

## Foraging site recursion by forest elephants *Elephas maximus borneensis*

Megan ENGLISH<sup>1\*</sup>, Marc ANCRENAZ<sup>2</sup>, Graeme GILLESPIE<sup>3</sup>,  
Benoit GOOSSENS<sup>4,5,6</sup>, Sen NATHAN<sup>6</sup>, Wayne LINKLATER<sup>1,7</sup>

<sup>1</sup> Centre for Biodiversity and Restoration Ecology, School of Biological Sciences, New Kirk Building, Kelburn Parade, Kelburn Campus, Victoria University of Wellington, 6012, New Zealand

<sup>2</sup> Hutan Kinabatangan Orangutan Conservation Project and Elephant Conservation Unit, Sukau, Kinabatangan, Sabah, Malaysia

<sup>3</sup> Zoology Department, University of Melbourne, Parkville, Victoria, 3010, Australia

<sup>4</sup> Danau Girang Field Centre, c/o Sabah Wildlife Department, Wisma Muis, 88100 Kota Kinabalu, Sabah, Malaysia

<sup>5</sup> Organisms and Environment Division, School of Biosciences, Cardiff University, Sir Martin Evans Building, Museum Avenue, Cardiff CF10 3AX, UK

<sup>6</sup> Sabah Wildlife Department, Wisma Muis, 88100 Kota Kinabalu, Sabah, Malaysia

<sup>7</sup> Centre for African Conservation Ecology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa

**Abstract** Recursion by herbivores is the repeated use of the same site or plants. Recursion by wild animals is rarely investigated but may be ubiquitous. Optimal foraging theory predicts site recursion as a function of the quality of the site, extent of its last use, and time since its last use because these influence site resource status and recovery. We used GPS collars, behaviour and site sampling to investigate recursion to foraging sites for two elephant *Elephas maximus borneensis* herds in the Lower Kinabatangan Wildlife Sanctuary, Borneo, over a 12 month period. Recursion occurred to 48 out of 87 foraging sites and was most common within 48 hours or between 151–250 days, indicating two different types of recursion. Recursion was more likely to occur if the site had previously been occupied for longer. Moreover, the time spent at a site at recursion was the same as the time spent at the site on the first occasion. The number of days that had passed between the first visit and recursion was also positively correlated with how much time was spent at the site at recursion. Habitat type also influenced the intensity of site-use, with more time spent at recursion within riverine/open grass areas along forest margins compared to other habitat types. Recursion is a common behaviour used by the elephants and its pattern suggests it may be a foraging strategy for revisiting areas of greater value. The qualities of recursion sites might usefully be incorporated into landscape management strategies for elephant conservation in the area [*Current Zoology* 60 (4): 551–559, 2014].

**Keywords** Asian elephant, Recursion, Site re-use, Herbivory, Megaherbivore, Optimal foraging

Understanding how animals utilise and navigate a landscape is essential to comprehending species ecological and population processes (Stephens and Krebs, 1986; Turchin, 1991; Bartumeus et al., 2005). Feed quality and the spatial distribution of foraging sites may influence foraging strategies of herbivores and the way in which they utilise the landscape (Owen-Smith and Novellie, 1982; Belovsky, 1984; Pyke, 1984; Senft et al., 1987; Adler et al., 2001). Recognising foraging patterns across the landscape has benefits for species and habitat conservation. The spatial and temporal variation in species foraging behaviour and habitat utilisation may be incorporated into landscape management strategies and habitat assessment.

The return by animals to previously utilised foraging

sites is known as recursion. Studies of recursion are few (Bar-David et al., 2009; Li et al., 2012; Riotte-Lambert et al., 2013). However, studies of animal behaviors that resemble recursion have been explored more extensively. Those studies used different terminology to recursion but have explored a similar process. Examples of foraging recursion include, the influence of spatial memory and resource relocation in bees (Kadmon, 1992; Williams and Thomson, 1998; Stout and Goulson, 2002; Menzel et al., 2005), nectar feeding birds returning to flowers (Gill, 1988; Burke and Fulham, 2003), sheep and cattle returning to grass patches (Bailey et al., 1989; Dumont and Petit, 1998) and primates returning to fruit trees (Garber, 1988; Garber and Jelinik, 2006; Erhart and Overdorff, 2008; Janson, 1998; Watts, 1998; Porter

---

Received April 12, 2014; accepted June 24, 2014.

\* Corresponding author. E-mail: Megan.English@vuw.ac.nz

© 2014 *Current Zoology*

and Garber, 2013; Janmaat et al., 2013).

Temporal patterns in site revisits have been related to resource recovery, for example in insects (Bell, 1990; Williams and Thomson, 1998) and birds (*Motacilla* sp.) (Davies and Houston, 1981). The predictability and order of repeated visits to previously utilised sites has been explored extensively in bumblebees (*Bombus* sp.) (Comba, 1999; Heinrich, 1976; Manning, 1956; Thomson, 1996; Thomson et al., 1982, 1987), euglossine bees (*Euglossini* spp.) (Janzen, 1971; Ackerman et al., 1982; Dressler, 1982), butterflies (*Danaus* sp.) (Gilbert, 1980), hummingbirds (*Phaethornis* spp.) (Gill, 1988; Garrison and Gass, 1999; Tiebout, 1991), wagtails (*Motacilla* sp.) (Davies and Houston, 1981), bats (*Glossophaga* sp., *Pipistrellus* sp.) (Lemke, 1984; Racey and Swift, 1985), and primates (*Saguinus* spp., *Cebus* sp., *Gorilla* sp.) (Garber, 1988; Janson, 1998; Watts, 1998). Additionally, the influence of resource renewal on site re-use has been explored using simulations of animal movement patterns (Possingham, 1989; Bar-David et al., 2009; Ohashi and Thomson, 2005). Nevertheless, only some studies have explored foraging site re-use in uncontrolled environments and these studies are largely limited to primates (Garber, 1988; Watts, 1998; Garber and Jetlinik, 2006; Erhart and Overdorff, 2008; Porter and Garber, 2013; Janmaat et al., 2013) and a few ungulates (*Syncerus* sp., *Aepyceros* sp.) (Bar-David et al., 2009; Riotte-Lambert et al., 2013).

Habitat quality and its importance to animals, or individual resource quality and its importance within foraging sites, might be best understood by measuring the amount of time animals spend at these sites and how frequently they return to them. Single point-in-time surveys, designed to identify selected resources or avoided habitat features, that do not take into account temporal variation in resource use might under- or over- estimate the relative importance of sites visited and their resource characteristics. If an animal repeatedly visits a site and spends more time at a site relative to others, this may help to identify high quality areas or more critical resources.

We investigated foraging site recursion by a wild population of Bornean elephants *Elephas maximus borneensis* and the foraging mechanisms that might explain recursion behavior. Our aims were to identify if recursion occurs, how often, and what environmental and biological variables may influence this behavior. In an optimally foraging herbivore, recursive site-use should be a function of the intensity of last use. Recursion should also relate to time since last use to allow for resource recovery after depletion (Ohashi and Thomson,

2005). The composition of the site should influence recursion because a herbivore will have specific resource requirements and site quality and recovery rates may vary with endogenous (for example, nutrient content) and exogenous (for example, climatic) influences. Recursion behavior may also, however, be an indicator of diminishing habitat of suitable quality or capacity because, as prime habitat becomes less available, recursion frequency should increase but time spent at sites decline. However, over time we would expect an optimally foraging herbivore to avoid unprofitable areas.

We expected elephants to spend more time at recursion sites compared to non-recursion sites if the former were higher quality, such as those sites containing preferred food plants like grasses and bamboos (English et al., 2014). Additionally, we expected elephants to return to sites at two temporal scales. Longer recursion times should occur in order for resources to sufficiently recover, especially where the site was used more extensively previously. Short-term recursions should occur as part of a site-sampling strategy (Owen-Smith, 2002). We also expected site characteristics such as habitat type, distance to water, distance to human habitation, shade and understorey cover to influence recursion and the intensity of site use. We expected more intensive use of sites within habitats containing preferred food plants of the Bornean elephant, such as within riverine and open grass areas along forest margins (English et al., 2014), sites closer to a water source (McKay, 1973; Sukumar, 1990), sites further from human habitation (Blake, 2002) and sites less shaded (Barnes et al., 1995; Powell, 1997) allowing for more understorey growth, in particular grasses and bamboos (McKay, 1973; Shoshani and Eisenberg, 1982).

## 1 Materials and Methods

### 1.1 Study site

The Lower Kinabatangan Wildlife Sanctuary (LKWS) is located in Eastern Sabah, Malaysia. The sanctuary is a lowland floodplain that comprises a matrix of habitat types in predominantly degraded forest ecosystems. The floodplain is characterized by a warm, wet and humid tropical climate. Mean monthly temperatures range between 21°C and 34°C (Ancrenaz et al., 2004). Flooding occurs mainly between November and March during the west monsoon. Rainfall averages 3000 mm y<sup>-1</sup> (Sooryanarayana, 1995). Soils are predominantly alluvial and derived from sedimentary deposits often rich in magnesium. In areas of freshwater swamps soils contain a high proportion of peat (Azmi, 1998).

This study focused on the area between the villages of Abai and Batu Puteh ( $5^{\circ}18'N$   $5^{\circ}42'N$ ,  $117^{\circ}54'E$   $118^{\circ}33'E$ ), which were the downriver and upriver limits of the LKWS elephant population's range. The study area contains 7 sections, each section referred to as a 'lot' (approximately  $218 \text{ km}^2$ ), including  $89 \text{ km}^2$  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.

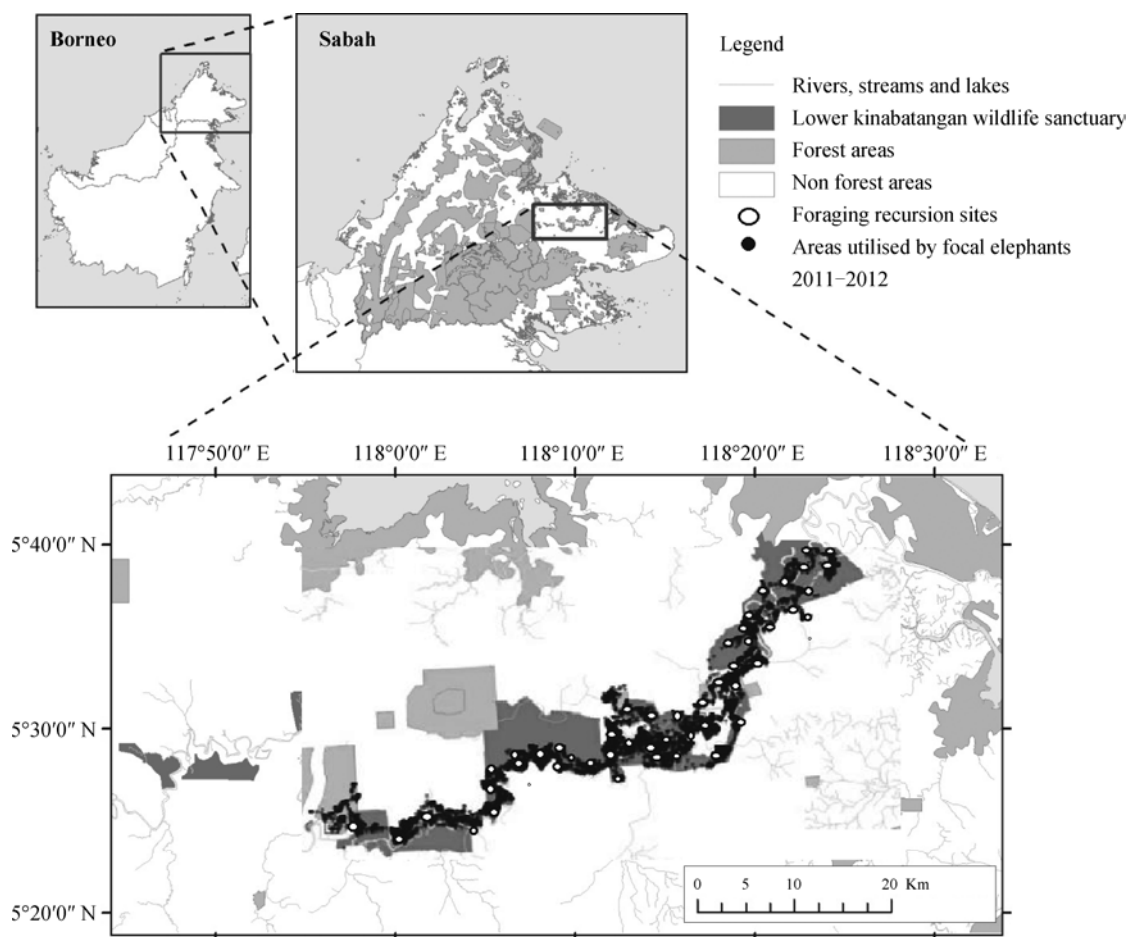
### 1.2 Focal species

The Bornean elephant, an endangered sub-species of Asian elephant *Elephas maximus* (IUCN, 2013) is found only in the eastern and central parts of Sabah (Alfred et al., 2010) as well as the extreme north of Indonesian Kalimantan. The main threats to Bornean elephants are changes in habitat particularly conversion of forest to

oil palm plantations and resulting elevation in human-elephant conflict. Elephants in LKWS are mostly restricted to the linear fragments of forest along the Kinabatangan River (Estes et al., 2012) (Fig. 1).

### 1.3 Site location

Two adult female elephants from separate herds, each consisting of approximately 20–30 individuals, were randomly selected to attach a collar with a GPS transmitter in 2011. Neither female was the matriarch to her herd which she belonged. Positions were recorded at hourly intervals for 12 months from April 2011 to May 2012. We identified and visited sites used by elephant throughout their range in April and May 2011, the early dry season. To identify sites used by the elephant herds, the latest GPS position recorded of each group on the days of observation was located and then fresh elephant sign, (footprints, dung, feed sign and vocalisations) was tracked until the focal female and her herd were located.



**Fig. 1** Map of the Lower Kinabatangan Wildlife Sanctuary, Sabah (Adapted from [www.cloudedleopard.org](http://www.cloudedleopard.org))

Black points illustrate the areas used by the two focal herds for 12 months from 1/04/11 to 1/04/2012. White points indicate the location of foraging sites that received recursion.

Once an elephant group was sighted we positioned ourselves at a distance so as not to disturb them. The activity of the majority of elephants at the site at the time of observation was recorded as either foraging, resting or moving. Moving sites were those where the focal female and her herd were seen walking without stopping to feed. Resting sites were areas where the majority of elephants in the group were seen standing motionless, apart from ear and tail movement, or lying down and not feeding. Foraging sites, the focus of this study, were areas where the majority of the herd were seen collecting and ingesting food at the time of observation. Once the activity of the group was categorised we then counted the number of elephants in the group and then waited and allowed the group to move before sampling the site. These observations were carried out on the two separate groups.

#### 1.4 Site characteristics

Foraging sites refer to areas in which we observed the herds during April–May 2011 (during the early to mid-dry season). These were the sites where recursion was measured. The habitat type of each site was categorised as one of riverine/open grass areas along forest margins, lowland dipterocarp forest, semi-inundated dipterocarp forest, swamp and highly disturbed/cultivated land according to previous classifications (Azmi, 1998; English unpub. data). Distance to the nearest water source (m), proximity to human habitation (m), shade (%) and understorey cover (%) were also recorded at each site. Distance to water and proximity to human habitation were measured using a Garmin 60csx Global Positioning System (GPS). Water sources included rivers, tributaries and ox-bow lakes but did not include swamps of stagnant, non-free flowing water. Proximity to human habitation was the distance in metres to areas with frequent human presence such as villages, dirt roads, bitumen roads and plantations. Shade percentage was measured using a spherical densiometer. This tool enabled calculation of the percentage of the forest canopy cover which was reflected onto a 24 cell grid convex mirror and measured near the centre of where the herd had been observed (see Lemmon 1956). Understorey cover was measured using a 2 m long PVC pipe marked every 2 cm along its length. The number of 2 cm marks covered by vegetation was counted from a distance of 5 m when the pipe was held horizontally 30 cm from the ground by an assistant. This was then converted to a percentage of understorey cover in an area resembling the understorey vegetation before elephant disturbance.

#### 1.5 Defining and measuring site recursion

A site was defined as the area that covered 100 m radius surrounding each measurement point taken from the centre of the elephant herd. The density of hourly GPS recordings was used as a measure of the amount of time spent within a 100-m diameter of the measurement point at each foraging site and was quantified for comparison between recursion and non-recursion foraging sites. The number of individuals in each group was counted on one hundred separate occasions for each group and was between 20–30 individuals per group (Group 1 =  $25 \pm 0.24$  and Group 2 =  $26 \pm 0.26$ ).

Using the recorded GPS positions from the elephant collars uploaded to Google Earth (Google Inc. 2010) along with the locations of foraging sites, we counted the number of returns to each site within 12 months, since the date of direct observation. The time period between each return was quantified. GPS points with a Positional Dilution of Precision (PDOP) of  $> 6$  were removed from analyses due to lack of precision (Langley, 1999).

#### 1.6 Statistical analyses

The data collected from both elephant groups was analysed using a *t*-test to compare differences in the frequency of recursion events, density of points at sites and the above mentioned habitat variables. The only variable that was significantly different between the two elephant groups was shade % (English unpub.data). However this variable was later removed from further analyses and so the datasets were pooled (see below).

A Principal Components Analysis (PCA) reduced confounding effects of partial correlation between environmental variables (distance to water, proximity to human habitation, shade % and understorey %). The PC identified that understorey and shade were strongly associated with Eigenvalues  $< 1$  and were therefore removed from further analyses, thus reducing the number of covariates in the model to distance to water and proximity to ongoing human habitation.

A Generalised Linear Model (GLM) (SPSS version 18.0, 2009) was used to determine if foraging site characteristics including distance to water, proximity to human habitation and habitat type influenced the dependent variable of recursion (1 = recursion, 0 = no recursion). The amount of time the herd spent at a foraging site at the first visit (when the herd was initially observed at the site) was also included to determine if this influenced whether the site was later returned to.

A further GLM was used to analyse foraging sites with recursion to determine if there was a relationship

between the time spent at the site at the first visit, time (days) between visits, proximity to human habitation, distance to water, habitat type and the dependent variable – time spent at the site at recursion.

The number of foraging sites where elephants were seen feeding on grasses/bamboo, gingers, palms, lianas and woody species (Table 1) was quantified and compared between recursion and non-recursion sites using a one-way ANOVA test. Food plants selected were measured from direct observation of elephants feeding, with plants seen ingested by the elephants identified to species level and later categorised into the above growth forms.

A chi-square test was used to determine if recursion frequency varied over temporal scales or if variation occurred randomly with no significant influence of time.

## 2 Results

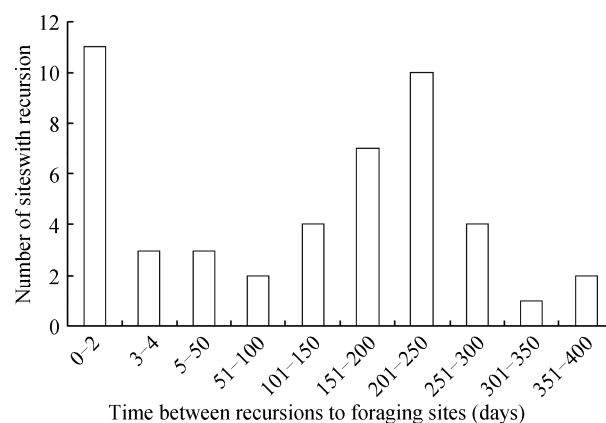
Eighty-seven foraging sites were measured. Seventy-five movement and 43 resting sites were also initially measured but not included in the analyses for this study, which focuses on recursion to foraging sites only.

**Table 1 Plant species and their growth form selected by elephants at foraging sites in the Lower Kinabatangan Wildlife Sanctuary, Sabah**

Family	Genus	Plant form
Poaceae	<i>Dinochloa scabrida</i>	Grass/Bamboo
Poaceae	<i>Panicum</i> sp.	Grass
Poaceae	<i>Phragmites karka</i>	Grass
Poaceae	<i>Pennisetum</i> sp.	Grass
Zingiberaceae	<i>Alpinia ligulata</i>	Ginger
Maranthaceae	<i>Donax caniniformis</i>	Ginger
Arecaceae	<i>Licuala</i> sp.	Palm
Arecaceae	<i>Calamus caesius</i>	Palm
Arecaceae	<i>Arenga</i> sp.	Palm
Leguminosae	<i>Spatholobus</i> sp.	Liana
Leguminosae	<i>Fordia splendidissima</i>	Liana
Lophopyxidaceae	<i>Lophopaxis mangai</i>	Liana
Dilleneaceae	<i>Dillenia excelsa</i>	Woody species
Sterculiaceae	<i>Pterospermum</i> sp.	Woody species
Euphorbiaceae	<i>Mollotus</i> sp.	Woody species
Euphorbiaceae	<i>Claoxylon</i> sp.	Woody species
Euphorbiaceae	<i>Maccaranga</i> sp.	Woody species
Myrtaceae	<i>Eugenia</i> sp.	Woody species
Moraceae	<i>Ficus</i> sp.	Woody species
Guttiferae	<i>Garcinia parvifolia</i>	Woody species

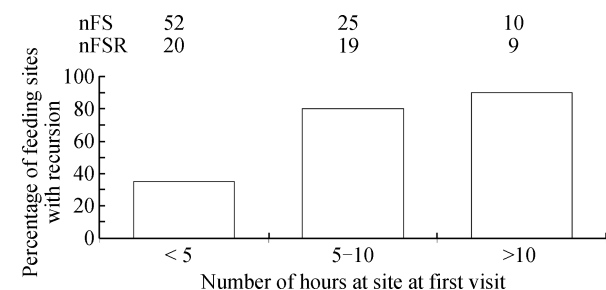
Foraging sites were returned to by each herd over varying temporal scales ranging from within days, to weeks and months of the previous visit. Forty-eight foraging sites were returned to within 12 months. A large percentage of sites were returned to within 48 hours of the previous visit and the remaining sites were returned to over varying time-scales peaking again between 151–250 days. The difference in recursion frequency through time, therefore, was not random (Chi-square,  $df = 10$ ,  $P < 0.01$ , Fig. 2). Elephants spent more time at the first visit compared to the second visit if they returned within 48 hours to a site ( $t$ -test,  $n = 11$ ,  $P = 0.00$ ).

We found a significant positive relationship between the hours at a site at the first visit and recursion ( $\chi^2_1 = 10.68$ ,  $P = 0.001$ , Fig. 3), with more time spent at sites that were returned to. No relationship was found between hours at the site on first visit and other biological or environmental site characteristics including distance to water, proximity to human habitation or habitat type.



**Fig. 2 Time period (days) between recursions by Bornean elephants in the Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysia over a 12 month period**

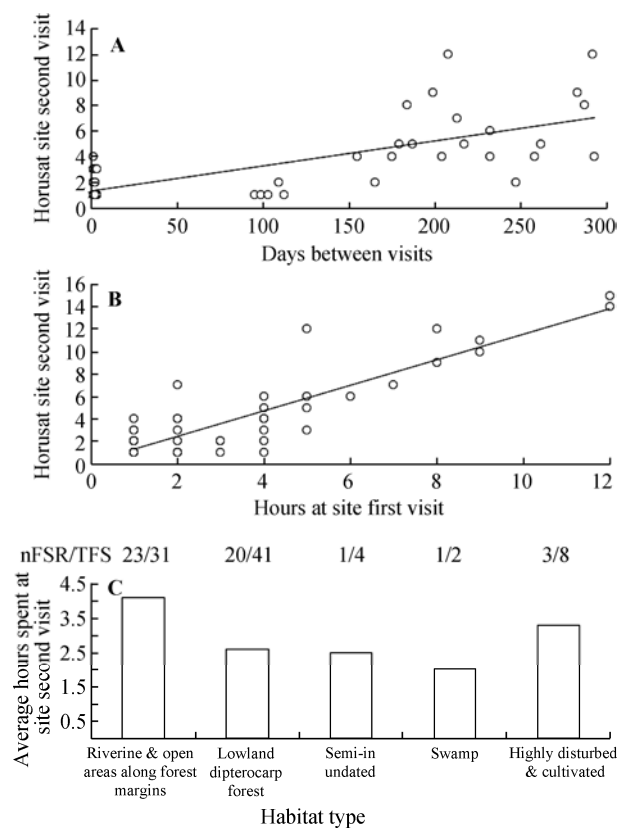
A total of 48 foraging sites out of 87 were returned to.



**Fig. 3 Comparison between the time spent (hours) at recursion and non-recursion sites within the Lower Kinabatangan Wildlife Sanctuary, Sabah**

The occurrence of recursion was higher to foraging sites where elephants had spent more time at the previous visit (nFS is the total number of feeding sites = 87, nFSR is the total feeding sites with recursion = 48).

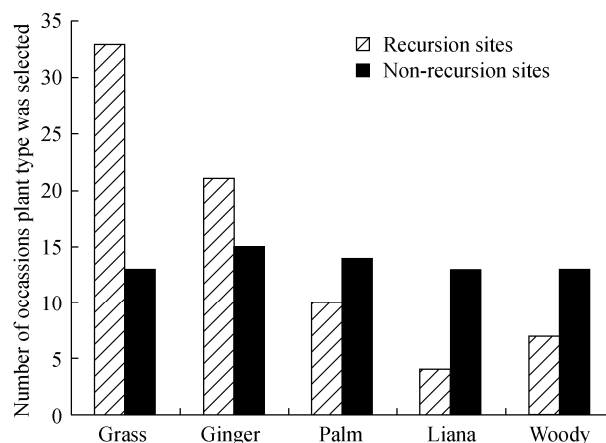
We also found a significant positive relationship between the number of days between visits (Fig. 4A), time spent at a site at the first visit (Fig. 4B) and habitat type (Fig. 4C) with the amount of time at a site at recursion (hours at first visit, Wald chi-square = 89.51,  $df = 1$ ,  $P < 0.01$ , days between returns, Wald  $\chi^2 = 13.77$ ,  $df = 1$ ,  $P = 0.00$ , habitat type, Wald  $\chi^2 = 3.44$ ,  $df = 1$ ,  $P = 0.043$ ).



**Fig. 4** Variables influencing time Bornean elephants spent within the Lower Kinabatangan Wildlife Sanctuary, Sabah spent at second visit to a site (i.e. 1<sup>st</sup> recursion)

A) days between visits B) time spent at sites at first visit and C) habitat. nFRS is the number of foraging sites that received recursion and nTFS refers to the total number of foraging sites within each habitat type.

From direct observations of the elephant herds foraging we found that there was a significant relationship between recursion and foraging sites where they were seen foraging on grasses and bamboos (ANOVA,  $df = 86$ ,  $F = 14.041$ ,  $P < 0.001$ ) and a significant relationship between foraging on lianas and sites that were not returned to within the 12 month study period (ANOVA  $df = 86$ ,  $F = 8.501$ ,  $F = 0.005$ ) (Fig. 5). Woody plants, palms and gingers had no significant influence on recursion ( $P = 0.095$ ,  $P = 0.157$  and  $P = 0.504$  respectively).



**Fig. 5** Plant types selected for feeding by Bornean elephants within LKWS at recursion and non-recursion sites

### 3 Discussion

Recursion by elephants in the LKWS was common. It most commonly occurred during two time periods: within 48 hours of the previous visit and between 151–250 days after the last visit, suggesting there are two different reasons for recursion.

We also found that the occurrence of recursion to foraging sites was influenced by the amount of time elephants had spent at a site previously, with recursions occurring more often to sites where they had spent more time in the past. A positive relationship was found between the number of days between the first visit and recursion, the number of hours spent at a site at the first visit, and the amount of time spent at a site at recursion. The habitat type of the site also influenced how much time was spent at a site during recursion. Additionally, elephants fed more on grasses and bamboos at recursion sites compared to sites they did not return to. Grasses and bamboos are most commonly found in the riverine and open grass habitats along forest margins (English et al., 2014) where elephants spent more time at recursion.

A relationship between the amount of time allocated to a particular area per visit and the resource quality of the area has previously been identified in large herbivore foraging behavior (Bailey et al., 1996). Our results suggest that, as more time was spent at recursion sites compared to non-recursion sites, then these sites, and sites with similar characteristics as recursion sites, are favourable to elephants and therefore should be considered high quality.

#### 3.1 Short-term recursions

Recursions to a foraging site within 48 hours of the previous visit were expected to be a site-sampling stra-

tegy where short duration visits were followed by longer duration visits, with the elephants returning to feed more extensively once the site quality was known relative to other sites in the area. We found the opposite, however. Elephants spent more time at sites at the first visit compared to the second visit (recursion) when they returned within 48 hours. This foraging strategy may be a way of reinforcing acceptance of a site over time (Owen-Smith, 2002). Alternatively, shorter second visits might be due to the elephants checking that all food within the site was exploited, resulting in less feeding time due to reduced food quality and insufficient regrowth of vegetation. Furthermore, induced responses in plants following herbivory, such as increased tannin content (Karban and Myers, 1989), could reduce the palatability of plants at sites recently visited.

### 3.2 Long-term recursions

Recursions after longer periods may be related to plant recovery rates (Bar-David et al., 2009) where herbivores return to exploit a feeding site once resources have sufficiently recovered. The more time elephants spent at sites at the first visit, the more days passed before they returned and the more time was spent at the site at recursion. This suggests that recursion occurring after 151–250 days is most likely related to resource recovery. To minimise energy expenditure and make optimal use of its home-range, a herbivore would benefit by monitoring vegetation depletion and renewal rates (McNaughton et al., 1997). This strategy would reduce the occurrence of returning to areas that had recently been exploited and facilitate the return after resource renewal.

Elephants may shift among sites in the same general region or move between a set of foraging areas. Recursions that occur after a longer time-period may occur after all sections have been exploited and enough time has passed for vegetation to regenerate in the areas previously visited (Bailey et al., 1996). This differs from recursions that occur within 48 hours where insufficient time has passed for resource regeneration. Long-term recursions to previously foraged areas, therefore, may be a beneficial foraging strategy for herbivores, enabling them to consume regrowing vegetation in a stage of high primary productivity and palatability (McNaughton, 1985; Gordon and Lindsay, 1990). Moreover, recursions may accelerate nutrient cycling in highly foraged sites (Gordon and Lindsay, 1990; McNaughton et al., 1997) and maintain them as nutrient hotspots (Winnie et al., 2008). Elephants may also select certain plants at a foraging site at specific times of the year.

This could explain why some sites received less recursions than others, for example where they had selected woody plants previously.

Both long- and short-term foraging strategies may be a form of associative learning, although in some species returning to a resource once it has been replenished is innate (Burke and Fulham, 2003). Innate foraging decisions associated with the spatial and temporal availability of resources may also occur in elephants. However, for such a highly social and long-lived species with large home-ranges, learned behavior within elephant herds is likely, especially considering their highly developed spatial and temporal memory (Hart et al., 2008). It is therefore probable that elephants remember areas containing their preferred food choices and return to them after sufficient time has passed for resources to replenish.

### 3.3 Implications for elephant habitat management

The identification and conservation of sites of recursion for elephants should be a priority in the design and management of reserves. For the LKWS population, riverine and open grass areas along forest margins appear to be key recursion sites and so these areas should be a conservation priority. Loss of access to recursion sites, or sites with similar characteristics, from either anthropogenic or natural disturbance may lead to increased human-elephant conflict due to resources being sought elsewhere, such as in oil palm plantations. Additionally, conservation practitioners and wildlife departments should establish protected corridors linking recursion sites to ensure accessibility for elephants.

The temporal pattern of site recursion described in this study is a reflection of elephant movement patterns amongst foraging sites. An investigation of movement was beyond the scope of the present study but further studies of recursion will benefit from investigations of the movement patterns that support recursion over different temporal scales. We observed recursion to occur over two time-scales: short- and long-term. Such a recursion could be supported by random or stratified random movement patterns, especially given spatial constraints of habitat boundaries, and so potentially modelled using random-walk models; for example, correlated random walks (McCulloch and Cain, 1989). Alternatively and much more likely, long-term recursions occur as a result of lengthy, directed moves to clusters of foraging sites followed by short-term recursions within the clusters. This type of movement would be expected to follow a Hidden Markovian Model (Langrock et al., 2012). The models that best explain movement pattern while also

generating observed patterns of recursion remain to be found.

**Acknowledgements** Thank you to Victoria University of Wellington for supporting the study and providing a doctoral scholarship and a completion scholarship for Megan English, and to the Economic Planning Unit and Sabah Wildlife Department for permitting the research in the Lower Kinabatangan Wildlife Sanctuary. Thank you to Sulaiman Ismail from HUTAN Elephant Conservation Unit for helping with data collection and Danau Girang Field Centre and Nurzhafarina Othman for allowing access to the collared elephant data. Thank you to Andrew Hearn from the Bornean Clouded Leopard Programme for use of the map of LKWS. This project was supported by funds to Megan English and Dr Wayne Linklater from Zoos Victoria, Australia.

## References

- Ackerman JD, Mesler MR, Lu KL, Montalvo AM, 1982. Food-foraging behavior of male Euglossini (Hymenoptera, Apidae): Vagabonds or trappers? *Biotropica* 14: 241–248.
- Adler P, Raff D, Lauenroth W, 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479.
- Alfred R, Ahmad AH, 2010. Density and population estimation of the Bornean elephants *Elephas maximus borneensis* in Sabah. *Online Journal of Biological Sciences*, 10: 92–102.
- 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.
- Bailey DW, Rittenhouse LR, Hart RH, Swift DM, Richards RW, 1989. Association of relative food availabilities and locations by cattle. *Journal of Range Management* 42: 480–482.
- Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB et al., 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49: 386–400.
- Bar-David S, Bar-David I, Cross PC, Ryan SJ, Knechtel CU et al., 2009. Methods for assessing movement path recursion with application to African buffalo in South Africa. *Ecology* 90: 2467–2479.
- Barnes RFW, Blom A, Alers MPT, Barnes KL, 1995. An estimate of the numbers of forest elephants in Gabon. *Journal of Tropical Ecology* 11: 27–37.
- Bartumeus F, Da Luz MGE, Viswanathan GM, Catalan J, 2005. Animal search strategies: A quantitative random-walk analysis. *Ecology* 86: 3078–3087.
- Blake S, 2002. The Ecology of Forest Elephant Distribution and Its Implications for Conservation. Ph.D. dissertation, Edinburgh, University of Edinburgh.
- Bell W, 1990. Searching behavior patterns in insects. *Annual Review Entomology* 35: 447–467.
- Belovsky GE, 1984. Herbivore optimal foraging: A comparative test of three models. *American Naturalist* 124: 97–115.
- Burke D, Fulham BJ, 2003. An evolved spatial memory bias in a nectar-feeding bird? *Animal Behaviour* 66: 695–701.
- Comba L, 1999. Patch use by bumblebees (Hymenoptera Apidae): Temperature, wind, flower density and traplining. *Ethology Ecology and Evolution* 11: 243–264.
- 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.
- Dressler RL, 1982. Biology of the orchid bees (Euglossini). *Annual Review Ecological Systems* 13:373–394.
- Dumont B, Petit M, 1998. Spatial memory of sheep at pasture. *Applied Animal Behaviour Science* 60: 43–53.
- English M, Gillespie G, Ancrenaz M, Ismail S, Goossens B et al., 2014. 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 et al., 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 fuscicollis*, 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 palliata*. In: Estrada A, Garber PA, Pavelka MSM, Luecke L ed. *New Perspectives in the Study of Mesoamerican Primates*. Springer US: 287–309.
- Garrison JSE, Gass CL, 1999. Response of a traplining hummingbird to changes in nectar availability. *Behavioural Ecology* 10: 714–725.
- Gilbert LE, 1980. Ecological consequences of a coevolved mutualism between butterflies and plants. In: Gilbert LE, Raven PH ed. *Coevolution of Animals and Plants*. Austin: University of Texas Press, 210–231.
- Gill FB, 1988. Trapline foraging by hermit hummingbirds: Competition for an undefended, renewable resource. *Ecology* 69: 1933–1942.
- Gordon I J, Lindsay WK, 1990. Could mammalian herbivores manage their resources? *Oikos* 59: 270–280.
- Hart BL, Hart LA, Pinter-Wollman N, 2008. Large brains and cognition: Where do elephants fit in? *Neuroscience and Biobehavioral Reviews* 32: 86–98.
- Heinrich B, 1976. The foraging specialisations of individual bumblebees. *Ecological Monographs* 46: 105–128.
- IUCN, 2013. IUCN Red List of Threatened Species. Version 2013.2.
- 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.
- Janson CH, 1998. Experimental evidence for spatial memory in foraging wild capuchin monkeys *Cebus apella*. *Animal Behaviour* 55: 1229–1243.
- Janzen DH, 1971. Euglossine bees as long-distance pollinators of



- tropical plants. *Science* 171: 203–205.
- Kadmon R, 1992. Dynamics of forager arrivals and nectar renewal in flowers of *Anchusa stigosa*. *Oecologia* 92: 552–555.
- Karban R, Myers JH, 1989. Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* 20: 331–348.
- Langley RB, 1999. Dilution of precision. *GPS World* 10: 52–59.
- Langrock R, King R, Matthiopoulos J, Thomas L, Fortin D et al., 2012. Flexible and practical modeling of animal telemetry data: Hidden Markov models and extensions. *Ecology* 93: 2336–2342.
- Lemke TO, 1984. Foraging ecology of the long-nosed bat *Glossophaga soricina*, with respect to resource availability. *Ecology* 65: 538–548.
- Lemmon PE, 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* 2: 314–320.
- Li Z, Han J, Ding B, Kays R, 2012. Mining periodic behaviors of object movements for animal and biological sustainability studies. *Data Min. Knowl. Discovery* 24: 355–386.
- Manning A, 1956. Some aspects of the foraging behaviour of bumble-bees. *Behaviour* 9: 164–201.
- McCulloch CE, Cain ML, 1989. Analyzing discrete movement data as a correlated random walk. *Ecology* 70: 383–388.
- McKay GM, 1973. Behavior and ecology of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology* 125: 1–113.
- McNaughton SJ, 1985. Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs* 55: 259–294.
- McNaughton SJ, Banikwa FF, McNaughton MM, 1997. Promotion of the cycling of diet enhancing nutrients by African grazers. *Science* 278: 1798–1800.
- Menzel R, Greggers U, Smith A, Berger S, Brandt R et al., 2005. Honey bees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences of the United States of America* 102: 3040–3045.
- Ohashi K, Thomson JD, 2005. Efficient harvesting of renewing resources. *Behavioral Ecology* 16: 592–605.
- Owen-Smith N, Novellie P, 1982. What should a clever ungulate eat? *American Naturalist* 119: 151–178.
- Owen-Smith RN, 2002. *Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments*. Cambridge: Cambridge University Press.
- 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.
- Powell JA, 1997. *The Ecology of Forest Elephants *Loxodonta africana cyclotis* in Banyang-Mbo and Korup Forests, Cameroon with Particular Reference to Their Role as Seed Dispersal Agents*. Doctoral dissertation, University of Cambridge.
- Possingham HP, 1989. The distribution and abundance of resources encountered by a forager. *American Naturalist* 133: 42–60.
- Pyke GH, 1984. Optimal foraging theory: A critical review. *Annual Review of Ecological Systems* 15: 523–575.
- Racey PA, Swift SM, 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera, Vespertilionidae) during pregnancy and lactation. 1. Foraging behavior. *Journal Animal Ecology* 54: 205–215.
- Riotte-Lambert L, Benhamou S, Chamaille-Jammes S, 2013. Periodicity analysis of movement recursions. *Journal of Theoretical Biology* 317: 238–243.
- Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE et al., 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37: 789–795.
- Shoshani J, Eisenberg JF, 1982. *Elephas maximus*. *Mammalian Species* 182: 1–8.
- Sooryanarayana S, 1995. Floods in Malaysia: Patterns and implications. *Malaysian Journal of Tropical Ecology* 26: 35–46.
- SPSS, 2009. *PASW Statistics for Windows, Version 18.0*. Chicago: SPSS Inc.
- Stephens DW, Krebs JR, 1986. *Foraging Theory*. Princeton: Princeton University Press.
- Stout JC, Goulson D, 2002. The influence of nectar secretion rates on the responses of bumblebees (*Bombus* spp.) to previously visited flowers. *Behavioral Ecology and Sociobiology* 52: 239–246.
- 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.
- Thomson JD, Maddison WP, Plowright RC, 1982. Behavior of bumble bee pollinators of *Aralia hispida* Vent (Araliaceae). *Oecologia* 54: 326–336.
- Thomson JD, Peterson SC, Harder LD, 1987. Response of traplining bumble bees to competition experiments: Shifts in feeding location and efficiency. *Oecologia* 71: 295–300.
- Thomson JD, 1996. Trapline foraging by bumblebees: I. Persistence of flight-path geometry. *Behavioural Ecology* 7: 158–164.
- Tiebout HM III, 1991. Daytime energy management by tropical hummingbirds: Responses to foraging constraint. *Ecology* 72: 839–851.
- Turchin P, 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72: 1253–1266.
- Watts DP, 1998. Long-term habitat use by mountain gorillas *Gorilla gorilla beringei*. 2. Reuse of foraging areas in relation to resource abundance, quality, and depletion. *Int. J. Primatol.* 19: 681–702.
- 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: 1457–1468.