoracicus* (B), the largest roller *Synapsis boonlongi* (C), and the largest tunneler *Catharsius molossus* (D). All species of these beetles removed gibbon feces and seeds from dung piles. Ball-rollers have relatively long hind legs adapted for constructing and rolling dung balls away from dung piles before burying them while tunnelers including *Catharsius molossus* with short legs remove dung and seeds directly under dung piles. (Scale = 1 mm) Photos by A. Yhamdee.



pendix 12. A dweller dung beetle *Aphodius lewisii* with about 3 mm body length. This dweller species were found almost all months of the year. Dwellers were always seen and found inside or 1–2 cm below dung piles. No seeds in gibbon feces were sighted to remove by dwellers. (Scale = 1 mm) Photo by A. Yhamdee.

pendix 13. A tunneler dung beetle *Onthophagus manipurensis* attracting to a gibbon dung pile containing some small-seeded species. Tunnelers make their underground tunnels or burrows under or short distances away from dung piles and remove dung accidentally with these seeds into them. Photo by A. Yhamdee.

Appendix 14. Rollers and their balls of feces and seeds; (A) *Sisyphus maniti*, (B) *S. thoracicus*, and (C) *Synapsis boonlongi*. Diameters of dung balls of these beetles were about 2 times their body lengths. Small-seeded species in gibbon feces including fig seeds were always contained in balls of *S. maniti* and *S. thoracicus* while both small and larger seeds were sighted in dung balls of *S. boonlongi* and were buried by *C. molossus*. Photos by A. Yhamdee.



Appendix 15. Rainfall and temperature (THav = average highest temperature, TLav = average lowest temperature) during the year 2000.

BIOGRAPHY

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