

Recursion to food plants by free-ranging Bornean elephant

Megan English¹, Graeme Gillespie², Benoit Goossens^{3,4,5}, Sulaiman Ismail⁶, Marc Ancrenaz⁶ and Wayne Linklater^{1,7}

¹ Centre for Biodiversity and Restoration Ecology, School of Biological Sciences, Victoria University of Wellington, New Zealand

² Department of Zoology, University of Melbourne, Parkville, Victoria, Australia

³ Danau Girang Field Centre, c/o Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia

⁴ Organisms and Environment Division School of Biosciences, Cardiff University, Cardiff, UK

⁵ Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia

⁶ HUTAN Elephant Conservation Unit and Kinabatangan Orangutan Conservation Project, Sukau Sabah, Malaysia

⁷ Centre for African Conservation Ecology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa

ABSTRACT

Plant recovery rates after herbivory are thought to be a key factor driving recursion by herbivores to sites and plants to optimise resource-use but have not been investigated as an explanation for recursion in large herbivores. We investigated the relationship between plant recovery and recursion by elephants (*Elephas maximus borneensis*) in the Lower Kinabatangan Wildlife Sanctuary, Sabah. We identified 182 recently eaten food plants, from 30 species, along 14 × 50 m transects and measured their recovery growth each month over nine months or until they were re-browsed by elephants. The monthly growth in leaf and branch or shoot length for each plant was used to calculate the time required (months) for each species to recover to its pre-eaten length. Elephant returned to all but two transects with 10 eaten plants, a further 26 plants died leaving 146 plants that could be re-eaten. Recursion occurred to 58% of all plants and 12 of the 30 species. Seventy-seven percent of the re-eaten plants were grasses. Recovery times to all plants varied from two to twenty months depending on the species. Recursion to all grasses coincided with plant recovery whereas recursion to most browsed plants occurred four to twelve months before they had recovered to their previous length. The small sample size of many browsed plants that received recursion and uneven plant species distribution across transects limits our ability to generalise for most browsed species but a prominent pattern in plant-scale recursion did emerge. Plant recovery time was a good predictor of time to recursion but varied as a function of growth form (grass, ginger, palm, liana and woody) and differences between sites. Time to plant recursion coincided with plant recovery time for the elephant's preferred food, grasses, and perhaps also gingers, but not the other browsed species. Elephants are bulk feeders so it is likely that they time their returns to bulk feed on these grass species when quantities have recovered sufficiently to meet their intake requirements. The implications for habitat and elephant management are discussed.

Submitted 4 March 2015

Accepted 26 May 2015

Published 4 August 2015

Corresponding author

Megan English,
megs.english@gmail.com

Academic editor

Richard Cowling

Additional Information and
Declarations can be found on
page 12

DOI 10.7717/peerj.1030

© Copyright
2015 English et al.

Distributed under
Creative Commons CC-BY 4.0

OPEN ACCESS

Subjects Animal Behavior, Biodiversity, Ecology, Ecosystem Science, Environmental Sciences

Keywords Recursion, Elephant feeding behaviour, Herbivore-resource relationships, Herbivore ecology, Re-browsing

INTRODUCTION

Recursion by wild herbivores is the repeated use of the same sites or finer-scale reuse of resources, such as individual plants, within a site over time. Importantly, recursion by wild herbivores to previously browsed or grazed sites and plants is thought to facilitate plant productivity (re-growth) and its consumption at stages of highest productivity (McNaughton, 1985; Gordon & Lindsay, 1990; English et al., 2014a). Recursion may also accelerate nutrient cycling at sites (Gordon & Lindsay, 1990; McNaughton, Banyikwa & McNaughton, 1997) and so maintain them as nutrient hotspots (Winnie, Cross & Getz, 2008). Thus, recursion is thought to trigger and maintain the positive feedback between large herbivore feeding, and vegetation regeneration and palatability (McNaughton, Banyikwa & McNaughton, 1997). Although recursion is consistent in these ways with optimal-foraging theory and strategies, and assumed to be ubiquitous (McNaughton, 1985), it has only rarely and recently been investigated amongst wild herbivores.

Recursion has been described at site and landscape scales for wild buffalo (*Syncerus caffer*; Bar-David et al., 2009; Benhamou & Riotte-Lambert, 2012) and impala (*Aepyceros melampus*; Riotte-Lambert, Benhamou & Chamaille-Jammes, 2013) but finer-scale recursion to individual plants has not been investigated. Nevertheless, recursion has been explored amongst nectivorous insects and birds where the reuse of individual plants was found to occur after nectar replenishment (Davies & Houston, 1981; Bell, 1990; Williams & Thomson, 1998). Recursion behaviour has also been described in frugivorous primates returning to the same trees for fruit (Garber, 1988; Garber & Jelinek, 2006; Erhart & Overdorff, 2008; Janmaat, Ban & Boesch, 2013; Porter & Garber, 2013). As for nectar and fruit feeders, plant recovery period is also expected to strongly influence the movements and recursion frequency (rate) of grazers and browsers amongst sites. Prior to this study, the expected correspondence between individual plant recovery and recursion by wild grazers or browsers as an explanation for site recursion has not been explored.

Studies of recursion have important implications for animal population and habitat management (Bar-David et al., 2009). Most evaluations of wild animal resource requirements and preferences are based largely on the premise that if animals use resources (e.g., sites or food species) in lower or higher proportion to their availability then this suggests that the resource is avoided or preferred, respectively (Johnson, 1980). This framework is most commonly applied in studies that occur over relatively short time-frames to provide an indicative 'snap-shot' of resource-use. However, in natural environments resources are not consistently available in distribution, proportion and density through time and animals may reuse some resources but not others. An uncommon species of food-plant, for example, may appear to be a minor or unimportant part of the diet at selected sites but might be the subject of repeated use such that recursion would indicate it is highly selected. Alternatively, a common species of food-plant may appear to be avoided until investigation of recursion reveals reuse. Thus, studies of recursion are necessary to elaborate on spatial variation in availability and selection when assessing food and habitat preferences.

Recursion patterns may also be a useful indicator of population relations with habitat. Large herbivores, like elephants, are a particularly interesting species in which to study recursion as they are ecosystem engineers—having complex, scale-dependent effects on habitat structure and vegetative community (Bond, 1993; Jones, Lawton & Shachak, 1996). A study of recursion at the individual plant scale can identify if elephants are potentially over-utilising and depleting resources by re-browsing plants before they have recovered, or if they are facilitating growth of preferred or bulk-food plants (Fornara & du Toit, 2007; Cromsigt & Kuijper, 2011). Thus, increases in rates of recursion that exceed plant recovery rates could indicate that a population exceeds habitat capacity and reveal how they are influencing vegetation community structure and composition. Alternatively, plant recovery rates that exceed recursion may be evidence of further capacity to support greater elephant densities. An understanding of recursion patterns, therefore, may augment evaluations of a habitat's capacity to support elephant and vegetation dynamics on the landscape under elephant grazing and browsing regimes.

In a previous study, English *et al.* (2014a) showed patterns of elephant recursion to sites consistent with site quality and optimal foraging theory. In this study we aim to test the hypothesis that recursion by elephants to sites in tropical rainforest also involves recursion to individual plants and corresponds with their plant recovery. We predict that elephant recursion would coincide with plant recovery and help to explain the periodicity of site recursion observed previously.

MATERIALS AND METHODS

Study site and focal species

The dominant landform of the Lower Kinabatangan region is the extensive floodplain and its swamps. Soils are predominantly alluvial and derived from sedimentary deposits often rich in magnesium. Beyond the floodplains, soils are derived from sedimentary rocks (Azmi, 1998). The Kinabatangan floodplain is characterized by a warm, wet and humid tropical climate. The larger temperature variations are diurnal rather than seasonal. Mean monthly temperatures range between 21 °C and 34 °C (Ancrenaz, Calaque & Lackman-Ancrenaz, 2004). The north-easterly monsoon brings high monthly rainfall from October to February, although rainfall is also common from March to September. Dry months, with mean monthly rainfall <60 mm, tend to occur at roughly 3-year intervals. The mean annual rainfall is 3,000 mm (Acres & Folland, 1975).

This study focused on the area between the villages of Abai and Batu Puteh (5°18'-N 117°42'-E, 117°54'-E 118°33'-E), which were the downriver and upriver limits of the Lower Kinabatangan Wildlife Sanctuary (LKWS) elephant population's range (approximately 200 individuals). The study area (approximately 218 km²) contains seven sections, each section referred to as a 'lot', including 89 km² of protected forest reserves (Estes *et al.*, 2012). The elephant herds utilised their whole range throughout the year including use of privately owned forests and cultivated land, particularly oil palm plantations that were adjacent to and between forested areas. Elephants in LKWS are mostly restricted to the linear fragments of forest along the Kinabatangan River (Estes *et al.*, 2012) (Fig. 1).

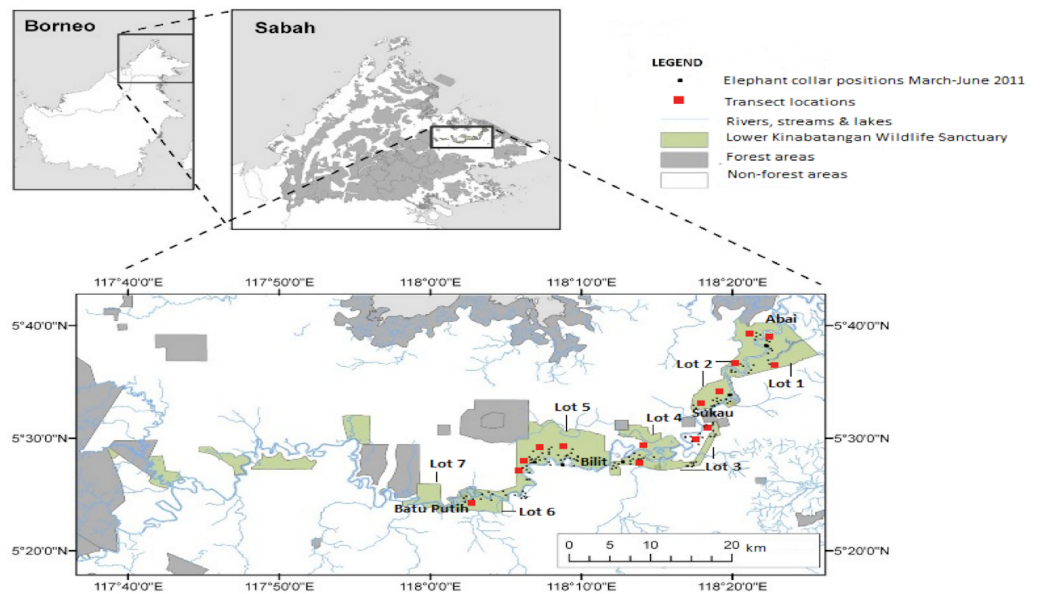


Figure 1 Map of study site. The Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysia (English et al., 2014b). Adapted from Clouded Leopard Project, Sabah www.cloudedleopard.org.

Plant recursion

Fourteen 50 m transects were located where elephants had fed previously. Transects were >300 m apart. One transect was established per day. We tracked fresh elephant signs including footprints, dung and signs of feeding to establish the transect along the group's feeding path. All plants showing signs of elephant feeding within 2 m either side of transect were marked and labelled with the date and a reference number. Samples of all plant species were collected for identification at the Sabah Forestry Department Herbarium (SAN), Sandakan. The growth and recovery of each plant after herbivory was measured each month from April to December 2011 or until the elephants re-browsed the plant's new growth. The length of the plant stem prior to browsing or grazing was determined by measuring the length of stems of the same plant that were not eaten, or remnants of the eaten stem, as a surrogate reference of original stem length. If the plant died or the new growth was re-browsed by other herbivores, thus preventing measurements of regrowth, this was recorded. It was possible to differentiate between elephant feeding signs and other herbivore feeding signs, such as from bearded pig (*Sus barbatus*) and sambar Deer (*Rusa unicolor*), because of the other sign and spoor left in the area, such as dung, footprints, the way in which the plant was eaten and the height of the sign. Recorded GPS positions of two collared elephants from the two main herds in LKWS confirmed when the focal group returned to the site and transect within the month and the age of the feeding signs allowed approximation of whether this coincided with the time of the focal elephant herd's visit. If food plants had been re-browsed by elephant, but the focal group had not returned within the month, this was not recorded as a recursion.

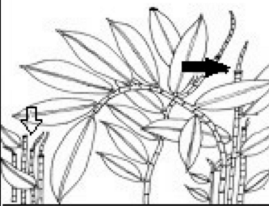
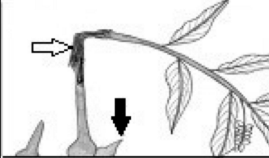
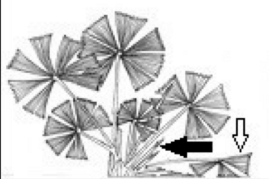
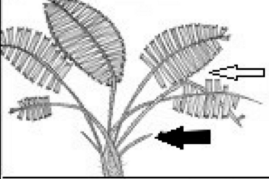
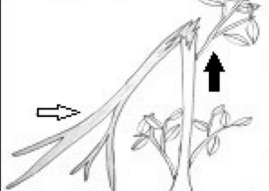
	Species examples	Growth form	Elephant feeding	Regrowth
	<i>Costus speciosus</i> (Costaceae) Scale 5cm=20cm	Ginger	Young and old stems, not sub-woody base. Leaves	Tuberous roots and at the tip of stem where breakage occurred
	<i>Alpinia ligulata</i> (Zingiberaceae) Scale 5cm=12cm	Ginger	Pith of pseudostem Young leaves	Rhizomatous plant spreads laterally forming ramets which produce aerial shoots
	<i>Licuala</i> sp. (Arecaceae) Scale 5cm=15cm	Palm	Base of stem Young leaves	Trunk develops axillary bud near the base from which a new shoot emerges
	<i>Arenga</i> sp. (Arecaceae) Scale 5cm=15cm	Palm	Young growth at apex	Trunk develops axillary bud near the base from which a new shoot emerges
	<i>Garcinia parvifolia</i> (Guttiferae) Scale 5cm=15cm	Woody	Young leaves Young stems	Along the length of the stem/trunk where epicormic buds produce shoots from the nodes and at the base forming from the tree roots.

Figure 2 Typical examples of plant growth forms. Examples of plants selected by elephants in LKWS showing plant growth forms and their recovery. White arrows indicate portions of the plant eaten by elephant and black arrows indicate recovery growth.

Plant physiognomy varies among species and between plants within a species. Regrowth measurements were taken on a selected new shoot closest to the growth node nearest the feeding sign, or from the plant base, depending on plant physiognomy and how it recovered (see Fig. 2 for typical examples). Measurements included new shoot growth in length and basal diameter, and a count of the number of new shoots produced each month. The approximate length and the basal diameter of the original feeding sign on each plant were compared to the length and basal diameter of the new growth when it was fed on again. If we returned to a plant and it had been fed on since the last measurement was taken, the growth measurements from the prior month were used for comparison. The same technique was used for the two grasses: *Phragmites karka*—a reed, and *Dinochloa scabrida*—a bamboo, as their structure is a main stem with new growth emerging from nodes along the main stem, or from the root system. Short grasses were not included due to

difficulty in identifying feeding signs (i.e., the whole plant is often ingested) and measuring recovery growth related to feeding by elephants. Student's T-tests were used to compare the lengths of the individual plant new growth with their lengths when first selected for feeding to determine any significant difference.

Plant recovery growth and recursion rate

The expected time required for each individual plant to recover was estimated by averaging the monthly growth in length (mm) of the plant, divided by its estimated length at the beginning of study which was based on what remained of the stem after elephant feeding. Other stems on the same plant were used as a surrogate reference. Based on this monthly growth average, we estimated how many months it would take for the individual plant to return to its previous length. The difference in the average recovery time (months) subtracted from the average recursion time (months) is shown for each growth form (grass, ginger, palm, liana and woody species) where the plant species are the replicates used to derive standard errors for each growth form.

Multi-model inference and selection

An information theoretic approach (linear mixed effects model) was applied to test the hypothesis for recursion time and plant recovery time. Individual plant recovery times and time to recursion were used in the statistical analysis. We predicted recursion would occur after individual plants had recovered to their pre-herbivory height. We evaluated the power of plant recovery to explain recursion in the absence of other *a priori* hypotheses by comparing a model of our hypothesis with models that included random effects for site (transect) and growth form. We described and evaluated models in the 'lme4' package in R ([Bates et al., 2014](#)). All plants browsed by elephants, including those plants that did not receive recursion but were located on transects that received recursion, were included in the analyses. We used maximum likelihood (MLE) to provide estimates of the model's parameters because fixed effects were different between models.

RESULTS

Individual food plants, recently eaten by elephants, were identified by following the herd that was allowed to select sites and plants without influence. As one would expect for a herbivore selecting from a diverse landscape and flora we identified many individuals of commonly eaten species but a larger number of species represented by a few individuals. Thus, our sampling is skewed towards a few commonly eaten plants with many other species being eaten little by elephants and sampled less.

We recorded a total of 182 plants from 30 species eaten by elephants over 14 transects. Eighty-six of these plants from 12 species were re-browsed, i.e., recursion to individual plants ([Fig. 3A](#)). Twenty-six plants died and did not recover after being partially eaten by elephants and were, therefore, not included in further analyses ([Fig. 3B](#)). Two transects were not returned to by the elephants (five plants each transect), resulting in 146 plants used for recursion analyses.

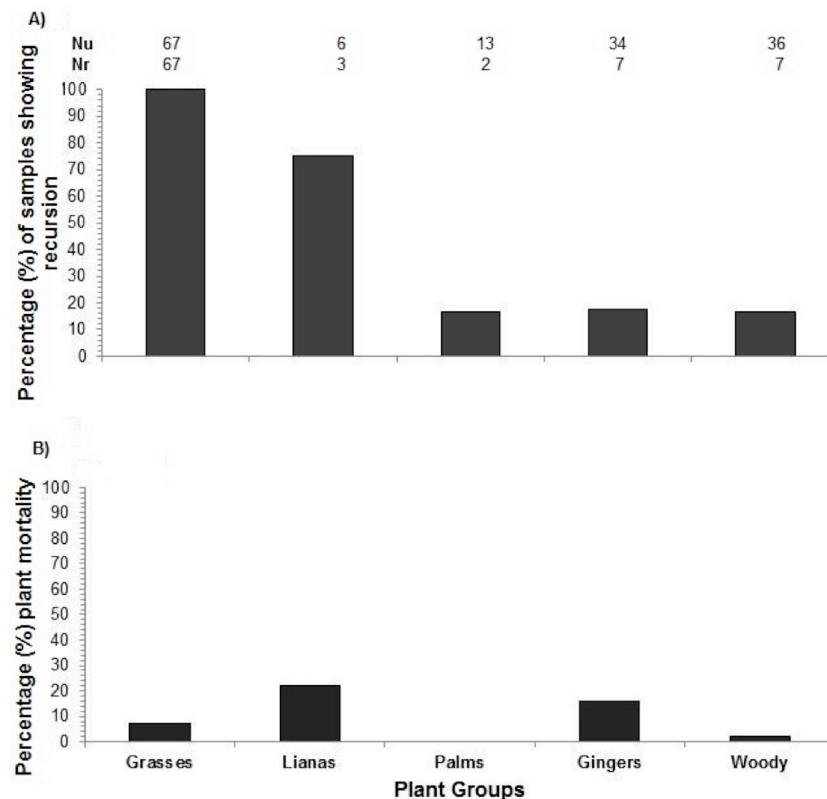


Figure 3 Plant recursion and plant mortality. (A) The percentage of plants along transects re-browsed by elephants. **Nu**, number of plants of each plant group eaten by elephants at the first visit; **Nr**, number of plants of each plant group that were re-browsed. (B) Plant mortality within plant growth forms.

The time to recursion for each plant species varied across the nine months of sampling (Table 1). Four species including ginger: *Costus speciosus*, grasses: *Dinochloa scabrida*, *Phragmites karka* and liana: *Spatholobus sp.*, had recovered to their previous size when they were re-browsed, whereas the remaining eight species were re-browsed before they had fully recovered (Figs. 4 and 5). Seventy-seven percent of re-browsed plants were grasses. A linear mixed-effects model found that the plant recovery time is a good predictor of time to recursion but this varies as a function of growth form (grass, ginger, palm, liana and woody) and differences between sites. A large amount of variation is unexplained by recovery time (Table 2).

Two species of grass, *Phragmites karka*—a reed, and *Dinochloa scabrida*—a bamboo, received recursion at a time when their length was not significantly different from when they had first been selected (Reed: t -test, $df = 50$, $P = 0.137$; Bamboo: t -test, $df = 17$, $P = 0.232$) (Fig. 4). However all other growth forms that were selected were re-browsed before they had recovered to their previous length except one ginger species, *Costus speciosus*, and one liana species, *Spatholobus sp.* Mean recursion time subtracted from mean recovery time to all growth forms illustrates that recursion to palms, lianas and woody species occurred many months before the individual plants had recovered (Table 1 and Fig. 5).

Table 1 Elephant food plants and recursion. Plant genus/species eaten by elephants and those re-browsed at recursion during the 9-month study period. The number of plants eaten, number returned to, average time to plant species recovery and time to re-browsing at recursion are shown.

Growth form	Family	Genus/species	Plant eaten	Plant recursion	Average recovery time range (months)	Time to re-browsing (months)
Grass	Poaceae	<i>Phragmites karka</i>	50	50	4–5	5
Grass	Poaceae	<i>Dinochloa scabrida</i>	17	17	2–3	3
Ginger	Costaceae	<i>Costus speciosus</i>	7	3	2–3	5
Ginger	Maranthaceae	<i>Donax canniformis</i>	19	4	8–9	7
Ginger	Zingiberaceae	<i>Alpinia ligulata</i>	8	0	8–11	^a
Palm	Arecaceae	<i>Calamus caesius</i>	3	1	8–9	4
Palm	Arecaceae	<i>Arenga</i> sp.	4	1	7–9	4
Palm	Arecaceae	<i>Daemonorops</i> sp.	3	0	11–14	^a
Palm	Arecaceae	<i>Licuala</i> sp.	3	0	10–15	^a
Liana	Leguminosae	<i>Spatholobus</i> sp.	3	1	3–4	4
Liana	Leguminosae	<i>Fordia</i> sp.	3	2	8–12	2
Woody	Guttiferae	<i>Garciniaparvifolia</i>	5	1	12–20	3
Woody	Euphorbiaceae	<i>Claoxylon</i> sp.	2	2	9–16	5
Woody	Dilleniaceae	<i>Dillenia</i> sp.	3	0	10–15	^a
Woody	Cornaceae	<i>Alangium</i> sp.	2	0	2–4	^a
Woody	Sapindaceae	<i>Lepisanthes</i> sp.	4	3	12–14	2
Woody	Melastomataceae	<i>Memecylon panniculium</i>	2	1	5–6	2
Woody	Myrtaceae	<i>Syzygium</i> sp.	2	0	12–14	^a
Woody	Rubiaceae	<i>Gardenia elata</i>	2	0	10–12	^a
Woody	Hypericaceae	<i>Cratoxylum</i> sp.	1	0	11	^a
Woody	Phyllanthaceae	<i>Bridelia</i> sp.	1	0	12	^a
Woody	Euphorbiaceae	<i>Mallotus</i> sp.	1	0	14	^a
Woody	Rutaceae	<i>Clausena excavata</i>	1	0	2	^a
Woody	Euphorbiaceae	<i>Macaranga</i> sp.	2	0	6–8	^a
Woody	Euphorbiaceae	<i>Paracroton</i> sp.	2	0	12–15	^a
Woody	Meliaceae	<i>Dysoxylum</i> sp.	1	0	3	^a
Woody	Lamiaceae	<i>Callicarpa</i> sp.	2	0	5–7	^a
Woody	Leeaceae	<i>Indica</i> sp.	1	0	12	^a
Woody	Phyllanthaceae	<i>Antidesma thwaites</i>	1	0	16	^a
Woody	Apocynaceae	<i>Rauvolfia</i> sp.	1	0	14	^a

Notes.

^a Represents plant species that did not receive recursion.

DISCUSSION

Plant recovery time after herbivory as an explanation for site and plant recursion is expected from optimal foraging theory and has been postulated for large wild herbivores (e.g., *Bar-David et al., 2009*) but had not yet been investigated in uncontrolled environments. We found plant recovery time to be a good predictor of time to plant recursion by elephant but also observed large variation with differences in growth form and amongst sites. The recovery time of the two primary species of grass—elephants' primary food species—coincided with plant and site recursion but this was not also true for browsed species. Palms, lianas and woody species were re-browsed before they had recovered.

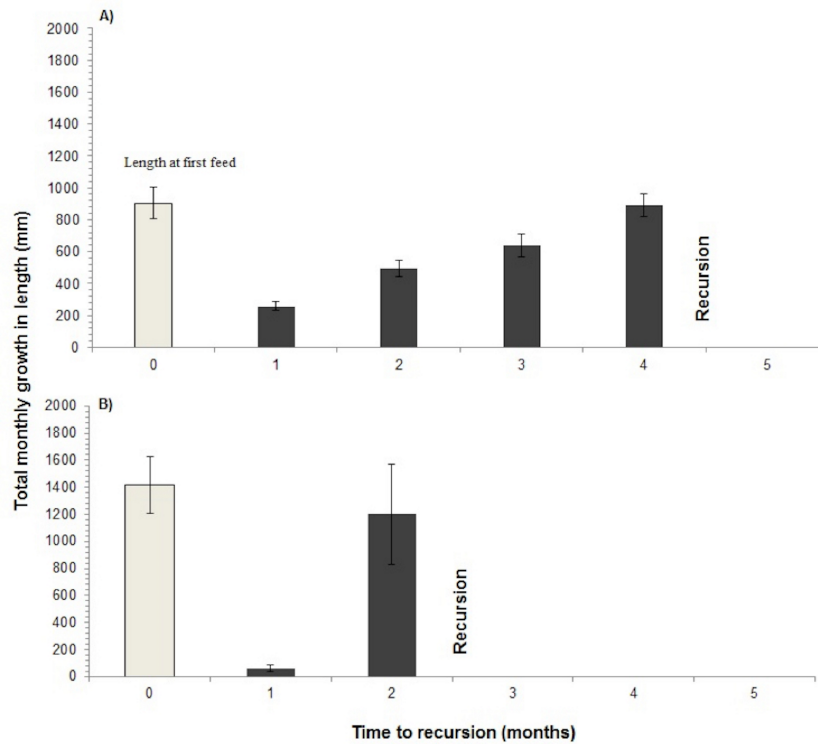


Figure 4 Recursion to grasses. Recursion to grasses showing the average length of the grass stem when initially fed on (shaded bar) and the average total length of new shoots per month until recursion occurred, for two grass species (A) *Phragmites karka* and (B) *Dinochloa scabrida*. Standard error bars represent ± 1 standard deviation of the sample distribution. Recovery has occurred when the black bar is the same length as the white bar.

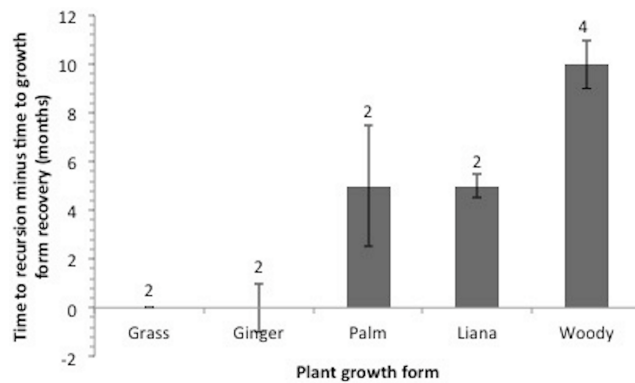


Figure 5 Time to recursion-Time to recovery. Time to recursion (months) minus Time to recovery (months) averages for each plant growth form. Numbers above bars represent the number of species within each growth form that received recursion. A positive value on the y -axis means that recursion occurred faster than plant recovery and a negative value means recursion occurred before plant recovery.

Table 2 Multimodel inference and selection. Four models ranked in order of AIC weights where recovery time (months) is the fixed-effect and plant growth form and site are random-effects, the response variable is time to recursion (months).

Model	Fixed effects	Random effects	<i>n</i>	K	AICc	Δ AIC	ω
1	Recovery time	Growth form & site ID	146	4	561.9	0	0.6300
2	(Base model)	Growth form & site ID	146	3	563.2	1.3	0.3300
3	Recovery time	Growth form	146	3	567.1	5.2	0.0500
4	Recovery time	Site ID	146	3	612.1	50.2	0.0000

The large amount of variation attributable to sites may pertain to a number of abiotic influences on plant recovery rates, such as soil fertility and micro-climate.

Recursion rate corresponded best with the recovery of grasses: *Dinochloa scabrida* and *Phragmites karka*, even though those grass species had very different recovery times: e.g., 2–3 and 4–5 months, respectively. In all cases these grazed plants were returned to after they had recovered. Grasses have also been identified as the preferred food plants of the elephants (*English et al., 2014b*) and they made up 43% of all plants selected and 77% of plants receiving recursion. Elephants are bulk feeders so it is likely that they time their returns to bulk feed on grasses and grassed sites when stands have recovered sufficiently to meet their intake requirements. Grasses were less likely to die and faster to recover compared to other growth forms. Other than grasses, most species did not receive recursion, or if they did, it occurred before the individual plants had recovered.

Recursion to a few poorly regenerated species, specifically woody trees, palms, lianas and one species of ginger, may be a result of elephants foraging on other nearby plants (i.e., grasses) and indiscriminately re-browsing those unrecovered plants. If this was the case we would expect the re-browsing of plants prior to their recovery would be most common when they are found within grass-dominated sites. Half of the browse plant samples found within grass-dominated sites were re-browsed before their recovery compared to 20% of those outside grassed areas. Thus, premature woody-plant re-browsing could be an ancillary to grazing sites.

Alternatively, recursion to unrecovered plants may be due to elephants specifically targeting those growth forms or their younger growth because they contribute a small but important component of the diet (e.g., trace elements). Forest plant productivity and nutritional quality has been found to be highest after around 5–6 months of plant regrowth (*Plumptre, 1993*), which might explain why some browsed plants were re-eaten after this many months of regrowth but before the recovery of their branch and stem lengths. Furthermore, elephants may select some food plants not just to facilitate re-growth productivity but also to manipulate the structure and composition of the plant community at sites. For example, *Jachman & Bell (1985)* proposed that African elephants selectively fell preferred tree species to stimulate coppicing but also to increase the availability of other palatable forage species. Elephants may, therefore, alter structure and floristic composition, especially of woody species, in ways that increase rather than reduce carrying capacity. If woody plants are re-browsed faster than they can recover then elephant feeding might

lead to the creation and maintenance of open, grassed areas. These areas are likely to become dominated by early successional species, thus providing the elephants with more of their preferred food such as grasses. Therefore, feeding on woody species faster than they can recover may augment grass patches and prevent woody invasion. This is a common observation of elephants. As ecosystem engineers they are known to alter the structure and composition of habitat and plant communities (*Laws, 1970; Bryant, 1981; Bergström & Danell, 1987; du Toit, Bryant & Frisby, 1990; Ben-Shahar, 1993; Prins et al., 1998*). Elephant impact on woody vegetation has led to decreasing numbers of trees and increase of open areas in Africa (*Conybeare, 2004; O'Connor, Goodman & Clegg, 2007*). The results of our study suggest that elephants in LKWS may be controlling re-forestation within open grass areas by re-browsing on woody species, lianas, and palms before their recovery. However, a long-term study on elephants as ecosystem engineers within the Lower Kinabatangan is required.

Another plausible explanation for recursion on poorly regenerated plants is that these plants are highly desirable and resources in the area are inadequate, perhaps due to spatial constraints, habitat fragmentation and overstocking. Resources may be insufficient to support a slower site recursion rate. Elephant feeding on plants before they have recovered might indicate that food species are being over-exploited and that the elephant population is approaching or exceeding habitat carrying capacity. However, with the exception of grasses, our results show that only 19 of 89 browse plants were returned to for feeding during the nine-month study period. This finding suggests that there is no evidence from recursion data that this elephant population has exceeded the area's carrying capacity. The two first explanations, individually or in combination, best explain the pattern.

Limitations in data collection in this study are imposed by the lack of independence between plant samples within species and amongst sites that were determined by elephant movements and choices and also due to plant distributions within the study area, particularly for Poaceae, which occur in homogenous stands at just a few sites that are highly favoured by the elephant (*English et al., 2014b*). Sites and transects are not balanced replicates for each plant species measured, and recursion occurred to most but not all selected sites. A lack of equal distribution of all species across all transects due to elephant food plant choices and plant species heterogeneity and distribution influenced the strength of the data. Moreover, despite a satisfactory sample size of browsed plants initially, a lack of re-browsing to plant samples across a variety of species resulted in reduced sample sizes of plants receiving recursion, especially for woody species, and therefore limited statistical power.

Despite these limitations, we established the likely importance of recovery time for recursion of elephants' bulk food, grass. It was a novel approach to establish the relationship between resource recovery and recursion by elephants in LKWS by measuring plant recovery rates in an uncontrolled environment. Our results recognised the importance of incorporating open land, for elephants to feed on grasses, into corridor design and reforestation programmes in the area. Future studies investigating recursion to plants could be improved by ensuring a relatively even distribution of plant samples across

all transects and increasing sample sizes of each species. For example, by establishing more transects or extending sampling distance (>2 m either side of transect) in order to incorporate a larger number of samples within each species for statistical comparison. It would also be beneficial to compare inter-annual variation in re-browsing and elephant impact on their resources as ecosystem engineers.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This project was funded by ZoosVictoria, Australia, and research scholarships provided by Victoria University of Wellington, New Zealand. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:

ZoosVictoria, Australia.

Victoria University of Wellington.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Megan English conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Graeme Gillespie conceived and designed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, reviewed drafts of the paper.
- Benoit Goossens and Marc Ancrenaz contributed reagents/materials/analysis tools, reviewed drafts of the paper.
- Sulaiman Ismail performed the experiments, contributed reagents/materials/analysis tools.
- Wayne Linklater conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

Victoria University of Wellington Animal Ethics Committee approved the research on the 30/3/2010. Elephants were not manipulated in any way for the purposes of this research. GPS tracking collars were attached to elephants for another student's research supervised by Dr. Benoit Goossens, who allowed Megan English to access the data information.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

Economic Planning Unit, Kuala Lumpur and Sabah Wildlife Department. Research pass number: 2833.

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.1030#supplemental-information>.

REFERENCES

- Acres BD, Folland CJ. 1975.** *The soils of the Sabah: Sandakan and Kinabatangan districts*. Land Resources Division, Directorate of Overseas Surveys.
- Ancrenaz M, Calaque R, Lackman-Ancrenaz I. 2004.** Orangutan nesting behaviour in disturbed forest of Sabah, Malaysia: Implications for nest consensus. *International Journal of Primatology* 25:983–1000 DOI 10.1023/B:IJOP.0000043347.84757.9a.
- Azmi R. 1998.** *Natural vegetation of the Kinabatangan Floodplain. Part 1: background and preliminary checklist report*. Kota Kinabalu, Sabah: WWF-Malaysia.
- Bar-David S, Bar-David I, Cross PC, Ryan SJ, Knechtel CU, Getz WM. 2009.** Methods for assessing movement path recursion with application to African buffalo in South Africa. *Ecology* 90:2467–2479 DOI 10.1890/08-1532.1.
- Bates D, Maechler M, Bolker B, Walker S. 2014.** *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.0-6. Available at <http://CRAN.R-project.org/package=lme4>.
- Bell W. 1990.** Searching behaviour patterns in insects. *Annual Review Entomology* 35:447–467 DOI 10.1146/annurev.en.35.010190.002311.
- Benhamou S, Riotte-Lambert L. 2012.** Beyond the utilisation distribution: identifying homerange areas that are intensively exploited or repeatedly visited. *Ecological Modelling* 227:112–116 DOI 10.1016/j.ecolmodel.2011.12.015.
- Ben-Shahar R. 1993.** Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* 65:249–256 DOI 10.1016/0006-3207(93)90057-8.
- Bergström R, Danell K. 1987.** Effects of simulated winter browsing by moose on morphology and biomass of two birch species. *The Journal of Ecology* 75:533–544 DOI 10.2307/2260432.
- Bond WJ. 1993.** *Keystone species*. In: Schulze ED, Mooney HA, eds. *Biodiversity and Ecosystem Function*. Springer-Verlag, 237–253.
- Bryant JP. 1981.** Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. *Science* 213:889–890 DOI 10.1126/science.213.4510.889.
- Conybeare AM. 2004.** Elephant impacts on vegetation and other biodiversity in the broadleaved woodlands of S-Central Africa. In: *Biodiversity of the four corners area: technical reviews volume two*. Harare: Biodiversity Foundation for Africa, Bulawayo/Zambezi Society, 477–508.
- Cromsigt JP, Kuijper DP. 2011.** Revisiting the browsing lawn concept: evolutionary interactions or pruning herbivores? *Perspectives in Plant Ecology, Evolution and Systematics* 13:207–215 DOI 10.1016/j.ppees.2011.04.004.
- Davies NB, Houston AI. 1981.** Owners and satellites-the economics of territory defense in the pied wagtail (*Motacilla alba*). *Journal of Animal Ecology* 50:157–180 DOI 10.2307/4038.

- du Toit JT, Bryant JP, Frisby K. 1990. Regrowth and palatability of Acacia shoots following pruning by African savanna browsers. *Ecology* 71:149–154 DOI 10.2307/1940255.
- English M, Ancrenaz M, Gillespie G, Goossens B, Nathan S, Linklater WL. 2014a. Foraging site recursion by forest elephants (*Elephas maximus borneensis*). *Current Zoology* 60:551–559.
- English M, Gillespie G, Ancrenaz M, Ismail S, Goossens B, Nathan S, Linklater WL. 2014b. Plant selection and avoidance by the Bornean elephant (*Elephas maximus borneensis*) in tropical forest: does plant recovery rate after herbivory influence food choices? *Journal of Tropical Ecology* 30:371–379 DOI 10.1017/S0266467414000157.
- Erhart EM, Overdorff DJ. 2008. Spatial memory during foraging in prosimian primates: *Propithecus edwardsi* and *Eulemur fulvus rufus*. *Folia Primatologica* 79:185–196 DOI 10.1159/000112911.
- Estes JG, Othman N, Ismail S, Ancrenaz M, Goossens B, Ambu LN, Palmiotto PA. 2012. Quantity and configuration of available elephant habitat and related conservation concerns in the Lower Kinabatangan floodplain of Sabah, Malaysia. *PLoS ONE* 7:e44601 DOI 10.1371/journal.pone.0044601.
- Fornara DA, du Toit JD. 2007. Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology* 88:200–209 DOI 10.1890/0012-9658(2007)88[200:BLROAN]2.0.CO;2.
- Garber PA. 1988. Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica* 20:100–106 DOI 10.2307/2388181.
- Garber PA, Jelinek PE. 2006. Travel patterns and spatial mapping in Nicaraguan mantled howler monkeys (*Alouatta palliate*). In: Estrada A, Garber PA, Pavelka MSM, Luecke Led, eds. *New perspectives in the study of mesoamerican primates*. US: Springer, 287–309.
- Gordon IJ, Lindsay KW. 1990. Could mammalian herbivores “manage” their own resources? *Oikos* 59:270–280 DOI 10.2307/3545544.
- Jachman H, Bell RHV. 1985. Utilisation by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology* 23:245–258 DOI 10.1111/j.1365-2028.1985.tb00955.x.
- Janmaat KR, Ban SD, Boesch C. 2013. Tai chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes. *Animal Cognition* 16:851–860 DOI 10.1007/s10071-013-0617-z.
- Johnson DH. 1980. The comparison of usage and availability for evaluating resource preference. *Ecology* 61:65–71 DOI 10.2307/1937156.
- Jones CG, Lawton JH, Shachak M. 1996. Organisms as ecosystem engineers. In: *Ecosystem Management*. New York: Springer, 130–147.
- Laws RM. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21:1–15 DOI 10.2307/3543832.
- McNaughton SJ. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55:259–294 DOI 10.2307/1942578.
- McNaughton SJ, Banyikwa FF, McNaughton MM. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* 278:1798–1800 DOI 10.1126/science.278.5344.1798.
- O’Connor TG, Goodman PS, Clegg B. 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation* 136:329–345 DOI 10.1016/j.biocon.2006.12.014.

- Plumptre AJ. 1993.** The effects of trampling damage by herbivores on the vegetation of the Parc National des Volcans, Rwanda. *African Journal of Ecology* **32**:115–129
[DOI 10.1111/j.1365-2028.1994.tb00563.x](https://doi.org/10.1111/j.1365-2028.1994.tb00563.x).
- Porter LM, Garber PA. 2013.** Foraging and spatial memory in wild Weddell's saddleback tamarins *Saguinus fuscicollis weddelli* when moving between distant and out-of-sight goals. *International Journal of Primatology* **34**:30–48 [DOI 10.1007/s10764-012-9644-x](https://doi.org/10.1007/s10764-012-9644-x).
- Prins HHT, Olf H, Newbery DM, Brown ND. 1998.** Species-richness of African grazer assemblages: towards a functional explanation. In: *Dynamics of tropical communities: the 37th symposium of the British Ecological Society, Cambridge University, 1996*. Blackwell Science Ltd, 449–490.
- Riotte-Lambert L, Benhamou S, Chamaille-Jammes S. 2013.** Periodicity analysis of movement recursions. *Journal of Theoretical Biology* **317**:238–243 [DOI 10.1016/j.jtbi.2012.10.026](https://doi.org/10.1016/j.jtbi.2012.10.026).
- Williams NM, Thomson JD. 1998.** Trapline foraging by bumble bees: III. Temporal patterns of visitation and foraging success at single plants. *Behavioural Ecology* **9**:612–621
[DOI 10.1093/beheco/9.6.612](https://doi.org/10.1093/beheco/9.6.612).
- Winnie JA, Cross P, Getz W. 2008.** Habitat quality and heterogeneity influence distribution and behaviour in African buffalo (*Syncerus caffer*). *Ecology* **89**:1457–1468 [DOI 10.1890/07-0772.1](https://doi.org/10.1890/07-0772.1).