Harvesting and chewing as constraints to forage consumption by the African savanna elephant (*Loxodonta africana*) (#11471)

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Harvesting and chewing as constraints to forage consumption by the African savanna elephant (*Loxodonta africana*)

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As a foundation for understanding the diet of African savanna elephants (*Loxodonta africana*), adult bulls and cows were observed over an annual cycle to determine whether harvesting, chewing and handling times differed across food types and harvesting methods (handling time is defined as the time to harvest, chew and swallow a trunkload of food). Bulls and cows were observed 105 and 26 times respectively (94 and 26 individuals), with a total of 64 hours of feeding recorded across 32 vegetation types. Some food types took longer to harvest and chew than others, which may influence intake rate and affect choice of diet. The method used to gather a trunkload of food had a significant effect on harvesting time, with simple foraging actions being comparatively rapid and more difficult tasks taking longer. Handling time was constrained by chewing for bulls, except for the processing of roots from woody plants, which was limited by harvesting. Time to gather a trunkload had a greater influence on handling time for cows compared to bulls. Harvesting and handling times were longer for bulls than cows, with the sexes adopting, within the limits of their strength, foraging behaviors that best suited their energy requirements.

do you have evidence of a strength limitation? I suspect not; suggest omit

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ABSTRACT

As a foundation for understanding the diet of African savanna elephants (*Loxodonta africana*), adult bulls and cows were observed over an annual cycle to determine whether harvesting, chewing and handling times differed across food types and harvesting methods (handling time is defined as the time to harvest, chew and swallow a trunkload of food). Bulls and cows were observed 105 and 26 times respectively (94 and 26 individuals), with a total of 64 hours of feeding recorded across 32 vegetation types. Some food types took longer to harvest and chew than others, which may influence intake rate and affect choice of diet. The method used to gather a trunkload of food had a significant effect on harvesting time, with simple foraging actions being comparatively rapid and more difficult tasks taking longer. Handling time was constrained by chewing for bulls, except for the processing of roots from woody plants, which was limited by harvesting. Time to gather a trunkload had a greater influence on handling time for cows compared to bulls. Harvesting and handling times were longer for bulls than cows, with the sexes adopting, within the limits of their strength, foraging behaviors that best suited their energy requirements.

Key words: bark, diet, foraging, forbs, grass, handling, leaves, roots

INTRODUCTION

African savanna elephants (*Loxodonta africana*) utilize a wide variety of forage types, consuming leaves, stems, roots and tubers from herbaceous vegetation (grass and forbs) (Barnes 1982; de Boer et al. 2000; de Longh et al. 2004; Wyatt & Eltringham 1974), and leaves, twigs, bark, roots, flowers and fruits from woody plants (Field 1971; Guy 1976). Although elephants harvest food from a range of plant life forms, it is their conspicuous impact on woodlands that has the greatest potential to cause long-term vegetation change (Lamprey et al. 1967; Laws 1970; Leuthold 1977). Extensive conversion of woodlands to shrubland by elephants (Spinage 1994) and the potential associated loss of biodiversity (Cumming et al. 1997; Herremans 1995; Kerley & Landman 2006) may require management intervention (O'Connor et al. 2007), but any action
“based”
should be founded on an understanding of why elephants choose to utilize woody plants in a destructive manner. Impact on woody vegetation is greatest when harvesting methods such as breaking branches, debarking stems, or toppling, pollarding or uprooting whole plants are used, and less when trunkloads of leaves are stripped without breaking branches (Clegg 2010). When diet is composed solely of grass and forbs there is no damage to woody plants. Therefore
“are”; there are 2 things being described
knowledge of the factors that influence choice of diet and mode of harvesting is required before impact on woody vegetation can be understood.

Elephants spend up to 18 hours per day foraging (Wyatt & Eltringham 1974). This involves locating suitable food patches, harvesting trunkloads, and chewing and swallowing harvested material. The time to complete these individual tasks may vary across forage types, potentially causing differences in the rate at which each forage type can be ingested. This in turn may influence diet and habitat selection because elephants possibly seek to maximize their rate of intake of food rich in easily digestible cell solubles (Clegg 2010; O'Connor et al. 2007). Food types that can be located, harvested and chewed quickly should have higher preference than those that take longer to ingest. Determinants of searching time (time to locate a food patch) have been investigated for elephants (Clegg & O'Connor 2016), but the potential for differences in harvesting and chewing times across the range of forage types consumed is yet to be explored. Adult females have half the body mass of adult males (Owen-Smith 1988) and this may cause differences in the strength and capacity available for harvesting and chewing fibrous food types. Consequently, the possibility that gender influences time to harvest and chew food is also explored in this study.

Early foraging models assumed that harvesting and chewing by herbivores were mutually exclusive processes (Farnsworth & Illius 1996; Farnsworth & Illius 1998; Spalinger & Hobbs 1992). However, harvesting and chewing have been shown to overlap for both cattle (Laca et al.

sentences are often too long. Break into 2 sentences instead of adding "and"

1994) and giraffe (Ginnett & Demment 1995), and this is also true for elephants because the trunk allows harvesting to take place while food is being chewed (Clegg 2010). This overlap means that handling time (time to harvest, chew and swallow a trunkload of food; H_t) is constrained by either harvesting time (P_t) or chewing time (C_t) depending on which action takes longest (i.e. when $P_t > C_t$, $H_t = P_t$, but when $H_t > P_t$, $H_t = C_t$) (Clegg 2010). Therefore harvesting

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methods that involve laborious, time consuming actions may considerably lower the rate of food intake even if trunkloads are rapidly chewed and swallowed. This study focused on foraging within a food patch. Movement between patches necessitates the inclusion of searching time as an additional constraint, and this is dealt with elsewhere using a more complete foraging model (Clegg 2010).

The aim of this study was to determine whether harvesting, chewing and handling time differ across food types as a foundation for understanding diet choice of elephants. The following specific questions were addressed. (1) Do some forage types take longer to harvest and chew than others? (2) Does the method used to gather a trunkload affect harvesting time? (3) Is handling time constrained by harvesting or chewing? (4) Does gender influence handling time?

MATERIALS & METHODS

Study area

The study was conducted in the semi-arid savanna of Malilangwe Wildlife Reserve (50 000 ha) in south-eastern Zimbabwe (20°58′–21°15′ S, 31°47′–32°01′ E). Permission to carry out the research was granted by The Malilangwe Trust. The reserve has a hot wet season from November to March, a cool dry season from March to August, and a hot dry season from September to October. Mean annual rainfall is 557 mm (n = 64; CV = 34.2 %), with approximately 84 % falling in the hot wet season. Rainfall during the year of study was 716 mm. The average minimum and maximum monthly temperatures range from 13.4 °C (July) to 23.7 °C (December), and 23.2 °C (June) to 33.9 °C (November) respectively (Clegg 2010). Frost is rare. Thirty-eight vegetation types, from open grassland to dry deciduous forest, have been identified on seven geological types, with soils ranging from 90 % sand to 41 % clay (Clegg & O'Connor 2012). Fire has been used as a tool for rangeland management since 1994. In October 2001 (5 months prior to the start of the study period), 28 % of the reserve was burnt for management purposes.

Data collection & analysis

P_t and H_t were estimated for different food types by observing elephants feeding between April 2002 and March 2003. C_t was not estimated directly, but because of the potential for complete overlap between harvesting and chewing, when $H_t > P_t$, it was assumed that $H_t = C_t$. Observations were made in as many vegetation types and times of day as possible. No observations were made at night. Once elephants were located, a focal individual was chosen. Random selection was impossible because of the dictates of wind direction, availability of cover for an undetected approach and the presence of other elephants, and therefore selection was restricted to the most accessible adult (approximately > 30 years old). The sex of the focal animal was recorded and characteristics such as tusk length, shape and size, and torn ears were noted to ensure recognition during sampling. Observations were made on foot or from a vehicle for the larger family groups at a distance of 20 to 50 m using binoculars. The time at the start of the feeding record was noted. The following was recorded for each trunkload by talking at the instant of each foraging action into a head-set microphone attached to a Dictaphone that was running continuously: (1) when the elephant began to harvest a trunkload, (2) harvesting method, (3) forage type, (4) plant species, and (5) when the trunkload was placed in the mouth. The point at which the elephant finished chewing a mouthful was assumed to take place the instant before the next trunkload was placed in the mouth. It was also noted when the elephant left a patch of food and started to feed in a new patch. The elephant was deemed to have left a woody patch if it abandoned the shrub or tree it had been feeding on or an herbaceous patch if it walked more than two paces without feeding from the herbaceous layer. If the focal elephant disappeared from view, recording was stopped. Recording continued when the elephant reappeared. If it became obvious that the elephant was walking to

water as opposed to actively feeding, or if feeding was disturbed in any other way, observation was abandoned. The route and distance travelled during the observation period was recorded by saving a track on a Global Positioning System. The Dictaphone recordings were transferred to a
does this need a Registered sign?
computer where they were analyzed using Winamp (a digital audio player) and Microsoft Excel. Because the Dictaphone was running continuously, the recording preserved the intervals between feeding actions. Consequently when recordings were played using Winamp the time at the start and end of each feeding action could be read to the nearest second off the digital timer. These times were transferred to Excel spreadsheets that were used to construct data sets for P_t and H_t that included forage type, harvesting method, vegetation type, month, and elephant gender and ID for each trunkload. H_t was calculated as the interval between consecutive mouthfuls of a food type gathered from a single patch using the same method of harvesting.

Many combinations of forage type and harvesting method had insufficient observations for
write out numbers <10, except where an SI unit or similar follows
analysis and therefore a single categorical variable called "Ftype" that included the 9 most common combinations was constructed. To account for spatial, temporal, and within subject non-independence of observations we used the glmer function of the lme4 package of R (Bates et al. 2015) to create generalized linear mixed-effects models (GLMM) with harvesting or handling time as the dependent variable, and forage type (factor with 9 levels) and sex (factor with 2 levels) as fixed effects. Vegetation type (spatial non-independence), month (temporal non-independence), and elephant ID (within subject non-independence) were used as crossed, uncorrelated, random intercept effects. Models failed to converge when slope was included in the structure of random
fullstop after "effects". Then "Therefore, only random…"
effects therefore only random intercepts were considered. Distributions of harvesting and handling
hyphenate
times were right skewed so models were specified with the gamma distribution and log link to achieve homoscedasticity of residuals. The interaction between main effects was not included

because data were missing for some forage type and gender combinations. Models with all possible
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groupings of random intercept effects were compared by assessing goodness of fit using Akaike
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and Bayesian information criteria acquired using the AIC (R Core Team 2016) and BIC (Pinheiro et al. 2016) functions of R respectively. The Anova (Fox & Weisberg 2011) and anova (R Core
suggest using italics so that the reader understands that these are specific statistical tests
Team 2016) functions, and lsmeans package (Lenth 2016) of R were then run on the outputs of the best models to determine the significance of the fixed effects and calculate the least squares means of harvesting and handling time (and 95 % confidence intervals) for the different forage type and gender combinations. The lsmeans package was used to conduct pairwise comparisons of the least squares means across forage types using Tukey’s adjustment. Within forage types, we tested for a significant difference between harvesting and handling times by calculating the 95 % confidence interval of the difference (intervals that included zero were not significant). We used the
why this? please explain
Pythagorean Theorem to calculate the standard error of the difference and a value of 1.96 for the
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Z-statistic. Labfit software (Silva & Silva 2011) was used to determine the function that best fit the relationship between mean handling time and the frequency of observations for each forage type.

RESULTS

Adult bulls and cows were observed 105 and 26 times respectively (96 and 26 individuals), with a total of 64 hours of feeding recorded across 32 vegetation types. Cows were observed less frequently than bulls because they tended to associate in large groups (up to 80 individuals) and were therefore more difficult to approach on foot. A total of 109 plant species were consumed.

Food types utilized were whole grass plants, grass inflorescences (only observed for cows), grass roots, whole forb plants, leaves and twigs of woody plants, bark from canopy branches of trees and shrubs, bark from the main stems of trees, bark from roots of trees and shrubs, roots of trees and shrubs, tubers (caudices), flowers and fruits. Often a trunkload was composed of more than one food type e.g. leaves and twigs or leaves and fruits.

Harvesting methods varied within and across food types. Grass plants were plucked by wrapping the trunk around the above ground portions of a tuft and pulling to uproot the plant. If soil was attached to the roots or a significant amount of senescent leaf material was present, this was removed by thrashing the tuft against the chest or front leg. Most often the entire grass plant was consumed, but when the base of tillers was particularly robust, only the upper portion of the tuft was eaten, the roots and bases of the tillers being discarded. Grass roots were harvested in the same way except the above ground portions of the plant were discarded and only the roots eaten. Grass inflorescences were gathered by wrapping the trunk around a number of culms and pulling. Forbs with an erect growth form were plucked in a similar way to grass tufts, with the entire plant being consumed. Forbs with a creeping or climbing growth habit were gathered by extracting a long length, bundling it in the trunk, and then inserting the bundle into the mouth. Leaves of woody plants were either stripped or plucked. Stripping was most commonly done by wrapping the trunk around a leafy branch and then pulling the trunk along the length of the branch. Leaves were also stripped by loosely grasping a leafy branch in the mouth and then allowing the branch to run through the mouth while moving away from the plant. Stripping often resulted in a substantial amount of twigs being included in the trunkload. Leaves were plucked using the projections at the end of the trunk. Plucking appeared to result in fewer twigs being included in the trunkload compared to stripping, but the mass of the trunkload was potentially reduced. Leaves and twigs were harvested by wrapping the trunk around a slender branch and then bending the branch until it snapped. The entire branch was then consumed. For woody species with bark of high tensile

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strength (e.g. *Acacia tortilis*), leaves and twigs were harvested by grasping the end of a branch in the mouth and then drawing the branch taught across the end of a tusk until it snapped. Preference for this harvesting technique was indicated by the development of a marked groove a few centimeters back from the tip of the working tusk. Often an additional action such as breaking down a branch or felling the tree was required before a trunkload of leaves or leaves and twigs could be harvested. Bark was harvested from the canopy branches of shrubs and trees by snapping off a branch (approximately 2 cm in diameter) with the trunk, placing it in the mouth and then chewing off the bark along the length of the branch. Bull elephants harvested bark from the main stems of trees by gouging and prizing out sections using their tusks. Once gouging had created a piece of bark that could be grasped by the trunk with sufficient purchase, the bark was stripped away by pulling upwards. This was only possible for tree species with bark of an adequate tensile strength. Bulls most frequently employed this technique. Cows preferred to either snap the main stem or locate a tree whose main stem had been snapped and then strip off small pieces of bark by pulling on the torn, jagged edges of bark that were created when the stem was snapped. Cows frequently employed this technique when harvesting bark from the main stems of small (main stems of approximately < 15 cm diameter) *Colophospermum mopane* trees. Roots were harvested by excavating with the feet, uprooting shrubs by plucking with the trunk, pushing over trees or by grasping exposed roots with the trunk and pulling to lift long sections out of the soil. Tubers (e.g. those of *Jatropha* spp.) were particularly sought after by cows after rain in areas with sandy soil. A unique method was used to harvest tubers. First the tuber would be partially excavated by ploughing backwards and forwards through the soil with a foot. The moist soil after rain facilitated digging because the soil did not slide back into the hole. Once part of the tuber was exposed the

I'm assuming that it is the elephant that is "rising"? Please clarify

elephant would kneel down and impale the tuber with a tusk. On rising it would remove the tuber from the tusk using the trunk and place it in the mouth. Fruits where either plucked from the plant or picked up from the ground after the tree had been shaken to dislodge the fruits. When gathering small fruits from the ground (e.g. pods from *Acacia tortilis*) the fruits were swept into a pile, which was then ladled into the mouth using the trunk.

Data used for the GLMM's had fewer observations for harvesting than handling (Table 1) because when elephants were feeding from a dense sward it was difficult to record precisely when harvesting began. The AIC and BIC scores indicated that the best model for harvesting included elephant ID and month as random effects, while that for handling also included vegetation type as an additional random effect (Table 2). Analysis of variance showed that both forage type and sex had a significant influence on harvesting and handling times (Table 3).

Harvesting times were short for trunkloads of green grass, forbs and leaves from woody plants; intermediate for trunkloads of mixed grass, leaves and twigs, and bark from canopy branches; and long for trunkloads of roots from woody plants and main stem bark (Fig. 1). Additional harvesting actions, such as shaking a tuft of grass to remove senescent material, significantly ($P < 0.05$) increased harvesting time relative to instances when additional actions were not required. Handling times were short for trunkloads of leaves from woody plants, forbs and green grass; intermediate for leaves and twigs, roots from woody plants and mixed grass; and long for canopy bark, main stem bark and roots from woody plants that had to be excavated before being broken off (Fig. 2). Cows had shorter harvesting and handling times ($P < 0.05$) than bulls.

Handling time was constrained by chewing for bulls, except for the processing of roots from woody plants which was limited by harvesting (Fig. 3). Time to gather a trunkload had a greater influence on handling for cows than bulls, with 4 out of the 9 food types being constrained by harvesting as opposed only 2 for bulls (Fig. 4). For both bulls and cows, trunkloads of food types with the shortest handling times were recorded most frequently (Fig. 5).

DISCUSSION

Time to harvest and chew food has been shown to influence the intake rate of many herbivore species (for examples see Ginnett & Demment 1997; Illius et al. 2002; Laca et al. 1994; Pastor et al. 1999), but to the best of our knowledge, this is the first published study to investigate this for African savanna elephants (*Loxodonta africana*). Large differences in harvesting and handling times were apparent across food types. For example, bulls took three times longer to process
“trunk”?
trunkloads of main stem bark than trunkloads of leaves from woody plants. Differences in handling times are possibly more conspicuous for elephants than other herbivores because an unusually broad assortment of forage types is utilized and a particularly diverse array of harvesting methods is employed. Variation in handling time might affect the rate of intake when feeding on different food types, which may in turn influence food preferences and choice of diet (Clegg 2010; O'Connor et al. 2007). Elephants have a fast rate of passage of ingesta (Eltringham 1982). To capitalize on this they should prefer food types that can be harvested and chewed rapidly compared to those that can only be processed more slowly (Clegg 2010; O'Connor et al. 2007). Our observations supported this hypothesis because when all food types were available during the rainy season elephants ate predominantly green grass, forbs and leaves from woody plants (Clegg 2010),
but they vary a lot in quality; e.g. grasses have far less crude protein than leaves of woody plants
which are the food types that can be harvested and chewed most rapidly. Only when these had senesced during the dry season did elephants feed more on bark and roots, which required more laborious harvesting methods and took longer to process. This seasonal change in diet has been frequently reported in the literature (Cerling et al. 2004; Owen-Smith 1988).

Mode of harvesting had a significant effect on harvesting time. Harvesting was shorter when trunkloads could be gathered by simply plucking or stripping and longer when additional actions were necessary. For example, it took bulls almost twice as long to harvest grass tufts with a mixture of green and dry leaves compared to those with only green leaves. This was because an additional action of thrashing the plucked tuft against the chest or front leg to remove senescent material was necessary before the trunkload could be ingested. Similarly, it took twice as long to harvest a trunkload of roots from woody plants if they had to be dug up first compared to situations where they were already exposed. This is consistent with the hypothesis that hedging of the tree layer by elephants facilitates foraging because it allows food to be harvested more rapidly and with less energy expenditure (Smallie & O'Connor 2000).

Food types that could be harvested rapidly were eaten most frequently and therefore handling time was most often constrained by chewing. Under these circumstances intake rate can be increased by selecting non-fibrous plant species and parts that can be rapidly chewed. This may partially explain why elephants prefer soft, broad-leaved grasses (e.g. *Panicum maximum*), climbing forbs that don't invest heavily in structural material, and leaves with a high specific area (Clegg 2010; O'Connor et al. 2007). When rapidly harvestable food types (generally those from the herbaceous layer) are not available, handling becomes constrained by harvesting. This generally leads to increased levels of impact to woody vegetation because the additional actions required to harvest food are often destructive.

how similar or different are these handling times to those described for other large mammalian herbivores? See e.g. Spalinger and Hobbs (1987), etc.

The longer handling times for bulls compared to cows were unexpected because the greater strength (body size) of bulls should allow them to harvest and chew food more rapidly. However, bulls extract larger trunkloads than cows and when this is taken into account, bulls do indeed process a greater mass of food per unit time, despite their longer handling times (Clegg 2010).

Harvesting methods such as pollarding or uprooting trees and using tusks to prize bark from main stems require considerable strength. Our observations suggest that these foraging techniques are largely the domain of adult bulls, presumably because their body size affords them the necessary strength. Cows appear to have fewer harvesting options available to them. This is supported by the observation that cows were often seen moving rapidly to a tree that had been felled by a bull, presumably to take advantage of a forage source that would otherwise have been inaccessible. This suggests that impact to woody vegetation should be more closely correlated to the density of adult bulls as opposed to that of the total population. Cows compensated for their apparent lack of strength by adopting different harvesting methods to bulls. For example, they often extracted main stem bark by first snapping the trunks of small mopane trees and then stripping short lengths of inner bark from the jagged edge of the breaks. Bulls were not observed using this technique. Cows appeared to adopt a strategy of harvesting small trunkloads that allowed for rapid harvesting and chewing. This gave a sense of urgency to their feeding behavior. Bulls on the other hand appeared to be focused on larger trunkloads that took longer to harvest and chew. This difference in foraging behavior is presumably driven by the two fold difference in body size that causes cows to have a greater energy requirement per unit body mass and bulls to have a greater absolute energy requirement per unit time (O'Connor et al. 2007).

interesting point - also made by Dobson; Midgley et al. 2005; Guy 1976, Croze, etc.

hyphenate multi-adjectival noun for clarity

CONCLUSION

Some forage types took longer to harvest and chew than others, with both gender and the method of gathering food affecting harvesting and handling times. Handling time was mostly constrained by chewing for both sexes, but harvesting did limit processing of some food types, especially for cows. The above differences may cause variation in the rate at which forage types can be ingested,

this is how a statistician would read this, but as an ecologist “gender” is an effect, not a cause which may in turn influence diet and habitat selection. This however can only be assessed by an intake model that also includes search time, trunkload mass, number of trunkloads harvested per patch, and the energy content of the forage as additional constraints.

I think that you need to say what some of the other constraints on elephant feeding are. See e.g. Owen-Smith and Chafota 2012; Shrader et al. 2012; Schmitt et al. 2016.

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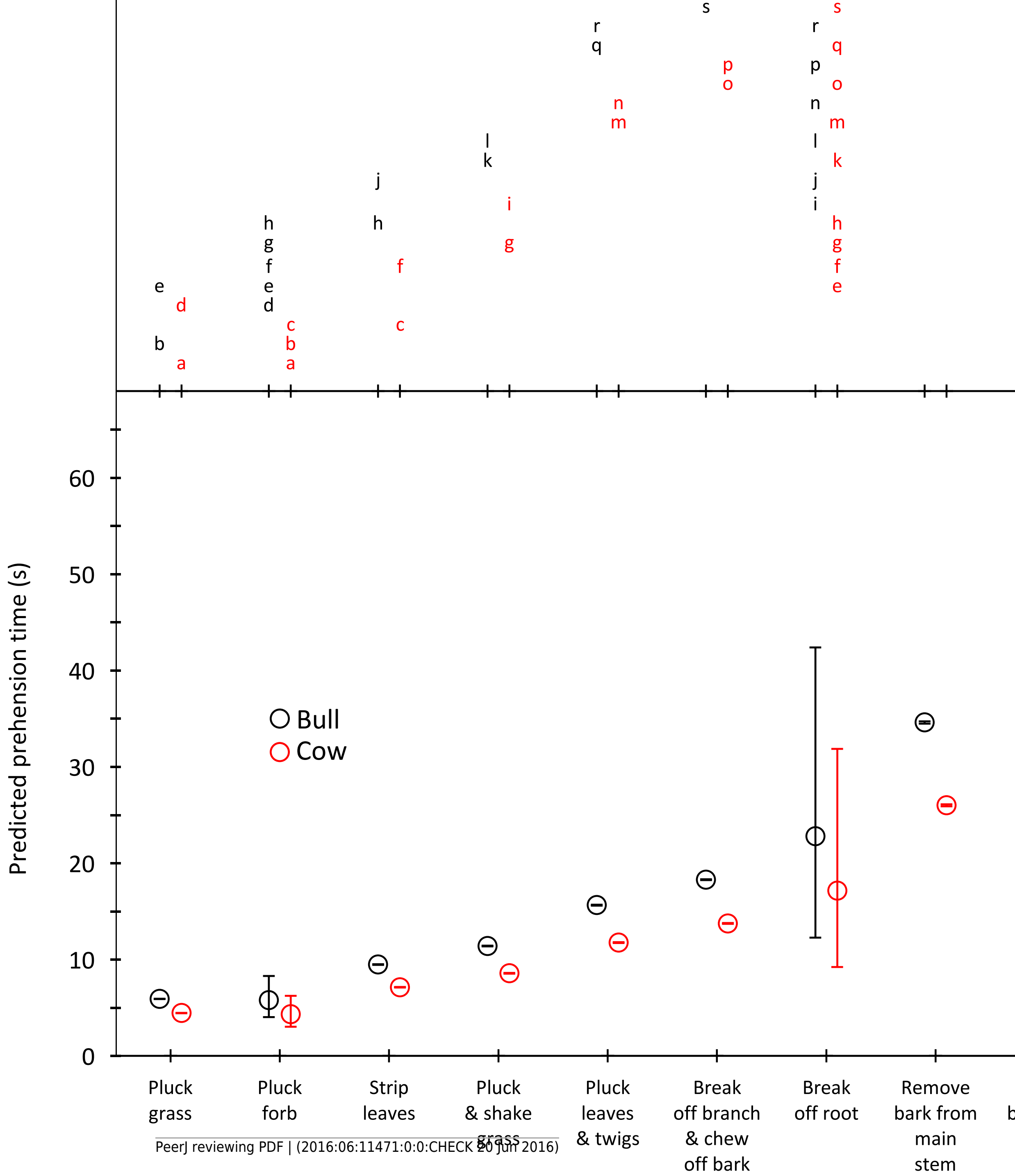
Figure 1(on next page)

Predicted harvesting times (least squares means) for adult bulls and cows across the commonly utilized forage types.

The compact letter display depicts the results of pairwise comparisons conducted using post hoc test, I assume you mean? Tukey's adjustment. Harvesting times were not significantly different ($P > 0.05$) for forage/gender combinations with letters in common. Bars represent 95 % confidence intervals (back transformed from log scale).

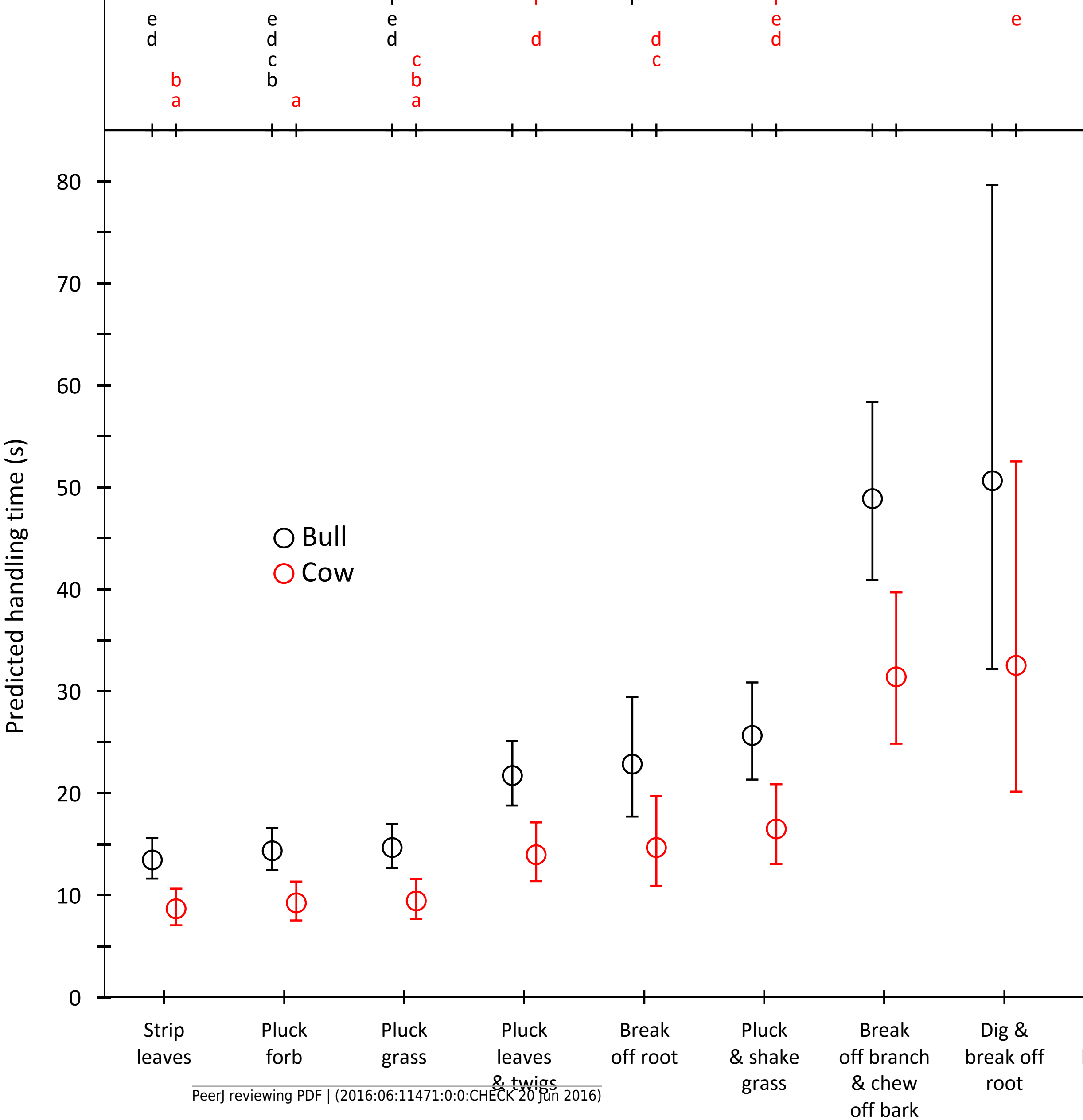


Predicted prehension time (s)
0
10
20
30
40
50
60
Bull
Cow
Pluck grass
Pluck forb
Strip leaves
Pluck & shake grass
Pluck leaves & twigs
Break off branch & chew off bark
Break off root
Remove bark from main stem

Figure 2 (on next page)

Predicted handling times (least squares means) for adult bulls and cows across the commonly utilized forage types.

The compact letter display depicts the results of pairwise comparisons conducted using post hoc test Tukey's adjustment. Handling times were not significantly different (P > 0.05) for forage/gender combinations with letters in common. Bars represent 95 % confidence intervals (back transformed from log scale).



Predicted handling time (s)
0
10
20
30
40
50
60
70
80
Bull
Cow
Strip leaves
Pluck forb
Pluck grass
Pluck leaves & twigs
Break off root
Pluck & shake grass
Break off branch & chew off bark
Dig & break off root
e d
b a
e d c b
a
e d
c b a
d
d c
e d
e

Figure 3(on next page)

Comparison of harvesting (P_t) and handling times (H_t) for adult bulls for the commonly utilized forage types.

Bars represent 95 % confidence intervals (back transformed from log scale). The significance of the difference between harvesting and handling times was tested for each forage type by calculating the 95 % confidence interval of the difference (intervals that included zero were not significant). Handling was assumed to be constrained by chewing when H_t > P_t. and by harvesting when H_t = P_t.

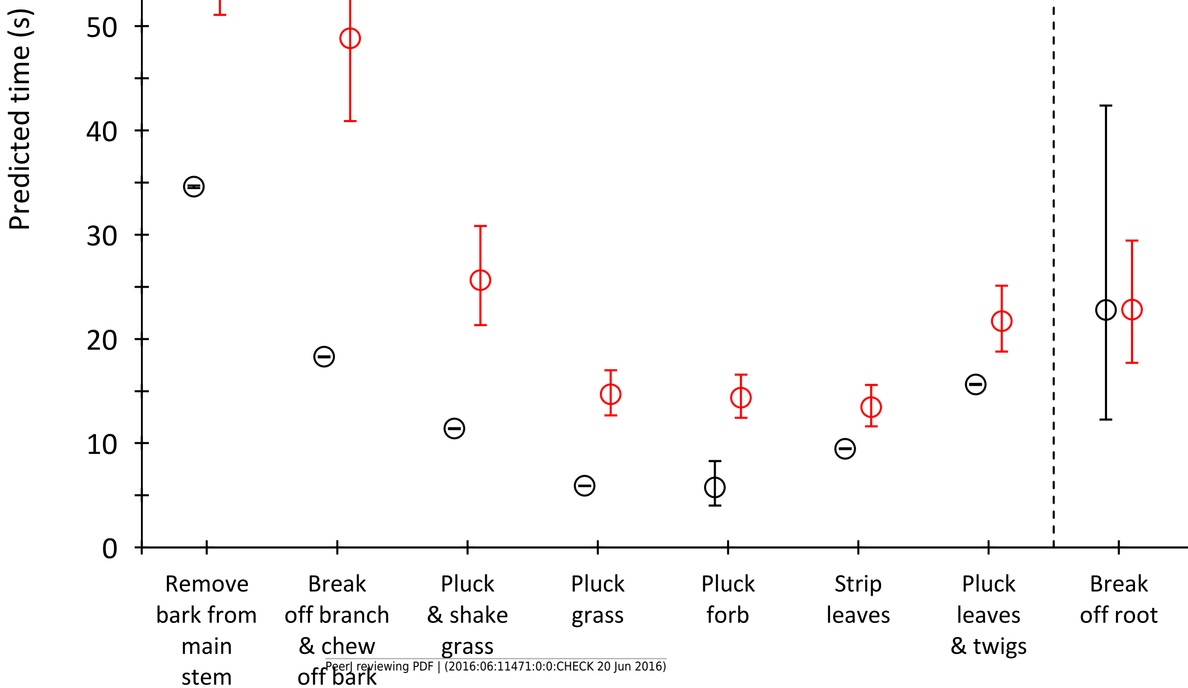

Predicted time (s)
0
10
20
30
40
50
Remove bark from main stem
Break off branch & chew off bark
Pluck & shake grass
Pluck grass
Pluck forb
Strip leaves
Pluck leaves & twigs
Break off root

Figure 4(on next page)

explain what “prehension time” means

Comparison of harvesting (P_t) and handling times (H_t) for adult cows for the commonly utilized forage types.

Bars represent 95 % confidence intervals (back transformed from log scale). The significance of the difference between harvesting and handling times was tested for each forage type by calculating the 95 % confidence interval of the difference (intervals that included zero were not significant ($P > 0.05$)). Handling was assumed to be constrained by chewing when $H_t > P_t$. and by harvesting when $H_t = P_t$.

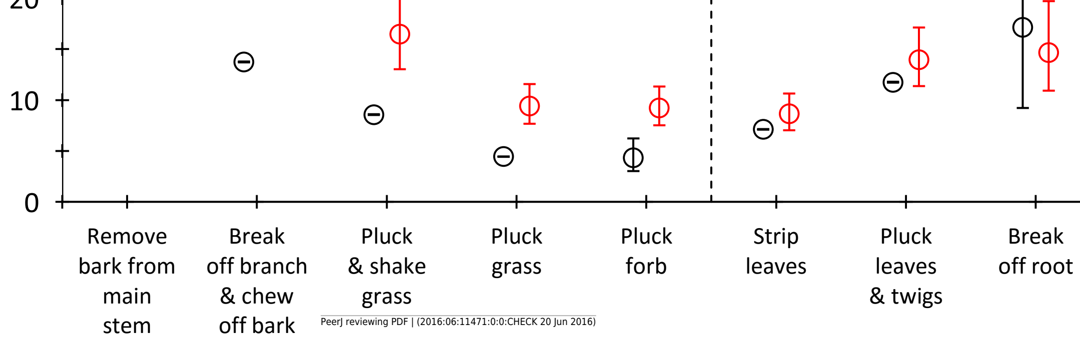

20
10
0
Remove bark from main stem
Break off branch & chew off bark
Pluck & shake grass
Pluck grass
Pluck forb
Strip leaves
Pluck leaves & twigs
Break off root

Figure 5 (on next page)

Relationship between handling time and percent of total trunkloads recorded.

The relationship for bulls (●) was best represented by a second order hyperbola (solid line, $Y=a/x^2$, where a = 2332.246, $P < 0.001$, adj. $R^2 = 0.729$) and for cows (○) by a first order hyperbola (dashed line, $Y=a/x$, where a = 179.374, $P < 0.002$, adj. $R^2 = 0.475$).

it would be nice to know how similar or how different these are to other curves for other large mammalian herbivores - should be mentioned in Discussion. See e.g. Spalinger and Hobbs, etc.

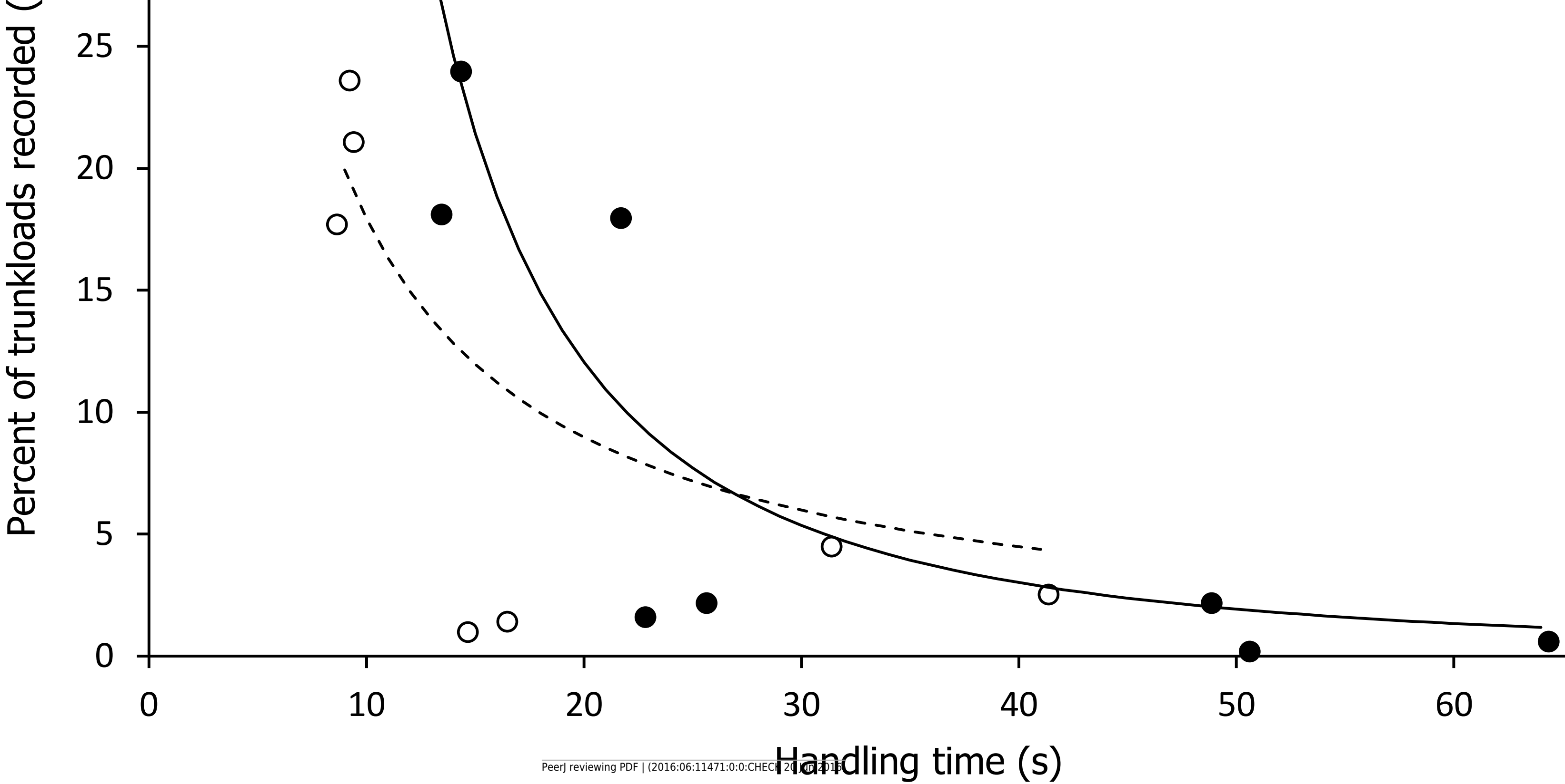

Percent of trunkloads recorded (
0
5
10
15
20
25
0
10
20
30
40
50
60
Handling time (s)

Table 1
(on next page)

Observations per combination of fixed effects used for modelling harvesting and handling times

	Forage type								
	Pluck grass	Pluck & shake grass	Pluck forb	Strip leaves	Pluck leaves & twigs	Break off branch & chew off bark	Remove bark from trunk	Break off root	Dig & break off root
Harvesting									
Bull	23	103	16	169	247	89	20	2	8
Cow	5	14	-	57	50	37	15	3	-
Handling									
Bull	1524	99	1097	829	822	99	27	73	8
Cow	150	10	168	126	201	32	18	7	-

Table 2 (on next page)

Results of the best GLMM's for harvesting and handling time.

The intercept, estimate (log scale) of the effect of breaking off a canopy branch and chewing off the bark, is a baseline against which the other fixed effects were compared. Forage types with positive estimates took longer to harvest or process than the baseline, and those with negative estimates took less time than the baseline. Negative estimates for sex indicate that cows had shorter harvesting and handling times than bulls fullstop at end of sentence

<table>
<tr><th colspan="5">Harvesting time ~ Forage type + Sex + (1|Month) + (1|Elephant ID)</th></tr>
<tr><th>Fixed effects</th><th>Estimate</th><th>Std. Err.</th><th>t value</th><th>Pr (>|z|)</th></tr>
<tr><td>Forage type</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Intercept (break off branch & chew off bark)</td><td>2.906</td><td>0.001</td><td>2345.8</td><td><0.001</td></tr>
<tr><td>Pluck forb</td><td>-1.153</td><td>0.184</td><td>-6.3</td><td><0.001</td></tr>
<tr><td>Pluck grass</td><td>-1.129</td><td>0.001</td><td>-910.6</td><td><0.001</td></tr>
<tr><td>Pluck & shake grass</td><td>-0.472</td><td>0.001</td><td>-369.0</td><td><0.001</td></tr>
<tr><td>Pluck leaves & twigs</td><td>-0.156</td><td>0.001</td><td>-126.2</td><td><0.001</td></tr>
<tr><td>Strip leaves</td><td>-0.658</td><td>0.001</td><td>-530.6</td><td><0.001</td></tr>
<tr><td>Remove bark from trunk</td><td>0.638</td><td>0.001</td><td>514.7</td><td><0.001</td></tr>
<tr><td>Break off root</td><td>0.221</td><td>0.316</td><td>0.7</td><td>0.485</td></tr>
<tr><td>Dig & break off root</td><td>-0.286</td><td>0.001</td><td>955.3</td><td><0.001</td></tr>
<tr><td>Sex</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Cow</td><td>-0.286</td><td>0.001</td><td>-230.3</td><td><0.001</td></tr>
<tr><th>Random effects</th><th>Variance</th><th>Std. Dev.</th><th></th><th></th></tr>
<tr><td>Elephant ID</td><td>0.088</td><td>0.296</td><td></td><td></td></tr>
<tr><td>Month</td><td>0.001</td><td>0.01</td><td></td><td></td></tr>
<tr><th colspan="5">Handling time ~ Forage type + Sex + (1|Vegetation type) + (1|Month) + (1|Elephant ID)</th></tr>
<tr><th>Fixed effects</th><th>Estimate</th><th>Std. Err.</th><th>t value</th><th>Pr (>|z|)</th></tr>
<tr><td>Forage type</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Intercept (break off branch & chew off bark)</td><td>3.889</td><td>0.091</td><td>42.85</td><td><0.001</td></tr>
<tr><td>Pluck forb</td><td>-1.225</td><td>0.066</td><td>-18.65</td><td><0.001</td></tr>
<tr><td>Pluck grass</td><td>-1.204</td><td>0.070</td><td>-17.18</td><td><0.001</td></tr>
<tr><td>Pluck & shake grass</td><td>-0.644</td><td>0.091</td><td>-7.06</td><td><0.001</td></tr>
<tr><td>Pluck leaves & twigs</td><td>-0.811</td><td>0.070</td><td>-11.65</td><td><0.001</td></tr>
<tr><td>Strip leaves</td><td>-1.289</td><td>0.071</td><td>-18.07</td><td><0.001</td></tr>
<tr><td>Remove bark from trunk</td><td>0.276</td><td>0.116</td><td>2.37</td><td>0.018</td></tr>
<tr><td>Break off root</td><td>-0.761</td><td>0.138</td><td>-5.49</td><td><0.001</td></tr>
<tr><td>Dig & break off root</td><td>0.035</td><td>0.236</td><td>0.15</td><td>0.881</td></tr>
<tr><td>Sex</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Cow</td><td>-0.442</td><td>0.098</td><td>-4.50</td><td><0.001</td></tr>
<tr><th>Random effects</th><th>Variance</th><th>Std. Dev.</th><th></th><th></th></tr>
<tr><td>Elephant ID</td><td>0.057</td><td>0.238</td><td></td><td></td></tr>
<tr><td>Vegetation type</td><td>0.025</td><td>0.16</td><td></td><td></td></tr>
<tr><td>Month</td><td>0.004</td><td>0.066</td><td></td><td></td></tr>
</table>

Table 3 (on next page)

Analysis of variance tables for the best GLMM's for harvesting and handling times

	Df.	Sum Sq.	Mean Sq.	F value	Chisq.	Pr (>chisq.)
Harvesting time						
Forage type	8	84.45	10.56	24.05	2322278.0	< 0.001
Sex	1	2.78	2.78	6.33	53050.0	< 0.001
Handling time						
Forage type	8	251.30	31.41	97.49	882.4	< 0.001
Sex	1	11.96	11.96	37.12	20.3	< 0.001