THE RAFFLES BULLETIN OF ZOOLOGY 2011 Supplement No. **24**: 115–122
Date of Publication: 30 Mar.2011

FEEDING OVERLAP AND SEED DISPERSAL EFFICIENCY BETWEEN SYMPATRIC HORNBILLS AND GIBBONS IN THAILAND

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ABSTRACT. **–** Gibbons and hornbills are often found in close sympatry in South-east Asian forest for which they play an important role as seed disperser. However, between the two species, the potential redundancy in dispersing seeds is currently debated. This potential redundancy might play an important role for forest regeneration as both species are facing drastic, but of different intensity, decline in their natural habitat. A closer investigation between the two species first show the presence of three feeding assemblages with gibbons isolated from hornbills and, within those a distinction between large and small body-sized birds. Secondly, each feeding assemblage show a different efficiency in seed dispersal capacity with an overall low redundancy recorded. Thirdly, we determine the effect of the raising habitat degradation observed in South-East Asia on the different feeding assemblage. Although no redundancy is observed between the two species, for which one assemblage can substitute another one in dispersing similar plant species, gibbons show a larger capacity than hornbill when limited to a small area, overall small home ranges. The importance of hornbills emerge when seed dispersal is analyzed over a larger area and, eventually between habitat fragments.

This paper was presented at the 5th International Hornbill Conference jointly organised by the National Parks Board (Singapore) and the Hornbill Research Foundation (Thailand), in Singapore on 22nd–25th March 2009.

KEY WORDS. **–** Diet redundancy, frugivore community, feeding assemblage, habitat regeneration.

INTRODUCTION

South-east Asian mixed-evergreen rain forest is home to both hornbills and arboreal gibbons (Kinnaird & O'Brien, 2007; Lappan & Whittaker, 2009). Both sympatric species are highly frugivorous (Kanwatanakid-Savini et al*.*, 2009) and play an important function in the regeneration of their habitat by dispersing a large proportion of the seeds consumed in their diet (Corlett, 1998; Kitamura et al*.*, 2004a; McConkey & Chivers, 2007). Not all frugivores provide the same dispersal service to a given plant species (Howe and Estabrook, 1977; Clark et al*.*, 1999) as different animal species can differ dramatically in their basic behaviour (i.e. moving, foraging, defecating) which will directly influence seed deposition (Clark et al*.*, 1999; Clark et al*.*, 2001). This difference in seed dispersal behaviour, as well as different plant species selection within a dispersed community is fundamental for habitat regeneration. Both species, gibbons and hornbills along with other dispersers, have been reduced in their natural range due to hunting (Kinnaird & O'Brien, 2007; Brodie et al*.*, 2009; Whittaker, 2009) and habitat destruction (Bodmer et al*.*, 1991; Kinnaird & O'Brien, 2007) which has clearly altered seed dispersal and habitat regeneration patterns (Brodie et al*.*, 2009). However, the two species seem to respond differently to degradation and hunting pressure which vary considerably across the landscape (Brodie et al*.*, 2009). From an overall forest conservation point of view, evaluation of the degree of overlap between the two species in their seed dispersal capacity would provide a better understanding of how the decline of hornbill s may or may not be compensated by the presence of the gibbons and vice versa.

In order to determine the efficiency of a seed disperser community composed of perhaps functionally similar hornbills and gibbons, we ask the following questions: 1) how many feeding assemblages are represented between gibbons and hornbills but also within hornbills? 2) what is the efficiency of each feeding assemblage on seed dispersion in pristine habitat? And finally, 3) what is the effect of the increased habitat degradation observed in South-East Asia (Laurance, 1999) on different feeding assemblages?

RESULTS AND DISCUSSION

General seed dispersal. **–** Plant-animal interactions in tropical habitat have serious conservation implications (Chapman, 1995). Up to 90% of tropical plant species produce fleshy fruits providing a large proportion of animal diets (Frankie et al*.,* 1973). In return, animals provide the "tool" to disperse plant seeds (Janzen, 1970) generating a stable equilibrium between plants and dispersers (Karr and Freemark, 1983; Swaine, et al. 1987). Without dispersers seeds will fall under the parent tree where they can face great resource competition from their parents and other seedlings (Janzen, 1970), fall victim to seed predators (Wright et al., 2000) or degraded by fungi and other pathogens (Packer and Clay, 2000). The behaviour of frugivores will indeed affect the distance seeds might be dispersed (Clark et al*.,* 2001), the amount that will be dropped in a single spot and the quality of the spot in which seeds are defecated (Howe, 1989). Moreover, through digestion and regurgitation process, frugivores will remove fleshy pulp and can modify the seed coat structure (Lambert, 1999) which can increase germination success in some plant species. In order to attract good dispersers, plants have evolved attractive fruit characteristics which include color, seed size and shape, and, ultimately, chemical composition (Gautier-Hion et al., 1985; Dew & Wright, 1998).

Overall, three main parameters have been suggested to define the quality of a seed disperser: 1) the number of seeds potentially dispersed; 2) the chance that the seeds will germinate after handling or gut passage; and 3) the quality of the microsite where seeds are deposited for germination (Chapman, 1995).

As all seed dispersing animals have differences in the type of fruit they can disperse as well as a marked differences in their dispersing success, it is of interest to investigate their effectiveness within a specific community (Poulsen et al*.,* 2002). Within the seed disperser community inhabiting tropical forests, primates and large frugivorous birds are considered of particular importance (Rowell & Mitchell, 1991; Chapman, 1995; Sun et al*.,* 1997; Dew & Wright, 1998; Kinnaird et al*.,* 1998; Whitney et al*.,* 1998; Holbrook & Smith, 2000; Poulsen et al*.,* 2002). Although both having a frugivorous diet, large birds and primates tend to feed and, as a consequence, disperse different types of plant species (Poulsen et al*.,* 2002).

Seed dispersal between primate (gibbons) and hornbills. **–** Primates are generally considered excellent seed dispersers (Wrangham et al., 1994; Dew & Wright, 1998) as most species are largely frugivorous (Chapman, 1995), not only ingesting large amount of fruits (Corlett & Lucas, 1990) but they tend not to harm the seeds (Chapman, 1989) and can carry them a significant distance away from parent trees (Garber & Lambert, 1998). Among them, gibbons are considered one of the most important seed dispersers of the forest of South-East Asia, consuming between 57 to 72% of all fleshy fruits available (McConkey et al*.,* 2003), discarding very few seeds under the feeding trees and maintaining almost all seeds vital after defecation (Chivers & Raemaekers, 1986; McConkey, 2000) which are likely to germinate (Whitington & Treesucon, 1991; McConkey, 2005).

Among large frugivorous tropical birds, hornbills are considered the most efficient group of seed dispersers (Kinnaird et al*.,* 1998; Holbrook & Smith, 2000), dispersing as much as 20% of the plant species community (Whitney et al*.,* 1994). Like gibbons, hornbills feed on ripe fruit at high rates and drop, un-harmed, seeds at relevant distances from parent trees (Howe & Smallwood, 1982). Moreover, hornbills can also consume fruits, and as a consequence seeds that, due to their large size, are ignored by most of the other frugivorous birds and smaller mammals (Kinnaird & O'Brien, 2007). However, a major difference with gibbons is that most of the fruits are stored in their crop and seed are later spitted after the pulp is detached and therefore rarely ingested (Kinnaird & O'Brien, 2007).

Besides being considered good seed dispersers, gibbons and hornbills share a similar niche in the forest by selecting mainly ripe, sugar-rich fruits (Leighton, 1998; Poonswad et al., 1998) of bright coloration (Suryadi et al., 1994, Kanwatanakid & Brockelman, 2005) which they both harvest on the outer part of the tree canopy (Carpenter, 1967; Kemp, 1995). This could suggest a major overlap in their diet which is expected to result in a redundancy of their seed dispersal activity within the forest community (Poulsen et al., 2002). In this case, a community-level approach will provide information both on smaller differences that might result in large variation in seed dispersal efficiency, and in the contribution of gibbons and hornbills to the seed shadows of plants (Poulsen et al., 2001).

Determination of feeding assemblage. **–** Hornbills range over all of tropical and sub-tropical Asia, as well as Papua New Guinea and Africa (Kemp, 1995), over this range they can be found in rich communities with several species living sympatrically (Holbrook & Smith, 2000; Gale & Thongaree, 2006; Kanwatanakid-Savini et al*.,* 2009) with often a simple ecological division into two sub-communities based on body size (Kanwatanakid-Savini et al., 2009). On the other hand, the overall distribution of gibbons appears smaller, ranging in tropical and sub-tropical Asia between East India to Indochina, Sumatra, Borneo and eastern Java (Chatterjee, 2009) and rarely occur sympatrically with other species of gibbons (Geissmann, 1995). However, three exceptions are observed in limited geographical areas usually at the headwaters of major rivers (Geissmann, 1995) where sympatry has resulted in both mixed species groups (Brockelman & Gittins, 1984) and low level of hybridization (Groves, 1972; Marshall & Brockelman, 1986; Chivers & Burton, 1991; Geissman, 1995). Concerning gibbons we can only talk about a "community" within the range of the siamang (*Symphalangus syndactylus*) who is generally found sympatrically with the agile gibbon (*Hylobates agilis*), in Southern Sumatra, and with the white-handed gibbon (*H. lar*) in northern Sumatra and the Malaya Peninsula (Chatterjee, 2009). The stability of this sympatry is explained by the difference in diet with the siamang which is largely folivorous (MacKinnon, 1977; but see Elder, 2009).

The work of Kanwatanakid-Savini et al. (2009) suggested a clear distinction between the gibbons and hornbills in the feeding assemblage in the largely undisturbed forest of Khao Yai National Park, Thailand, where one species of gibbon was found sympatrically with four species of hornbills. Moreover, two feeding assemblages were described within the four sympatric hornbill species based on large body size (Great and Wreathed Hornbills) and small body size (Oriental Pied and White-throated Brown Hornbills). Similar body size variation, also related to the microhabitat used, was observed between the Red-knobbed and the Sulawesi Tarictic Hornbills (Kinnaird & O'Brien, 2007).

Differences in foraging strategy exist between the two hornbill feeding assemblages with large-bodied hornbill flying over the canopy looking for large emergent fruiting trees (Kemp, 1995) while small-bodied hornbill tend to move through the forest also using smaller fruiting crowns similar to gibbons (Kanwatakid-Savini et al., 2009). It is this difference in feeding behaviour that generate a slightly higher diversity in the diet of small-bodied hornbills compared to large-bodied hornbills (Kanwatakid-Savini et al., 2009), as the birds will not only feed on the few species that generate large crowns but also on smaller fruiting species typical of the understory. Like other Asian primates (Kappeler & Heymann, 1996) greater diet diversity, significantly higher than observed in hornbills, was observed in gibbons. Not only do they move within the forest canopy, as in small-bodied hornbills, foraging in smaller understory crowns, gibbons also have the capacity, like other primates (Fleagle, 1988), to access a larger variety of species by manipulating their food as well as detaching the pulp from seeds through digestion (Kanwatanakid, 2000) which does not limit them to dehiscent fruits as in hornbills (Poonswad et al., 1998). Poulsen et al. (2001) using the number of dispersed species as an indicator of disperser quality suggested that the primate community dispersed more species than the hornbill community in the Dja Reserve, Cameroon.

Overall only a minimal redundancy in diet composition (plant species) is observed between the two species based mainly on fig consumption (Kanwatakid-Savini et al., 2009). The selection of the fruit species to be consumed is based on their size, color, shape, and ease of harvest, which also indicate their nutritional content (Grether et al., 1992). Gibbons provide their dispersal services to a larger number of species, also due to their lower selectivity. During the first six months of the year, gibbons selected 35 plant species between trees and climbers, while, for the same period of the year, both hornbill assemblages selected 26 plant species (Kanwatanakid-Savini, 2009). Like gibbons (McConkey, 2009), hornbills also show a particular interest in climbers (Kitamura et al., 2004b).

In primates, we observe a consistency in the traits selected in fruits (Sourd & Gautier-Hion, 1986, Wrangham et al., 1998) with the priority given to fruits which are yellow or orange in color, covered by a rind-like skin, a sweet juicy pulp, with one or a few well-protected seeds (Gautier-Hion et al., 1985; Sourd & Gautier-Hion, 1986). Gibbons seems to reflect the "primate pattern" in selecting their food with a particular preference for large, yellow colored fruit (red and black appears to be underselected) showing a juicy soft pulp (McConkey et al., 2002). However, the work of McConkey and coauthors (2002) showed that, in addition to fruit characteristics, fruit abundance in the habitat is the major force driving food selection by gibbons.

Fruit selected by Asian hornbills are often of large size as, due to their large bill, they often are among the only consumers (Kitamura et al., 2002); however, smaller fruits are also consumed (Kitamura et al., 2004b). Selected fruits are usually of easy access within the canopy, due to their limited manipulation capacity, show dark colorations such as red, purple or black (Suryadi et al., 1994; Kitamura et al., 2004b) which reflect a general selection pattern in frugivorous birds (Corlett, 1996). As mentioned above, fruit selected by hornbills are generally dehiscent, or indehiscent but only when coated by a thin husk (Kitamura et al., 2004b). In order to limit their body weight while in flight, hornbill consume predominantly dehiscent fruit (Johnson et al., 1985) for which seeds can be easily detached from the flesh with the use of their large bill and then spat out.

Determination of the efficiency of each feeding assemblage. – Following Chapman (1995), seed dispersers can be evaluated based 1) on the number of seeds potentially dispersed, 2) the potential germination of those seeds after dispersal, and 3) the quality of the sites they are deposited. Moreover, we can add 4) the distance from the parent tree at which seeds are dropped (Schupp, 1993).

Size and number of seeds potentially dispersed. – A major distinction between the two taxa is related to what happens to the seed after the fruit containing it is selected. Gibbons generally ingest fruits with an average seed length of 20 mm (McConkey et al., 2002). Larger seeds, up to 40 mm, were sporadically ingested but were considered infrequent in their diet (McConkey, 2000). In hornbills, seed ingested and later regurgitated are smaller, with an average length of 11 mm with maximum length between 32 and 35 mm, during both breeding (Kitamura et al., 2004b) and non-breeding seasons (Kanwatanakid-Savini unpublished PhD data). Hornbills tend to digest usually only very small seeds, 0.05 g in weight, generally from the genus *Ficus* (Kinnaird & O'Brien, 2007).

The amount of ingested fruit, which indicates the number of ingested seeds, is often defined by the time an animal spends in a selected fruiting tree (Savini et al., 2008). This time period is on average similar between gibbons, 20 to 30 minutes (T. Savini unpublished data), and hornbills, between 10 to 30 minutes (Suryadi et al., 1998). When we look at the potential seed dispersal capacity among the different assemblages, we need to take into account the overall density for each assemblage and its relative biomass; as biomass is often used to define the amount of resources consumed in a given area (Kinnaird & O'Brien, 2005) from which the number of dispersed seeds can be extrapolated. White-handed gibbon density at the Mo Singto study area was approximately 17.5 animals per km^2 in 2005 (T. Savini unpublished data). The total hornbill density in the same area was of about 41.4 animals per km^2 with 5.5 animals per km^2 for the large-bodied birds (Great and Wreathed Hornbills) and 35.9 animals per km^2 for the small-bodied birds (Oriental Pied and White-throated Brown Hornbills) for the 2004 – 2006 period (G. A. Gale unpublished data). The total biomass for gibbons was about 105 kg per km^2, higher than what was observed for similar body-sized Hylobatidae (Yanuar, 2009); the total biomass for hornbill 38.7 kg per km^2 with 13 kg per km^2 for the large-bodied birds and 25.8 kg per km^2 for the smaller-bodied birds. From these differences, we can conclude that gibbons overall have the potential to transport a larger amount of seeds followed by smaller-bodied hornbills and lastly by larger-bodied hornbills. However, in the Dja Reserve in Cameroon, Clark et al. (2001) showed that, despite their low density, large frugivorous birds, including hornbills, contributed more seeds to the seed rain than the four sympatric primate species. However, no data on biomass differences between the two taxa were reported, but substantial differences exist between other primates and gibbons with this last group considered, among Asian primates, as one of the most efficient seed dispersers (Corlett, 1998).

Potential germination after dispersion. – A very large proportion of ingested seeds are dispersed by hornbills and gibbons. Hornbills disperse almost 100 % of what they ingest (Kinnaird & O'Brien, 2007), while gibbons disperse 90% (McConkey & Chivers, 2007). Hornbills, due to their "gentle" feeding behaviour, do not harm any of the ingested seeds (Kinnaird & O'Brien, 2007) while gibbons destroy up to 12% of what they ingest (McConkey, 2000). Germination rates for defecated seeds were estimated at 95.5 % for gibbons with 41 % of ingested species having a higher germination after digestion, while only 12 % of the ingested species had a lower germination rate after gut passage (McConkey, 2000). For hornbills, 95.8 % of defecated seeds germinated successfully (Whitney et al., 1998).

Gut passage time, mainly related to seed size both in birds (Holbrook & Smith, 2000; Fukui, 2003) and in primates (Wrangham et al., 1994), was reported to be between 15 and 50 hours for gibbons (McConkey, 2000). Hornbills have a much shorter gut passage time (83 minutes) (Kinnaird & O'Brien, 2007) mainly because of the smaller size of the seeds that they typically ingest. However, for sporadic large seeds ingested, a gut passage time of more than 10 hours was recorded (Holbrook & Smith, 2000). Due to their behaviour of storing seeds in their crops, a regurgitation time was even faster (67 minutes) (Kinnaird & O'Brien, 2007).

Quality of the sites where seeds are deposited. – When seeds accumulate in particular sites, this is typically detrimental for seedling survival, causing similar mortality rates to those found in seeds dropped under parent trees (Krijger et al., 1997). Due to their behaviour, both hornbills and gibbon can cause seed accumulation.

Large seed deposition rate under nesting trees was observed in hornbills (Kinnaird, 1998) probably as a direct consequence of their nesting behaviour and their particularly long nesting period, between 90 and 120 days (Poonswad et al., 2004). For most of the dispersed species, this large deposition under nesting trees indirectly causes high seed mortality as seeds are attacked by the same organisms as if they were dropped, un-dispersed, under their mother tree (Kitamura et al., 2004c). For example, very low survival was found in figs as hornbills mainly consume large stranglers (Kitamura et al*.,* 2002), which do not survive well when dropped on the forest floor (Kitamura et al*.,* 2004c). Overall, accumulations under nesting trees appear limited to breeding hornbills, as the adults which are not breeding due to nest-site limitations (Poonswad, 1995) and the animals not yet sexually mature deposit seeds throughout the forest (Kinnaird, 1998).

During the non-breeding season, seed accumulation occurs under roosting sites re-used on consecutive days, where hornbills can gather in extremely large numbers. Up to 1000 Wreathed Hornbills (*Aceros undulatus*) where observed at a single roosting site in Khao Yai National Park (Poonswad & Kemp, 1993). Low survival under roosting tree crowns, where seedling density was high, was observed as few of the seedlings hardly survived their first year of life, making the dispersion under roosting trees disadvantageous from the plant's perspective (Kitamura et al*.,* 2008). However, due to short gut passage times and regurgitation times in hornbills, only a small proportion of ingested seeds are likely to be deposited under roosting crowns and probably derived from plant from the last feeding bout of the day (Kitamura et al., 2008).

Seeds also often accumulate at primate sleeping nests (Julliot, 1997; Rogers et al., 1998). However, accumulation of dispersed seeds under sleeping trees was less important in gibbons. Overall, only 1.2% of ingested seeds were dispersed under sleeping trees (McConkey, 2000) as gibbons defecate before entering their sleeping tree in the evening and after leaving it in the morning (T Savini personal observation). Overall re-use of night trees on consecutive nights in gibbons is rarely observed, as animals tend to avoid the same trees as an anti-predator strategy (Phoonjampa et al*.,* 2010). Due to their long gut passage time, seeds are never defecated under the parent tree while foraging. However, due to the small size of their home range, gibbons can revisit on consecutive days the same fruiting tree. Because of this, approximately 5.6 % of seeds were defecated by chance under the parent tree (McConkey, 2000). Under fruiting trees, a relatively high defecation rate is observed as gibbon stop here for a long period of time while foraging; however eventual seed accumulation did not seem to affect germination success (McConkey, 1999). As for hornbills, defecated seeds by gibbons do not appear evenly distributed through the forest but can accumulate along frequently used travel pathways, generating regions with higher concentrations of seeds (McConkey, 2000).

Distances from the parent tree seeds are dropped. – Gibbons travel on average 1300 m per day over a home range of approximately 25 ha (Savini et al., 2008) with a maximum linear distance of approximately 500 m (T. Savini unpublished data). In large-bodied hornbills, average daily travel route ranged between 11 and 8.5 km (non-breeding vs. breeding season respectively) over a home range of between 42 and 8 km^2 with an average distance travelled per hour ranging from >1 km in the non-breeding season to 0.6 km in the breeding season (Kinnaird & O'Brien, 2007). Smaller-bodied hornbills travelled on average 4.5 km daily, and 0.4 km per hour, over a home range of about 1 km^2 (Kinnaird & O'Brien, 2007). Thus, both hornbills and gibbons are likely to disperse seeds away from parent trees as seeds deposited only a few crowns from the parent, between 2 to 10 meters, is typically all that is required to increase germination and survival (Becker & Wong, 1985; Schupp, 1988).

Effect of habitat loss on each assemblage. – A botanically intact forest appears beautiful today but will not have a future if the decline of their resident animal community, providing seed dispersal services, continues to decline (Redford, 1992). Due to their importance in forest regeneration, a decline in primate (Wright et al*.,* 2000) and hornbill (Kinnaird & O'Brien, 2007) communities may speed the forest degradation process by altering seed dispersal, seed predation and seedling recruitment processes.

When comparing the general seed dispersal efficiency between gibbons and hornbills, the three major assemblages are similar and both taxa are among the few forest species that can ingest large seeds and disperse them (see table 3 in Kitamura et al*.,* 2002). In pristine habitats, gibbons tend to disperse a larger number of species but over a small area constantly over the year. On the other hand, hornbills tend to disperse over a larger area which, however, changes drastically between breeding and non-breeding seasons. In fragmented habitats, as seed disperser may help re-colonize new sites (Dalling et al., 2002; Levine & Murrell, 2003), gibbons are limited to primary forest patches, as they tend to inhabit only these habitats (Whittaker & Lappan, 2009), where they do not guarantee genetic variability in plants; while hornbills, depending on their body size, can potentially disperse seeds between fragments and increase plant genetic variability. In addition, because some hornbills use disturbed habitats for nesting, they probably serve as agents to their regeneration (Datta, 1998; Kinnaird & O'Brien, 1999). Moreover, small-bodied hornbills such as Oriental Pied Hornbill (*Anthracoceros albirostris*) have been observed nesting in highly disturbed habitat composed of a mix of secondary forest with old plantation in Pulau Ubin, an island off Singapore (Chan et al*.,* 2007).

When looking at animal biomass, we assume a larger importance for gibbons as seed dispersers in intact forest due to their capacity of ingesting a larger number of seeds from an overall larger number of species. However, some redundancy was observed between the two taxa mainly regarding *Ficus*, which appeared to be best dispersed by gibbons as seeds were dropped directly on tree branches while hornbills tended to drop them on the forest floor. However, their seed dispersal activity remain limited to small home ranges located exclusively in pristine habitat. On the other hand, hornbill tend to feed mainly on dehiscent fruits which are usually a low proportion of gibbon diet (T. Savini personal observation). Moreover, due to their capacity for long distance flight, hornbills may play an important role in the maintenance and regeneration of South-east Asian forests which have high rates of deforestation, fragmentation, and disappearance of megafauna (Poonswad & Kemp, 1993; Kinnaird, 1998; Whitney et al*.,* 1998; Holbrook & Smith, 2000; Poulsen et al*.,* 2002; Corlett, 2007; Kinnaird & O'Brien, 2007). However, two questions need to be raised here: (1) what is the capacity of hornbills to fly over disturbed areas to connect forest patches? Species such as the Great Hornbill have been reported flying over agricultural land while moving between closely located forest fragments. However, other species, such as the Helmeted Hornbill do not even fly in proximity of forest edge (Kinnaird & O'Brien, 2007). In this case, other species such as Green and Imperial Pigeon might have a more important role in connecting fragments as they are reported to consume seeds of similar size as hornbills (Kitamura et al., 2002). (2) What is the effect of habitat degradation and fragmentation on hornbill survival? As hornbills are known to prefer large patches of pristine forest (Kemp, 2001) and their numbers have been already reduced by habitat degradation in several areas (Kinnaid & O'Brien, 2007).

In conclusion, both taxa are complementary to each other in the regeneration of tropical forest and the disappearance of either one may drastically affect forest regeneration. Furthermore, the function of macaques, which are also typically found throughout Southeast Asia, as seed dispersers, should be investigated in greater detail. The genus is usually found in sympatry with gibbons, with which they share most of their diet but are capable of surviving in highly degraded habitats, which together with small-bodied hornbill, could actively help in habitat regeneration. However, their function as seed disperser remains controversial as macaque have been shown to be both efficient seed dispersers (Latine et al., 2008) and seed predators (McConkey, 2009).

ACKNOWLEDGEMENTS

A first version of this work was presented at the 5th International Hornbill Conference, 22–25 March 2009, Singapore. We are grateful to the conference organizers, in particular to Bee Choo Ng, for their assistance and financial support. G.A. Gale and R.T. Corlett provided valuable comments on the manuscript.

LITERATURE CITED

Becker, P. & M. Wong, 1985. Seed dispersal, seed predation, and juvenile mortality of *Aglaia* sp. (Meliaceae) in lowland dipterocarp rainforest. *Biotropica*, **17**: 230–237.

Bodmer, R. E., R. Mather & D. J. Chivers, 1991. Rain forests of central Borneo – threatened by modern development. *Oryx*, **25**: 21–26.

Brockelman, W. Y. & S. P. Gittins, 1984. Natural hybridization in the *Hylobates lar* species group: implications for speciation in gibbons. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman & N. Creel (eds.), *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh University Press. Pp. 498-532.

Brodie, J. F., O. E. Helmy, W. Y. Brockelman & J. L. Maron, 2009. Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecology Appications*, **19**: 854–863.

Carpenter, C. R., 1967. *A Field Study in Siam of the Behavior and Social Relations of the Gibbon (*Hylobates lar*).* The John Hopkins Press, New York. 212 pp.

Chan, Y. H., M. Zafirah, M. Cremades, M. Divet, C. H. R. Teo & S. C. Ng, 2007. Infanticide-cannibalism in the Oriental Pied Hornbill *Anthroceros albirostris*. *Forktail*, **23**: 170–173.

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

Chapman, C. A., 1995. Primate seed dispersal: coevolution and conservation implication. *Evolutionary Anthropology* **4**: 74–82.

Chatterjee, H. J., 2009. Evolutionary relationships among the gibbons: a biogeographic perspective. In S. Lappan & D. J. Whittaker (eds.), *The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology*. Springer. Pp. 13-36.

Chivers, D. J. & J. J. Raemaekers, 1986. Natural and synthetic diets of Malayan gibbons. In J. G. Else & P. C. Lee (eds.), *Primate Biology and Conservation*. Cambridge University Press. Pp. 39-56.

Chivers, D. J. & Burton, K.M., 1991. Some observations on the primates of Kalimantan Tengah, Indonesia. *Primate Conservation*, **9**: 138–146.

Clark, J. S., M. Silman, R. Kern, E. Macklin, & J. HilleRisLamers, 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**: 1475–1494.

Clark, C. J., J. R. Poulsen & V. T. Parker, 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica*, **33**: 606–620.

Corlett, R. T., 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. *Journal of Tropical Ecology*, **12**: 819–833.

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

Corlett, R. T., 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica*, **39**: 292–303.

Corlett, R. T. & P. W. Lucas, 1990. Alternative seed-handling strategies in primates: seed spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia*, **82**: 166–171.

Dalling, J. W., H. C. Muller-Landau, S. J. Wright, & S. P. Hubbell, 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology*, **90**: 714–727.

Datta, A., 1998. Hornbill abundance in unlogged forest, selectively logged forest and a forest plantation in Arunachal Pradesh, India. *Oryx*, **32**: 285–294.

Dew, L. J. & P., Wright, 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica*, **30**: 425–437.

Elder, A. A., 2009. Hylobatid diets revisited: The importance of body mass, fruit availability, and interspecific competition. In S. Lappan & D. J. Whittaker (eds.), *The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology*. Springer. Pp. 133-159.

Fleagle, J. G., 1988. *Primate Adaptation and Evolution*. Academic Press, San Diego. 596 pp.

Frankie, E. J., H. G. Baker & P. A. Opler, 1973. Comparative phonological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, **62**: 881–919.

Fukui, A., 2003. Relationship between seed retention time in bird's gut and fruit characteristics. *Ornithological Science*, **2**: 41–48.

Gale, G. A. & S. Thongaree, 2006. Density estimate of nine hornbill species in lowland forest site in southern Thailand. *Bird Conservation International*, **16**: 57–69.

Garber, P. A. & J. E. Lambert, 1998. Introduction to primate seed dispersal. Primate as seed disperser: ecology processes and direction for future research. *American Journal of Primatology*, **45**: 3–8.

Gautier-Hion, A., J. M. Duplantier, R. Quris, R. Feer, C. Sourd, J. P. Decoux, G. Dubost, C. Emmons, C, Erard, D. Hecketswecker, A. Moungazi, C. Roussilhon, & J. M. Thiollay, 1985. Fruits characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, **65**: 324–337.

Geissmann, T., 1995. Gibbon systematics and species identification. *International Zoo News*, **42**: 467–501.

Grether, G. F., R. A. Palombit & P. S. Rodman, 1992. Gibbon foraging decisions and the marginal value model. *International Journal of Primatology*, **13**: 1–17.

Groves, C. P., 1972. Systematics and phylogeny of gibbons. In Rumbaugh, D. M. (ed.), *Gibbon and Siamang. Vol. 1: Evolution, Ecology, Behavior, and Captive Maintenance*. Karger. Pp. 1-89.

Holbrook, K. & T. B. Smith, 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, **125**: 249–257.

Howe, H. F., 1989. Scatter- and clump-dispersal and seedling demography: hypotheses and implications. *Oecologia*, **79**: 417–426.

Howe, H. F. & G. F. Estabrook, 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist*, **111**: 817–832.

Howe, H. & J. Smallwood, 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**: 201–228.

Janzen, D. H., 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**: 501–528.

Johnson, R. A., M. F. Willson, J. N. Thompson & R. I. Berton, 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology*, **66**: 819–827.

Julliot, C., 1997. Impact of seed dispersal by red howler monkeys *Alouatta seniculus* on the seedling population in the understorey of tropical rain forest. *J. Ecol.*, **85**: 431–440

Kanwatanakid, C., 2000. Characteristics of fruit consumed by the white-handed gibbon (*Hylobates lar*) in Khao Yai National Park, Thailand. M.Sc. dissertation. Mahidol University, Bangkok. 130 pp.

Kanwatanakid, C. & W. Y. Brockelman, 2005. Characteristics of fruits consumed by the White-handed gibbon *(Hylobates lar)* at Khao Yai National Park, Thailand. In: Poonswad, P. (ed.), *Proceedings the Third International Hornbill Workshop*, *The Ecology of Hornbills: Reproduction and Populations.* Pimdee Karnpim. Pp. 97-116.

Kanwatanakid-Savini, C., P. Poonswad & T. Savini, 2009. An assessment of food overlap between gibbons and hornbills. *The Raffles Bulletin of Zoology*, **57**: 189–198.

Kappeler, P. M. & E. W. Heymann, 1996. Nonconvergence in the evolution of primate life history and socio-ecology. *Biological Journal of the Linnean Society*, **59**: 297–326.

Karr, J. R. & K. E. Freemark, 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. *Ecology*, **64**: 1481–1494.

Kemp, A. C., 1995. *The Hornbills: Bucerotiformes*. Oxford University Press, Oxford. 302 pp.

Kemp, A. C., 2001. Family Bucerotidae (hornbills). In: del Hoyo, J., A. Elliott & J. Sargatal (eds.), *Handbook of the Birds of the World. Vol. 6: Mousebirds to Hornbills*. Lynx Edicions. Pp. 436-523.

Kinnaird, M. F., 1998. Evidence for effective seed dispersal by the Sulawesi red-knobbed hornbill, *Aceros cassidix. Biotropica*, **30**: 50–55.

Kinnaird, M. F. & T. G. O'Brien, 1999. Breeding ecology of the Sulawesi red-knobbed hornbill *Aceros cassidix*. *Ibis*, **141**: 60–69.

Kinnaird, M. F. & T. G. O'Brien, 2005. Fast food in the forest: the influence of figs on primate and hornbills across Wallacea's line. In: Dew, J. L. & J. P. Boubli (eds.), *Tropical Fruit and Frugivores*. Springer. Pp. 155-184.

Kinnaird, M. F. & T. G. O'Brien, 2007. *The Ecology and Conservation of Asian Hornbills*. The University of Chicago Press, Chicago. 302 pp.

Kinnaird, M. F., T. G. O'Brien, & J. R. Sinclair, 1998. The role of Sulawesi red-knobbed hornbills *Aceros cassidix* in seed dispersal. In: Poonswad, P. (eds.), *The Asian Hornbills: Ecology and Conservation*. Thai Studies in Biodiversity No 2, BIOTEC, NSTDA. Pp. 124-136.

Kitamura, S., T. Yumoto, P. Poonswad, P. Chuailua, K. Plongmai, T. Maruhashi & N. Noma, 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia*, **133**: 559–572.

Kitamura, S., S. Suzuki, T. Yumoto, P. Poonswad, P. Chuailua, K. Plongmai, N. Noma, T. Maruhashi & S. Suckasam, 2004a. Dispersal of *Aglaia spectabilis*, a large-seeded tree species in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, **20**: 421–427.

Kitamura, S., T.,Yumoto, P. Poonswad, P. Chuailua & K. Plongmai, 2004b. Characteristics of hornbill-dispersed fruits in a tropical seasonal forest in Thailand. *Bird Conservation International*, **14**: S81–S88.

Kitamura, S., T. Yumoto, P. Poonswad, N. Noma, P., Chuailua, K. Plongmai, T. Maruhashi & S. Suckasam, 2004c. Pattern and impact of hornbill seed dispersal at nest trees in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, **20**: 545–553.

Kitamura, S., T., Yumoto, N., Noma, P., Chuailua, T., Maruhashi, P. Wohandee, and P. Poonswad, 2008. Aggregated seed dispersal by wreathed hornbills at a roost site in a moist evergreen forest of Thailand *Ecological Research*, **23**: 943–952

Krijger, C. L., M. Opdam, M. Thery & F. Bongers, 1997. Courtship behaviour of manakins and seed bank composition in a French Guianan rain forest. *Journal of Tropical Ecology*, **13**: 631–636.

Lambert, J. E., 1999. Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *American Journal of Physical Anthropology*, **109**: 365–386.

Lappan, S. & D. J. Whittaker, 2009. *The Gibbons: New Perspective on Small Ape Socioecology and Population Biology*. Springer, New York. 523 pp.

Latine, A, M.-C. Huynen, & T. Savini, 2008. Feeding ecology and seed dispersal of pigtail macaque (*Macaca nemestrina*) in Khao Yai National Park, Thailand. *Folia Primatologica*, **79**: 348.

Lawrence, W. F., 1999. Reflection on the tropical deforestation crisis. *Biological Conservation*, **91**: 109–117.

Leighton, D. R., 1998. Gibbons, territoriality and monogamy. In: Smuts, B.B., D. L. Cheney, R. M. Syfarth, R. W. Wrangham & T. T. Struhsaker (eds.), *Primate Societies.* Chicago University Press. Pp. 135-145.

Levine, J. M. & D. J. Murrell, 2003. The community level consequences of seed dispersal patterns. *Annual Review of Ecology and Systematics*, **34**: 549–574.

MacKinnon, J., 1977. A comparative ecology of Asian apes. *Primates*, **18**: 747–772.

Marshall, J. T. & W. Y. Brockelman, 1986. Pelage of hybrid gibbons (*Hylobates lar*×*H. pileatus*) observed in Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society*, **34**: 145–157.

McConkey, K. R., 1999. Gibbons as seed dispersers in the rain-forests of central Borneo. Ph.D. dissertation. Cambridge University, Cambridge. 286 pp.

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**: 13–29.

McConkey, K. R., 2005. The influence of gibbon primary seed shadows on post-dispersal seed fate in a lowland dipterocarp forest in Central Borneo. *Journal of Tropical Ecology*, **21**: 255–262.

McConkey, K. R., 2009. The seed dispersal niche of gibbons in Bornean dipterocarp forests. In: Lappan, S. & D.J. Whittaker (eds.), *The Gibbons: New Perspective on Small Ape Socioecology and Population Biology*. Springer. Pp. 189-207.

McConkey K. R. & D. J. Chivers, 2007. Influence of gibbon ranging patterns on seed dispersal distance and deposition site in a Bornean forest. *Journal of Tropical Ecology*, **23**: 269–275.

McConkey, K. R., F. Aldy, A. Ario & D. J. Chivers, 2002. Selection of fruit by gibbons (*Hylobates muelleri* x *agilis*) in the rain forest of Central Borneo. *International Journal of Primatology*, **23**: 123–145.

McConkey, K. R., A. Ario, F. Aldy & D. J. Chivers, 2003. The influence of forest seasonalityongibbon food choice in the rain-forests of central Borneo. *International Journal of Primatology*, **24**: 19–32.

Packer, A. & K. Clay, 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, **404**: 278–281.

Phoonjampa, R., A. Koenig, C., Borries, G. A. Gale, & T. Savini, 2010. Selection of sleeping trees in pileated gibbons (*Hylobates pileatus*). *American Journal of Primatology*, **72**: 617–625.

Poonswad, P., 1995. Nest site characteristics of four sympatric species of hornbills in Khao Yai National Park, Thailand. *Ibis*, **137**: 183–191.

Poonswad, P. & A. C. Kemp, 1993. *Manual to the Conservation of Asian Hornbills*. Hornbill Project Thailand, Bangkok. 370 pp.

Poonswad, P., A., Tsuji, N. Jirawatkavi & V. Chimchome, 1998. Some aspects of food and feeding ecology of sympatric hornbills in Khao Yai National Park, Thailand. In: Poonswad, P. (eds.), *The Asian Hornbills: Ecology and Conservation*. Thai Studies in Biodiversity No 2, BIOTEC, NSTDA. Pp. 137-157.

Poonswad, P., A. Tsuji, & N. Jirawatkavi, 2004. Estimation of nutrients delivered to new inmates by four sympatric species of hornbill in Khao Yai National Park, Thailand. *Ornithological Science*, **3**: 99–112.

Poulsen, J. R., C. J., Clark & T. B. Smith, 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, **17**: 787–808.

Poulsen, J. R., C. J., Clark, E. F. Connor & T. B. Smith, 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, **83**: 228–240.

Redford, K. E., 1992. The empty forest. *BioScience*, **42**: 412–422.

Rogers, M. E., B. C. Voysey, K. E., McDonald, R. J. Parnell & C. E. G. Tutin, 1998. Lowland gorillas and seed dispersal: the importance of nest sites. *American Journal of Primatology*, **45**: 45–68.

Rowell, T. E. & B. J. Mitchell, 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology*, **7**: 269–274.

Savini, T., C., Boesch & U. H. Reighard, 2008. Home range characteristics and the influence of seasonality on female reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. *American Journal of Physical Anthropology*, **135**: 1–12.

Schupp, E. W., 1988. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia*, **76**: 525–530.

Schupp, E. W., 1993. Quantity, quality and the effectiveness dispersal by animals. *Vegetatio*, **107/108**: 15–29.

Sourd, C. & A. Gautier-Hion, 1986. Fruit selection by a forest guenon. *Journal of Animal Ecology*, **55**: 235–244.

Sun, C., A. R. Ives, H. J. Kraeuter & T. C. Moermond, 1997. Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia*, **112**: 94–103.

Suryadi, S., M. F. Kinnard, T. G. O'Brien, J., Supriatna & S. Somadikarta, 1994. Food preferences of the Sulawesi Red-knobbed Hornbill during the non breeding season. *Tropical Biodiversity*, **2**: 377–384.

Suryadi, S., M. F. Kinnard & T. G. O'Brien, 1998. Home range and daily movement of the Sulawesi Red-knobbed hornbill *Aceros cassidix* during the non-breeding season. In: Poonswad, P. (eds.), *The Asian Hornbills: Ecology and Conservation*. Thai Studies in Biodiversity No 2, BIOTEC, NSTDA. Pp. 159-170.

Swaine, M. D., D. Lieberman & F. E. Puts, 1987. The dynamics of tree populations in a tropical forest. *Journal of Tropical Ecology*, **3**: 356–367.

Whitington, C. & U. Treesucon, 1991. Selection and treatment of food plants by white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society*, **39**: 111–122.

Whitney, K. D., M. F. Fogiel, A. M. Lamperti, K. M. Holbrook, D. J. Stauffer, B. D. Hardesty, V. T. Parker & T. B. Smith, 1998. Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, **14**: 351–371.

Whittaker, D. J., 2009. Saving the Small Apes: Conservation Assessment of Gibbon Species at the 2006 Asian Primate Red List Workshop In: Lappan, S. & D.J. Whittaker (eds.), *The Gibbons: New Perspective on Small Ape Socioecology and Population Biology*. Springer. Pp. 497-499.

Whittaker, D. J. & S., Lappan, 2009. The Diversity of Small Apes and the Importance of Population-Level Studies. In: Lappan, S. & D.J. Whittaker (eds.), *The Gibbons: New Perspective on Small Ape Socioecology and Population Biology*. Springer. Pp. 3-10.

Wrangham, R. W., C. A. Chapman & L. J. Chapman, 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology*, **10** :355–368.

Wrangham, R. W., N. L. Conklin-Brittain & K. D. Hunt, 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I Antifeedants. *International Journal of Primatology*, **19**: 949–970.

Wright, S. J., H. Zeballos, I. Dominguez, M. M. Gallardo, M. C. Moreno & R. Ibanez, 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology*, **14**: 227–239.

Yanuar, A., 2009. The population, distribution and abundance of Siamangs (*Symphalangus syndactylus*) and Agile Gibbons (*Hylobates agilis*) in West Central Sumatra, Indonesia. In: Lappan, S. & D.J. Whittaker (eds.), *The Gibbons: New Perspective on Small Ape Socioecology and Population Biology*. Springer. Pp. 453-465.