Recursion to food plants by free-ranging Bornean elephant

Megan English, Graeme Gillespie, Benoit Goossens, Sulaiman Ismail, Marc Ancrenaz, Wayne Linklater

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 × 50m 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 and 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.
Recursion to food plants by free-ranging Bornean elephant

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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 et al., 1997) and so maintain them as nutrient hotspots (Winnie et al., 2008). Thus, recursion is thought to trigger and maintain the positive feedback between large herbivore feeding, and vegetation regeneration and palatability (McNaughton et al., 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 et al., 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 & Jelinik, 2006; Erhart & Overdorff, 2008; Janmaat et al., 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 and, therefore, 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 illustrate it to be 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 et al., 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. 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 habitats 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 et al., 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 5° 42’ -N, 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).

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 herds 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.

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 typological 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 and other stems on
the same plant 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 elephant, 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
elephant 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.
The time to recursion for each plant species varied across the nine months of sampling
(Table 1). Four species including ginger: Costus speciousus, 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 (Fig 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 speciousus*, 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).

**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 has 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. 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 microclimate.

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 recursions, 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 browsed plants were re-eaten before the recovery of their branch and
stem lengths that takes longer. 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 and 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 et al., 1990; Ben-Shahar, 1993; Prins & Olff, 1998). Elephant impact on woody vegetation has led to decreasing numbers of trees and increase of open areas in Africa (Conybeare, 2004; O’Connor et al., 2007). The results of our study suggest that elephants in LKWS may be controlling reforestation 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 but 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 elephant’s bulk food, grass. This was a novel approach for establishing 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, increasing sample sizes of each species, i.e. 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.

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.

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.
Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. http://CRAN.R-project.org/package=lme4.

Bell W. 1990. Searching behaviour patterns in insects. Annual Review Entomology 35: 447–467.

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.

Ben-Shahar R. 1993. Patterns of elephant damage to vegetation in northern Botswana. Biological Conservation 65: 249-256.

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.

Bond WJ. 1993. Keystone species. In: Schulze, E.D., Mooney, H.A. (Eds.), Biodiversity and Ecosystem Function. Springer-Verlag, pp. 237–253.

Bryant JP. 1981. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. Science 213: 889-890.

Conybeare AM. 2004. Elephant impacts on vegetation and other biodiversity in the broadleaved woodlands of S-Central Africa. Biodiversity of the Four Corners Area: Technical Reviews Volume Two. Biodiversity Foundation for Africa, Bulawayo/Zambezi Society, Harare, Zimbabwe, pp. 477-508.

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.
du Toit J T, Bryant JP, Frisby K. 1990. Regrowth and palatability of Acacia shoots following pruning by African savanna browsers. *Ecology* 71: 149-154.

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.

Erhart EM, Overdorff DJ. (2008). Spatial memory during foraging in prosimian primates: *Propithecus edwardsi* and *Eulemur fulvus rufus*. *Folia Primatologica* 79: 185–196.

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.

Garber PA. 1988. Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicolis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica* 20: 100–106.

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. Springer US: New Perspectives in the Study of Mesoamerican Primates. pp. 287–309.

Gordon IJ, Lindsay KW. 1990. Could mammalian herbivores “manage” their own resources? *Oikos* 59: 270-280.

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.
Janmaat KR, Ban SD, Boesch C. 2013. Taï chimpanzees use botanical skills to discover fruit: What we can learn from their mistakes. *Animal Cognition* 16: 851–860.

Johnson DH. 1980. The comparison of usage and availability for evaluating resource preference. *Ecology* 61: 65-71.

Jones CG, Lawton JH, Shachak M. 1996. Organisms as ecosystem engineers. In *Ecosystem Management*. Springer New York. pp. 130-147.

Laws RM. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21: 1-15.

McNaughton SJ. 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs* 55: 259-294.

McNaughton SJ, Banyikwa FF, McNaughton MM. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* 278: 1798-1800.

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.

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.

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.

Prins HHT, Olff 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. (pp. 449-490).

Price PW. 1991. The plant vigour hypothesis & herbivore attack. *Oikos* 244-251.

Riotte-Lambert L, Benhamou S, Chamaille-Jammes S. 2013. Periodicity analysis of movement recursions. *Journal of Theoretical Biology* 317: 238-243.

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.

Winnie JA, Cross P, Getz W. 2008. Habitat quality and heterogeneity influence distribution and behaviour in African buffalo (*Syncerus caffer*). *Ecology* 89: 1457-146
Map of study site

The Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysia (English et al., 2014b).
(Adapted from Clouded Leopard Project, Sabah www.cloudedleopard.org).
Typological 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.

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

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. * represents plant species that did not receive recursion.
| Growth form | Family             | Genus/species               | Plant eaten | Plant recursion | Average recovery time range (months) | Time to re-browsing (months) |
|------------|-------------------|-----------------------------|-------------|----------------|-------------------------------------|-----------------------------|
| Grass      | Poaceae           | *Phragmites karka*          | 50          | 50             | 4-5                                 | 5                           |
| Grass      | Poaceae           | *Dinochloa scabra*          | 17          | 17             | 2-3                                 | 3                           |
| Ginger     | Costaceae         | *Costus speciousus*         | 7           | 3              | 2-3                                 | 5                           |
| Ginger     | Maranthaceae      | *Donax canniformis*         | 19          | 4              | 8-9                                 | 7                           |
| Ginger     | Zingiberaceae     | *Alpinia ligulata*          | 8           | 0              | 8-11                                | *                           |
| Palm       | Arecaceae         | *Calamus caesius*           | 3           | 1              | 8-9                                 | 4                           |
| Palm       | Arecaceae         | *Arenga sp.*                | 4           | 1              | 7-9                                 | 4                           |
| Palm       | Arecaceae         | *Daemonorops sp.*           | 3           | 0              | 11-14                               | *                           |
| Palm       | Arecaceae         | *Licuala sp.*               | 3           | 0              | 10-15                               | *                           |
| Liana      | Leguminosae       | *Spatholobus sp.*           | 3           | 1              | 3-4                                 | 4                           |
| Liana      | Leguminosae       | *Fordia sp.*                | 3           | 2              | 8-12                                | 2                           |
| Woody      | Guttiferae        | *Garcinia parvifolia*       | 5           | 1              | 12-20                               | 3                           |
| Woody      | Euphorbiaceae     | *Claoxylon sp.*             | 2           | 2              | 9-16                                | 5                           |
| Woody      | Dilleniaceae      | *Dillenia sp.*              | 3           | 0              | 10-15                               | *                           |
| Woody      | Cornaceae         | *Alangium sp.*              | 2           | 0              | 2-4                                 | *                           |
| Woody      | Sapindaceae       | *Lepisanthes sp.*           | 4           | 3              | 12-14                               | 2                           |
| Woody      | Melastomataceae   | *Memecylon panniculum*      | 2           | 1              | 5-6                                 | 2                           |
| Woody      | Myrtaceae         | *Szygium sp.*               | 2           | 0              | 12-14                               | *                           |
| Woody      | Rubiaceae         | *Gardenia elata*            | 2           | 0              | 10-12                               | *                           |
| Woody      | Hypericaceae      | *Cratoxylum sp.*            | 1           | 0              | 11                                  | *                           |
| Woody      | Phyllanthaceae    | *Bridelia sp.*              | 1           | 0              | 12                                  | *                           |
| Woody      | Euphorbiaceae     | *Mallotus sp.*              | 1           | 0              | 14                                  | *                           |
| Woody      | Rutaceae          | *Clausena excavata*         | 1           | 0              | 2                                   | *                           |
| Woody      | Euphorbiaceae     | *Macaranga sp.*             | 2           | 0              | 6-8                                 | *                           |
| Woody Family       | Tribe            | Species                   | Abundance | Death | *  |
|-------------------|------------------|---------------------------|-----------|-------|----|
| Woody Euphorbiaceae | Paracron sp.     | 2                         | 0         | 12-15 | *  |
| Woody Meliaceae    | Dysoxylum sp.    | 1                         | 0         | 3     | *  |
| Woody Lamiaceae    | Callicarpa sp.   | 2                         | 0         | 5-7   | *  |
| Woody Leaceae      | Indica sp.       | 1                         | 0         | 12    | *  |
| Woody Phyllanthaceae | Antidesma thwaites | 1                     | 0         | 16    | *  |
| Woody Apocynaceae  | Rauvolfia sp.    | 1                         | 0         | 14    | *  |
### 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       | n   | K  | AICc | Δ   | AIC | ω   |
|-------|------------------|----------------------|-----|----|------|-----|-----|-----|
| 1     | Recovery Time    | Growth Form & SiteID | 146 | 4  | 561.9| 0   | 561.9| 0.6300|
| 2     | (base model)     | Growth Form & SiteID | 146 | 3  | 563.2| 1.3 | 564.5| 0.3300|
| 3     | Recovery Time    | Growth Form          | 146 | 3  | 567.1| 5.2 | 572.3| 0.0500|
| 4     | Recovery Time    | SiteID               | 146 | 3  | 612.1| 50.2| 662.3| 0.0000|