Journal of Tropical Ecology (2005) **21**:117–120. Copyright © 2005 Cambridge University Press
DOI: 10.1017/S0266467404001968 Printed in the United Kingdom

SHORT COMMUNICATION

Influence of faeces on seed removal from gibbon droppings in a dipterocarp forest in Central Borneo

Kim R. McConkey

Wildlife Research Group, Department of Anatomy, University of Cambridge, Cambridge CB2 3DY, UK

(*Accepted 20 May 2004*)

Key Words: Borneo, civet, dung beetles, gibbon, Indonesia, rodent, seed predation, *Sus barbatus*

Many frugivorous animals disperse seeds in their faeces (Corlett 1998, van der Pijl 1982), which may enhance the ability of secondary seed dispersers and post-dispersal seed predators to locate seeds (Andresen 2001, Chapman 1989, Feer 1999, Janzen 1982). By destroying and moving seeds these animals can radically alter the primary seed shadows generated by frugivorous animals and, consequently, have the potential to influence plant recruitment (Alcántara *et al*. 2000, Crawley 1992). Nevertheless, the influence of faeces on seed removal in South-East Asian forests has not previously been investigated and our knowledge currently comes from studies in Neotropical forests (Andresen 2001, Chapman 1989, Feer 1999, Janzen 1982).

In this study, I monitored seed removal from experimental gibbon droppings in a lowland dipterocarp forest in Central Kalimantan, Indonesia. Gibbons (Hylobatidae) are one of the main frugivores inhabiting the forests of Kalimantan (Blouch 1997, McConkey & Chivers 2004). They disperse large numbers of seeds in their faeces and the seed shadow they generate is almost completely altered by subsequent post-dispersal processes (McConkey 2000). Most activity occurs within a few days of seeds being deposited in the forest (Blate *et al*. 1998, Chapman 1989, McConkey in press), so this was the period of study. There were two main aims: (1) to determine if faeces enhances the location of seeds; (2) to identify some of the animal groups responsible for seed removal.

Field data were collected at the Barito Ulu Research Area (BURA) in April and September 1997. BURA occurs virtually at the geographic centre of the island of Borneo (0°12′N, 114°6′E), in the watershed of the upper Barito River. The area has a rugged, hilly to mountainous terrain (100–350 m asl) and the main forest type is lowland dipterocarp forest, interspersed with heath forest (Mirmanto 1996). The latter study month coincided with the start of a severe drought, causing lower than average rainfall (2585 mm in 1997 compared to 3738 mm per year between 1990–1996).

Ninety seed piles were formed using three different conditions (30 piles of each). The fate of artificial gibbon droppings (seeds and faeces combined; SF) was compared with piles of only seeds (S) and only faeces (F). For the SF and F piles, approximately 15 g of gibbon (*Hylobates mulleri* × *agilis* Marshall & Sugardjito 1986) faeces was used, since this mimics natural gibbon droppings (McConkey 2000); droppings were less that 1 d old and had not been handled directly (all manipulation was done within a clear plastic bag). Seeds in the SF piles were taken from natural gibbon droppings, while seeds in the S piles were taken from fresh fruit and cleaned of any pulp residue. This ensured that the appropriate smell, or lack of, was associated with each pile. I was interested in documenting how the presence of faeces influenced the ability of animals to locate droppings rather than actual seed removal; hence I used the seeds of several species (all found in wild gibbon droppings; McConkey 1999) to minimize the chances of excluding a particular granivore. Seed number used per pile varied according to the species used (to account for different sized seeds), but species and numbers were kept constant across all conditions (Table 1).

Piles were located every 20 m along an established transect, but the actual condition (F, SF, S) was selected randomly. A small area (approximately 30 cm) surrounding the pile was cleared of debris and vegetation, and was spread with sand to gain foot imprints of vertebrates. Piles were marked by a piece of flagging tape tied 1.5–2 m

---

Current address: A. V. Ramarao Research Foundation, 7-102/54 Sai Enclave, Habshiguda, Hyderabad 500007, India. Email: kimm@sancharnet.in

https://doi.org/10.1017/S0266467404001968 Published online by Cambridge University Press

Table 1. Plant species used in the experiment and their seed mass. Number of seeds in each experimental pile is shown for each species (these mimicked seed numbers found in wild gibbon droppings; McConkey 1999). The number of seed piles the species was used for in each condition is also shown (a total of 30 seed piles were used in each of three conditions).

Species (Family*)	Fresh seed mass (g)	No. seeds per pile	No. piles in each condition
Calamus sp. (Arec.)	1.7	4	7
Calophyllum soulattri Burm. (Clusi.)	0.5	10	2
Garcinia sp. (Clusi.)	0.3	20	3
Erycibe maingayi Hoogl. (Convolvul.)	1.4	6	3
Beilschmiedia dictyoneura Kosterm. (Laur.)	2.0	4	2
Lauraceae sp. 1 (Laur.)	1.8	4	5
Aglaia rubigonosa (Hiern.) Pannell (Meli.)	4.4	4	2
Ziziphus sulvensis Lam. (Rhamn.)	3.4	4	2
Xerospermum noronhianum (Bl.) Bl. (Sapind.)	1.7	5	1
unidentified sp. (indet.)	3.4	4	3

*'aceae' omitted.

above the site. Although the proportion of removed seeds in the SF (60% of 30 'droppings') condition was not significantly different from rates in naturally gibbon defaecated seeds (75% of 183 droppings, McConkey 1999; $Z = 1.57$, $P > 0.05$), the rates reported here should be considered to be relative rates of detection (between the different conditions), rather than absolute rates.

Piles were set at 06h00 (11 sets) and 14h00 (19 sets), checked after 1 h, 2 h and 4 h (to evaluate removal by dung beetles), then every 4 h for 1 d; they were then checked once a day for 1 wk. A pile was considered located when the first seed had been removed from the pile or when the faeces had disappeared. An animal was associated with faecal or seed removal if it was observed directly (invertebrates only) or if footprints in the sand were seen at the same time as the removal was recorded. Footprints were identified from Payne *et al.* (1985) and also from prints left in camp from a Malay civet (*Viverra tangalunga* Gray) that regularly consumed seeds set for germination. The civet was observed directly on several occasions and seed remains were found after the animal had been scared away by my presence (the sound of seeds being crushed caused me to investigate, leading to these sightings). These observations indicated that this species tended to discard the pulp of fruit if available and consume the endocarp (often leaving remnants of the seed testa).

Data were analysed using Cox's F-test in the Kaplan–Meier Survival Analysis procedure (STATISTICA, version 4.1); (Test 1) time to first seed removal in the SF and S piles; (2) time for removal of faeces in the SF and F piles; (3) time to first seed removal in the SF pile, distinguishing between piles from which dung beetles had removed faeces, and those that still had faeces. In addition, I compared time to (i) first seed removal and (ii) faecal removal between the two study months (April, September) and two start times (06h00, 14h00) to determine if the sampling procedure influenced the results.

Over the 7 d, seeds from SF piles were located quicker and more often (18 piles, 60%) than those from S piles (9 piles, 30%) ($F = 2.65$, $P = 0.006$; Figure 1a). There was no difference in the location of faeces from SF piles (19 piles, 63%) and F piles (15 piles, 50%) ($F = 1.34$, $P = 0.19$; Figure 1b). Removal of faeces by dung beetles in the first 4 h did not alter the persistence of SF seed piles over 7 d ($F = 1.48$, $P = 0.21$; Figure 1c). Month ($F = 1.14$, $P = 0.36$) had no influence on seed removal, but time of day did ($F = 3.27$, $P = 0.004$; Figure 1d). Seeds were located quicker and more often when piles were placed in the forest at 14h00 (55% of piles found), than at 06h00 (23% of piles found). Neither month ($F = 1.42$, $P = 0.16$), nor time of day ($F = 1.02$, $P = 0.46$) influenced faecal removal.

Dung beetles were the most frequently observed animal associated with removal of faeces (Figure 2) and regardless of time of day they were the first animals seen to arrive at the droppings and were not recorded after 4 h. However, dung beetles only removed one seed. Ants were also seen removing faeces, including an entire pile at 168 h. Vertebrate prints were recorded between 18h00 and 06h00. Pig and civet prints were associated with faecal removal, but usually this involved the removal of seeds as well. Rodent prints were the most frequently observed print associated with the removal of seeds (Figure 2).

Location of experimental seed piles was enhanced two-fold by the presence of faeces in this study. Granivores were even able to locate seeds from which dung beetles had removed the surrounding faeces. This suggests that the faecal smell is still prominent (although faeces are absent) and acting as an attractant to granivores for at least 1 wk after removal of the faeces. The effect of faeces as an attractant may diminish given sufficient time. In Costa Rica, Chapman (1989) found that 20% more seeds were found by seed predators if faeces were present, but this difference had diminished to 8% after 3 wk and to 0.06% after 17 mo. A similar trend would be expected if the present study had been conducted over a longer time period. Nevertheless, the initial higher location rate of defaecated seeds may still have an important influence on seed survival. Of 11 seed species dispersed by gibbons and germinated in trials, five germinated within 3 wk and one of these within 5 d (McConkey 2000). For fast-germinating species such as these the presence of faeces may significantly decrease the chances of seeds germinating before being located by granivores.

Most activity at the faeces occurred within the first day after deposition, beginning with the arrival of mainly

https://doi.org/10.1017/S0266467404001968 Published online by Cambridge University Press

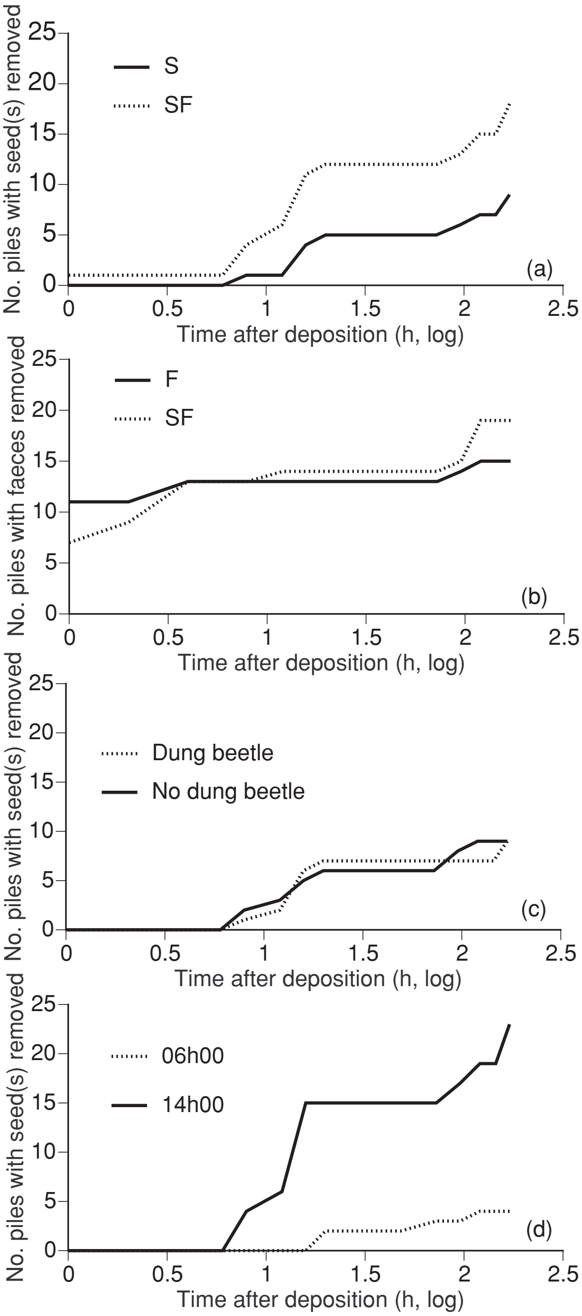

Figure 1. Cumulative removal of seeds or faeces over the monitoring period according to different conditions: (a) time to first seed removal in SF (seeds and faeces) and S (seeds only) piles, (b) removal of faeces in SF and F (faeces only) piles, (c) time to first seed removal in SF piles from which dung beetles have, and have not, removed faeces from, (d) time to first seed removal in SF and S piles (combined) placed in the forest at two different time periods (06h00 and 14h00).

dung beetles and ants. Dung beetles are considered important secondary seed dispersers in Neotropical forests, and while they only removed one seed in this study, smaller seeds are probably removed more frequently (Andresen 2001, Engel 2000).

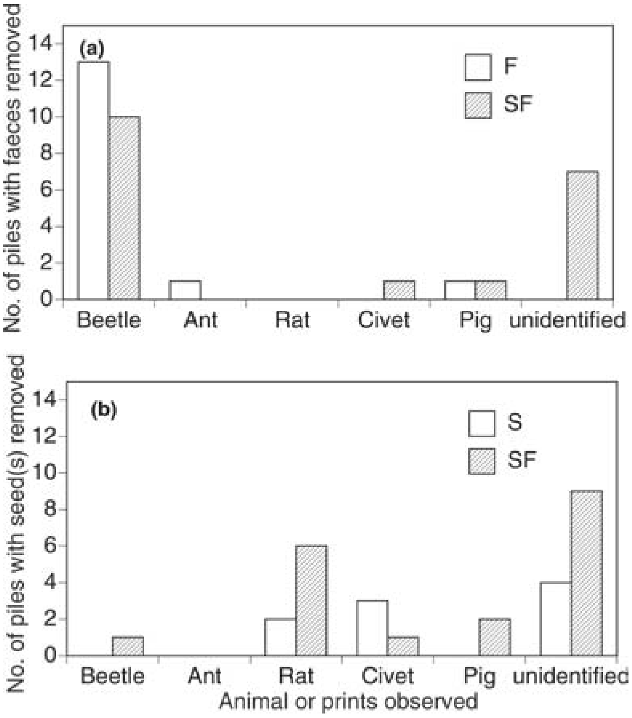

Figure 2. Number of piles that had (a) faeces or (b) seeds removed and the animal directly observed (dung beetles and ants) or whose prints were seen at the time the removal was noted. Piles either had seeds only (S), faeces only (F) or both seeds and faeces (SF).

Three groups of potential seed predators were identified in this study (rats, pigs and civets). Rodents are recognized as significant predators in South-East Asia (Blate *et al.* 1998, Miura *et al.* 1997), but recent evidence suggest they also hoard seeds (Yasuda *et al.* 2000). This has yet to be shown to result in significant plant recruitment, however, as it does in the Neotropics (Forget 1996). A single hoard of *Litsea ferruginea* seeds were found at the study site that had been formed by an individual of *Maxomys rajah* (K. R. McConkey, unpubl. data.) and *Rattus* spp. (also found at the study site) husking stations in the tropical Pacific do occasionally generate seedlings (McConkey *et al.* 2002); hence it is likely that some seeds removed by rodents at the study site may establish seedlings.

Pigs have been identified as important seed predators in Asian forests (Blate *et al.* 1998, Curran & Leighton 2000, Miura *et al.* 1997), but civets have not previously been noted as potential seed predators. Civets are generally regarded as being frugivorous/omnivorous (Corlett 1998, Engel 2000) and this may indeed be the case for most species. Brush-tailed porcupines (*Hystrix brachyura* Linn.) and long-tailed porcupines (*Trichys fasiculata* Shaw) may have been responsible for the prints found at the piles that I attributed to civets, but the prints can be distinguished (Payne *et al.* 1985) and I already had prior knowledge of *Viverra tangalunga* prints and their seed-eating behaviour. This species feeds almost entirely on

https://doi.org/10.1017/S0266467404001968 Published online by Cambridge University Press

the ground (MacDonald & Wise 1979), and has been previously reported to include a high proportion of fruits or seeds in its diet (15% of faeces, MacDonald & Wise 1979, Harrison 1962). I suggest that this species should be considered as a potential seed predator in the forests where it occurs.

At present, researchers looking at post-dispersal seed removal often mimic the distribution of dispersed seeds, but not the presence of faeces – even though endozoochory is a common dispersal mechanism in the tropics (Corlett 1998, Engel 2000, van der Pijl 1982). While this is beginning to be addressed in the Neotropical work (Andresen 2001, Estrada *et al.* 1993, Feer 1999, Janzen 1982), no studies have been done in South-East Asia. As this study shows, however, faeces may significantly influence seed removal rates in the short term and is an important component of the primary seed shadow.

ACKNOWLEDGEMENTS

I thank the Ministry of Forestry and LIPI in Indonesia for their support and permission to conduct the research at the Barito Ulu Site. Rupert Ridgeway and D. J. Chivers provided logistical support and Nurdin and Mulyadi provided unlimited field assistance. Thanks to D. J. Chivers, P. A. Jansen, T. Engel and an anonymous reviewer for advice on the manuscript. Financial assistance was provided by the New Zealand Federation of University Women, Cambridge Commonwealth Trust, Leakey Foundation, Selwyn College, Cambridge University Board of Graduate Studies, Primate Conservation Inc. and Sophie Danforth Conservation Biology Fund of the Roger Williams Park Zoo and Rhode Island Zoological Society.

LITERATURE CITED

ALCÁNTARA, J. M., REY, P. J., SÁNCHEZ-LAFUENTE, A. M. & VALERA, F. 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. *Oikos* 88:362–370.

ANDRESEN, E. 2001. Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. *Journal of Tropical Ecology* 17:61–78.

BLATE, G. M., PEART, D. R. & LEIGHTON, M. 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* 82:522–538.

BLOUCH, R. A. 1997. Distribution and abundance of Orangutans (*Pongo pygmaeus*) and other primates in the Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia. *Tropical Biodiversity* 4:259–274.

CHAPMAN, C. A. 1989. Primate seed dispersal: the fate of dispersed seeds. *Biotropica* 21:148–154.

CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. *Biological Reviews* 73:413–448.

CRAWLEY, M. J. 1992. Seed predators and plant population dynamics. Pp.157–191 in Fenner, M. (ed.) *Seeds: the ecology of regeneration in plant communities*. CAB International, Wallingford.

CURRAN, L. M. & LEIGHTON, M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs* 70:101–128.

ENGEL, T. R. 2000. *Seed dispersal and forest regeneration in a tropical lowland biocenosis* (*Shimba Hills, Kenya*). Ph.D. dissertation. Bayreuth University, Germany.

ESTRADA, A., HALFFTER, G., COATES-ESTRADA, R. & MERITT, D. A. 1993. Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 9:45–54.

FEER, F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. *Journal of Tropical Ecology* 15:129–142.

FORGET, P. M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *Journal of Tropical Ecology* 12:751–761.

HARRISON, J. L. 1962. The natural food of some Malayan mammals. *Bulletin of the Singapore National Museum* 31:5–18.

JANZEN, D. H. 1982. Removal of seeds from horse dung by tropical rodents: influence of habitat and amount of dung. *Ecology* 63:1887–1900.

MACDONALD, D. W. & WISE, M. J. 1979. Notes on the behaviour of the Malay civet. *The Sarawak Museum Journal* 48:295–299.

MARSHALL, J. T. & SUGARDJITO, J. 1986. Gibbon systematics. *Comparative Primate Biology* 1:137–185.

McCONKEY, K. R. 1999. *Gibbons as seed dispersers in the rain-forests of central Borneo*. Ph.D. dissertation. Cambridge University, Cambridge, UK.

McCONKEY, K. R. 2000. The primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. *American Journal of Primatology* 52:1–17.

McCONKEY, K. R. in press. The influence of gibbon primary seed shadows on post-dispersal seed fate in a lowland dipterocarp forest in central Borneo. *Journal of Tropical Ecology*.

McCONKEY, K. R. & CHIVERS, D. J. 2004. Low mammal and hornbill abundance in the forests of Barito Ulu, Central Kalimantan. *Oryx* 38: in press.

McCONKEY, K. R., DRAKE, D. R., MEEHAN, H. J. & PARSONS, N. 2002. Husking stations provide evidence of seed predation by introduced rodents in Tongan rain forests. *Biological Conservation* 109:221–225.

MIRMANTO, E. 1996. *A lowland rain forest fertilization experiment in Central Kalimantan, Indonesia*. M.Sc thesis, University of Stirling.

MIURA, S., YASUDA, M. & RATNAM, L. C. 1997. Who steals the fruits? Monitoring frugivory of mammals in a tropical rain forest. *Malayan Nature Journal* 50:183–193.

PAYNE, J., FRANCIS, C. & PHILLIPS, C. 1985. *A field guide to the mammals of Borneo*. Sabah Society and WWF Malaysia, Kota Kinabalu.

VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants*. Springer-Verlag, New York.

YASUDA, M., MIURA, S. & HUSSEIN, N. A. 2000. Evidence for food hoarding behaviour in terrestrial rodents in Pasoh forest reserve, a Malaysian lowland rain forest. *Journal of Tropical Forest Science* 12:164–173.

https://doi.org/10.1017/S0266467404001968 Published online by Cambridge University Press