

Chapter 5

Frugivory and Seed Dispersal by Large Herbivores of Asia

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Abstract Seed dispersal is a key ecological process with ~50–80 % of all tropical plants depending on animals to provide this service. Wide-ranging and large-bodied species are believed to play a disproportionately important role in the seed dispersal process. Although mounting evidence demonstrates a strong role for large herbivores in seed dispersal, our broad knowledge of this interaction remains surprisingly rudimentary. In this chapter, we partially bridge this knowledge gap for South and Southeast Asia (SSEA). We start by synthesizing known information on how the sensory ecology of these animals aid in locating fruit. Next, we review the fruits consumed and dispersed by distinct large herbivore groups, and the influence of their digestive physiology on seed dispersal patterns. We collated more than 300 records of frugivory and/or seed dispersal for 27 species of large herbivores. The data suggests that smaller species of large herbivores may be constrained in the size of fruits they can consume while larger species are not. An assessment of overlap in the traits of fruits consumed indicates much more dissimilarity between groups of large herbivores than previously thought. Finally, we examine the implications of

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this interaction both from a historical perspective and for the future. Despite the broad-scale synthesis achieved, we conclude that information on seed dispersal services provided by large herbivores in SSEA remains largely incomplete.

Keywords Large herbivores · Ungulates · Seed dispersal · Frugivory · Plant animal interactions

5.1 Introduction

Seed dispersal is a key ecological process influencing the spatial patterns and population dynamics of plants (Wang and Smith 2002). Low rates of seedling recruitment under the canopies of parent trees make seed dispersal essential for many plant species (Nathan and Muller-Landau 2000; Matthesius et al. 2011). Disruptions to the seed dispersal process can have profound consequences for ecosystem function and resilience (Terborgh 2013). In tropical ecosystems, 50–80 % of plants are dispersed by vertebrate fauna (Jordano 2000). However, vertebrate frugivores are highly variable in their effectiveness as seed dispersers. Within the community of seed dispersers, certain frugivore species tend to have disproportionately important functional roles (Jordano et al. 2007; Donatti et al. 2011). Large and highly mobile frugivores often have non-redundant seed dispersal roles in the habitats they occupy (Lundberg and Moberg 2003). Due to constraints on the size of seeds that can be processed by smaller frugivores, large-bodied frugivores can consume fruits that are accessible only to a limited number of frugivores, such as large or well protected fruits (Janzen and Martin 1982; Kitamura et al. 2002). Large frugivores also disperse very large quantities of seeds and over much longer distances compared to smaller frugivores within communities (Janzen and Martin 1982; Spiegel and Nathan 2007; Lundberg and Moberg 2003).

Large herbivores constitute some of the most wide-ranging fruit-eating animals in the world, with the incidence of frugivory being greatest among tropical species (Bodmer 1990). Tropical Asia supports over 80 species of large herbivores (>2 kg) belonging to nine families (Groves and Grubb 2011, see Table 1.1) and occupying a wide range of habitats, from arid zones to rainforests (Wilson and Mittermeier 2011). Asia is a hot spot for deer radiation (Geist 1998, also see Chap. 2), has the highest diversity of extant pig species (Meijaard et al. 2011), and the only forest-dependent rhinoceros species (van Strien et al. 2008). This high diversity and abundance of large herbivores may have been a key causative factor for the differences in the flora and fauna between tropical Asia and other tropical regions (Corlett 2007). Fruits are consumed by species from all herbivore families to varying degrees (Bodmer 1990; Corlett 1998), yet relationships between large herbivores and the seeds they disperse are poorly understood.

The relative role of large herbivores in seed dispersal can be understood when compared with the rest of the disperser community. However, comprehensive

assessments of seed dispersal at community scales, especially for diverse tropical regions, are very limited. In an undisturbed tropical dry forest with an intact faunal assemblage in India, large herbivores had the greatest contribution to seed dispersal of the plant community; dispersing 31 % of the 67 plants available (Prasad 2011). In a disturbed tropical wet forest in Malaysia, large herbivores interacted with 26 % of 49 plant species (Yasuda et al. 2005), while in a relatively undisturbed tropical wet forest site in Thailand, large herbivores dispersed only 6 % of the plant species, although they interacted with 18 % of the plant community (Kitamura et al. 2002). One report from an African wet forest indicates that large herbivores interact with over 50 % of the plant community (Gautier-Hion et al. 1980, 1985). However, except for Prasad (2011), few studies have used approaches that allowed robust sampling of frugivory by large herbivores which are mostly terrestrial frugivores feeding on fallen fruit. Consequently, these studies may have under-estimated the contribution of large herbivores to seed dispersal processes. Additionally, most sites in tropical Asia have already suffered a decline of large fauna due to hunting and habitat degradation, and thus large herbivores are likely to be under represented in these communities. While existing community-wide datasets from tropical Asia, though incomplete, suggest variability in the relative role of large herbivores as dispersers, they nevertheless highlight a community-wide influence. Given the enormous potential of large herbivores in SSEA to play a functionally unique role in seed dispersal, a better understanding of their interactions with associated plant communities is essential.

Insights into the relationships between large herbivores and fruits in Asia are also vital due to the widespread population declines of many species caused by hunting, habitat destruction and competition from domestic livestock (Corlett 2007, see Chap. 11). Hunting in many parts of Asia has depressed large herbivore populations to critically low levels or extirpated them locally (Robinson and Bennett 2000; Corlett 2007). Additionally, the habitats of Asian large herbivores are among the most fragmented in the world (Riitters et al. 2000; Karanth et al. 2010). The consequences of such large-scale disturbances for seed dispersal can be dramatic, from preventing plant migration in the face of climate change to a total collapse of dispersal function (McConkey et al. 2012; Corlett and Westcott 2013). Mitigating such effects requires a deeper understanding of the role of large herbivores as seed dispersers. In this chapter, we examine the nature of these interactions by reviewing known information on fruits consumed and seeds dispersed by large herbivores. First, we summarize studies examining the role of sensory cues in large herbivores to locate fruit in the forest. Next, we review fruit selection, the nature and outcome of fruit processing by large herbivores, and examine the relationship between fruit size and herbivore body size. Finally, we conclude by discussing the effects historical and recent declines in large herbivores have had at the community level, in light of the interactions we describe above.

5.2 Data Compilation

We compiled a database of fruits known to be consumed by large herbivores across tropical Asia and noted whether the seeds within them were either dispersed or destroyed. Data were collated from published articles, books, reports, theses, unpublished results and personal observations of researchers. Information on fruit traits such as length, width and weight of fruits and seeds, and fruit type were obtained from both primary and secondary sources. Secondary sources included digital floras, information from herbariums and databases maintained by individual researchers or institutions. Fruit and seed measurements were restricted to two dimensions—maximum length and width. When multiple measures existed or were provided as a range, the mean or mid-point was recorded, respectively. The diameter of globular fruits and seeds was taken as both length and width. Plants that were not identified to a species level, but had associated fruit trait data, were retained for the analysis. Herbivore action on seeds was recorded as dispersed or destroyed when available. If dispersal or predation records were ambiguous, fruits were recorded as being “consumed” only.

Herbivore traits were obtained from a combination of primary and secondary sources. A single mean value was computed when ranges or multiple values were available. Traits recorded included body weight (kg), home range size (ha), daily movement range (m), digestive physiology, and IUCN status. All binomial names follow the IUCN listing.

5.3 How Do Large Herbivores Locate and Select Fruit?

It is unlikely that large herbivores rely solely (or even largely) on sensory cues when locating fruits. Fruit crops last days or weeks, so returning to previously rewarding locations is a strategy that is probably used by all frugivores (Corlett 2011). A combination of spatial and temporal memory would allow long-lived animals to return annually to preferred fruiting plants (Campos-Arceiz and Blake 2011). However, sensory information is needed for precise location of individual fruits and for the detection of newly ripened fruit crops. As far as is known, all large herbivore species have the “typical” forms of all the major mammalian senses: vision, touch, hearing, smell and taste.

Vision enables the herbivore to locate and identify food resources, including fruits. All large herbivore species that have been tested appear to be typical dichromats, with two spectrally distinct cone types. They are most sensitive in the blue to yellow-green part of the human visual spectrum and lack discrimination ability at the orange-red end (Ahnelt and Kolb 2000; Peichl 2005; Schiviz et al. 2008; Corlett 2011; Jacobs 2012). Fruits that are red or orange and eaten by large herbivores are likely to be eaten most by trichromatic primates or tetrachromatic birds (Corlett 2011). In low light the cones are inactive and rods take over, making

vision monochromatic, with peak sensitivity in the blue–green. As in most mammals, rods dominate the retinas of all herbivores that have been studied. As well as colour, herbivores can potentially use brightness (lightness) to distinguish fruits from their background, under both high and low light conditions, but the relative importance of this is unknown.

Visual acuity may be more important than colour or brightness discrimination in locating fruit, but lack of standardization in the methods by which this is measured makes comparisons among taxa difficult. In general, it appears that acuity is low in large herbivores (Corlett 2011). Visual acuity is relatively higher in open-country species, such as horses, where it is presumably essential for predator avoidance, and lower in forest species, such as pigs and mouse deer (Schiviz et al. 2008; Sugnaseelan et al. 2013). Even at close range, domestic pigs failed to discriminate visual cues <20 mm across (Zonderland et al. 2008). In contrast, Asian elephants can apparently discriminate cues 5 mm across at a distance of 2 m (i.e. at the tip of the trunk) (Shyan-Norwalt et al. 2010).

If an animal cannot see a fruit, it may be able to detect the fruit by either touch, the sound the fruit makes when falling, or by the smell of the fruit. The vibrissae (tactile hairs or whiskers) around the mouths of all herbivores are tactile sense organs (Ahl 1986) that may help detect fruits on the ground, although this has not been studied. A pig's entire snout seems to have the same function, and fallen fruits hidden in litter are presumably detected snout-first. Hearing is potentially useful for not only detecting the sound of falling fruits, but also the noise from feeding arboreal frugivores that many terrestrial frugivores follow (Prasad and Sukumar 2010). The ability to accurately localize sounds seems to vary considerably across large herbivores, being high in pigs and elephants, but low in domestic cattle (Heffner and Heffner 1992).

Olfaction is often assumed to have a dominant role in the mammalian sensory system, with the exception of primates (Corlett 2011), but comparisons between senses are difficult to make. Asian elephants are better at odour discrimination than humans, mice and macaques (Rizvanovic et al. 2013) and indirect evidence suggests that this may also be true for pigs and deer (Graves 1984; Rizvanovic et al. 2013). The sense of taste offers the last opportunity for rejecting a fruit before swallowing (Corlett 2011). Large herbivores appear to have the same five basic tastes as humans (sweet, salty, sour, umami and bitter) (Ginane et al. 2011; Jiang et al. 2012). However, the details of what is detected as sweet or, in particular, bitter, are known to vary considerably across mammalian taxa and it is possible that this influences fruit choice in herbivores.

Finally, a diet based on sensory cues alone would inevitably be nutritionally unbalanced, since these cues are imperfect proxies for nutritional value (Corlett 2011; Cazetta et al. 2012). Preferences for colours, odours and tastes need to be fine-tuned by the post-ingestive physiological feedbacks that enable an animal to eat more of what it needs and less of what it does not need. This “diet learning” ability has been widely demonstrated in domestic herbivores and can be assumed to be present in their wild relatives too (Provenza 1995; Yearsley et al. 2006).

5.4 Fruit (or Seed) Selection, Processing and Deposition

In addition to variation in sensory ecology outlined above, differences in body size, digestive physiology, nutritional requirements, and habitat specificity may influence fruit choice by large herbivores. The nature of seed processing, seed retention times and consequently the seed shadows generated by large herbivores for endozoochorously dispersed seeds are primarily influenced by the digestive anatomy and physiology of herbivores, which shows tremendous variation among herbivore families. The outcome of this plant–herbivore interaction determines whether the herbivore is a disperser or a seed predator, the distances to which seeds are transported and the deposition of seeds to particular habitats (Brodie et al. 2009a, b; Velho et al. 2012a, b; Jadeja et al. 2013). In this section, we summarize relationships between fruit traits and the outcome of seed processing by large herbivores in relation to the digestive anatomy and physiology of large herbivores.

Based on their digestive anatomy and physiology, Asian large herbivores can be broadly classified into three groups which reflect similarities in seed processing: (1) foregut fermenters or ruminants (mouse–deer, muntjac, deer, antelope and wild cattle), (2) simple-stomach frugivores (pigs, babyrusa) and (3) simple-stomach folivores (tapirs, wild ass, rhinoceros and elephant). Although processing varies within these groups, the overlap in characteristics merits a synthesis among the distinct groups.

5.4.1 Foregut Fermenters (*Tragulidae*, *Cervidae* and *Bovidae*)

In SSEA, extant ruminants belonging to three families—*Tragulidae* (eight species), *Cervidae* (20 species), and *Bovidae* (30 species)—constitute the majority of large herbivores. We were unable to find information on frugivory and seed dispersal by *Moschidae* (musk deer, 5 species) and so do not consider them any further here. Ruminants range in size from 2 to 1000 kg; chevrotains (*Tragulidae*) and muntjacs (*Cervidae*) occupy the lower end of this spectrum (2–20 kg), while wild cattle (*Bovidae*; 240–850 kg) are comparable in size to rhinoceroses (Table 5.1). It has been suggested that the digestive physiology of ruminants may have evolved for a frugivorous diet, later diversifying for folivory (Bodmer 1989; Gagnon and Chew 2000; Clauss et al. 2003).

Theories based on energetics, digestive physiology and allometry predict that smaller ruminants should consume more fruits than larger species (Jarman 1974; Hofmann 1989; Wenninger and Shipley 2000; Clauss et al. 2003). Specifically, energy requirements per unit mass increase with declining body size, necessitating small ruminants to ingest food items of high quality, such as fruits. Additionally, their smaller digestive tracts have faster passage rates associated with lower digestion efficiency (Hofmann and Stewart 1972; Demment and van Soest 1985;

Table 5.1 Traits of large herbivores recorded to consume fruits, listed by increasing weight; IS–IUCN status: DD–data deficient, LC–least concern, NT–near threatened, VU–vulnerable, EN–endangered, CE–critically endangered; SC–number of species whose fruits were consumed; WT–body weight in kg; HR–home range in hectares; DMR–daily movement rate in m; HAB–habitat type; DA–digestive anatomy: R-3C–ruminant with three chambered stomach, R-4C–ruminant with four chambered stomach, S-FR–simple-stomach frugivore, S-FO–simple-stomach folivore

Species	Family	IS	SC	WT	HR	DMR	HAB	DA	Ref
<i>Tragulus javanicus</i>	Tragulidae	DD	22	2	4.85	546	Forest	R-3C	1, 2
<i>Moschiola indica</i>	Tragulidae	LC	6	3	–	–	Forest	R-3C	3
<i>Tragulus napu</i>	Tragulidae	LC	10	7	2.5	–	Forest	R-3C	2
<i>Muntiacus atherodes</i>	Cervidae	LC	18	16	6.2	–	Forest	R-4C	1
<i>Muntiacus muntjak</i>	Cervidae	LC	78	20	6	–	Forest	R-4C	1, 3, 4
<i>Tetracerus quadricornis</i>	Bovidae	VU	2	20	–	–	Open forest	R-4C	5
<i>Gazella bennettii</i>	Bovidae	LC	10	23	–	–	Grassland	R-4C	6
<i>Antilope cervicapra</i>	Bovidae	NT	1	30	766	–	Grassland	R-4C	7
<i>Axis porcinus</i>	Cervidae	EN	11	37	51.25	252	Grassland	R-4C	8
<i>Sus cebifrons</i>	Suidae	CE	2	45	–	–	Forest	S-FR	9
<i>Sus celebensis</i>	Suidae	NT	1	55	–	–	Generalist	S-FR	9
<i>Sus barbatus</i>	Suidae	VU	31	70	–	500	Forest	S-FR	9
<i>Babyrousa babyrussa</i>	Suidae	VU	8	70	–	–	Forest	S-FR	10
<i>Axis axis</i>	Cervidae	LC	40	72	169	–	Open forest	R-4C	3, 11
<i>Sus verrucosus</i>	Suidae	EN	2	90	–	–	Open forest	S-FR	9
<i>Rucervus eldii</i>	Cervidae	EN	8	100	814.5	–	Open forest	R-4C	12, 13
<i>Babyrousa togeanensis</i>	Suidae	EN	6	100	–	–	Forest	S-FR	9
<i>Sus scrofa</i>	Suidae	LC	62	135	1800	8400	Generalist	S-FR	9, 14
<i>Rusa unicolor</i>	Cervidae	VU	73	200	900	–	Forest	R-4C	3, 11, 15
<i>Boselaphus tragocamelus</i>	Bovidae	LC	15	240	8800	2150	Open forest	R-4C	16
<i>Equus hemionus</i>	Equidae	EN	15	250	2800	7500	Desert	S-FO	17
<i>Tapirus indicus</i>	Tapiridae	EN	16	350	1275	2160	Forest	S-FO	18, 19
<i>Dicerorhinus sumatrensis</i>	Rhinocerotidae	CE	18	750	2500	7500	Forest	S-FO	20

(continued)

Table 5.1 (continued)

Species	Family	IS	SC	WT	HR	DMR	HAB	DA	Ref
<i>Bos gaurus</i>	Bovidae	VU	23	850	11200	4000	Forest	R-4C	11, 21
<i>Rhinoceros sondaicus</i>	Rhinocerotidae	CE	5	1350	14500	–	Forest	S-FO	22
<i>Rhinoceros unicornis</i>	Rhinocerotidae	VU	14	2350	5000	–	Grassland	S-FO	23, 24
<i>Elephas maximus</i>	Elephantidae	EN	84	4000	41700	4000	Generalist	S-FO	25, 26, 27

1-Heydon (1994), 2-Yasuda et al. (2005), 3-Prasad (2011), 4-Kitamura et al. (2002), 5-Baskaran et al. (2011), 6-Dookia and Jakher (2007), 7-Jadeja et al. (2013), 8-Dhungel and O’Gara (1991), 9-Meijaard et al. (2011), 10-IUCN species account, 11-Schaller (1967), 12-Aung et al. (2001), McShea et al. (2001), 14-Mitchell et al. (2009), 15-Sankar (1994), 16-Jamal (1994), 17-Ghasemi et al. (2012), 18-Campos-Arceiz et al. (2012), 19-O’Farrill et al. (2013), 20-Flynn (1978), 21-Krishnan (1972), 22-Corbet and Hill (1992), 23-Dinerstein and Wemmer (1988), Dinerstein (1991), 25-Samansiri and Weerakoon (2008), 26-Kitamura et al. (2007), 27-Campos-Arceiz and Blake (2011)

Clauss et al. 2003). Conversely, fruits may not be dominant in the diet of larger ruminants, which are more efficient at processing more abundant lower quality food items such as grass and leaves (Clauss et al. 2013). Nevertheless, frugivory is reported from several species of ruminants (Table 5.2) and medium-sized ruminants can be seasonally very frugivorous (John Singh 1981). There are fewer reports of frugivory by larger ruminants such as wild cattle (genera *Bos* and *Bubalis*), nilgai (*Boselaphus tragocamelus*) or sambar (*Rusa unicolor*) compared to small and medium-sized ruminants such as muntjac (*Muntiacus muntjac*) and chital (*Axis axis*). From available records, it appears that the extent of frugivory may be higher in small to medium-sized ruminants (e.g. tragulids, muntjacs and *Axis* deer).

All ruminants house symbiotic bacteria in their fore-stomachs. While cervids and bovids have a four-chambered stomach, the third stomach chamber in tragulids is poorly developed or completely absent (Agungpriyono et al. 1992). Ruminants have strong molars and seeds can be destroyed during repeated chewing (Bodmer 1989). While some ruminants have been documented to swallow fruits whole (Chen et al. 2001; Prasad et al. 2006; Jadeja et al. 2013), others may chew fruits too large to swallow (Feer 1995). The orifice between the first and second stomach chambers constrains the size of food particles that can pass through the fore-stomach, resulting in two distinct seed dispersal mechanisms. First, seeds that are small enough to pass through the fore-stomach (typically <1 mm) are defecated intact (Demment and van Soest 1985; Mouissie et al. 2005; Jadeja et al. 2013). Second, larger seeds, typically drupes (fleshy fruit which have seeds encased in a stony wall, providing strong protection) that can survive repeated mastication during rumination are spat out after being stored in the rumen (first stomach chamber) for several hours (Chen et al. 2001; Prasad et al. 2006). These two distinct mechanisms of dispersal are perhaps associated with significantly different seed retention times, survival probabilities, and germination success, all of which eventually determine the efficacy of ruminants as dispersers. Based on the limited number of both plant and ruminant species that have been examined for damage or germination,

Table 5.2 Traits of fruit and seed consumed or dispersed by large herbivores of Asia. Numbers indicate the total in each category

Group	Life form of plants	Fruit type	Fruit colour	Largest fruit consumed (mm)	Largest seed dispersed (mm)
<i>Traquilidae</i>	Tree 32	Drupe 15; Berry 5; Capsule 3; Pod 2	Green 10; Yellow 3; Brown 3	80 × 80	23 × 17
<i>Muntjacs</i>	Tree 78; Liana 6; Shrub 3; Palm 1	Drupe 30; Berry 17; Capsule 10; Fig. 6; Pod 1	Yellow 30; Red 12; Black 12; Purple 7; Orange 6	87 × 84	80 × 80
<i>Large cervids</i>	Tree 53; Shrub 6; Vine 4; Liana 3	Drupe 30; Berry 17; Pod 8; Fig. 2	Yellow 11; Green 8; Red 6; Black 5	548 × 19	35 × 17
<i>Bovidae</i>	Tree 27; Shrub 5; Vine 3; Herb 2	Drupe 12; Pod 8; Berry 7	~3 each of Black, Green, Yellow, Red	548 × 19	9 × 7
<i>Babirusa</i>	Tree 11; Vine 1	Drupe 6; Complex fruit 3; Berry 2; Pod 2	Yellow, Green, Black, Brown ~ 2 each	350 × 125	48 × 28
<i>Pigs</i>	Tree 47; Shrub 8; 4 of Palm & Grass; 3 of Vine & Herb	Drupe: 23; Dry fruit 15; Berry 12; Complex fruit 6; Pod 5	Red 18; Yellow 11; Brown 8; Green 5; Black 4; Orange 4; Purple 4; White 3; Blue 2; Pink 1	350 × 125	48 × 28
<i>Elephants</i>	Tree 45; Herb 19; Vine 10; Grass 8; Shrub 6; Palm 2	Pod 22; Berry 20; Drupe 16; Complex fruit 9; Grass 7; Capsule 4; Dry fruit 1	Yellow 13; Brown 10; Red 9; Green 5; Black 3; Purple 3; Orange 1	375 × 175	39 × 26
<i>Rhinoceros</i>	Tree 19; Herb 6; Vine 4; Shrub 3	Berry 9; Drupe 6; Capsule 5; Complex fruit 4; Pod 4	Brown 7; Red 4; Yellow 4; Green 3; Purple 2; Orange 1; White 1	300 × 200	30 × 23
<i>Tapirs</i>	Tree 15	Complex fruit 6; Capsule 4; Drupe 4; Berry 2	Green 4; Yellow 3; Brown 2; 1 each of Red, Purple, Black and Orange	132 × 100	39 × 26
<i>Wild ass</i>	Herb; Shrub; Tree	NA	NA	NA	NA

ruminants appear to play a key role in the dispersal of certain tropical plants, typically with drupes (Chen et al. 2001; Prasad et al. 2006; Brodie et al. 2009a, b). However, the fate of most seeds consumed by ruminants (i.e. whether they are dispersed or destroyed) remains unknown. There is a need to examine the exact nature of the interaction between ruminants and fruits, particularly for newly described ruminant species from tropical Asia (Van Dung et al. 1993; Rabinowitz et al. 1999; Groves and Grubb 2011).

5.4.1.1 Tragulidae

The small body size, crepuscular habits, elusive behaviour, and tendency to prefer dense undergrowth (Sridhara et al. 2013) has precluded reliable observations of frugivory by tragulids until the more recent use of camera-traps (Prasad et al. 2010). From the literature we were able to tabulate fruits from 32 tree species in the diets of tragulids. Accounts of frugivory were restricted to three tragulid species, although eight occur in Asia. Records of fruits consumed by tragulids were restricted to trees, mostly drupaceous and coloured green. Dispersal was confirmed for 6 species (all drupes), and seed predation recorded for one dry-fruited species (Yasuda et al. 2005). The largest fruits consumed and seeds dispersed by tragulids were smaller than for other ruminant groups (Table 5.2).

5.4.1.2 Cervidae

We found frugivory records for only two species of muntjac, although nine species are recognized in SSEA. For these, we were able to record instances of fruit consumption of 88 plant species. Fruits consumed were largely from trees, predominantly drupaceous, and were mostly yellow. A total of 15 species were recorded as being dispersed (11 drupes, 3 berries), and the largest fruits consumed and dispersed were similar in size (Table 5.2). Seeds that were consistently destroyed (7 species—4 drupes, 2 berries and 1 capsule) ranged in size from 10×8 to 25×15 mm.

We documented a total of 67 plant species whose fruit were consumed by larger cervids belonging to three genera: *Rucervus*, *Rusa* and *Axis*. Accounts of frugivory were restricted to four species, although 10 large cervid species occur in tropical Asia. Fruits consumed were mostly from trees, largely drupaceous, and predominantly yellow or green (Table 5.2). Dispersal records were confined to 24 plant species (15 drupes, 4 berries, 2 figs and 1 capsule). Seeds consistently destroyed (2 drupes, 2 berries and 1 capsule) varied from 15×9 to 25×15 mm.

5.4.1.3 Bovidae

Fruits from 38 plant species were documented to be consumed by bovids. Records of frugivory were restricted to one species each from the genera *Gazella*, *Naemorhedus*,

Tetracerus, *Antelope*, *Capricornis*, *Boselaphus* and *Bos*, although several other species of bovids are found in tropical Asia. Fruits consumed were mostly from trees, drupaceous and equally likely to be black, green, yellow, or red. Twelve species were recorded as being dispersed (including 5 pods, 2 berries, 1 each of drupe and capsule), while no information was available on destruction of seeds.

5.4.1.4 Seed Deposition

In general, there is surprisingly little information on the seed deposition patterns by ruminants. Brodie et al. (2009a, b) found that muntjacs (*Muntiacus muntjac*) alone deposit seeds of *Choerospondias axillaris* in open microhabitats where their germination success is the highest, although sambar (*Cervus unicolor*) and gibbons (*Hylobates lar*) also disperse *C. axillaris*. Gut passage rates or seed retention times, which affect deposition patterns, are unknown for all but one species of ruminant, chital (*Axis axis*). Chital retain the seeds of *Phyllanthus emblica* for 7–27 h before regurgitating them (Prasad et al. 2006). Studies on wild and domesticated ruminants from Europe and America indicate that gut passage rates range from 20 h to 5 days for medium to large ruminant species (Janzen et al. 1985; Schmidt et al. 2004). The uneven retention time of seeds combined with the large home ranges of medium–large ruminants (<114 km²—Table 5.1) is expected to result in scattered seed deposition patterns and long seed dispersal distances (Vellend et al. 2003; Myers et al. 2004).

5.4.2 Simple-Stomach Frugivores (Suidae)

In Asia, the family *Suidae* comprises 13 species in three genera (IUCN 2014). Pigs and their relatives are primarily frugivorous, but are unique in comparison with other ungulates in supplementing their diet with a wide range of other food types including animal matter.

Both pigs and babirusa are of medium-size, with weights ranging from 45–135 kg (pigs) and 70–100 kg (babirusa) (Table 5.1). The strong jaws and teeth, and irregular molar surfaces of pigs and babirusa make them well suited for crushing seeds (Meijaard et al. 2005). Domestic pigs have a well-developed caecum and spiral colon that are major sites for microbial digestion, with efficient cellulose digestion (Leus and Macdonald 1997). However, wild suid digestive physiology has rarely been investigated. Reports indicate that they are more folivorous than domesticated pigs (Leus and Macdonald 1997). The diet of *Sus scrofa* varies greatly among the habitats and regions in which it occurs (Ickes et al. 2001); both this species and *S. barbatus* appear to prefer fruit and consume it in abundance when available. Similarly, the digestive physiology of babirusa suggests that it is primarily frugivorous, or a frugivore-folivore (Leus 1994). Indeed, babirusa do show a preference for fruit (Leus 1994; Clayton 1996) and are more specialized in

digesting fruit components and less efficient in digesting grass fibre than pigs (Leus 1994). Babirusa have enlarged stomachs compared to pigs as more fermentation occurs here than in the large intestine.

Published accounts also indicate significant variability in whether *Sus* are considered dispersers (Hamann and Curio 1999; Donatti et al. 2011) or predators of seeds (Campos and Ojeda 1997; Curran and Leighton 2000; Lynes and Campbell 2000; Meijaard et al. 2005), even for congeneric plant species (Campos and Ojeda 1997; Lynes and Campbell 2000). While the seeds of some fruit types (e.g. dry) are consistently destroyed (Curran and Leighton 2000), seed treatment is probably type- and species-specific and there may be significant differences in seed handling. Seeds from berries (10 of 12 species dispersed), pods (4 of 5 species) and complex fruit (6 of 6 species) were more likely to be dispersed than destroyed, while seeds from dry fruits (15 species) were always destroyed. Plant species with drupe fruit were equally likely to have their seeds dispersed (11 species) as destroyed (12 species). Seed predation by *Sus* can have profound effects on seed recruitment (Curran and Leighton 2000), while its potential role as a seed disperser in most Asian habitats may be less significant, albeit understudied (Hamann and Curio 1999). In temperate regions, fruit forms 32–42 % of the diet of *S. scrofa* (Diong 1982; Thomson and Challies 1988), while in *S. barbatus* stomachs investigated in Asia, crushed seeds were often dominant (Caldecott 1991; Meijaard et al. 2005; Wulffraat 2006). There have been an increasing number of studies indicating an important dispersal role for introduced pigs outside of their native range, particularly where alternative native dispersers are scarce (Diong 1982; Fedriani and Delibes 2009; Matias et al. 2010; Donatti et al. 2011; O'Connor and Kelly 2012).

5.4.2.1 Babirusa

Information about frugivory by babirusa is largely anecdotal and the only evidence of seed dispersal comes from stomach contents (Clayton 1996). We found 21 records of frugivory for *B. babyrussa* and *B. togeanensis*, while no information exists for *B. celebensis*. Most records of frugivory were of drupaceous fruits from trees, equally likely to be coloured yellow, green, black or brown. Even if babirusa destroys the seeds of some species, they are one of the largest fruit-eating animals in their range, exceeded in size only by the anoa (*Bubalus depressicornis*) (Whitten et al. 1987).

5.4.2.2 Pigs

Available information on frugivory in *Sus* comes largely from the widespread *Sus scrofa* and *S. barbatus*, with limited records for *S. celebensis*, *S. cebifrons*, and *S. verrucosus*. In total, fruits of 97 species were recorded as being consumed, of which 30 species were reported as destroyed and 32 dispersed. Fruits were mostly from trees and were predominantly drupaceous and red in colour. Generally, the

seeds dispersed by *Sus* are small to medium sized ($n = 12$ species, with fruit length <10 mm), but seeds up to 48×28 mm have been recorded as dispersed.

5.4.2.3 Seed Deposition

With gut passage rates of 2–4 days (O'Connor and Kelly 2012) and home range sizes of 6–34 km² (Saunders and Kay 1991; Caley 1997; Mitchell et al. 2009), *Sus scrofa* (and perhaps other pig species) may be effective long distance seed dispersers for some plant species (O'Connor and Kelly 2012). Further, defecation of seeds can be spaced over multiple days, producing scattered seed deposition patterns (O'Connor and Kelly 2012), which can be beneficial for seedling recruitment. *Sus barbatus* has unique ranging behaviour, whereby periodic mass migrations of individuals occur every few years, probably to coincide with predictable fruiting in *Dryobalanops* forests in the Malayan peninsula (Kawanishi et al. 2008) or seasonally fruiting *Dinochloa* bamboo in Borneo (Davies and Payne 1982). At other times the populations are mostly small and exhibit local movements only, although movements may increase as populations expand to exploit food sources (Kawanishi et al. 2008). During annual migrations, *S. barbatus* may cover distances of 8–22 km per month, and 250–650 km in all (Caldecott 1991) and thus have the potential to disperse seeds over long distances.

5.4.3 Simple-Stomach Folivores (*Elephantidae*, *Rhinocerotidae*, *Equidae* and *Tapiridae*)

Unlike ruminants (4.1) and pigs (4.2), simple-stomach folivores belong to four different families with different phylogenetic histories: Elephantidae (1 Asian species), Rhinocerotidae (3 Asian species), Equidae (1 species in tropical Asia) and Tapiridae (1 Asian species) (see Table 1.1; also refer to Chap. 2 for further details). However, these species display similarities in their digestive systems and consequently show some similarities in their seed dispersal behaviour. Although collectively called “hindgut fermenters”, fermentation in these animals actually occurs in the mid-gut, which results in distinctly different seed processing compared to foregut fermenters or simple-stomach frugivores. These large herbivores have simple stomachs, with symbiotic bacteria housed in the caecum and colon (Clemens and Maloiy 1982). The breakdown of cellulose is less efficient compared to foregut fermenters and faecal particle size is significantly larger, with faeces containing poorly digested forage (Fritz et al. 2009). Thus, fruits and seeds are poorly digested and often pass undamaged through their guts. Since fermentation occurs in the caecum and colon, these animals can process low-nutrient food rapidly. This rapid food processing gives them an advantage at large body sizes, as they are able to take in significantly larger quantities of food (Clauss et al. 2003). Perissodactyls (rhinoceroses, equids, and tapirs) have a compartmentalized colon (Stevens and

Hume 1995), which makes their digestive systems more complex than elephants. Although fruit is typically not a predominant food item in the diet of elephants, rhinoceroses, wild asses and tapirs, the regular appearance of seeds in their dung indicate that they do consume a wide range of fruit, sometimes in significant quantities (Table 5.2).

5.4.3.1 Elephants

Asian elephants (4000 kg) are the largest fruit-eating animals in Asia (Table 5.1). The extent of frugivory exhibited by elephants is highly variable (Campos-Arceiz and Blake 2011). Their mild masticatory action results in little or no seed damage in the mouth, although digestive seed predation in the gut has been reported (Campos-Arceiz et al. 2012). However, they are probably primarily seed dispersers.

Elephants consume fruits from a diverse range of life forms, but mostly from trees and herbs (Table 5.2), reflecting their diverse habitat use. Elephants were recorded to consume fruits from 84 species in our review. Types of fruit eaten were diverse, but most were pods, berries or drupes, and the seeds were usually dispersed. Fruits were mostly yellow, green or brown (Table 5.2). Elephants consume the largest fruits among large herbivores in Asia and can disperse seeds as large as 39×28 mm.

5.4.3.2 Perissodactyls (Rhinoceroses, Tapirs and Equids)

Rhinoceroses

Rhinoceroses (750–2350 kg), second in size only to elephants, are predominantly folivorous. However, seeds and fruits are regularly found in their dung and latrines (Flynn 1978; Dinerstein 1991). The rarity of most rhinoceros species has prevented detailed investigation of the proportion of fruit in their diet. Frugivory has nevertheless been reported, and fruit of 37 plant species are recorded as consumed by Asian rhinoceroses. These fruits are mostly from trees, usually dull coloured (green, brown or yellow), and are either berries or drupes. The relatively less diverse range of fruits consumed by rhinoceroses perhaps reflects their current rarity and habitat specialization.

Tapirs

Tapirs (350 kg) have been documented to disperse and destroy seeds. The dentition of tapirs is well suited for seed crushing (Campos-Arceiz et al. 2012) and seed fragments have been reported from dung of Neotropical tapir species (Janzen 1981). Like pigs, their function as dispersers or seed predators is variable. Captive tapirs

have been documented to spit or swallow seeds whole and also defecate both viable and destroyed seeds (Campos-Arceiz et al. 2012). However, the extent of frugivory in tapirs in the wild is unclear, making any comparison with other simple-stomached herbivores difficult.

In our review, we found records of tapirs feeding on fruits from 21 species of plants. These fruits were all from trees, yellow, green or brown, and were complex fruits, berries or drupes. Tapirs are extremely variable in their seed treatment and often both disperse and destroy seeds from the same species (Campos-Arceiz et al. 2012). Of the 21 species we recorded as consumed by tapirs, five usually had the seeds destroyed, four had seeds destroyed as well as dispersed, two were dispersed and the remaining 10 were observations of frugivory only. Further, tapirs have difficulty handling large fruits and frequently spit seeds from large fruits (Campos-Arceiz et al. 2012). *Durio zibethinus* seeds (39×26 mm) are the largest reported to be dispersed by Asian tapirs (Holden et al. 2003; Campos-Arceiz et al. 2012).

Equids

The Asiatic wild ass (250 kg) is the smallest simple-stomached herbivore. Equids have small stomachs relative to their body size and tend to process fruit slowly, limiting the quantity of food that can be consumed (Giffin and Gore 1989). The Asiatic wild ass has been studied in Israel, Iran and India, and seeds are frequently reported in dung and seedlings have been found near dung piles (Shah 1993; Peled 2010; Ghasemi et al. 2012), but detailed reports on extent of frugivory are unavailable. Similarly, there is no information on seed predation, although digestive seed predation has been reported for domestic horses (Janzen et al. 1985). In general, asses in the tropics are found only in desert regions, limiting their fruit consumption to berries, capsules and pods of herbs, shrubs and sometimes trees.

5.4.3.3 Megafaunal Fruit

It has been proposed that the largest fruit within tropical plant communities evolved in response to frugivory by “megafauna”—the largest terrestrial vertebrate frugivores (>1000 kg; Guimaraes et al. 2008). Analyses of elephant fruit and plant communities in South America suggest that megafaunal fruit fall into two categories: fruits 4–10 cm in diameter with up to five large seeds, and fruits >10 cm diameter with numerous small seeds (Guimarães et al. 2008). In tropical Asia, elephants and rhinoceroses are able to swallow and disperse the largest seeds in the habitats they occupy (Cochrane 2003; Corlett 2011). In our review, fruit that fit the “megafaunal fruit” syndrome featured prominently in the diets of elephants (19 of 50 plant species for which fruit width was available), rhinoceroses (10 of 24

plant species) and tapirs (9 of 13 plant species). The role of tapirs, however, in the dispersal of large seeds is variable; from studies on captive individuals, seeds of large fruits were less likely to be swallowed and more likely to be damaged, and only small-seeded species were regularly defecated in a viable condition (Campos-Arceiz et al. 2012). Fruits that fit the “megafaunal fruit” syndrome are known to be dispersed by smaller frugivores as well as other dispersal mechanisms such as wind or water (Cochrane 2003), and in a staggered successive manner with back-up dispersal mechanisms being invoked when megafauna fail to disperse the fruit (Sekar and Sukumar 2013). It remains to be tested if these fruit evolved in response to features of the sensory and digestive systems of large simple-stomached herbivores. No data on dispersal of megafaunal fruits exist for Asian equids, but in the Neotropics introduced horses appear to have replaced some of the seed dispersal services that were lost with the extinction of the megafauna around 10,000 years ago (Janzen and Martin 1982).

5.4.3.4 Seed Deposition

Large simple-stomached herbivores process vast quantities of forage within a day, consequently exhibiting the longest known daily displacements rates and home ranges for terrestrial mammals. They also have long gut passage times (rhinoceroses 61–122 h, elephants 40–122 h, tapirs 63–235 h, ass 34–39 h), although this may not scale with body size, since the retention times of smaller foregut herbivores overlap (2–96 h, S. Prasad unpublished data). These large herbivores also undertake long, directed seasonal movements to access water, grasses in different stages of growth, or salt licks (Campos-Arceiz et al. 2008). Estimated seed dispersal distances for tapirs (Campos-Arceiz and Blake 2011) and elephants (Campos-Arceiz et al. 2008), indicate that these animals are effective long-distance seed dispersers. Asses and rhinoceroses are likely to be similarly capable of long-distance seed dispersal, although no data exist; Asiatic wild ass have daily movements of 4–11 km, and home ranges of 8–19 km², while rhinoceroses have home ranges of 5–50 km² and may travel up to 10 km within a day (van Strien et al. 2008).

Both elephants and rhinoceroses deposit seeds within large dung piles, which can provide suitable conditions for seedling recruitment although this advantage may be partially offset by high seedling density and associated competition (Campos-Arceiz and Blake 2011). Rhinoceroses and tapirs frequently deposit seeds in latrines (Dinerstein 1991; O’Farrill et al. 2013), which can have both positive and negative consequences for seed recruitment (González-Zamora et al. 2012; O’Farrill et al. 2013). While these are untested in rhinoceroses, latrines of *R. unicornis* were associated with distinct floras (Dinerstein 1991).

5.4.4 Relationship Between Body Size of Herbivores and Size of Fruit Consumed

Seed size and weight are key determinants of recruitment success and seedling survival, consequently influencing the reproductive success of plants (Moles and Westoby 2006). Because frugivores can exert selective pressures on fruit and seed size (Forget et al. 2007), the constraint of frugivore body size on fruit traits needs closer examination. For instance, fruits with very large seeds are accessed only by a few frugivores that are often non-redundant in dispersal function, whereas fruits with smaller seeds usually have a wider suite of consumers and dispersers (Gautier-Hion et al. 1985; Kitamura et al. 2002). Indeed, recent evidence suggests that the functional extinction of large frugivores can cause rapid evolution in trees towards smaller seed sizes (Galetti et al. 2013) or shifts in plant communities in ecological time (Velho et al. 2012a, b).

Here, we examine the nature of the relationship between body size of large herbivores and the largest fruit they can consume. Fruit size is highly correlated to seed size and is therefore a good measure of the limits imposed by gape width of large herbivores on the size of seeds potentially dispersed (Forget et al. 2007). We analyzed fruit and seed width (seed width = second largest axis of the fruit or seed), which often determines if a fruit or seed is swallowed (Corlett 1998). Each species of plant and herbivore was considered to be an independent data point. We used generalized linear models and quantile regressions to examine whether the average and maximum width of fruit and seed consumed were constrained by the body size of large herbivores. To linearize the allometric relationship we log-transformed the predictor (i.e. body weight of herbivores) and used the log link function for Gaussian error distributions. We checked for over-dispersion and examined residuals graphically to check for normality and heteroscedasticity. All analyses were performed in R 3.0.1 (R-Core-Team 2013).

Results indicate that body size may limit the size of fruits that can be consumed by large herbivores (Fig. 5.1). Although maximum fruit length, seed length, and width of seed consumed increased with body weight of large herbivores, the only significant relationship was with fruit width, suggesting that body size (correlated with gape width) of large herbivores can limit the sizes of fruits consumed (Fig. 5.1). Results from the quantile regressions however, suggest that maximum fruit length alone shows a positive relationship with body weight (Fig. 5.2a). Fruit width, seed length and seed width however, do not show any pattern with body size (Fig. 5.2b–d) for the upper quantile (0.95). Because these three traits show a positive relationship for the other quantiles used (0.25, 0.5, 0.75) we could perhaps infer that minimum fruit sizes consumed by herbivores increases with body size, and the fruit sizes consumed by smaller herbivores are on an average smaller than their larger bodied counterparts. Although larger bodied herbivores appear to

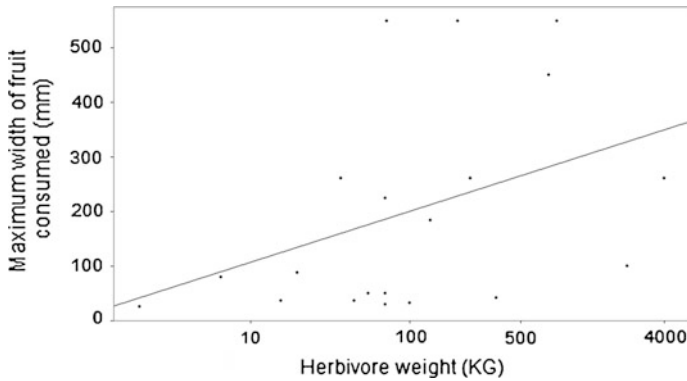


Fig. 5.1 Relationship between body weight of large herbivores in tropical Asia, and the maximum width of fruits consumed

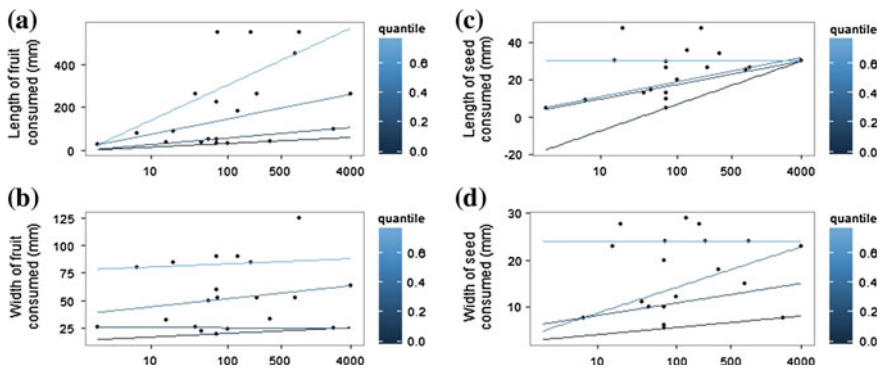


Fig. 5.2 Quantile regressions of fruit traits **a** length of fruit consumed, **b** width of fruit consumed, **c** length of seed consumed and **d** width of seed consumed as a function of herbivore body weight. The quantile regressions were carried out using all available data, but for ease of interpretation we only plot maximum fruit and seed dimensions as points. The four different lines in each graph represent the 25th, 50th, 75th and 95th quantiles

consume fruits that span a wider range of fruit lengths than smaller bodied herbivores (Fig. 5.2a), overall our results do not suggest a strong link between disperser body mass and fruit or seed size likely to be consumed or dispersed. More data are needed to better elucidate these links, and we advise caution against dismissing the importance of larger bodied herbivore species until such data has been assembled. Nevertheless, plant species dependent on large herbivores that are especially threatened (Table 5.1) may still be vulnerable in the absence of redundant dispersers (Corlett and Westcott 2013).

5.4.5 *Overlap in Fruit Choice Among Asian Herbivores*

We also assessed the similarity in the traits of fruits consumed by the different families of large herbivores found in Asia. We compiled data on the digestive system, maximum and minimum fruit length and width, maximum and minimum seed length and width, maximum and minimum fruit and seed weight, fruit type and fruit colour associated with each of the large herbivore species. This data was collated for seven of the nine families of large herbivores; Equidae and Moschidae were excluded due to the lack of information on fruit traits. We used the package “FD” in software R to compute the dissimilarity in traits. Gower’s dissimilarity index was used since it allows for categorical traits (fruit type and colour, in this case). Numbers close to 0 indicate greater similarity in fruit choice while numbers close to 1 indicate dissimilarity.

In general, our results suggest a degree of dissimilarity in the fruit choice by the different families of large herbivores, providing the first family-wise comparisons at a continental scale. Results indicate that fruit choice is most similar between cervids and elephants, followed by cervids and bovids (Table 5.3). The similarity between cervids and bovids may reflect the overlap in their digestive physiology and body size. The similarity between elephants and cervids, however, is surprising given the differences in their digestive physiology and sensory capabilities. Fruit choice may overlap based on the limited fruit characteristics we found and used in the analysis, perhaps due to sympatry of cervids and elephants throughout SSEA until recent times. Incorporating currently unknown information such as nutritional characteristics of fruits and the relative abundances of these fruits in the diet may alter the dissimilarity metrics when reassessed in the future. This similarity may also be due to the incomplete nature of the dataset. Nevertheless, our results, although preliminary, call into question the assumed non-redundancy of large herbivores as seed dispersers, specifically small–medium species in the families Cervidae and Bovidae. Tapirs are consistently dissimilar to most families, but it is unclear whether this reflects scarcity of information on frugivory or the uniqueness in their fruit choice. As other animals including bears, civets, macaques, and orangutans, also compete with large herbivores for fruits on the ground, fruit characteristics are

Table 5.3 Dissimilarity in the traits of fruits consumed by the different families of large herbivores of Asia

	Tragulidae	Cervidae	Bovidae	Suidae	Tapiridae	Rhinocerotidae	Elephantidae
Tragulidae	0.00	0.63	0.63	0.60	0.49	0.67	0.69
Cervidae	0.63	0.00	0.28	0.44	0.72	0.58	0.23
Bovidae	0.63	0.28	0.00	0.47	0.75	0.48	0.42
Suidae	0.60	0.44	0.47	0.00	0.58	0.64	0.53
Tapiridae	0.49	0.72	0.75	0.58	0.00	0.75	0.61
Rhinocerotidae	0.67	0.58	0.48	0.64	0.75	0.00	0.55
Elephantidae	0.69	0.23	0.42	0.53	0.61	0.55	0.00

Values towards 0 indicate similarity in traits, while values towards 1 indicate dissimilarity

as likely to have been shaped by these frugivores too. Finally, these results must be interpreted cautiously due to the incomplete nature of the dataset. Studies from more landscapes covering the entire suite of frugivores can help verify these patterns across regional, continental and global scales.

5.5 Other Modes of Seed Dispersal by Large Herbivores

Apart from locating fruits actively, the consumption of fruits may be a passive activity when other plant parts (e.g. foliage, twigs) are being eaten. Janzen (1984) proposed that small fruits interspersed in the foliage may be consumed inadvertently, even though the animals are not actively seeking them. Because small fruits may not provide sufficient rewards to the consumers, foliage serves the function of the fruit by “packaging” seeds, which potentially leads to endozoochorous dispersal (Janzen 1984). Known as the “foliage-as-fruit” hypothesis, this mechanism of dispersal is relevant to large herbivores, whose diet often consists predominantly of foliage. Several grasses, herbs and a few trees seemingly fit the requirements for this mechanism of seed dispersal in Asia (R. Corlett pers. obs.), although the hypothesis remains largely untested. Preliminary evidence supporting this hypothesis was found for elephants in Sri Lanka (Samansiri and Weerakoon 2008), three ruminants, and wild pigs in India (Middleton and Mason 1992), but was rejected for rhinoceroses in Nepal (Dinerstein 1991). More studies that test the hypothesis are necessary to assess its extent and significance for plant species.

Seeds of herbs and grasses can also be transported by adhering to the pelage or fur of animals. This mode of dispersal, referred to as epizoochory, has been reported for large herbivores because the body hair on these mammals enables the transport of certain kinds of seeds. European populations of *Sus scrofa* and certain temperate deer species effectively disperse seeds that attach to hair (Couvreux et al. 2004; Schmidt et al. 2004). However, there are no reports of epizoochory for any of the large herbivores from tropical Asia, although fruits and seeds with adaptations for external attachment are widespread in open habitats, where they often attach to human clothing (R. Corlett pers. obs). Reports suggest that pigs transport seeds of *Rafflesia* in their hooves (MacKinnon et al. 1996).

5.6 Large Herbivore Distributions and Consequences for Seed Dispersal: Past, Present and Future

The Asian tropics still harbour a number of large herbivores, but the abundance and range of most extant species have contracted over historical and recent times (Groves and Grubb 2011, Chap. 11), and several additional species have become extinct since the Late Pleistocene (also see Chap. 2). In this section, we summarize

past and present distributions of herbivores, and assess the range of dispersal services that might have been lost in the Asian tropics.

All tropical terrestrial ecosystems, including several islands, have lost at least one megafaunal species (>44 kg) since the Pleistocene (Corlett 2011, also see Chap. 2). Tropical Asia has experienced significant megafaunal losses at rates that are higher than some other continents (Corlett 2011). The drivers of this region-wide extinction of megafauna remain unclear, with both climate change and the arrival of *Homo* species being plausible explanations (Louys 2012). Herbivorous mammals, including elephants, stegodons, rhinoceroses, horses, bovids, and tapirs, constitute the largest group of extinct megafauna. Since the Late Pleistocene, at least two species each of elephants, stegodons, rhinoceroses and bovids, one species of giraffe, and at least one species of horse have gone extinct from south Asia (Chauhan 2008). The number of Late Pleistocene rhinoceros species is uncertain (Antoine 2012), but the distribution of the family has certainly declined (Corlett 2011). Similarly, at least one species each of elephant, stegodon, rhinoceros, horse and bovid, in addition to a giant tapir, have been lost from Southeast Asia (Mishra et al. 2010; Corlett 2011). All of these extinct species are likely to have consumed at least some fruit, like their extant relatives (Corlett 2010). Since their diversity, distributions and abundances were greater than today (Corlett 2010), they may have played a significant role in the evolution of modern fruits.

At present, ruminants are widely distributed, from the arid zones of western India to the rainforests of Indonesia and Philippines, but are predominantly found in woody habitats, ranging from savannah to rainforest (Eisenberg and Seidensticker 1976), and attain their highest densities in tropical dry forests and woody savannas (Karanth and Sunquist 1992). Most ruminants occur in woody environments and avoid disturbed environments, possibly restricting their functional roles to these habitats. A few ruminants, however, may occur at high densities in human dominated landscapes (e.g. Nilgai *Boselaphus tragocamelus*). *Sus* (pigs) is the most diverse and widely distributed genus among suids. *Sus* species are scattered across tropical Southeast Asia, primarily in forested habitats, with some species being able to persist in grasslands and cultivated areas. Most pig species partly forage in disturbed regions, and can occupy both forest and non-forest habitats (Table 5.1). The disturbance tolerance of suids varies considerably and only *S. scrofa* is a true habitat generalist and potentially a disperser of seeds across modified habitats. The three *Babyrousa* (babirusa) species are confined to Sulawesi or nearby islands (Indonesia), where they persist in forests and occasionally cultivated regions. *Porcula* comprises a single species found in tall grasslands in India and no frugivory information exists for this species. Elephants are found in a range of habitats, from alluvial grasslands to rainforest and are distributed widely from India to Indonesia. With the exception of the Indian Rhino, *Rhinoceros unicornis*, all Asian rhinoceroses have highly restricted ranges within the rain forests of southeast Asia (IUCN 2014). The Indian rhinoceros is found in grasslands and riverine forests in northern India and Nepal, a tiny fraction of its historical and Pleistocene ranges. The Asiatic wild ass is restricted to deserts and very dry regions of western India, while tapirs are found only in the rainforests of Southeast Asia (IUCN 2014).

In summary, with few exceptions, most large herbivores are currently restricted to specific habitats within the continent, perhaps limiting the spatial extent of their seed dispersal function. However, elephants, often within a population, continue to utilize a range of habitats and probably remain responsible for long-range seed dispersal in a large mosaic of heterogeneous habitats for a wide range of plant species.

Apart from native large herbivores, free-ranging or feral buffalo, cows, horses and goats occur in many parts of tropical Asia (Dinerstein and Wemmer 1988; Middleton and Mason 1992). Although these feral and introduced animals have been documented to have detrimental impacts on plant populations (Scowcroft and Hobdy 1987; Moriarty 2004), they also function as seed dispersers (Middleton and Mason 1992; Giordani 2008), including dispersal of large fruits (Dinerstein and Wemmer 1988). Several Asian herbivores, including spotted deer (*Axis axis*), sambar (*Rusa unicolor*), blackbuck (*Antelope cervicapra*), and wild boar (*Sus scrofa*) have been introduced to other continents and become invasive in their introduced ranges (Moriarty 2004). These populations of introduced large herbivores may assist in the spread of both invasive and native plants (e.g. Moriarty 2004).

Most Asian large herbivores species are threatened by some combination of hunting, habitat loss, fragmentation, logging, competition from livestock, and hybridization with domestic species (IUCN 2013, Chaps. 1 and 11). Populations of many species are declining and their distributions are contracting, with larger species consistently more threatened than smaller ones (Table 5.1). Some smaller herbivore species, especially those that are habitat-specialists with very restricted ranges, are also at risk (Groves and Grubb 2011). It is not surprising therefore, that studies predicting future distributions of large herbivores in Asia present a grim prospect of further declines in their ranges and densities (Karanth et al. 2010; Corlett 2011). However, the impacts of these declines on seed dispersal processes are poorly understood. It has been suggested the loss of large mammals, including herbivores, can lead to declines in dispersal of large-seeded species, leading to a slow shift in forest community composition towards small-seeded, bird- and wind-dispersed species (Wright et al. 2007). Indeed, excessive harvest of muntjac (*Muntiacus muntjac*) in Thailand resulted in the decline of both seedling densities and seed dispersal of *Cheorospondias axillaris* (Brodie et al. 2009a, b).

Large, wide-ranging, habitat generalists such as elephants and pigs are especially important. They are likely to be regular dispersers of seeds across heterogeneous habitats and there is probably very low redundancy in their dispersal role in some habitats (Campos-Arceiz and Blake 2011). In the short term, plants may decline simultaneously with their key seed dispersers as has been noted in an elephant (Cochrane 2003) and deer (Brodie et al. 2009a, b) dispersed species. Long-term consequences of herbivore declines on plants with no redundant seed dispersers may include range contraction and local extinctions (Corlett and Westcott 2013). However, plants that are seemingly dependant on megafaunal dispersers may have evolved mechanisms to be dispersed by other frugivores. For instance, rodents and introduced livestock disperse seeds of plants thought to be entirely dependant on

megafauna extinct 10,000 years ago (Janzen and Martin 1982; Guimarães et al. 2008). Recent evidence from India also demonstrates that small and medium-sized herbivores, specifically native ruminants such as deer can provide “back-up” dispersal services to megafauna-dispersed trees, albeit to a much lesser extent (Sekar and Sukumar 2013). Additionally, these small to medium-sized herbivores, although not capable of accessing the wide range of fruits available to much larger megafauna, have been documented to disperse more plant species than their larger counterparts in both wet and dry tropical forests of Asia (Prasad 2011). We therefore suggest a rethinking of the importance placed on small and medium-sized herbivores as seed dispersers. While conservation efforts have often focussed on charismatic megafauna and should continue to do so, the unique and diverse dispersal services provided by small- and medium-sized herbivores should also be integrated into conserving planning.

5.7 Conclusion

We set out to produce a quantitative summary of frugivory and seed dispersal by large herbivores in tropical Asia. However, we found very little quantitative information on plant–herbivore interactions in the region. Our understanding of the extent of frugivory by herbivores, especially for smaller species, is incomplete. We also understand very little about fruit choice, seed processing and gut retention times of seeds dispersed by herbivores. These gaps in our understanding severely restrict our ability to assess dispersal services lost due to extinctions of large herbivores, and the potential future impacts if herbivore species currently under threat continue to decline. Most importantly, with the current limitations in our understanding of seed dispersal by large herbivores in tropical Asia, we are unable to predict shifts in herbivore–plant interactions for the future under changing climates and land-use. A robust understanding of plant–herbivore interactions in heterogeneous landscapes is critical to plan management strategies that address the anticipated impacts of climate change and associated drivers on biodiversity (McConkey et al. 2012; Corlett and Westcott 2013). Large herbivores can effectively disperse seeds very long distances away from parent trees (Vellend et al. 2003; Myers et al. 2004), potentially facilitating migration of plants at rates suitable to track climatic changes as predicted for the future (Corlett and Westcott 2013).

It has been suggested that lost ecological services may be reinstated by reintroducing species into their former ranges, or by introducing ecologically equivalent species (taxon substitutes) into areas that have experienced extinctions of fauna involved in key ecological processes (Ehrlich and Mooney 1983). Faunal reintroductions to address lost seed dispersal services have been undertaken at a few sites (e.g. Aldabra tortoises in Mauritius—Hansen et al. 2008). However, before attempting this in tropical Asia we need a better understanding of the seed dispersal services provided by large herbivores and of the community-level consequences of species reintroductions, especially novel introductions. Additionally, given the high

human pressures and the continued use of forests in tropical Asia, it is imperative that we mitigate these threats (e.g. fragmentation or hunting) that have led to the decline of large herbivores, before attempting reintroductions.

We hope this review will initiate further enquiry into seed dispersal services provided by large herbivores in tropical Asia, and extend the emphasis of research beyond documenting their distributions and abundances to studying their ecological function.

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References

- Agungpriyono S, Yamamoto Y, Kitamura N et al (1992) Morphological study on the stomach of the lesser mouse deer (*Tragulus javanicus*) with special reference to the internal surface. *J Vet Med Sci/Japan Soc Vet Sci* 54:1063–1069
- Ahl A (1986) The role of vibrissae in behavior: a status review. *Vet Res Commun* 10:245–268
- Ahnelt PK, Kolb H (2000) The mammalian photoreceptor mosaic-adaptive design. *Prog Retin Eye Res* 19:711–777
- Antoine P-O (2012) Pleistocene and Holocene rhinocerotids (Mammalia, Perissodactyla) from the Indochinese Peninsula. *CR Palevol* 11:159–168
- Aung M, Mcshea WJ, Htung S et al (2001) Ecology and social organization of a tropical deer (*Cervus eldi thamin*). *J Mammal* 82:836–847
- Baskaran N, Kannan V, Thiyagesan K et al (2011) Behavioural ecology of four-horned antelope (*Tetracerus quadricornis* 'de Blainville, 1816) in the tropical forests of southern India. *Mammalian Biology-Zeitschrift für Säugetierkunde* 76:741–747
- Bodmer RE (1989) Frugivory in Amazon ungulates. Dissertation, University of Cambridge
- Bodmer RE (1990) Ungulate frugivores and the browser-grazer continuum. *Oikos* 57:319–325
- Brodie JF, Helmy OE, Brockelman WY et al (2009a) Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecol Appl* 19:854–863
- Brodie JF, Helmy OE, Brockelman WY et al (2009b) Functional differences within a guild of tropical mammalian frugivores. *Ecology* 90:688–698
- Caldecott J (1991) Eruptions and migrations of bearded pig populations. *Bongo* 18:233–243
- Caley P (1997) Movements, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. *Wildlife Res* 24:77–87
- Campos-Arceiz A, Blake S (2011) Megagardeners of the forest—the role of elephants in seed dispersal. *Acta Oecol* 37:542–553
- Campos-Arceiz A, Larrinaga AR, Weerasinghe UR et al (2008) Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants. *Ecology* 89:2684–2691
- Campos-Arceiz A, Traeholt C, Jaffar R et al (2012) Asian tapirs are no elephants when it comes to seed dispersal. *Biotropica* 44:220–227
- Campos CM, Ojeda RA (1997) Dispersal and germination of *Prosopis flexuosa* (Fabaceae) seeds by desert mammals in Argentina. *J Arid Environ* 35:707–714
- Cazetta E, Galetti M, Rezende EL et al (2012) On the reliability of visual communication in vertebrate-dispersed fruits. *J Ecol* 100:277–286

- Chauhan PR (2008) Large mammal fossil occurrences and associated archaeological evidence in Pleistocene contexts of peninsular India and Sri Lanka. *Quatern Int* 192:20–42
- Chen J, Deng XB, Bai ZL et al (2001) Fruit characteristics and *Muntiacus muntjak vaginalis* (Muntjac) visits to individual plants of *Choerospondias axillaries*. *Biotropica* 33:718–722
- Clauss M, Frey R, Kiefer B et al (2003) The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia* 136:14–27
- Clauss M, Steuer P, Müller DWH et al (2013) Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. *PLoS ONE* 8:e68714
- Clayton LM (1996) Conservation biology of the babirusa, *Babyrousa babyrussa* in Sulawesi, Indonesia. Dissertation, University of Oxford
- Clemens E, Maloiy G (1982) The digestive physiology of three East African herbivores: the elephant, rhinoceros and hippopotamus. *J Zool* 198:141–156
- Cochrane EP (2003) The need to be eaten: balanites wilsoniana with and without elephant seed-dispersal. *J Trop Ecol* 19:579–589
- Corbet GB, Hill JE (1992) The mammals of the Indomalayan region: a systematic review. Oxford University Press, Oxford
- Corlett RT (1998) Frugivory and seed dispersal by vertebrates in the oriental (Indomalayan) region. *Biol Rev Camb Philos Soc* 73:413–448
- Corlett RT (2007) The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* 39:292–303
- Corlett RT (2010) Megafaunal extinctions and their consequences in the tropical Indo-Pacific. *Terra Australis* 32:117–131
- Corlett RT (2011) How to be a frugivore (in a changing world). *Acta Oecol* 37:674–681
- Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? *Trends Ecol Evol* 28:482–488
- Couvreur M, Christiaen B, Verheyen K et al (2004) Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. *Appl Veg Sci* 7:229–236
- Curran L, Leighton M (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol Monogr* 70:101–128
- Davies G, Payne J (1982) A faunal survey of Sabah World Wildlife Fund Malaysia
- Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am Nat* 125:641–672
- Dhungel SK, O'gara BW (1991) Ecology of the hog deer in Royal Chitwan National Park, Nepal. *Wildlife Monographs* 119:3–40
- Dinerstein E (1991) Seed dispersal by greater one-horned rhinoceros (*Rhinoceros unicornis*) and the flora of Rhinoceros latrines. *Mammalia* 55:355–362
- Dinerstein E, Wemmer CM (1988) Fruits Rhinoceros eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. *Ecology* 69:1768–1774
- Diong CH (1982) Population biology and management of the feral pig (*Sus scrofa* L.) in Kipahulu Valley, Maui. Dissertation, University of Hawaii
- Donatti CI, Guimaraes PR, Galetti M et al (2011) Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecol Lett* 14:773–781
- Dookia S, Jakher G (2007) Food and feeding habit of Indian Gazelle (*Gazella bennettii*), in the Thar Desert of Rajasthan. *Indian Forester* 133:1327–1340
- Ehrlich PR, Mooney HA (1983) Extinction, substitution, and ecosystem services. *Bioscience* 33:248–254
- Eisenberg JF, Seidensticker J (1976) Ungulates in southern Asia: a consideration of biomass estimates for selected habitats. *Biol Conserv* 10:293–308
- Fedriani JM, Delibes M (2009) Seed dispersal in the Iberian pear, *Pyrus bourgaeana*: a role for infrequent mutualists. *Ecoscience* 16:311–321
- Feer F (1995) Seed dispersal in African forest ruminants. *J Trop Ecol* 11:683–689

- Flynn R (1978) The Sumatran rhinoceros in the Endau-Rompin National Park of Peninsular Malaysia. *Malayan Naturalist* 4:5–12
- Forget P-M, Dennis A, Mazer S et al (2007) Seed allometry and disperser assemblages in tropical rainforests: a comparison of four floras on different continents. In: Dennis AJ, Schupp EW, Green R, Westcott DA (ed) *Seed dispersal: theory and its application in a changing world*. CAB International Publishing, Wallingford, UK, pp 5–36
- Fritz J, Hummel J, Kienzle E et al (2009) Comparative chewing efficiency in mammalian herbivores. *Oikos* 118:1623–1632
- Gagnon M, Chew AE (2000) Dietary preferences in extant African Bovidae. *J Mammal* 81: 490–511
- Galetti M, Guevara R, Côrtes MC et al (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340:1086–1090
- Gautier-Hion A, Duplantier JM, Quris R et al (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65:324–337
- Gautier-Hion A, Emmons L, Dubost G (1980) A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels and ruminants). *Oecologia* 45:182–189
- Geist V (1998) *Deer of the world: their evolution, behaviour, and ecology* Stackpole Books. Mechanicsburg, USA
- Giffin JM, Gore T (1989) *Horse owner's veterinary handbook* Howell Book House. New York, USA
- Ginane C, Baumont R, Favreau-Peigné A (2011) Perception and hedonic value of basic tastes in domestic ruminants. *Physiol Behav* 104:666–674
- Giordani L (2008) *The role of goats in germination and dispersal of Mimosa luisana Brandege (Leguminosae-Mimosoideae) seeds in Tehuacán-Cuicatlán valley, Puebla State, Mexico*. Dissertation, Norwegian University of Life Sciences
- Ghasemi A, Hemami M, Irvani M Senn J (2012) Seed dispersal by Persian wild ass (*Equus hemionus onager*) in Qatruiyeh National Park, south central Iran. Conference Paper
- González-Zamora A, Arroyo-Rodríguez V, Oyama K et al (2012) Sleeping sites and latrines of spider monkeys in continuous and fragmented rainforests: implications for seed dispersal and forest regeneration. *PLoS ONE* 7:e46852
- Graves H (1984) Behavior and ecology of wild and feral swine (*Sus scrofa*). *J Anim Sci* 58: 482–492
- Groves C, Grubb P (2011) *Ungulate taxonomy* John Hopkins University Press. Baltimore, USA
- Guimarães PR Jr, Galetti M, Jordano P (2008) Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE* 3:e1745
- Hamann A, Curio E (1999) Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. *Conserv Biol* 13:766–773
- Hansen DM, Kaiser CN, Müller CB (2008) Seed dispersal and establishment of endangered plants on oceanic islands: the Janzen-Connell model, and the use of ecological analogues. *PLoS ONE* 3:e2111
- Heffner RS, Heffner HE (1992) Visual factors in sound localization in mammals. *J Comp Neurol* 317:219–232
- Heydon MJ (1994) *The Ecology and management of Rainforest Ungulates in Sabah, Malaysia*. Technical Report. Institute of Tropical Ecology, Aberdeen University
- Hofmann R (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443–457
- Hofmann R, Stewart D (1972) Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia* 36:226–240
- Holden J, Yanuar A, Martyr DJ (2003) The Asian tapir in Kerinci Seblat National Park, Sumatra: evidence collected through photo-trapping. *Oryx* 37:34–40
- Ickes K, Dewalt SJ, Appanah S (2001) Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. *J Trop Ecol* 17:191–206
- IUCN (2013) *The IUCN Red List of Threatened Species*. Version 2013-09. <http://www.iucnredlist.org>. Downloaded on 10 October 2013

- IUCN (2014) The IUCN Red List of Threatened Species. Version 2014-04. <http://www.iucnredlist.org>. Downloaded on 24 April 2014
- Jacobs GH (2012) The evolution of vertebrate color vision. *Adv Exp Med Biol* 739:156–172
- Jadeja S, Prasad S, Quader S et al (2013) Antelope mating strategies facilitate invasion of grasslands by a woody weed. *Oikos* 122:1441–1452
- Jamal A (1994) Food habits of ungulates in dry tropical forests of Gir Lion Sanctuary, Gujarat, India. *Acta Theriol* 39:185–193
- Janzen D, Demment M, Robertson J (1985) How fast and why do germinating guanacaste seeds (*Enterolobium cyclocarpum*) die inside cows and horses? *Biotropica* 17:322–325
- Janzen DH (1981) Digestive seed predation by a Costa Rican Baird's tapir. *Biotropica* 13:59–63
- Janzen DH (1984) Dispersal of small seeds by big herbivores: foliage is the fruit. *Am Nat* 123:338–353
- Janzen DH, Martin PS (1982) Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215:19–27
- Jarman P (1974) The social organisation of antelope in relation to their ecology. *Behaviour* 215–267
- Jiang P, Josue J, Li X et al (2012) Major taste loss in carnivorous mammals. *Proc Natl Acad Sci* 109:4956–4961
- John Singh A (1981) Importance of fruit in the diet of chital in dry season. *J Bombay Nat Hist Soc* 78:594
- Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) *Seeds: the ecology of regeneration in plant communities*. CAB International, Wallingford, pp 125–166
- Jordano P, Garcia C, Godoy JA et al (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proc Natl Acad Sci* 104:3278–3282
- Karanth KK, Nichols JD, Karanth KU et al (2010) The shrinking ark: patterns of large mammal extinctions in India. *Proc Roy Soc B: Biol Sci* 277:1971–1979
- Karanth KU, Sunquist ME (1992) Population structure, density and biomass of large herbivores in the tropical forests of Nagarhole, India. *J Trop Ecol* 8:21–35
- Kawanishi K, Sunquist ME (2008) Food habits and activity patterns of the Asiatic golden cat (*Catopuma temminckii*) and dhole (*Cuon alpinus*) in a primary rainforest of Peninsular Malaysia. *Mammal Study* 33:173–177
- Kitamura S, Yumoto T, Poonswad P et al (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133:559–572
- Kitamura S, Yumoto T, Poonswad P et al (2007) Frugivory and seed dispersal by Asian elephants, *Elephas maximus*, in a moist evergreen forest of Thailand. *J Trop Ecol* 23:373–376
- Krishnan M (1972) An ecological survey of mammals in India: the Gaur. *J Bombay Nat Hist Soc* 69:322–349
- Leus K (1994) Foraging behaviour, food selection and diet digestion of *Babyrousa babyrussa* (Suidae, Mammalia). Dissertation, University of Edinburgh
- Leus K, Macdonald AA (1997) From babirusa (*Babyrousa babyrussa*) to domestic pig: the nutrition of swine. *Proc Nutr Soc* 56:1001–1012
- Louys J (2012) The future of mammals in Southeast Asia: Conservation insights from the fossil record. In: Louys J (ed) *Paleontology in ecology and conservation*. Springer, Hiedelberg, pp 227–238
- Lundberg J, Moberg F (2003) Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6:0087–0098
- Lynes B, Campbell S (2000) Germination and viability of mesquite (*Prosopis pallida*) seed following ingestion and excretion by feral pigs (*Sus scrofa*). *Trop Grasslands* 34:125–128
- Mackinnon K, Hatta G, Halim H et al (1996) *The ecology of Kalimantan* Oxford University Press, Oxford
- Matías L, Zamora R, Mendoza I et al (2010) Seed dispersal patterns by large frugivorous mammals in a degraded mosaic landscape. *Restor Ecol* 18:619–627
- Matthiesius A, Chapman H, Kelly D (2011) Testing for Janzen-Connell effects in a West African montane forest. *Biotropica* 43:77–83

- Mcconkey KR, Prasad S, Corlett RT et al (2012) Seed dispersal in changing landscapes. *Biol Conserv* 146:1–13
- Mcshea WJ, Aung M, Poszig D et al (2001) Forage, habitat use, and sexual segregation by a tropical deer (*Cervus eldi thamin*) in a dipterocarp forest. *J Mammal* 82:848–857
- Meijaard E, D’huart J, Oliver W (2011) Family Suidae (Pigs). *Handbook of the mammals of the world*, vol 2
- Meijaard E, Sheil D, Nasi R et al (2005) Life after logging: reconciling wildlife conservation and production forestry in Indonesian Borneo CIFOR, Bogor, Indonesia
- Middleton BA, Mason DH (1992) Seed herbivory by nilgai, feral cattle, and wild boar in the Keoladeo National Park, India. *Biotropica* 538–543
- Mishra S, Gaillard C, Hertler C et al (2010) India and Java: contrasting records, intimate connections. *Quatern Int* 223:265–270
- Mitchell J, Dorney W, Mayer R et al (2009) Migration of feral pigs (*Sus scrofa*) in rainforests of north Queensland: fact or fiction? *Wildl Res* 36:110–116
- Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life cycle. *Oikos* 113:91–105
- Moriarty A (2004) The liberation, distribution, abundance and management of wild deer in Australia. *Wildl Res* 31:291–299
- Mouissie A, Van Der Veen CE, Veen GC et al (2005) Ecological correlates of seed survival after ingestion by fallow deer. *Funct Ecol* 19:284–290
- Myers JA, Vellend M, Gardescu S et al (2004) Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139:35–44
- Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol Evol* 15:278–285
- O’connor S-J, Kelly D (2012) Seed dispersal of matai (*Prumnopitys taxifolia*) by feral pigs (*Sus scrofa*). *N Z J Ecol* 36:228
- O’farrill G, Galetti M, Campos-Arceiz A (2013) Frugivory and seed dispersal by tapirs: an insight on their ecological role. *Integrative zoology* 8:4–17
- Peichl L (2005) Diversity of mammalian photoreceptor properties: adaptations to habitat and lifestyle? *Anat Rec Part A: Discover Mol Cell Evol Biol* 287:1001–1012
- Peled T (2010) Reintroductions as an ecosystem restoration tool: a case study of reintroduced ungulates as vectors for seed-dispersal. Dissertation, Ben-Gurion University of the Negev
- Prasad S (2011) Seed dispersal in the tropical dry forests of Mudumalai, Southern India. Dissertation, Indian Institute of Science
- Prasad S, Krishnaswamy J, Chellam R et al (2006) Ruminant-mediated seed dispersal of an economically valuable tree in Indian dry forests. *Biotropica* 38:679–682
- Prasad S, Pittet A, Sukumar R (2010) Who really ate the fruit? a novel approach to camera trapping for quantifying frugivory by ruminants. *Ecol Res* 25:225–231
- Prasad S, Sukumar R (2010) Context-dependency of a complex fruit–frugivore mutualism: temporal variation in crop size and neighborhood effects. *Oikos* 119:514–523
- Provenza FD (1995) Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *J Range Manage Arch* 48:2–17
- R-Core-Team (2013) R: A Language and Environment for Statistical Computing. R Development Core Team, Vienna, Austria
- Rabinowitz A, Myint T, Khaing ST et al (1999) Description of the leaf deer (*Muntiacus putaoensis*), a new species of muntjac from northern Myanmar. *J Zool* 249:427–435
- Robinson JG, Bennett EL (2000) Hunting for sustainability in tropical forests. Columbia University Press
- Riitters K, Wickham J, O’neill R et al (2000) Global-scale patterns of forest fragmentation. *Conserv Ecol* 4:3
- Rizvanovic A, Amundin M, Laska M (2013) Olfactory discrimination ability of Asian elephants (*Elephas maximus*) for structurally related odorants. *Chem Senses* 38:107–118

- Samansiri K, Weerakoon DK (2008) A study on the seed dispersal capability of Asian elephants in the northwestern region of Sri Lanka. *Gajah* 28:19–24
- Sankar K (1994) The ecology of three large sympatric herbivores (chital, sambar and nilgai) with special reference for reserve management in Sariska Tiger Reserve. University of Rajasthan, Jaipur
- Saunders G, Kay B (1991) Movements of Feral Pigs (*Sus Scrofa*) at Sunny Corner, New South Wales. *Wildlife Research* 18:49–61
- Schaller GB (1967) The deer and the tiger. University of Chicago Press
- Schiviz AN, Ruf T, Kuebber-Heiss A et al (2008) Retinal cone topography of artiodactyl mammals: influence of body height and habitat. *J Comp Neurol* 507:1336–1350
- Schmidt M, Sommer K, Kriebitzsch W-U et al (2004) Dispersal of vascular plants by game in northern Germany. Part I: Roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). *Eur J Forest Res* 123:167–176
- Scowcroft PG, Hobdy R (1987) Recovery of goat-damaged vegetation in an insular tropical montane forest. *Biotropica* 19:208–215
- Sekar N, Sukumar R (2013) Waiting for Gajah: an elephant mutualist's contingency plan for an endangered megafaunal disperser. *J Ecol* 101:1379–1388
- Shah N (1993) Ecology of wild ass (*Equus hemionus khur*) in Little Rann of Kutch. Dissertation, Baroda University
- Shyan-Norwalt MR, Peterson J, Milankow King B et al (2010) Initial findings on visual acuity thresholds in an African elephant (*Loxodonta africana*). *Zoo biology* 29:30–35
- Spiegel O, Nathan R (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecol Lett* 10:718–728
- Sridhara S, Edgaonkar A, Kumar A (2013) Understorey structure and refuges from predators influence habitat use by a small ungulate, the Indian chevrotain (*Moschiola indica*) in Western Ghats, India. *Ecol Res* 28:427–433
- Stevens CE, Hume ID (1995) Comparative physiology of the vertebrate digestive system. Cambridge University Press, Cambridge
- Sugnaseelan S, Prescott NB, Broom DM et al (2013) Visual discrimination learning and spatial acuity in sheep. *Appl Anim Behav Sci* 147:104–111
- Terborgh J (2013) Using Janzen-Connell to predict the consequences of defaunation and other disturbances of tropical forests. *Biol Conserv* 163:7–12
- Thomson C, Challies C (1988) Diet of feral pigs in the podocarp-tawa forests of the Urewera Ranges. *N Z J Ecol* 11:73–78
- Van Dung V, Giao PM, Chinh NN et al (1993) A new species of living bovid from Vietnam. *Nature* 363:443–445
- van Strien NJ, Steinmetz R, Manullang B, Sectionov Han KH, Isnain W, Rookmaaker K, Sumardja E, Khan MKM Ellis S (2008) Rhinoceros sondaicus. The IUCN Red List of Threatened Species 2008: e.T19495A8925965. <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T19495A8925965.en>
- Velho N, Isvaran K, Datta A (2012a) Rodent seed predation: effects on seed survival, recruitment, abundance, and dispersion of bird-dispersed tropical trees. *Oecologia* 169:995–1004
- Velho N, Ratnam J, Srinivasan U et al (2012b) Shifts in community structure of tropical trees and avian frugivores in forests recovering from past logging. *Biol Conserv* 153:32–40
- Vellend M, Myers JA, Gardescu S et al (2003) Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology* 84:1067–1072
- Wang BC, Smith TB (2002) Closing the seed dispersal loop. *Trends Ecol Evol* 17:379–386
- Wenninger PS, Shipley LA (2000) Harvesting, rumination, digestion, and passage of fruit and leaf diets by a small ruminant, the blue duiker. *Oecologia* 123:466–474
- Whitten T, Mustafa M, Henderson GS (1987) The Ecology of Sulawesi Gajah Mada. University Press, Yogyakarta
- Wilson DE Mittemeier RA (2011) Handbook of the Mammals of the World-Volume 2. Hoofed Mammals. Lynx Edicions

- Wright SJ, Hernández A, Condit R (2007) The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica* 39:363–371
- Wulffraat S (2006) Diet studies of Bearded Pigs in Kayan Mentarang National Park, Borneo, Indonesia. *Suiform Soundings* 6:17–18
- Yasuda M, Miura S, Ishii N et al (2005) Fallen fruits and terrestrial vertebrate frugivores: a case study in a lowland tropical rain forest in Peninsular Malaysia. In: Forget P-M, Lambert JE, Vander Hulme P E, Wall SB (eds) *Seed fate: predation, dispersal and seedling establishment*. CABI Publishing, Wallingford, pp 151–174
- Yearsley JM, Villalba JJ, Gordon IJ et al (2006) A theory of associating food types with their postingestive consequences. *Am Nat* 167:705–716
- Zonderland JJ, Cornelissen L, Wolthuis-Fillerup M et al (2008) Visual acuity of pigs at different light intensities. *Appl Anim Behav Sci* 111:28–37