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Authors: Beirne, Christopher, Nuñez, Chase L., Baldino, Melissa, Kim, Seokmin, Knorr, Julia, et al.

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Estimation of gut passage time of wild, free roaming forest elephants

Christopher Beirne, Chase L. Nuñez, Melissa Baldino, Seokmin Kim, Julia Knorr, Taylor Minich, Lingrong Jin, Shuyun Xiao, Walter Mbamy, Guichard Ndzeng Obiang, Juliana Masseloux, Tanguy Nkoghe, Médard Obiang Ebanega, Colin Rundel, Justin P. Wright and John R. Poulsen

C. Beirne, C. L. Nuñez, M. Baldino, S. Kim, J. Knorr, T. Minich, J. Masseloux, J. P. Wright and J. R. Poulsen ✉ *(john.poulsen@duke.edu), Nicholas School of the Environment, PO Box 90328, Duke Univ., Durham, NC 27708, USA. – L. Jin and S. Xiao, Dept of Biology, Duke Univ., Durham, NC, USA. – W. Mbamy, G. N. Obiang, T. Nkoghe and M. O. Ebanega, Dépt de Géographie, Univ. Omar Bongo, Libreville, Gabon. – C. Rundel, Dept of Statistical Science, Duke Univ., Durham, NC, USA.*

Seed gut passage times, the time from ingestion to defecation, and frugivore movement patterns determine patterns of seed deposition across the landscape and are thus crucial parameters to quantify in wild populations. Recent advancements in satellite and telemetry technologies mean that animal movement patterns are readily quantifiable in increasingly high resolution. However, data on wild frugivore gut passage times are scarce to non-existent due to the difficulty of monitoring seed ingestion and defecation in natural habitats; therefore, GPT estimates are often extrapolated from captive species whose diets and activity patterns may have limited transferability to free-ranging populations. Here we develop, trial and deploy a suite of model seeds to address this shortfall in wild African forest elephants *Loxodonta cyclotis* – one of the most effective seed dispersers in the tropics. We use a combination of 'active' seed mimics, which indirectly measure gut passage through recording temperature fluctuations, and 'passive' seed mimics, which serve to mark the point of defecation to allow gut passage estimation from time-stamped GPS collar data. In doing so, we present the first ever GPT estimates from wild forest elephants: mean = 39.8 h (min = 16.6 h; max = 113.7 h). The estimates were derived exclusively from passive seed mimics (plastic beads and modified native seeds) as all active seed mimics were rejected by the focal elephant. The methods described are translatable to other free-ranging, GPS-collared, species and if widely adopted, will begin to address the current gap in our understanding of seed dispersal by wild frugivores.

Keywords: biologger, digesta retention time, forest elephant, gut passage time, iButton

Accurate estimation of gut passage time (GPT; also known as digesta retention time), from ingestion to defecation, is essential for understanding vertebrate-mediated ecological processes, such as seed dispersal (Cochrane 2003, Levine and Murrell. 2003, Spiegel and Nathan 2007, Campos-Arceiz and Blake 2011, Sadeghayobi et al. 2011). Patterns of dispersed seeds vary drastically among different frugivore species (Cochrane 2003), and are governed by a myriad of factors including the frugivore's diet, movement patterns and gut passage times (Schupp 1993). Gut passage time affects both the proportion of seeds that germinate and the timing of germination through exposure to the chemical environment of the digestive tract (Traveset 1998). Gut passage time and frugivore movement patterns together determine where seeds are deposited across the landscape, the probability of arriving at suitable microsites for recruitment, and their likelihood of escaping density-dependent mortality (Connell 1970, Janzen 1970). With recent advancements in satellite and telemetry technologies (Kays et al. 2015), data on animal movements are increasingly available and accurate, whereas data on gut passage times of wild frugivores are sparse because of the difficulty in monitoring seed ingestion and defecation in natural habitats (but see Yumoto et al. 1999 and Tsuji et al. 2010 for examples of GPT estimation in habituated groups of primates).

African forest elephants *Loxodonta cyclotis* are one of the most effective seed dispersers in the tropics (Dudley 1999, Campos-Arceiz and Blake 2011). In comparison to the other extant taxa of elephants – African savanna elephants *Loxodonta africana* and Asian elephants *Elephas maximus* – they disperse a higher number and a greater diversity of seeds (Blake 2002, Campos-Arceiz and Blake 2011). As the largest frugivores in tropical forests, African forest elephants are exclusive dispersers for many plant species (White 1994) and can ingest larger seeds, cross more significant geographical barriers, and travel longer distances

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than most other terrestrial seed dispersers (Blake et al. 2009). To date, the effectiveness of wild elephants as seed dispersers has been assessed primarily by analyzing dung content, monitoring visits to focal trees, tracking consumption rates of marked fruits and collecting GPS data from collared elephants (Cochrane 2003, Babweteera et al. 2007, Kitamura et al. 2007). However, lack of data on the GPT of wild elephants limits a full understanding of their effectiveness as seed dispersers because we cannot not accurately model seed dispersal distance without understanding the distribution of GPT. Data on elephant GPT are available on captive Asian and African savanna elephants (Rees 1982, Dudley 1999, Kinahan et al. 2007, Campos-Arceiz and Blake 2011, Harich et al. 2016, Bunney et al. 2017); but diet differences among species and changes in behavior and physiology associated with captivity raise questions about their application to wild African forest elephants (Campos-Arceiz et al. 2008).

To overcome the lack of GPT data on wild forest elephants, we developed and tested methods for the accurate measurement of GPT in the field. Taking advantage of GPS-collared forest elephants, we conducted GPT trials using modified seeds, colored plastic pellets and Thermocron temperature logging iButtons with and without VHF tags. Here we describe our experimental methods, assess their effectiveness and estimate, for the first time, GPT for wild forest elephants.

Methods

Study area

We conducted GPT trials in the vicinity of the Ipassa Research Station in the Ivindo National Park, Gabon. This region of Gabon (Fig. 1) experiences bimodal rainfall with two dry (January–March and June–August) and two rainy (September–December and April–May) seasons, with a mean annual precipitation of approximately 1700 mm and mean annual temperature of 23.9°C (Koerner et al. 2017). Ivindo National Park is approximately 300 000 ha and is predominantly forested (Sassen and Wan 2006). We selected this study area as, at the time of the study, there were five GPS-collared forest elephants present within the park (two in the north and three in the south).

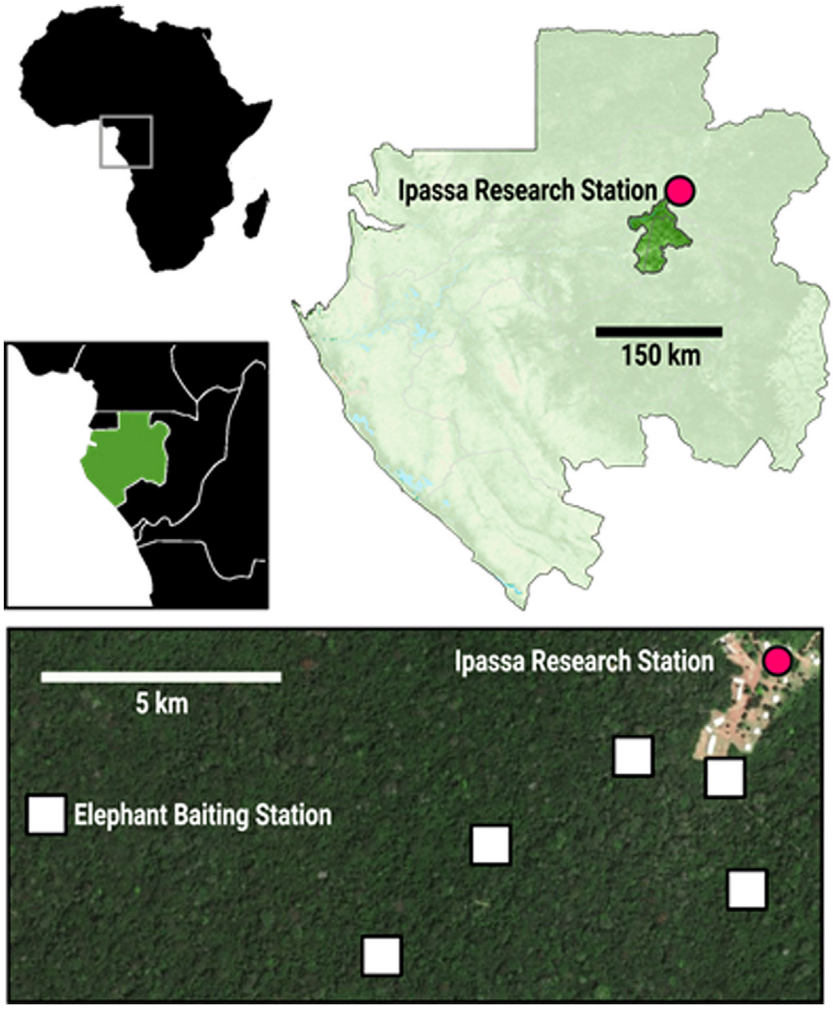


Figure 1. The location of the research site in the Ivindo National Park, Gabon as well as the locations of the six elephant baiting spots. We determined each location by assessing the movement patterns of the target elephant and identifying places it traveled to frequently.

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Focal elephant

We intended to incorporate multiple GPS-collared elephants in the study. However, only one elephant – a female named Amelia (age 30–40) – reliably ranged near the research station during the study period. Amelia was collared on 24 March 2017 by the Agence Nationales des Parcs Nationaux. Camera trap footage and dung size distributions (Turkalo 2013, Turkalo et al. 2018) demonstrated that Amelia was consistently accompanied by a seven or eight years old juvenile, Porkchop and a two–three-year-old juvenile, Rosebud. Both camera trap footage and the size distribution of dung-piles encountered suggested that the group remained together during the study period, therefore we assumed that the juveniles mirrored Amelia's movements.

Experimental seeds

Four types of experimental seeds were selected to mimic natural seeds of different sizes to measure elephant gut passage time. Two of the four experimental seeds were 'passive' – used to mark the point of defecation by the elephant. Passive seeds have been used previously to determine the gut passage time of a variety of captive vertebrate species where defecation time can be directly observed (Sadeghayobi et al. 2011, Steuer et al. 2011, Bunney et al. 2017), whereas here we infer the gut passage time of free-roaming, wild individuals from dung location and GPS collar data. Two of the seeds were 'active' – they recorded the actual gut passage times on the device through ambient temperature fluctuations.

The smallest 'passive' experimental seeds were colored plastic pellets (6 mm diameter Airsport Ammo; 0.11 g) – from here on referred to as 'pellets' (Fig. 2A). Different colored pellets were employed for each baiting trial to distinguish the origin of recovered pellets.

The second type of 'passive' seeds consisted of hollowed out *Chrysophyllum lacourtianum* seeds filled with aluminum foil and sealed with medical safe epoxy (Henkel Loctite Hysol M-31Cl Medical Device Epoxy) – from here on referred to as 'tin seeds' (Fig. 2B). *Chrysophyllum lacourtianum* is a large tree with large succulent globose fruits (mean mass = 320 g) that contain three to five seeds (mean mass = 2.8 g, mean length = 29 mm, mean width = 14 mm) and is consumed by elephants in the region (Rosin and Poulsen 2017). We harvested seeds from ripe fruits collected under wild fruiting trees. Insertion of the aluminum foil made it possible to detect the tin seeds in elephant dung using a metal detector (Garrett Ace 150 Metal Detector). Once hollowed out and filled with aluminum foil, the mass of the tin seeds was reduced by approximately 2.25 g on average relative to the unmodified seeds. To discriminate the origin of different tin seeds, a soldering iron was used to mark each seed with a unique pattern of dots corresponding to each baiting event.

The first 'active' experimental seeds consisted of iButton thermocouples (Thermochron DS1921H-F5, Maxim Integrated) (17.4 mm in diameter, 4.5 g) encapsulated in medical safe epoxy (Henkel Loctite Hysol M-31Cl Medical Device Epoxy) for protection – here on referred to as 'iButtons' (Fig. 2C). iButtons can be calibrated to record ambient temperature (with an accuracy of ±1°C) at defined time intervals (here we used 60 s) and have unique identification numbers so that each device can be individually identified. Therefore, after consumption by an elephant, the length of time in which the recorded temperature is consistent with the body temperature of an elephant (~36°C/96.8°F) is roughly equivalent to the GPT. Previously, Kinahan et al. (2007) fed iButtons embedded in apples to captive African savanna elephants to estimate GPT. We performed a similar baiting trial with three captive savanna elephants at the North Carolina Zoo to test the effectiveness of our encapsulation methods (Supplementary material Appendix 1).

The second 'active' experimental seed was similar to the first with the addition of a VHF transmitter (R1170, Advanced Telemetry Systems) (34 mm in diameter, 4 g) to improve the probability of recovering iButtons from free-roaming, wild elephants – here on referred to as 'VHF tag' (Fig. 2D). The VHF tags emit a signal that can be detected with a hand-held receiver and antennae. The maximum detection distance when the VHF tags were embedded in elephant dung was 120 m in the open and 58 m in the forest.

Baiting

We tracked Amelia's movements in real-time between 11 June 2018 and 2 August 2018 using an smartphone application developed by save the elephants (STE) and Vulcan, Inc. To focus our baiting efforts, we identified places Amelia visited repeatedly from the GPS tracking data and selected

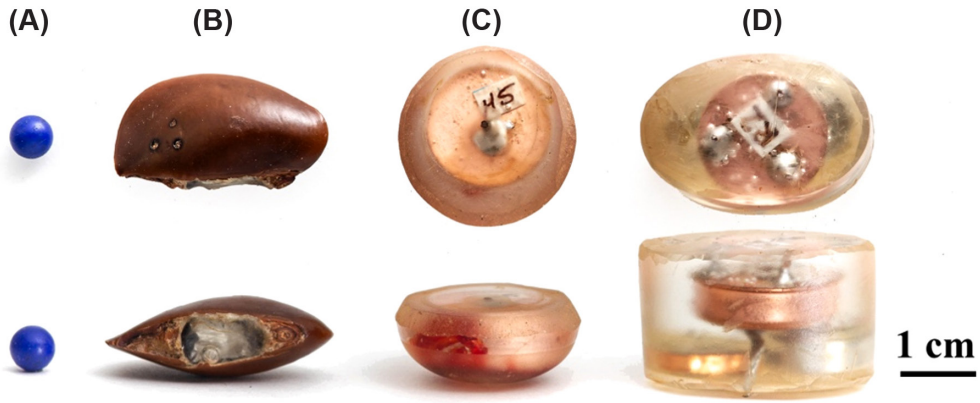


Figure 2. Photographs of the experimental seeds from above (top row) and the side (bottom row). Where: A = 'pellet'; B = 'tinned seed'; C = 'iButton'; D = 'VHF tag'.

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six elephant baiting locations (Fig. 1). At each location, we cleared the ground of vegetation and attached two camera traps (Bushnell Natureview Camera Viewer Model 119740 or Bushnell Trophy camera HD Brown Model 119676) to nearby trees, one aimed at the bait on the ground to directly observe feeding events and the other aimed at approximately 1.5 m in height to aid with individual identification (as non-collared elephants occurred in the area).

When Amelia and her juveniles approached the baiting stations, we selected the three most likely sites and baited them with all four experimental seed types embedded within real fruit. The fruit pile consisted of wild *C. lacourtianum* fruits, a seasonally and locally abundant elephant-dispersed fruit, and market bought mangos (*Mangifera* spp.) and ripe plantains (*Musa* spp.), both of which are known to be consumed by crop-raiding elephants in the study region. Each *C. lacourtianum* fruit was hollowed out, embedded with up to six tin seeds, no more than one iButton or VHF tag, and stuffed with a mixture of *C. lacoutianum* and plantain fruit flesh, and colored pellets. Each plantain contained a single epoxied iButton or VHF tag and was also stuffed with the fruit/pellet mixture. Prepared fruits were washed with stream water to reduce the possibility of seed rejection through human handling. In total, each pile contained 250 g of pellets (~2270 beads), between 19 and 46 tinned seeds and up to five iButtons and VHF tags. Additional fruit, such as mangos, undisturbed *C. lacourtianum* and plantains were added to each pile to make them more attractive to the elephants.

Once the sites were baited, we monitored the STE app periodically to see if Amelia approached the active bait locations. After a potential feeding event (the focal elephant coming within 50 m of the bait pile), the feeding stations were checked for signs of fruit consumption. If the fruit piles were disturbed, we reviewed the camera trap footage to determine if Amelia or her juveniles had consumed fruit. If they did, we began an 'elephant follow'.

Elephant follows

To recover dispersed seeds, we followed the focal elephant's GPS track and searched for dung piles. We conducted the follows a minimum of one hour behind Amelia to avoid altering her movement behavior. An experienced local Baka tracker followed the physical trail of the elephants through the forest. During our first follow, we tracked Amelia from the initial baiting station, and the first seeds were recovered 18 h after ingestion. On subsequent follows, we initiated tracking from Amelia's GPS location 10 h after fruit ingestion. We continued follows for 10 days after fruit ingestion.

For every elephant dung encountered, we measured the circumference of the three largest boli to identify the age of the individual. All boli were hand searched for experimental seeds, then spread into a thin layer and swept with a metal detector. For each dung pile with experimental seeds, we recorded the location and counted the number and type of seeds recovered.

Measuring GPT

In order to estimate gut passage time of passive experimental seeds, we developed a moving window algorithm in the R statistical environment. Briefly, for each dung encountered the elephant track of the focal elephant was subset to only contain the movement data from the time of feeding for the first dung encounter, or 6 h before the previous dung encounter for all subsequent dung, to the time the dung was discovered. We then determined the nearest available GPS point from the track subset to the located dung pile. The difference in time from the initial feeding event to the time at the nearest elephant location to the dung pile was considered to be the GPT (Supplementary material Appendix 2).

Results

In total, we set 21 baiting stations across five independent baiting trials. Elephants successfully consumed one baiting station from each of the first four baiting trials: three by the focal elephant and one by an unknown group. The fifth baiting trial was unsuccessful. Interference with baiting stations by non-target species was minimal, although a pouched rat removed several whole fruits in one isolated feeding event. We conducted three complete elephant follows (referred to as follows one, three and four). Follow two was abandoned as an unknown, non-collared group consumed the fruit at the baiting station, making it impossible to reliably track the dungs produced.

During the three complete elephant follows, we encountered 437 elephant dungs, 118 of which contained experimental seeds. A total of 845 experimental seeds were recovered, with the mean GPT estimated to be 39.8 h, and a range of 16.6–113.7 h. The types of experimental seeds recovered were as follows:

Passive experimental seeds: pellets

Overall, we recovered 842 pellets across the three follows (215, 534 and 93 in each follow respectively). The average number of pellets found per dung pile during follow one was seven, with a minimum of one and a maximum of 60. During follows three and four, the number of pellets were not counted to exhaustion, as the counting process would have compromised our ability to remain in close proximity to the focal elephant, therefore searches were limited to ~2 min. The rate of recovery diminished with increasing GPT, plateauing at around 60 h (Fig. 3). Estimates of GPT based on pellet-containing dung piles and GPS location data resulted in a GPT distribution ranging from 16.6 h to 79.7 h. The mean GPT was 39.7 h (SD = 14.5 h) (Fig. 4).

Passive experimental seeds: tin seeds

Three out of 48 tin seeds were retrieved from dung piles, two on follow three and one on follow four. Two of the tin seeds were found in two dung piles that also contained plastic pellets, with GPT's of 29.2 h and 53.8 h. The third tin seed was found by itself in dung, and had a GPT of 113.7 h. The mean GPT calculated using tin seeds was 65.6 h.

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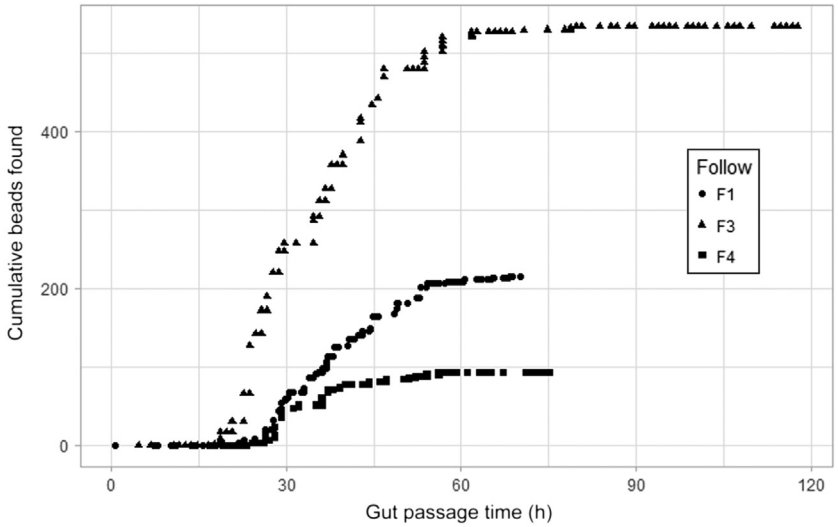


Figure 3. Cumulative number of pellets over estimated gut passage times, in hours, for three elephant follows.

Active experimental seeds

We did not recover any iButtons or VHF tags on the elephant follows (despite similar experimental seeds being recovered in trials with captive savannah elephants; Supplementary material Appendix 1). This is likely because Amelia spat out the encapsulated seeds shortly after consuming them. During the first baiting trial we recovered six iButtons that had been spat out on the ground at the baiting site, leaving only two that were potentially ingested. The unlocated seeds could also have been spat out after leaving the feeding station. During the third baiting trial, the elephants (Amelia and/or her juveniles) spat out five tin seeds, four iButtons and one VHF tag. We did not recover any rejected active seeds from the feeding site of the fourth trial, most likely due to the presence of tall grasses making them difficult to relocate. Our fifth and final baiting trial was unsuccessful, Amelia did not swallow any of the experimental seeds. She investigated the fruit pile and chewed some fruits, but threw most fruits away upon smelling them.

Discussion

Using a novel approach to quantify gut passage time (GPT) in wild forest elephants, we estimate an average GPT of 39.8 h (SD = 14.5 h). Our approach consisted of baiting a GPS-collared elephant with fruits filled with four types of experimental seeds so that we could later recover the seeds and calculate the time from ingestion to defecation. After three elephant follows, only colored plastic pellets provided substantial GPT data. Below we discuss the advantages and disadvantages of different types of experimental seeds to inform future field efforts.

All experimental seeds tested in this study can survive consumption by elephants and passage through the acidic gut environment, but they differ substantially in their rate of ingestion and detectability in the field. Of the four types of experimental seeds, wild forest elephants most easily ingested the plastic pellets. Few of the tin seeds, iButtons and VHF tags were ingested as the focal elephant, Amelia, tended to spit them out upon detection. The colored plastic pellets

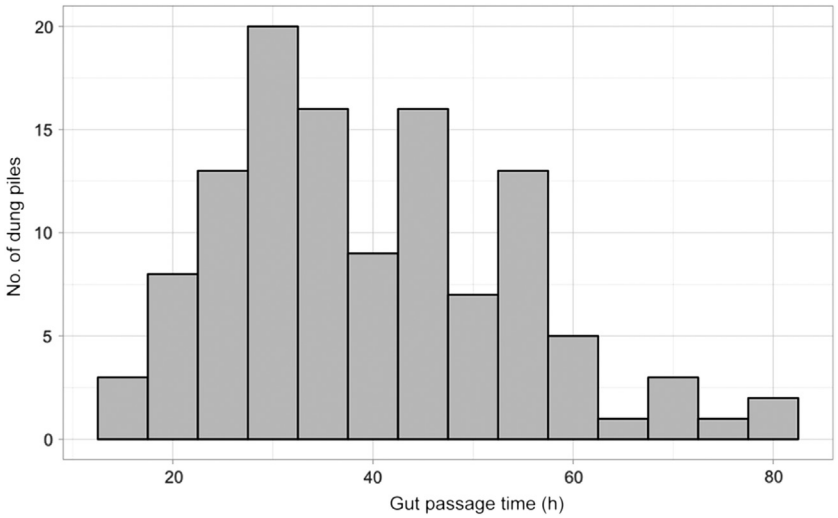


Figure 4. The frequency distribution of gut passage time (GPT) in hours from dung piles with plastic pellets. See Supplementary material Appendix 3 for the frequency table.

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were easy to find in elephant dung through a quick visual inspection, and the tin seeds were easily detected at close range with a metal detector. While the plastic pellets can mimic dispersal of small seeds like *Ficus* spp., the tin seeds are advantageous because they consist of actual, medium-to-large seeds and thus reflect natural dispersal of the majority of elephant-consumed seeds. As passive models of seeds, neither the plastic pellets nor the tin seeds can log gut passage time in real-time. Thus, calculations of GPT depend on being able to track elephants remotely using GPS collars, and estimating the time interval using known consumption and estimated deposition times of the seeds. Because GPS collars emit locations at user-defined intervals, the precise seed deposition time is not known and is potential source of error. However, as we used a high GPS reporting frequency (every 15 min) in this study, the error in estimated gut passage time is negligible.

Compared to the passive seed models, iButtons provide a more straightforward GPT measurement, as they log the temperature difference between the ambient forest environment and the elephant gut. In the zoo setting, iButtons worked reliably (Supplementary material Appendix 1). However, the focal wild forest elephant consistently spat out the iButtons, and we were not able to gather any GPT's from this method. Without further trials, it is impossible to know if all wild forest elephants will reject the larger active experimental seed types or if the focal elephant was a particularly sensitive individual. That said, we found no evidence of experimental seed rejection in the unknown group feeding event, and, on several occasions, we found large wild seeds spat onto the ground surrounding fruiting trees which the focal elephant had visited the previous night. Furthermore, captive savannah elephants ingested the iButtons in our Zoo trials and in previous studies (Kinahan et al. 2007). Future studies should take steps to the minimize handling and manipulation of fruits and experimental seeds in order to limit the possibility of individuals rejecting sensors due to strange smells or tastes. This is of particular importance where researchers are working in a location with species which are conditioned to avoid humans due to poaching or other anthropogenic disturbances. Nonetheless, if un-collared elephants had ingested the iButtons, they would have been near impossible to relocate as the VHF tags had a very limited range in the forest. Therefore, our ability to follow the GPS-collared elephants was key to our success. The mean GPT estimated from our data (39.8 h) is ~10% greater than the mean reported GPTs from captive Asian and savannah elephants (Dudley 1999, Harich et al. 2016, Bunney et al. 2017), however owing to potential species-specific GPTs, these differences must be interpreted with caution.

Our experiment was limited by several factors. First, we were only able to collect GPT data from one family of elephants, which may not be representative of different age and sex groups, especially males which are said to have larger home ranges (Mills et al. 2018). Furthermore, the work was conducted in the dry season in one locality. Future work should address how regional and seasonal variation in dietary intake or feeding behavior (Blake and Inkamba-Nkulu 2006, Buij et al. 2007, Mills et al. 2018) could drive local and landscape scale variation in GPT. The average GPT that we report here was principally estimated from plastic pellets that mimic small seeds, but GPT's could differ with seed size or shape. Future work will focus on encapsulating active data loggers into actual seeds consumed by forest elephants to further improve the ecological validity of the GPT's estimated. Even so, we demonstrate a novel method of determining GPT's of wild forest elephants and fill a gap in data on the GPT of wild African forest elephants, an important component to determining the ecological effects of elephants on forests (Poulsen et al. 2018).

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Supplementary material (available online as Appendix wlb-00543 at <www.wildlifebiology.org/appendix/wlb-00543>). Appendix 1.

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