Food preference of the Bornean elephant (Elephant maximus borneensis) in North Kalimantan Province, Indonesia, and its conservation implications

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Food preference of the Bornean elephant (*Elephas maximus borneensis*) in North Kalimantan Province, Indonesia, and its conservation implications

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Abstract. The preference to feed on particular plant species may reflect the most desirable components that an animal perceives, in relation to what is available. The food preference of the Bornean elephant (*Elephas maximus borneensis* Deraniyagala, 1950) in the Sebuku area of North Kalimantan was studied by chemical analysis on the metabolites of several known food plant species. We analysed the chemical properties of the Bornean elephant diet from thirteen food-plant species which represented the level of food-plant categories utilised by the Bornean elephant in the study area. All samples were analysed for nutritional value, and their metabolic profiles were obtained using ^{1}H nuclear magnetic resonance spectroscopy. These data were subjected to multivariate data analyses to identify the common components. This study confirmed that Bornean elephants tend to follow a strategy to maximise their energy intake by selecting food items rich in sugar and crude protein and minimise fibrous elements. The fact that they also prefer food items with high glutamate suggests that taste plays a role and this element may be a cue for the Bornean elephant to assist in foraging and searching for palatable food.

Key words. Bornean elephant, cue, glutamate, nuclear magnetic resonance, nutritional value, plant preference

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INTRODUCTION

Optimal foraging theory has been developed to explain the movements of foraging animals (Pyke, 1983; Sinclair, 1983). It suggests that herbivores maximise energy intake, digestion rate or protein content (McNaughton, 1979). Larger body size is characterised by increased metabolic demands and extended ingesta passage rates in comparison to small body sizes. Together, these are pre-requisites for the evolution of gut structures that result in greater digestibility of slowly digestible fractions of forage (Demment & Van Soest, 1985; Clauss et al., 2003). Mega-herbivores such as elephants have evolved non-ruminant hindgut fermentation that allows them to meet their energy requirements. While a ruminant has physical restrictions, due to the complex structure of the stomach, in the rate of passage of food and, hence, in the quantity of food it can consume, a non-ruminant does not have such a limitation (Sukumar, 2003). As hindgut fermenters, elephants more efficiently extract high-fibre diet per unit time, while ruminants have more efficient extraction rates per unit material (Jachmann & Bell, 1985). Elephants have a relatively fast digestive passage, thus allowing them to tolerate food of lower nutritional quality (Bell, 1971; Demment & Van Soest, 1985; Clauss et al., 2003). Based on their body size and metabolism, the elephants thus represent the upper end of a tolerance class, tolerating lower-quality food compared to smaller herbivores and ruminants.

To extract sufficient energy from high-quality plant species, hindgut fermenters expand their range of foods and increase the bulk of food ingestion (Demment & Van Soest, 1985; Sukumar, 1990). An adult Asian elephant (*Elephas maximus*) can consume between 150 and 350 kg in wet weight per day (Shoshani & Eisenberg, 1982). Elephants exploit a wide range of plant resources (Sukumar, 2006) due to their ability to digest cellulose through the presence of symbiotic microbes in their large caecum and in the colon, and by enhanced grinding of fibrous materials with their specialised trunks and high-crowned molar teeth. As a result, more than 250 plant species (in 60 families) have been reported to be consumed by the Asian elephant (Sitompul, 2011). Whenever available, elephants still show a preference for high-quality food, that is easy to digest and high in energy, protein, and minerals but low in certain secondary compounds such as saponins and lignin due to their deleterious properties and

limiting effects on digestibility (Jachmann, 1989; Rosenthal & Janzen, 1991). Larger herbivores and hindgut fermenters are less adapted to deal with these secondary compounds than foregut or ruminant herbivores, although they are known to reduce the negative effect of these compounds by diversifying diet composition (Clauss et al., 2003). As yet, a complete understanding of the elephant's foraging strategy is still beyond our knowledge (Sukumar, 2003).

Since 1986, the Asian elephant *Elephas maximus* has been listed as an endangered species (EN) on the IUCN Global Red List (Choudhury et al., 2008). Around 2,000 of the Bornean elephants subspecies (*Elephas maximus borneensis* Deraniyagala, 1950) are estimated to live in the wild, mostly in Sabah, Malaysia (Alfred et al., 2011). The species is severely threatened by habitat loss, degradation, and fragmentation (Choudhury et al., 2008). The elephant population within the Kalabakan Forest Reserve (FR) in central Sabah is estimated to consist of 280–330 individuals. The Sebuku forest (about 49,500 ha) in North Kalimantan, Indonesia is occasionally visited by 20–60 elephants (Wulffraat, 2006; Alfred et al., 2011) that are reproductively connected with the population at the Kalabakan FR (Riddle et al., 2010). The suitability of the Sebuku area to support a resident population in the long-term, however, needs further investigation. The fact that Bornean elephants have occurred here for thousands of years and that the area is connected to a vital elephant habitat in Sabah (Olivier, 1978; Payne et al., 1994; Yasuma, 1994; MacKinnon et al., 1996; Jepson et al., 2002; Riddle et al., 2010) would at least render such conservation efforts justified. Under Indonesian law (Government Regulation Nr. 7/1999), the Asian elephant (including Bornean elephant) is also listed as a protected species (Noerdjito & Maryanto, 2001).

In 2005, the elephant population in the Sebuku forest drew the attention of the provincial government as a result of local media reporting on incidents of human-elephant conflict, concerning solitary males that had entered village gardens and agricultural fields in the Sebuku area (Wulffraat, 2006). Within small-scale farming land, elephants move between refuges and feeding grounds at night and at high speed to avoid people (Sukumar, 1989; Nyhus et al., 2000; Chiyo et al., 2005; Galanti et al., 2006; Kumar et al., 2010; Webber et al., 2011; Gubbi, 2012). This type of dispersal is categorised as transient and corresponds with mostly solitary behaviour (Cote et al., 2016). It is, therefore, not surprising that incidents of crop-raiding by elephants in the Sebuku area are generally associated with solitary male elephants rather than herds (Suba et al., 2017). There are no known records of multiple elephants disturbing agricultural fields here, whereas several male individuals are suggested to have increased the frequency in which they visit some of the village gardens and fields (Wulffraat, 2006). In addition, the movement pattern of the elephants in this area has likely not changed for over a century. Knowledge of the feeding preferences of the Bornean elephants will help to inform options for the management of human-elephant conflict (Suba et al., 2018). From the initial study conducted by Suba et al. (2018), 52 food plants are distinguished based on feeding

signs consisting of 45 wild species and seven cultivated crops. Among wild species, the study revealed that all species of rattan, an arrowroot species (*Donax canniformis*), bamboo (*Bambusa* spp., *Dendrocalamus* sp., *Schizostachyum* sp.), wild banana (*Musa borneensis*), and all species of palms, are essential in the diet of Bornean elephants. In the vicinity of the villages, Bornean elephant mainly raid *Elaeis guineensis* (oil palms), *Saccharum officinarum* (sugarcane), *Cocos nucifera* (coconut), and *Artocarpus heterophyllus* (jackfruit) with various degrees of utilisation.

Besides nutritional values, preference for certain food plant species may also be based on perception; some animals select food components based on what they find most desirable, in relation to what is available (Loehle & Rittenhouse, 1982). Such behavioural preferences are driven by a range of stimuli: smell, taste, sight, touch, or sound, which may be 'patch-specific' (Bell, 1991; Sukumar, 2003; Blake & Inkamba-Nkulu, 2004). Provenza (1995) suggested that food selection involves interactions between the senses of taste and smell, as well as mechanisms to sense the consequences of food ingestion, such as satiety (experienced when animals ingest adequate kinds and amounts of nutritious food) and malaise (experienced when animals ingest excesses of nutrients or toxins or experience nutrient deficits). Taste, smell, and sight could also interact, e.g., a taste cue could potentiate a visual cue. Garcia (1989) thus suggested that taste is the most powerful arbiter of what is fit to eat, and smell comes after. Due to their highly developed sense of taste (Joshi, 2009; Garstang, 2015), it has been suggested that elephants select 'better tasting' food plant species.

Here, we applied different methodological approaches to analyse essential and possible secondary compounds in food plants which may be associated with the dietary preferences of Bornean elephants and crop-raiding behaviour. We also asked how nutritional values and chemical content would predict feeding frequency. Specifically, we addressed the following questions: (1) Which nutritional values have positive or negative effect on food preference? (2) Which metabolites are responsible for the separation of food preference rank?

MATERIAL AND METHODS

Study site. Our study was conducted in the Sebuku area of the Nunukan District, located in the northeast of the Province of North Kalimantan, Indonesia (Fig. 1). As the only remaining suitable habitat for Bornean elephants in the Nunukan District of North Kalimantan Province, the Sebuku forest is currently subject to a conflict over land-use claims by the government (central, provincial, and local), the private sector, and other stakeholders. Within the framework of the government-supported 'one million hectares of oil palms' programme since 2002, oil palm plantations have been established in the Nunukan District (Bureau of Estate of East Kalimantan, 2015; East Kalimantan Provincial Government, 2015). As the district is quickly becoming the main centre of the oil palm plantation programme, conversion of large parts of the Sebuku forest into oil palm is ongoing and is
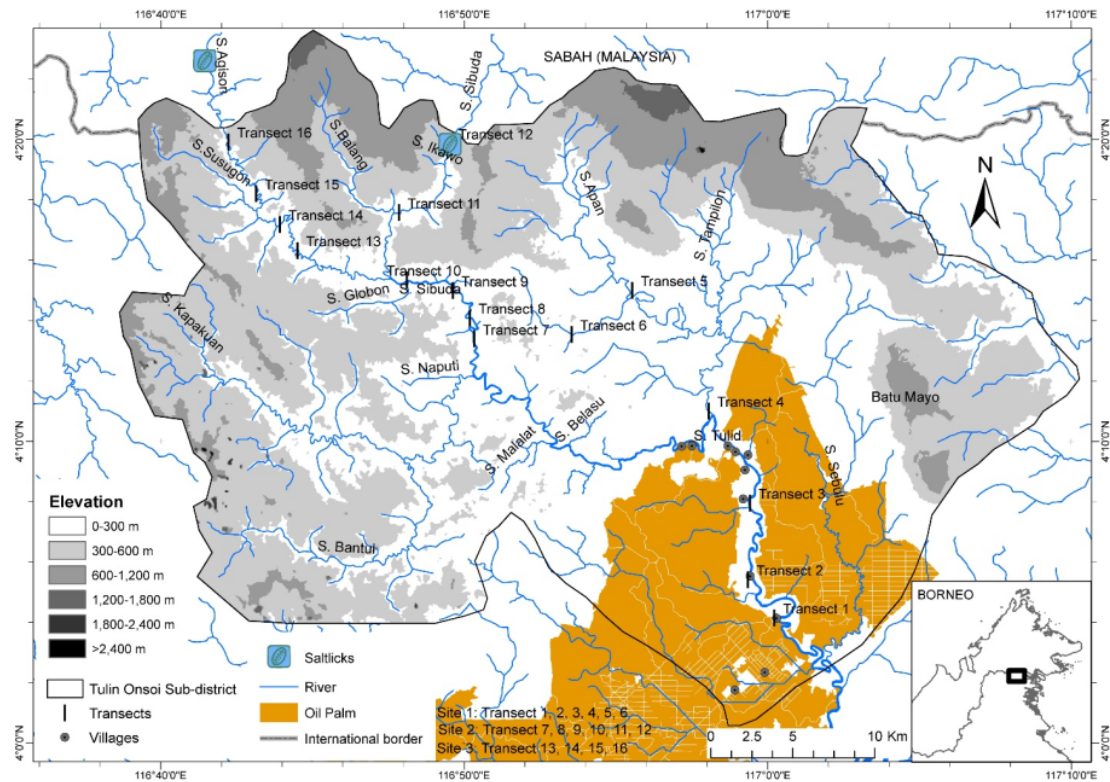
Fig. 1. Map of the study area showing transects containing feeding signs of Bornean elephant in the study area in Tulin Onsoi Sub-district, North Kalimantan Province (after Suba et al., 2018).

therefore considered as the major threat to the local elephant population (Wulffraat, 2006). Two main oil palm estates are operating in the Tulin Onsoi Sub-district: the Karangjoang Hijau Lestari (KHL) Group and the Tirtamadu Sawit Jaya (TSJ) Group, with respectively 20,000 and 7,900 ha of oil palms (Bureau of Estate of East Kalimantan, 2015).

The Sebuku forest shares its western boundary with the Kayan Mentarang National Park, which is characterised by an undisturbed sequence of all major habitats in Kalimantan, ranging from the mangrove tidal swamp, freshwater swamp, peat swamp, riverine, and lowland forests of Sebuku Sembakung, up to the hill and mountain habitats of Kayan Mentarang. The western area of the Sebuku watershed comprises forested hills with limestone areas and outcrops (Wulffraat, 2006). The Sebuku lowland forest used to be one of the most species-rich forests of Borneo (MacKinnon et al., 1996; Jepson et al., 2002), but has been logged to a great extent in the 1990s. Between 1996 and 2003, primary forest area decreased from 915,183 ha to 697,695 ha, a 24% decline in 7 years (Lusiana et al., 2005; Widayati et al., 2005). The proportion of trees from families such as the Euphorbiaceae, Moraceae, and Lauraceae is higher in these logged forests than in primary forest (MacKinnon et al., 1996). The herbaceous layer is also more pronounced in the logged areas. There are still areas of primary hill

dipterocarp forests in the upper North and West (Wulffraat, 2006) and riverine forests stretching in narrow strips along the larger streams and rivers. The vegetation is typically composed of dominant *Dipterocarpus oblongifolius* and several other species that are more or less restricted to this habitat. Degraded riverine vegetation in the lowlands is often dominated by *Saccharum* spp. grasses (Wulffraat, 2006). The canopy height in this forest ranges from 20–40 m, but giant emergent trees can reach a height of more than 60 m. Densities of non-woody plants on the forest floor depend largely on light penetration. In primary forests this group of plants is usually less abundant because the closed canopy prevents light from reaching the forest floor (Whitmore, 1998).

Ten villages located along the Tulid River were included in our study area, i.e., Balatikon, Tau Baru, Tinampak II, Tinampak I, Salang, Naputi, Tembalang, Kalunsayan, Sekikilan, and Semunad (Fig. 1). These villages have experienced the presence of the Bornean elephant. The predominant livelihood strategy in the Tulin Onsoi Sub-district is small-scale subsistence farming, nowadays complemented with wage labour for oil palm companies. Crops grown in the area include cassava *Manihot esculenta*; the staple food crop of the local community in the study area (i.e., the Dayak Agabag), rice (*Oryza sativa*), corn (*Zea*

Table 1. Thirteen Bornean elephant food samples based on frequency (F) of feeding signs found in the study area arranged according to overall preference by Bornean elephants (N = number of subplots; N_{total}-forest = 120; N_{total}-village = 40; Frequency (F)$_{selected}$ = N$_{selected}$/N$_{total}$).

No.	Elephant food	Symbol	Family	Life Form	Wild plants or Crop	Transect	N$_{selected}$	F$_{selected}$ (%)	Plant parts sampled	Sample Identity [Location (F=Forest, V=Village); Transect (T); Individual plant/part (n-th)]
1	*Calamus* sp.	C	Arecaceae	Palm	Wild plant	Forest	14	11.6	Shoots	F-5-1, F-7-1, F-8-1, F-9-1, F-13-1
2	*Donax canniformis*	Dc	Marantaceae	Shrub	Wild plant	Forest	5	4.2	All parts	F-6-1, F-9-1, F-10-1
						Village	3	7.5	All parts	V-1-1, V-3-1
3	*Elaeis guineensis*	Eg	Arecaceae	Palm	Crop	Village	4	10.0	Shoots (early stage plant)	V-1-1, V-2-1, V-3-1, V-3-2, V-4-1
4	*Etlingera* sp.	E	Zingiberaceae	Herb	Wild plant	Forest	12	10.0	All parts	F-7-1, F-9-1, F-10-1, F-10-2, F-13-1
5	*Musa borneensis*	Mb	Musaceae	Herb	Wild plant	Village	4	10.0	Stem pith and shoots	V-1-1, V-1-2, V-2-1, V-3-1, V-4-1
6	*Saccharum spontaneum*	Ss	Poaceae	Herb	Wild plant	Village	4	10.0	Stem and leaves	V-1-1, V-2-1, V-2-2, V-3-1, V-4-1
7	*Bambusa oldhamii*	Bo	Poaceae	Bamboo	Wild plant	Forest	12	10.0	Shoots	F-10-1, F-13-1, F-13-2, F-14-1, F-15-1
8	*Saccharum officinarum*	So	Poaceae	Herb	Crop	Village	3	7.5	Stem and leaves	V-1-1, V-1-2, V-2-1, V-2-2, V-3-1
9	*Cocos nucifera*	Cn	Arecaceae	Palm	Crop	Village	3	7.5	Shoots (early stage plant)	V-1-2, V-2-1, V-2-2, V-3-1
10	*Artocarpus heterophyllus*	Ah	Moraceae	Tree	Crop	Village	2	5.0	Twigs, young leaves, shoots	V-1-1, V-1-2, V-2-1, V-2-2, V-2-3
11	*Licuala spinosa*	L	Arecaceae	Palm	Wild plant	Forest	3	2.5	Shoots and stem pith of new clump	F-13-1, F-13-2
						Village	1	2.5	Shoots and stem pith of new clump	V-3-1, V-3-2, V-3-3,
12	*Caryota mitis*	Cm	Arecaceae	Palm	Wild plant	Village	1	2.5	Shoots and stem pith of new clump	V-3-1, V-3-2, V-3-3, V-3-4, V-3-5
13	*Arenga pinanga*	Ap	Arecaceae	Palm	Wild plant	Village	1	2.5	Shoots and stem pith of new clump	V-3-1, V-3-2, V-3-3, V-3-4, V-3-5

mays), legumes, coconut (*Cocos nucifera*), banana (*Musa* spp.), sugarcane (*Saccharum officinarum*), vegetables, fruits, and spice trees.

Data collection. We sampled the Bornean elephant diet from thirteen food-plant species which represented the level of food-plant categories utilised by the Bornean elephant in the study area, both from forest and village transects (Suba et al., 2018). Feeding signs on three wild food plant species were solely detected on the forest transects (i.e., *Calamus* sp., *Etlingera* sp., and *Bambusa oldhamii*). Two wild food plant species were represented on both forest and village transects (i.e., *Donax canniformis* and *Licuala* sp.), and four wild food plant species on the village transect only (i.e., *Musa borneensis*, *Saccharum spontaneum*, *Caryota mitis*, and *Arenga pinanga*). Four crop plant species had feeding signs on the village transects [i.e., *Elaeis guineensis* (oil palm), *Saccharum officinarum* (sugarcane), *Cocos nucifera* (coconut), and *Artocarpus heterophyllus* (jackfruit)]. Plant samples were taken from five individuals of each plant species, randomly sampled from different transects in both forest and village locations (for details see Table 1 and link to Fig. 1).

Plant preference levels were predicted by ranking them according to the frequency of feeding signs ($F_{selected}$) found in the study area for each food plant species (Table 1). *Calamus* sp. and *Donax canniformis* appeared to be the most preferred species ($F_{selected}$ = 11.6%), followed by five species with $F_{selected}$ = 10.0%, i.e., *Elaeis guineensis*, *Etlingera* sp., *Musa borneensis*, *Saccharum spontaneum*, and *Bambusa oldhamii*. The less preferred species were indicated by lower frequency respectively, i.e., *Saccharum officinarum* and *Cocos nucifera* (7.5%), *Artocarpus heterophyllus* and *Licuala* sp. (5% respectively), *Caryota mitis* and *Arenga pinanga* (2.5% respectively).

Chemical analysis. Chemical properties of elephant diets were determined by content analyses of the plant samples. For nutritional analysis, plant samples were sieved through a 1 mm mesh and analysed for chemical composition on a dry matter basis. For chemical profiling, dried powder (50 mg) of each plant sample was subjected to extraction by ultrasonication for 20 min with 1.5 ml mixture of KH_2PO_4 buffer (pH 6.0) in D_2O containing 0.005% of trimethyl silyl propionic acid sodium salt (w/w) (TMSP) and methanol-d_4 (1:1). Extracts were centrifuged at 13,000 rpm for 10 min at 25°C and the supernatant (300 μL) was transferred to a 3-mm NMR tube.

To determine the significant chemical attributes on which preference was based, all samples were analysed for dry matter (DM), organic material (OM), crude protein (CP), four fibrous components (the total structural carbohydrate content/neutral detergent fibre (NDF), cellulose plus lignin/ acid detergent fibre (ADF), hemicellulose (NDF-ADF), and acid detergent lignin (ADL)), and five mineral elements (phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na)). N, P, K, Ca, Mg, and Na were measured after destruction with a mixture of H_2SO_4, salicylic

acid, H_2O_2 and selenium (Se), with a Skalar Sanplus autoanalyzer (Novozamsky et al., 1983). The percentage of CP was obtained by multiplying the total N by 6.25 (%CP = %N × 6.25). NDF and ADL were determined according to Van Soest et al. (1991) using the ANKOM Technology Technique. This analysis was done at the Laboratory of the Wildlife Ecology and Conservation Group at Wageningen University and Research, The Netherlands.

Chemical profiles were obtained by comprehensive, qualitative and quantitative analysis, referred to as 'Metabolomics' (Kim et al., 2010). In the field of metabolomics, ^1H nuclear magnetic resonance spectroscopy (NMR) is considered to be a suitable method for a macroscopic analysis for a wide range of metabolic groups compared with other methods (e.g., mass spectrometry-based) because it allows the simultaneous detection of diverse groups of secondary metabolites (flavonoids, alkaloids, terpenoids, etc.) besides abundant primary metabolites (sugars, organic acids, amino acids, etc.), both essential and non-essential components. This analysis was conducted at Natural Products Laboratory at Leiden University, The Netherlands.

^1H NMR analysis was performed using the parameters explained in Kim et al. (2010). Briefly, ^1H NMR spectra were recorded at 25°C on a Bruker 600 MHz AVANCE II NMR spectrometer (Bruker, Karlsruhe, Germany) operating at a proton NMR frequency of 600.13 MHz. Methanol-d_4 was used as the internal lock. Each ^1H NMR spectrum consisted of 64 scans requiring 4 min and 26 s acquisition time with the following parameters: 0.16 Hz per point, pulse width (PW) = 30° (11.3 μs), and relaxation delay (RD) = 1.5 s. A pre-saturation sequence was used to suppress the residual H_2O signal with low-power selective irradiation at the H_2O frequency during the recycle delay. FIDs were Fourier-transformed with LB = 0.3 Hz. The resulting spectra were manually phased and baseline corrected, and calibrated to TMSP at 0.0 ppm, using XWIN NMR (version 3.5, Bruker).

Statistical analysis. The mean and standard error for each nutritional value of consumed plants was calculated. Different chemical characteristics of Bornean elephant food items were compared to detect differences among consumed plants and differences between consumed wild and crop plants in general.

The ^1H NMR spectra were automatically reduced to ASCII files. Spectral intensities were scaled to TMS signal (δ 0.0) and reduced to integrated regions of equal width (δ 0.04) corresponding to the region of δ 0.0–10.0. The regions of δ 4.85–4.95 and δ 3.2–3.4 were excluded from the analysis because of the residual signal of D_2O and CD_3OD, respectively. Bucketing was performed by AMIX software (Bruker) with scaling to the standard internal region (TMSP, from δ 0.02 to -0.02).

The projections to latent structures (PLS), an extended form of principal component analysis (PCA), are generally used to establish the relationship between two data sets, i.e., predictors and responses. For the present study, the predictor

Table 2. Nutrient and mineral composition of Bornean elephant's wild and crop food [Mean and S.E. (standard error) in parentheses].

Plant species	Wild plant or crop	C (%)									
		CP	NDF	ADF	Hemi	ADL	P	K	Ca	Mg	Na
Calamus sp.	Wild plant	34.0 (0.60)	39.2 (0.82)	18.3 (0.88)	20.9 (0.51)	6.7 (1.28)	0.61 (0.01)	3.02 (0.03)	0.44 (0.00)	0.29 (0.01)	0.03 (0.02)
Donax canniformis	Wild plant	2.1 (0.07)	72.0 (2.36)	49.3 (1.81)	22.7 (0.54)	6.7 (0.21)	0.08 (0.00)	4.37 (0.21)	0.07 (0.01)	0.14 (0.00)	0.01 (0.01)
Elaeis guineensis	Crop	16.8 (0.15)	48.7 (1.25)	24.5 (0.90)	24.2 (0.48)	8.6 (0.06)	0.57 (0.01)	4.18 (0.28)	0.82 (0.03)	1.18 (0.09)	0.11 (0.07)
Etlingera sp.	Wild plant	3.3 (0.14)	65.1 (2.58)	43.1 (2.42)	22.0 (0.16)	14.7 (1.97)	0.06 (0.00)	3.41 (0.17)	0.26 (0.05)	0.51 (0.06)	0.02 (0.01)
Musa borneensis	Wild plant	14.2 (0.51)	61.6 (0.74)	36.9 (0.43)	24.7 (0.32)	11.9 (0.24)	0.35 (0.02)	7.18 (0.23)	0.28 (0.03)	0.29 (0.02)	0.00 (0.00)
Saccharum spontaneum	Wild plant	15.2 (0.56)	55.8 (2.45)	27.6 (1.73)	28.2 (0.76)	2.9 (0.81)	0.39 (0.02)	4.27 (0.23)	0.57 (0.06)	0.45 (0.04)	0.03 (0.02)
Bambusa oldhamii	Wild plant	18.8 (0.28)	44.4 (0.29)	21.9 (1.00)	22.5 (0.71)	6.7 (1.56)	0.39 (0.01)	3.54 (0.06)	0.14 (0.02)	0.15 (0.01)	0.00 (0.00)
Saccharum officinarum	Crop	2.8 (0.18)	60.4 (0.80)	33.0 (0.30)	27.4 (0.72)	7.4 (0.30)	0.08 (0.00)	1.87 (0.05)	0.12 (0.00)	0.17 (0.01)	0.00 (0.00)
Cocos nucifera	Crop	5.9 (1.72)	54.6 (1.14)	34.3 (1.11)	20.4 (0.07)	10.7 (1.36)	0.23 (0.05)	2.39 (0.15)	0.40 (0.06)	0.30 (0.05)	0.21 (0.00)
Artocarpus heterophyllus	Crop	11.2 (0.26)	42.1 (0.44)	32.5 (0.28)	9.6 (0.27)	17.3 (0.45)	0.15 (0.01)	1.84 (0.03)	0.43 (0.01)	0.17 (0.00)	0.04 (0.01)
Licuala sp.	Wild plant	4.8 (0.02)	79.3 (0.03)	56.2 (0.07)	23.1 (0.04)	14.4 (0.19)	0.05 (0.00)	1.26 (0.07)	0.00 (0.00)	0.13 (0.00)	0.00 (0.00)
Caryota mitis	Wild plant	14.6 (0.50)	47.5 (2.51)	29.2 (1.15)	18.3 (1.38)	11.8 (0.51)	0.39 (0.03)	3.71 (0.06)	1.13 (0.04)	0.54 (0.01)	0.00 (0.00)
Arenga pinanga	Wild plant	15.3 (0.30)	56.5 (6.72)	35.7 (5.07)	20.8 (1.66)	7.7 (0.53)	0.48 (0.01)	4.47 (0.09)	0.69 (0.09)	0.56 (0.01)	0.36 (0.02)

CP: crude protein; NDF: neutral detergent fibre; ADF: acid detergent fibre; Hemi: hemicellulose; ADL: acid detergent lignin; P: phosphorus; K: kalium (potassium); Ca: calcium; Mg: magnesium; Na: natrium (sodium)

represents the nutritional values and metabolomics data and the response-data represents the predictive preference level based on the frequency of feeding signs of each food plant ($F_{selected}$). PLS modelling was primarily used to predict the chemical shifts from the nutritional values and metabolomics data responsible for the food preference of the Bornean elephant. The score plot of PLS with two components shows the samples grouped by preference.

Since structured noise present in the predictor-data set could cause systemic variation, this was eliminated by extension of the PLS method known as orthogonal PLS (OPLS). OPLS modelling determines relationships between the two data blocks and divides the systemic variation of predictors into two model parts: the predictive or parallel part which correlates the predictor and response-data, and the orthogonal part which indicates the variation in the predictor-data unrelated to the response-data set (Trygg & Wold, 2002; Eriksson et al., 2006). By applying the OPLS method, the samples with different preferences levels were separated by the predictive component with positive and negative scores.

PLS and orthogonal PLS (OPLS) with scaling based on Unit Variance were performed with the SIMCA-P+ software (v. 14.1, Umetrics, Umeå, Sweden).

RESULTS

Nutritional value of individual plants. Nutritional value of plants varied across species. Table 2 shows the content of crude protein, fibre, and lignin. *Calamus* sp., the most preferred wild plant, contained the highest value of CP (33.4–34.6%). Other wild food plants with a relatively high CP value were *Bambusa oldhamii* (18.5–19.1%), *Saccharum spontaneum* (14.6–15.7%), and *Musa borneensis* (13.7–14.7%). Low-level ADL was found in wild plant species which were assumed to be more preferred (based on Jachmann, 1989), i.e., *Saccharum spontaneum* (2.1–3.8%), *Donax canniformis* (6.4–6.9%), *Bambusa oldhamii* (5.1–8.2%) and *Calamus* sp. (5.4–8.0%). *Calamus* sp. and *Bambusa oldhamii* were among wild food plants which were low in ADF (17.4–19.2% and 20.9–22.9%, respectively). *Elaeis guineensis* was identified as high in CP (16.7–17.0%), but relatively low in ADF (23.6–25.4%) and ADL (8.5–8.7%). *Saccharum spontaneum* (wild plant) and *Saccharum officinarum* (crop) were high in hemicellulose (27.5–29.0% and 26.7–28.1%, respectively).

Table 2 also shows the content of mineral microelements in plants. *Calamus* sp. and *Elaeis guineensis* had the highest content of P (0.60–0.62% and 0.56–0.58%, respectively). The highest level of K was found in *Musa borneensis* (7.0–7.4%), followed by *Donax canniformis* (4.2–4.6%), *Saccharum spontaneum* (4.0–4.5%), and *Elaeis guineensis* (3.9–4.5%). In general, *Elaeis guineensis* had a higher concentration of the analysed minerals than most of the wild food plants. Ca and Na were less abundant in the most-preferred food plants and more abundant in the food plants with lower preference. *Arenga pinanga* (wild plant) and *Cocos nucifera* (crop plant)

had the highest concentration of Na (0.3–0.4% and 0.2%, respectively). *Caryota mitis* had the highest content of Ca (1.1–1.2%).

Fig. 2a shows the OPLS score plot with the correlation between nutritional data and food preference. In the OPLS model, two orthogonal components explained 52% of the variation of the total, and the cross-validation predictive ability $Q^2(y)$ value was 0.40, indicating good predictability of the model. Response-related (food preference) variables are shown in Fig. 2b. Crude protein, P, K, and hemicellulose (HC) appeared to be positively correlated with preference while fibrous components (ADF and ADL) were negatively correlated with preference. In contrast, Ca and Na, although also significant in their level of separation, were negatively correlated with predictive preference (Fig. 2b).

NMR analysis and correlation with food preference. Mostly large metabolites (protein, fibre) and inorganic components were subjected to nutritional composition analysis. During ^{1}H-NMR spectroscopy, all proton-containing compounds were detected, providing broader profiles of all metabolites present in the plant. Resonances were assigned according to an in-house library. Various metabolites such as amino acids, organic acids, sugars and other secondary metabolites (flavonoids, phenyl propanoids or terpenoids) were detected. Due to the considerable variation in plant profiles, it was necessary to apply chemometric tools such as PCA, partial least squares (PLS), or orthogonal projections to latent structures (OPLS) to quantify the differences between the spectra and extract latent spectral information correlated to a feeding preference.

No separation was found between crop plants and wild plants based on PCA and PLS-DA (data not shown). However, when applying the OPLS method, the plants with high and low preference are well separated and a clear correlation of the preference was observed (Fig. 3). The OPLS model was constructed using the NMR data as predictor variable and the food preference (F, %) as response variable. Two orthogonal components that explain 70% variation of the total were calculated for the model to remove the variation in the NMR spectra unrelated to feeding preference. Validation of the model was performed through cross-validation (CV)-ANOVA with P < 0.01, resulting in a cross-validation predictive ability $Q^2(y)$ of 0.65, indicating good predictability of the model. The R^2, which represents the total explained variation for predictor, was approximately 28%. Samples with different preference were well separated along the first component indicating that NMR-based profiles could reveal specific metabolites in plants from high and low feeding preference.

Since OPLS concentrated all discriminating information into the first component, it is sufficient to plot the S-line which allows the visualisation of both the covariance and the correlation structure between predictor-variables (NMR data) and predictive scores. The most dominant resonances responsible for separation were identified as glucose (δ 5.20, d, J = 3.4 Hz, α-form; δ 4.65, d, J = 8.0, β-form), glutamate
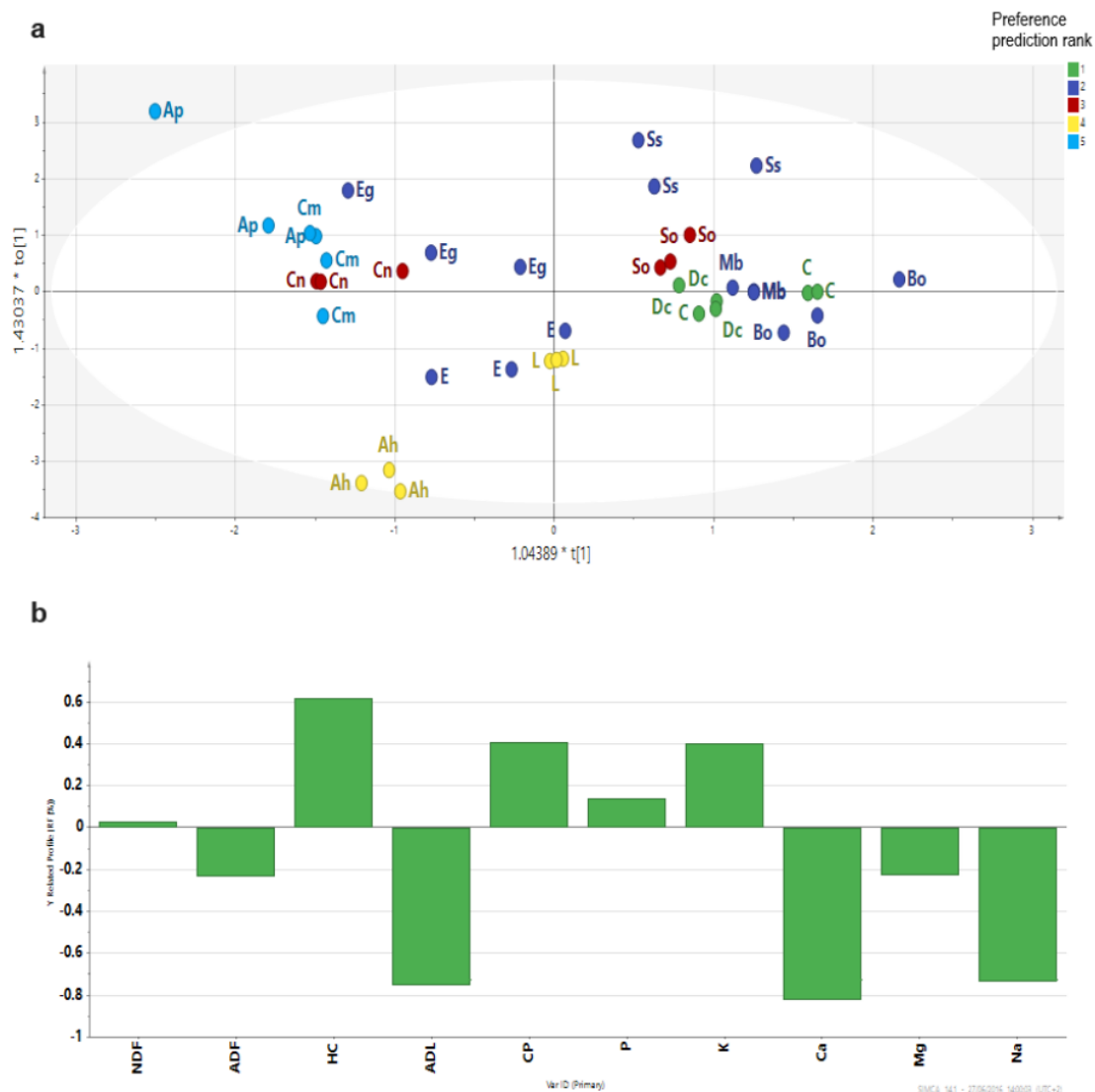
a

b

Fig. 2. The orthogonal projections to latent structures (OPLS) score plot (a) showing separation of nutritional values among the samples [C = *Calamus* sp., Dc = *Donax canniformis*, Eg = *Elaeis guineensis*, E = *Etlingera* sp., Mb = *Musa borneensis*, Ss = *Saccharum spontaneum*, Bo = *Bambusa oldhamii*, So = *Saccharum officinarum*, Cn = *Cocos nucifera*, Ah = *Artocarpus heterophyllus*, L = *Licuala* sp., Cm = *Caryota mitis*, Ap = *Arenga pinanga*] The response-related profile (b) showing signals that are positively and negatively correlated to the preference prediction [NDF = Neutral detergent fibre, ADF = Acid detergent fibre, HC = Hemicellulose, ADL = Acid detergent lignin, CP = Crude protein, P = Phosphorus, K = Potassium, Ca = Calcium, Mg = Magnesium, Na = Sodium].

(δ 2.10, m, δ 2.36, m) and glutamine (δ 2.14, m, δ 2.46, m) (Fig. 3b). In contrast, the presence of gallic acid derivatives (δ 7.10, δ 6.80) made the plant less preferable as food.

DISCUSSION

The NMR-based metabolomics approach showed that glucose and glutamate/glutamine appear to be determinant components in the food preference of Bornean elephants. In contrast, the presence of tannin-derivatives reduced the feeding preference of the plants, which is in accordance with previous reports on tannins acting as allelochemicals due to their deleterious properties (Freeland & Janzen, 1974; Jachmann, 1989; Rosenthal & Janzen, 1991). For the other nutritional values, the OPLS showed that crude protein, phosphorus, potassium, and hemicellulose were actual discriminants in the Bornean elephant food preference. Other fibrous elements (ADF and lignin) had a negative correlation. This revealed that the Bornean elephant avoids high-fibre concentrations, which appears to be common across several elephant populations (Jachmann, 1989; Nakamura, 1996).
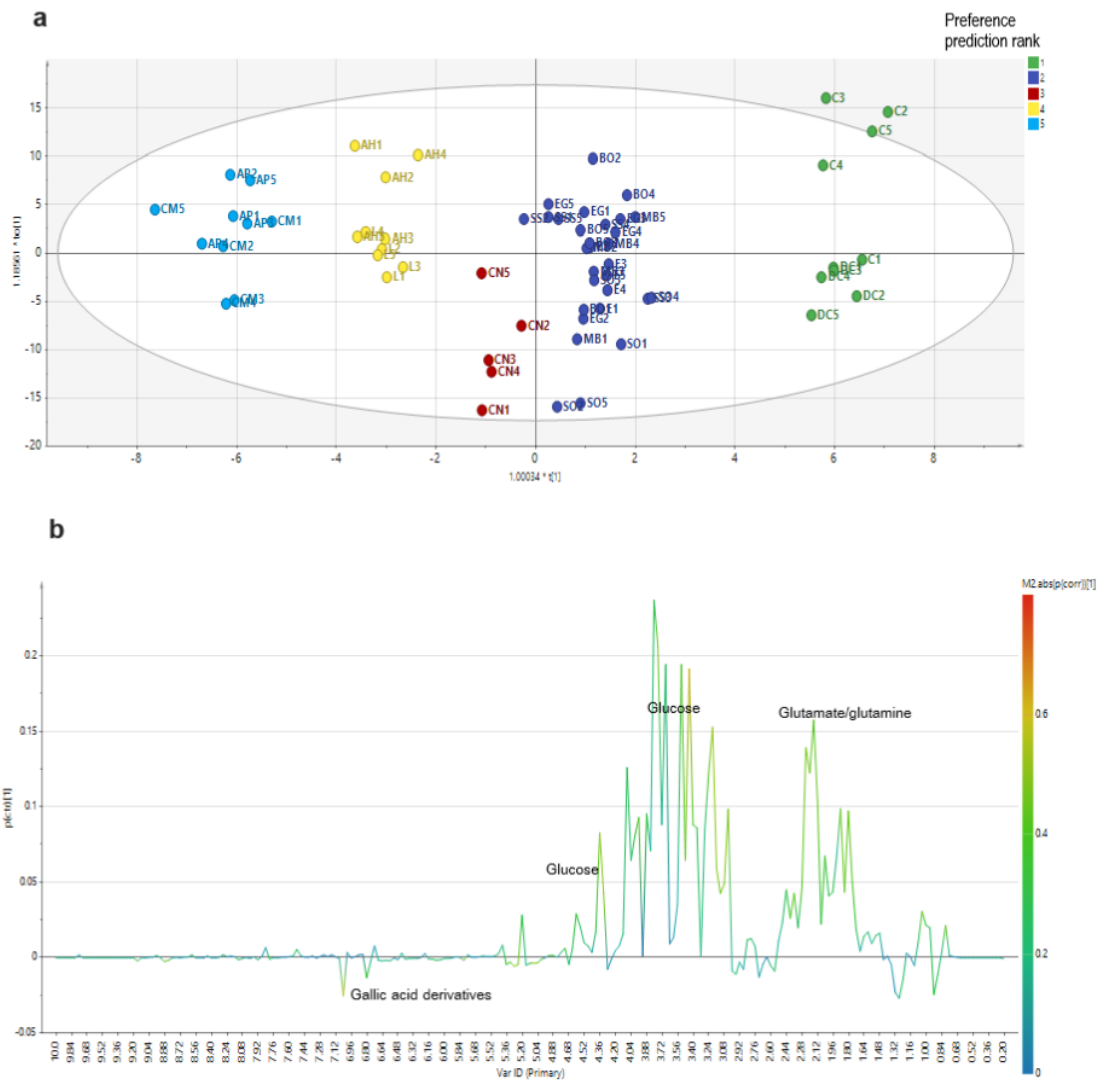
Fig. 3. The OPLS score plot (a) showing the correlation between ¹H NMR data and Bornean elephant predictive food preference level. The loading coefficient plot (b) showing the signals that are positively (on the positive y-axis) and negatively (negative y-axis) correlated to the preference prediction [C = *Calamus* sp., DC = *Donax canniformis*, EG = *Elaeis guineensis*, E = *Etlingera* sp., MB = *Musa borneensis*, SS = *Saccharum spontaneum*, BO = *Bambusa oldhamii*, SO = *Saccharum officinarum*, CN = *Cocos nucifera*, AH = *Artocarpus heterophyllus*, L = *Licuala* sp., CM = *Caryota mitis*, AP = *Arenga pinanga*].

Lignin reduces the digestibility of plant cell wall matter, and its adverse effect on elephant food selection is apparent (Jachmann, 1989).

The NMR-based metabolomics approach revealed a high amount of glutamate in most of the wild food plants preferred by the Bornean elephant. The concept that the presence of glutamate/glutamine in food allows human consumers to benefit from palatable food might also apply to elephants. Glutamate stimulates sensory working in two ways: (1) by acting on taste receptors and (2) by affecting brain neurons in an excitatory fashion to trigger and facilitate eating (Bellisle,

1999). Glutamate may intensify the savoury flavour of food suggested to be favoured by elephants, thus enhancing palatability (Bellisle, 1999; Forde & Lea, 2007). As hugely social and long-lived species with large home ranges, elephants could develop a spatial and temporal memory (Hart et al., 2008) that allows them to select 'tasty' food and to go back to specific areas after sufficient time has elapsed, in search for resources that could provide replenishment (English et al., 2014). This preference suggests that taste plays a role in the selection of food and could influence food searching behaviour and thus the movement pattern of Bornean elephants.

The results confirm that the Bornean elephant follows a strategy to maximise energy intake by selecting food items rich in sugar, protein, and hemicellulose. This is in accordance with several other studies demonstrating that elephants are energy maximisers (McCullagh, 1969; Pyke et al., 1977; McNaughton, 1979; Demment & Van Soest, 1985; Jachmann, 1989; Rode et al., 2006; Sitompul, 2011; Pretorius et al., 2012). This study showed that food preference is also correlated with crude protein, which is in agreement with Pyke et al. (1977) and Sitompul (2011). Plant material consists of chemical components that react differently to digestive enzymes within the gastrointestinal tract. Protein, sugars, and carbohydrates constitute the active fraction of plant metabolism and can rapidly be digested directly by vertebrate enzymes or can be fermented rapidly by microbes (Demment & Van Soest, 1985).

Sodium and protein are inversely related because plants that accumulate sodium typically contain low concentrations of protein (Masters et al., 2001), e.g., *Cocos nucifera* in this study. The consumption of young/growing tissues increases potassium intake (Jachmann, 1989), which at surplus concentrations will be excreted, followed by the excretion of sodium. In the present study, the wild food plant, *Arenga pinanga*, was found to have a high sodium concentration. This plant had, however, a lower frequency and abundance in the preference prediction. This confirms that the sodium availability of elephants may be very critical and in general, sodium concentrations of elephant food plants throughout their ranges in Asia and Africa are deficient (Weir, 1972; Jachmann, 1989; Sukumar, 1989; Holdo et al., 2002; Rode et al., 2006).

The ingestion of sodium through sodium-rich plants (Jachman, 1989; Nakamura, 1996; Holdo et al., 2002; Rode et al., 2006) as well as through soils (geophagy) has been widely observed in elephants (Houston et al., 2001; Chandrajith et al., 2009). At locations where high sodium concentrations are provided through so-called 'natural licks', geochemical and mineralogical composition differ from the surrounding soils. In the study area, at least two natural licks were frequently visited by elephants (Fig. 1). Besides being a mineral replenishment source (especially for sodium and magnesium), natural licks have been suggested to serve as a neutraliser of toxic secondary plant compounds and as a digestive stimulus (Jachmann, 1989). Clay minerals and in particular kaolinite ($Al_2Si_2O_5(OH)_4$) are absorptive agents of toxic compounds (Houston et al., 2001; Chandrajith et al., 2009) and elephants that have access to such minerals may be able to feed on a broader range of forest plant species (Houston et al., 2001). The presence of natural salt licks in Borneo has even been suggested to determine the limited distribution of Bornean elephants partially (e.g., Wulffraat, 2006; Matsubayashi et al., 2007).

Two crops in this study were identified as a source of sodium, i.e., *Cocos nucifera* and *Elaeis guineensis*, and were part of the elephants' diet. Crop raiding could thus be part of an optimal foraging strategy by the Bornean elephant. Findings of other studies suggesting that elephants select crops (Jachmann & Bell, 1985; Holdo et al., 2002; Rode et al., 2006) because of high sodium content, which is generally also associated with increased digestibility, confirm this assumption. The higher percentage of sugar (hemicellulose) in cultivated crops is also likely to be an essential incentive for elephants to raid crops.

Our knowledge of what the elephants feed on and what possible factors determine their dietary preference could contribute to a more conservative estimation of home range and movement patterns for better management practices.

Preserving elephants' habitat and food resources will provide for the elephants' requirements from inside their habitat (Oelrichs et al., 2016). The observation of movement patterns in the Sebuku area indicates that solitary male elephants mainly optimise their food intake, and crop-raiding exclusively might be an extension to optimal-foraging behavioural patterns. To effectively protect the Bornean elephants and to avoid more severe human-elephant conflict, it is, therefore, essential to prevent further encroachment to the Sebuku forest and expansion of oil palm plantations. Appropriate conservation measures should recognise the Bornean elephant's core habitats and their ecological requirements regarding feeding ecology and movement, for which the results of this study could provide a basis.

ACKNOWLEDGEMENTS

LITERATURE CITED

Alfred R, Ambu L, Nathan SKSS & Goossens B (2011) Current status of Asian elephants in Borneo. Gajah, 35: 29–35.

Bell RHV (1971) A grazing ecosystem in the Serengeti. Scientific American, 225: 86–93.

Bell WJ (1991) Searching Behavior: The Behavioral Ecology of Finding Resources. Chapman and Hall, London, 358 pp.

Bellisle F (1999) Glutamate and the UMAMI taste: sensory, metabolic, nutritional and behavioural considerations. A review of the literature published in the last 10 years. Neuroscience & Biobehavioral Reviews, 23: 423–438.

Blake S & Inkamba-Nkulu C (2004) Fruit, minerals, and forest elephant trails: do all roads lead to Rome? Biotropica, 36: 392–401.

Bureau of Estate of East Kalimantan (2015) http://disbun.kaltimprov.go.id (Accessed 18 March 2015).

Chandrajith R, Kudavidanage E, Tobschall HJ & Dissanayake CB (2009) Geochemical and mineralogical characteristics of elephant geophagic soils in Udawalawe National Park, Sri Lanka. Environmental Geochemistry & Health, 31: 391–400.

Chiyo PI, Cochrane EP, Naughton L & Basuta GI (2005) Temporal patterns of crop raiding by elephants: A response to changes in forage quality or crop availability? African Journal of Ecology, 43: 48–55.

Choudhury A, Lahiri Choudhury DK, Desai A, Duckworth JW, Easa PS, Johnsingh AJT, Fernando P, Hedges S, Gunawardena M, Kurt F, Karanth U, Lister A, Menon V, Riddle H, Rübel A & Wikramanayake E (IUCN SSC Asian Elephant Specialist Group) (2008) *Elephas maximus*. The IUCN Red List of Threatened Species 2008: e.T7140A12828813. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T7140A12828813.en (Accessed 19 October 2020).

Clauss M, Loehlein W, Kienzle E & Wiesner H (2003) Studies on feed digestibility in captive Asian elephants (*Elephas maximus*). Journal of Animal Physiology & Animal Nutrition, 87: 160–173.

Cote J, Bocedi G, Debeffe L, Chudzinska ME, Weigang HC, Dytham C, Gonzalez G, Matthysen E, Travis J, Baguette M & Hewison AJM (2016) Behavioral synchronization of large-scale animal movements – disperse alone, but migrate together? Biological Reviews of the Cambridge Philosophical Society, 92: 1275–1296.

Demment MW & Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. The American Naturalist, 125: 641–672.

East Kalimantan Provincial Government (2015) www.kaltimprov.go.id (Accessed 14 April 2015).

English M, Ancrenaz M, Gillespie G, Goossens B, Nathan S & Linklater W (2014) Foraging site recursion by forest elephants *Elephas maximus borneensis*. Current Zoology, 60: 551–559.

Eriksson L, Johansson E, Kettaneh-Wold N, Trygg J, Wikström C & Wold S (2006) Multi- and Megavariate Data Analysis: Basic Principles and Applications. Umetrics AB, Umeå, Sweden, 490 pp.

Forde BG & Lea PJ (2007) Glutamate in plants: metabolism, regulation, and signaling. Journal of Experimental Botany, 58: 2339–2358.

Freeland WJ & Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. The American Naturalist, 108: 269–289.

Galanti V, Preatoni D, Martinoli A, Wauters LA & Tosi G (2006) Space and habitat use of the African elephant in the Tarangire–Manyara ecosystem, Tanzania: Implications for conservation. Mammalian Biology, 71: 99–114.

Garcia J (1989) Food for Tolman: Cognition and cathexis in concert. In: Archer T & Nilsson L (eds.). Aversion, Avoidance and Anxiety: Perspectives on Aversively Motivated Behavior. Lawrence Erlbaum Associates, Inc., New Jersey. Pp. 45–85.

Garstang M (2015) Elephant Sense and Sensibility: Behavior and Cognition. Academic Press, London, 152 pp.

Gubbi S (2012) Patterns and correlates of human-elephant conflict around a south Indian reserve. Biological Conservation, 148: 88–95.

Hart BL, Hart LA & Pinter-Wollman N (2008) Large brains and cognition: where do elephants fit in? Neuroscience & Biobehavioral Reviews, 32: 86–98.

Holdo RM, Dudley JP & McDowell LR (2002) Geophagy in the African elephant in relation to availability of dietary sodium. Journal of Mammalogy, 83: 652–664.

Houston DC, Gilardi JD & Hall AJ (2001) Soil consumption by elephants might help to minimize the toxic effects of plant secondary compounds in forest browse. Mammal Review, 31: 249–254.

Jachmann H (1989) Food selection by elephants in the 'Miombo' biome, in relation to leaf chemistry. Biochemical Systematics & Ecology, 17: 15–24.

Jachmann H & Bell RHV (1985) Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. African Journal of Ecology, 23: 245–258.

Jepson P, Momberg F & Van Noord H (2002) A review of the efficacy of the protected area system of East Kalimantan Province, Indonesia. Natural Areas Journal, 22: 28–42.

Joshi R (2009) Asian elephant's *Elephas maximus* behavior in the Rajaji National Park, North-West India: Eight years with Asian elephants. Natural Science, 7: 49–77.

Kim HK, Choi YH & Verpoorte R (2010) NMR-based metabolomic analysis of plants. Nature Protocols, 5: 536–549.

Kumar MA, Mudappa D & Raman TS (2010) Asian elephant *Elephas maximus* habitat use and ranging in fragmented rainforest and plantations in the Anamalai Hills, India. Tropical Conservation Science, 3: 143–158.

Loehle C & Rittenhouse LR (1982) An analysis of forage preference indices. Journal of Range Management, 35: 316–319.

Lusiana B, Shea GA & Van Noordwijk M (2005) Introduction: Why monitor carbon in Nunukan? In: Lusiana B, Van Noordwijk M & Rahayu S (eds.). Carbon Stocks in Nunukan, East Kalimantan: A Spatial Monitoring and Modeling Approach. World Agroforestry Centre: Carbon Monitoring Team of the Forest Resources Management for Carbon Sequestration (FORMACS) Project. Pp. 1–8.

MacKinnon K, Hatta G, Halim H & Mangalik A (1996) The Ecology of Kalimantan. Oxford University Press, Oxford, 832 pp.

Masters DG, Norman NC & Dynes RA (2001) Opportunities and limitations for animal production from saline land. Journal of Animal Science, 14: 199–211.

Matsubayashi H, Lagan P, Majalap N, Tangah J, Abd Sukor JR & Kitayama K (2007) Importance of natural licks for the mammals in Bornean inland tropical rain forests. Ecological Research, 22: 742–748.

McCullagh K (1969) The growth and nutrition of the African elephant. II. The chemical nature of the diet. African Journal of Ecology, 7: 91–97.

McNaughton SJ (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. The American Naturalist, 113: 691–703.

Nakamura C (1996) Seasonal Variation in African Elephant Nutrition in Tsavo National Park, Kenya. Unpublished Master's Thesis. Michigan State University, Lansing, Michigan, 510 pp.

Noerdjito M & Maryanto I (2001) Jenis-jenis Hayati yang Dilindungi Perundang-undangan Indonesia. Balitbang Zoologi (Museum Zoologicum Bogoriense), Puslitbang – LIPI & the Nature Conservancy, Cibinong, 221 pp.

Novozamsky I, Houba VJG, Van Eck R & Van Wark W (1983) A novel digestion technique for multi-element plant analysis. Communications in Soil Science & Plant Analysis, 14: 239–248.

Nyhus PJ, Tilson R & Sumianto (2000) Crop-raiding elephants and conservation implication at Way Kambas National Park, Sumatra, Indonesia. Oryx, 34: 262–274.

Oelrichs CM, Lloyd DJ & Christidis L (2016) Strategies for mitigating forest arson and elephant conflict in Way Kambas National Park, Sumatra, Indonesia. Tropical Conservation Science, 9: 565–583.

Olivier R (1978) Distribution and status of the Asian elephant. Oryx, 14: 379–424.

Payne J, Francis CM & Phillipps K (1994) A Field Guide to the Mammals of Borneo. The Sabah Society, Kota Kinabalu, Malaysia, 386 pp.

Pretorius Y, Stigter JD, De Boer WF, Van Wieren SE, De Jong CB, De Knegt HJ, Grant CC, Heitkoenig I, Knox N, Kohi E, Mwakiwa E, Peel MJS, Skidmore AK, Slotow R, Van Der Waal C, Van Langevelde F & Prins HHT (2012) Diet selection of African elephant over time shows changing optimization currency. Oikos, 121: 2110–2120.

Provenza FD (1995) Postingestive feedback as an elementary determinant of food preference and intake in ruminants. Journal of Range Management, 48: 2–17.

Pyke GH (1983) Animal movements: an optimal foraging approach. In: Swingland IR & Greenwood PJ (eds.). The Ecology of Animal Movements. Clarendon Press, Oxford. Pp. 32–53.

Pyke GH, Pulliam HR & Charnov EL (1977) Optimal foraging: a selective review of theory and tests. The Quarterly Review of Biology, 52: 137–154.

Riddle HS, Schulte BA, Desai AA & Van Deer Meer L (2010) Elephants – a conservation overview. Journal of Threatened Taxa, 2: 653–661.

Rode KD, Chiyo PI, Chapman CA & McDowell LR (2006) Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behavior. Journal of Tropical Ecology, 22: 441–449.

Rosenthal GA & Janzen DH (1991) Herbivores, Their Interaction with Secondary Plant Metabolites. Second Edition. Academic Press, New York, 452 pp.

Shoshani J & Eisenberg JF (1982) *Elephas maximus*. Mammalian Species, 182: 1–8.

Sinclair ARE (1983) The function of distance movements in vertebrates. In: Swingland IR & Greenwood PJ (eds.). The Ecology of Animal Movements. Clarendon Press, Oxford. Pp. 240–258.

Sitompul AF (2011) Ecology and conservation of Sumatran elephants (*Elephas maximus sumatranus*) in Sumatra, Indonesia. PhD dissertation. University of Massachusetts-Amherst, Amherst, Massachusetts, 105 pp.

Suba RB, van der Ploeg J, van't Zelfde M, Lau YW, Wissingh TF, Kustiawan W, de Snoo GR & de Iongh HH (2017) Rapid expansion of oil palm is leading to human-elephant conflict in North Kalimantan Province of Indonesia. Tropical Conservation Science, 10: 1–12.

Suba RB, Beveridge NGP, Kustiawan W, de Snoo GR & de Iongh HH (2018) Foraging ecology and diet of Bornean elephants (*Elephas maximus borneensis*) in the Sebuku forest area, North Kalimantan Province of Indonesia: Do the choices matter? Integrative Zoology, 13: 219–223.

Sukumar R (1989) Ecology of the Asian elephant in southern India. I. Movement and habitat utilization patterns. Journal of Tropical Ecology, 5: 1–18.

Sukumar R (1990) Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. Journal of Tropical Ecology, 6: 33–53.

Sukumar R (2003) The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation. Oxford University Press, Oxford, 478 pp.

Sukumar R (2006) A brief review of the status, distribution and biology of wild Asian elephants *Elephas maximus*. Proceedings of the Zoological Society of London, 40: 1–8.

Trygg J & Wold SJ (2002) Orthogonal projections to latent structures (O-PLS). Journal of Chemometrics, 16: 119–128.

Van Soest PJ, Robertson JB & Lewis B (1991) Methods for dietary fiber, neutral detergent fiber, and non-starch polysaccharides in relation to animal nutrition. Journal of Dairy Science, 74: 3583–3597.

Webber CE, Sereivathana T, Maltby MP & Lee PC (2011) Elephant crop-raiding and human-elephant conflict in Cambodia: crop selection and seasonal timing of raid. Oryx, 45: 243–251.

Weir JS (1972) Spatial distribution of elephants in an African National Park in relation to environmental Na. Oikos, 23: 1–13.

Whitmore TC (1998) An Introduction to Tropical Rain Forest. Oxford University Press, Oxford, 296 pp.

Widayati A, Ekadinata A & Syam R (2005) Land-use change in Nunukan: Estimating landscape level carbon-stocks through land cover types and vegetation density. In: Lusiana B, Van Noordwijk M & Rahayu S (eds.) Carbon Stocks in Nunukan, East Kalimantan: A Spatial Monitoring and Modeling Approach. World Agroforestry Centre: Carbon Monitoring Team of the Forest Resources Management for Carbon Sequestration (FORMACS) Project. Pp. 35–53.

Wulffraat S (2006) The Elephants of East Kalimantan. Preliminary Report WWF Indonesia, unpublished, 45 pp.

Yasuma S (1994) An Invitation to the Mammals of East Kalimantan. PUSREHUT Special Publication No. 3. Samarinda, East Kalimantan, 384 pp.

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