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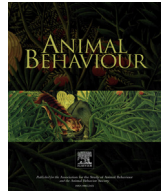
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## Discrete choices: understanding the foraging strategies of wild chimpanzees

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Optimal foraging theory has guided much of the research on foraging behaviour in the past five decades, with the notion of optimality deeply embedded in most models today. However, assuming that all foragers strive to maximize a certain predefined currency, such as amount of food per unit time, restricts what can be learned about the factors influencing foraging decisions. Here we applied a different approach: the discrete-choice model, which does not assume an optimal strategy as the starting point, but instead examines foraging decisions directly, modelling interpatch movements as the consequence of a choice of destination from a limited set of options. We analysed a set of foraging decisions by both adult male and female chimpanzees, *Pan troglodytes*, from two habituated communities in the Budongo forest, Uganda, to investigate the influence of foraging variables including food patch characteristics and interpatch distance on patch choice, with a view to identifying the strategy underlying these decisions. Despite differences in habitat between communities, we found that foraging strategies were remarkably similar across both communities and sexes, with chimpanzees exhibiting a clear preference for closer and novel (not previously visited) food patches. Individuals of both communities frequently chose to forage on food patches providing young leaves, highlighting the importance of this food type in their diet. Contrary to expectation, patch size did not predict foraging decisions, except for adult males of one community that chose larger patches, while both sexes aimed to minimize travel distance between consecutive patches. This study provides the first direct evidence that chimpanzees consider travel distance and whether they have recently visited a patch when choosing between potential foraging sites and demonstrates that new insights can be gained (even in a well-studied system) from integrating several important variables describing feeding ecology into a coherent model of patch choice.

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Studies of foraging behaviour have traditionally made use of optimality models (Charnov, 1976; Parker & Maynard Smith, 1990; Schoener, 1971). In this approach, foraging organisms are assumed to make decisions as if they have complete spatial and temporal knowledge of available resources, and are therefore able to choose foraging options which allow them to optimize net intake rates (Davies et al., 2012; Giraldeau & Caraco, 2000). This central assumption has, however, been questioned since it seems more plausible that individual foragers are to some extent uncertain about foraging conditions (Houston et al., 2007; Mangel, 1990; Pyke, 1984). Further, the environments in which social animals forage are often highly complex, making it unlikely that even

experienced foragers constantly make optimal decisions (Fawcett et al., 2014).

Discrete-choice models (Ben-Akiva & Lerman, 1985; Train, 2009) allow for an alternative approach that does not assume an optimal strategy as the starting point (Cooper & Millsaugh, 1999; Manly et al., 2002), and have recently been used to study foraging decisions in wild populations of chacma baboons, *Papio ursinus* (Marshall et al., 2012), black bears, *Ursus americanus* (Lewis et al., 2015), and mantled howler monkeys, *Alouatta palliata* (Hopkins, 2016). These models are based on the concept of utility, which can be thought of as the most profitable of the options available to the animal, for example in terms of energy intake (Emlen, 1966) or nutrient balancing (Felton et al., 2009; Raubenheimer & Boggs, 2009). Instead of judging the foraging success of animals on the capability to optimize a predefined currency, discrete-choice

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models allow foraging animals to choose, from a set of resources (the 'choice set'), whichever option at that moment provides maximum utility. Such models can accommodate multiple currencies, such as an animal trying to maximize energy intake and meet nutritional requirements (Felton et al., 2009), and explore how individual foragers attempt to meet such goals across contrasting habitats (Marshall et al., 2012).

Behavioural strategies can be considered to be sets of one or more contingent decision rules of the form 'if X, do Y'. Strategies thus mediate between an animal's environment and the behaviour that it performs. While identifying ecological correlates of foraging behaviours allows strategies to be inferred, unpicking the details of a foraging strategy (i.e. identifying the decision rules) requires more than this. Through the direct investigation of individual decisions, and by accommodating interindividual variation between decision makers, the discrete-choice approach allows the identification of key factors, with established ecological correlates facilitating a focused investigation. Where these key factors remain constant across differing arrays of resources, we can have confidence that we have identified the underlying decision rules, the strategy, driving foraging behaviour.

Here, we used this approach to establish (at least part of) the foraging strategy of East African chimpanzees, *Pan troglodytes schweinfurthii*, from the Budongo Forest Reserve, Uganda. Specifically, we addressed patch choice decisions, asking the question: given a set of possible patches in which to feed, what characteristics of a food patch determine that choice? Our aim in this study was both to demonstrate the benefits of using discrete-choice modelling to understand such foraging decisions, and so identify the strategy that generates these, and to seek new insights into a well-studied system, the foraging behaviour of chimpanzees.

Chimpanzees have proved a popular species for the testing of foraging models (Chapman & Chapman, 2000; Lehmann & Boesch, 2004; Newton-Fisher et al., 2000; Normand et al., 2009; Snaith & Chapman, 2005; Villioth et al., 2022; Watts et al., 2012; White & Wrangham, 1988) due to their pronounced fission–fusion social dynamics whereby individuals travel and forage either alone or in subgroups of varying size that change frequently in both their size and composition throughout the day (Aureli et al., 2008; Sugiyama, 1968). Such social systems are rare and found in only a few mammal species, for example lions, *Panthera leo* (Schaller, 1972), spotted hyaenas, *Crocuta crocuta* (Holekamp et al., 1997), dolphins, *Tursiops truncatus* (Connor et al., 2000), sperm whales, *Physeter macrocephalus* (Whitehead et al., 1991) and elephants, *Loxodonta africana* (Wittemyer et al., 2005), and several species of nonhuman primate including spider monkeys, *Ateles* spp. (Chapman et al., 1995; Symington, 1990; Wallace, 2008) and chimpanzees (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987). This flexible grouping behaviour is typically interpreted as a direct response to varying levels of feeding competition induced by short-term fluctuations in the distribution and availability of resources (Chapman et al., 1995; Lehmann & Boesch, 2004) and makes these species particularly attractive to researchers when compared to species with more stable social groupings, which are, in consequence, obligate group foragers (Chapman & Chapman, 2000). For present purposes, chimpanzees are particularly suitable because the degree of fluidity in their social system is such that foraging decisions can be considered on an individual basis. Since chimpanzees are group-living animals, these decisions can be investigated over multiple individuals under the same ecological conditions, while habituation of multiple social groups (to human observation) allows for investigation across varying ecological conditions. In addition, their diets and basic foraging ecology are well understood (e.g. Doran, 1997; Fawcett, 2000; Ghiglieri, 1984; Hockings et al., 2009; Isabirye-Basuta, 1988; Lehmann & Boesch, 2004; Newton-Fisher,

1999b; Newton-Fisher et al., 2000; Normand et al., 2009; Potts et al., 2011; Tweheyo & Obua, 2001; Watts et al., 2012; White & Wrangham, 1988; Wrangham, 1977, 1986; Wrangham et al., 1993, 1998) and so we can make clear predictions about how foragers should choose patches on the basis of previously identified ecological correlates of foraging behaviour.

As for other species that exploit discrete depletable patches, selection of a food patch by chimpanzee foragers should be a trade-off between the value of a particular patch and the travel costs to reach it. Foraging theory predicts that energetic costs of travel should have a strong impact on foraging strategies (Chapman & Chapman, 2000; Majolo et al., 2008). Multiple studies have shown that travel distance to food patches is a significant influence during foraging behaviour, constraining group size (Chapman et al., 1995; Isbell, 1991; Janson & Goldsmith, 1995; Steenbeek & van Schaik, 2001) and predicting both size and productivity of the patches in which animals forage (Normand et al., 2009; Pokempner, 2009; Suarez, 2014). Detailed studies of travel distance to food patches in chimpanzees have thus far focused on sex differences: in several communities, females tend to travel shorter distances and move in a more linear way in between feeding trees (Tai forest: Normand & Boesch, 2009; Kibale National Park: Pokempner, 2009; Budongo Forest, Sonso community: Bates & Byrne, 2009). Such sex differences, however, are less clear when all food patches (rather than just fruiting trees) are considered (Pokempner, 2009) or when individual movement phases are analysed instead of daily averages (Bates & Byrne, 2009). As a conservative hypothesis, we expected chimpanzees of both sexes to minimize travel distances between patches: all other things being equal, chimpanzees will choose closer feeding patches over those further away (Prediction 1).

The value of any given patch will depend upon the quantity and quality of available resources in that patch; when making multiple visits to the same patch, foragers might also use information from previous feeding bouts to decide whether to revisit (Vogel & Janson, 2007). Larger patches (those with more food) can accommodate a greater number of foragers (Asensio et al., 2009; Symington, 1990) or provide food for longer periods than can smaller patches (Chapman, 1990; Chapman et al., 1995; Janson & van Schaik, 1988; Snaith & Chapman, 2005). Given that the number of foragers within a chimpanzee foraging party is known to increase with patch size (Ghiglieri, 1984; Isabirye-Basuta, 1988; Lehmann & Boesch, 2004; Newton-Fisher et al., 2000; White & Wrangham, 1988), we predicted that chimpanzees would, across all food types, choose larger patches (Prediction 2).

Available resources within a patch also depend upon levels of resource depletion (Charnov, 1976). The influence of patch depletion has been investigated across taxa largely in terms of patch departure times (i.e. when foraging animals should decide to leave a patch: Altmann, 1998; Grether et al., 1992; Johnson et al., 2017; Plante et al., 2014), although patch depletion has rarely been used to assess patch value or to predict probabilities of foragers returning to a given patch in studies of primate foraging ecology (cf. Suarez, 2014). As ripe fruit specialists, chimpanzees might be expected to prefer patches that show low depletion of ripe fruit and return to these in preference to seeking newly available patches. Indeed, chimpanzees will sometimes return to large fruiting trees over multiple days (J. Villioth & N.E. Newton-Fisher, personal observations). However, a forager's prior knowledge of resource abundance and depletion may be rendered unreliable if there is significant scramble competition imposed by individuals of other species (various monkeys and birds, in the case of chimpanzees) and/or by conspecifics: a consequence of the chimpanzee's fluid social system is the co-occurrence of simultaneous foraging by multiple individuals/parties, each making independent visits to the same set of food patches. Thus, our prediction was that foragers will

tend to avoid recently visited patches and instead choose novel patches where possible (Prediction 3). A novel patch in this sense is a feeding site (tree) where food has recently become available (fruit ripening, young leaves or flowers emerging), and stands specifically as a contrast to a previously visited patch.

From a forager's perspective, the quality of a patch will depend strongly on the kind of resource that patch offers. Chimpanzees try to maintain a frugivorous diet even when fruit availability is low (Ghiglieri, 1984; Watts et al., 2012; Wrangham et al., 1998), selecting foods with high levels of easily digestible macronutrients such as nonstructural carbohydrates and lipids (Hohmann et al., 2010; Remis, 2002). Although research at Budongo has shown that Sonso chimpanzees incorporate a comparatively high proportion of young leaves into their diet (Newton-Fisher, 1999b; Newton-Fisher et al., 2000; Okecha & Newton-Fisher, 2006), ripe fruit remains the dominant component (see Ngogo community chimpanzees, Watts et al., 2012, for a comparable situation). We therefore predicted that foraging chimpanzees would show a marked preference for ripe fruit over other food types when choosing between food patches (Prediction 4).

Feeding bout length is a subject-based measure of patch value and is a reliable correlate of patch size (Chapman, 1990; Chapman et al., 1995; Janson & van Schaik, 1988; Symington, 1988). Bout length is also predictive of food-related agonism (Vogel & Janson, 2007), so may reflect the quality of a patch (Normand et al., 2009; Suarez, 2014). While a short feeding bout might not necessarily indicate a patch of low quality or size, as duration of feeding might depend on energy and nutrients acquired from previous patches, and patch departure can be influenced by social factors such as the number of co-feeders (Kazahari & Agetsuma, 2008; Snaith & Chapman, 2005) rather than patch depletion, on average feeding bout length should reflect both patch size and quality. Thus, we predicted that foragers would on average choose patches where previously chimpanzees had engaged in long feeding bouts (Prediction 5).

## METHODS

### *Study Site and Communities*

We collected data in the Budongo Forest Reserve (1°35'–1°55'N, 31°08'–31°42'E) over a period of 16 months. Foraging decisions were investigated in two neighbouring chimpanzee communities, Sonso (October 2015 to June 2016) and Waibira (October 2016 to June 2017), to increase the range of ecological variation against which to investigate patch choice decisions, and thus the generalizability of our findings. Floristic differences between the home ranges of these two communities existed as a consequence of variation in their respective histories of forest management and natural forest dynamics (Eggeling, 1947; Plumptre, 1996). Much of the Budongo forest was selectively logged during the 20th Century, increasing its mosaic nature (Plumptre, 1996; Reynolds, 1992), and this logging was more recent (1963–1964 versus 1947–1952) for forest within the Waibira home range compared to that within the Sonso home range (Plumptre, 1996). Waibira has also suffered more heavily from illegal pit-sawing during subsequent decades. Sonso, but not Waibira, chimpanzees also had access to groves of *Broussonetia papyrifera* (an exotic tree species introduced in the 1950s) which provided a significant source of food (Newton-Fisher, 1999b; Villioth, 2018). At the time of our study, food was more available for Sonso chimpanzees, with 11–30% of trees providing food in each month in contrast to 11–17% of trees within the Waibira home range (Villioth, 2018). Data on dietary diversity (standardized Shannon–Wiener index: Sonso: 0.67; Waibira: 0.76; Villioth, 2018) similarly suggested greater food abundance for Sonso chimpanzees (see Fawcett, 2000; Wrangham et al., 1998).

During our study, the Sonso community consisted of 71 individuals, including 12 adult males ( $\geq 16$  years old) and 24 adult females ( $\geq 14$  years old). All members of this community could be observed at close quarters ( $< 5$  m) and were individually recognizable, as this community has been studied continuously since the early 1990s (Newton-Fisher, 1997; Reynolds, 2005). Following study site health protocols, we endeavoured to remain at least 7 m from these chimpanzees. The Waibira community consisted of at least 88 known individuals, including 17 adult males and 29 adult females; habituation of this community started in 2011 (Samuni et al., 2014). At the time of this study, almost all adult members could be individually recognized, and minimum observation distances (10–15 m) permitted the studying of foraging behaviour. Observation distances were inevitably greater for both communities when chimpanzees foraged in the crowns of larger trees.

### *Behavioural Data Collection*

To obtain a complete record of the individual's foraging decisions during a follow, we started focal follows at the first feeding tree of the day and continued with this focal animal for as long as conditions allowed (mean duration of follows: Sonso:  $5.6 \pm 3.1$  h, range 1–12 h, median 5 h; Waibira:  $4.1 \pm 2.6$  h, range 1–12 h, median 4 h). We selected one focal individual from a randomized list at the beginning of each day. If the initial focal individual was lost, we attempted to increase the number of focal samples from individuals that were still underrepresented in the overall sample to maintain a balanced sampling regime. For the Sonso community, six adult males and five adult females were selected as focal individuals, while in the larger Waibira community we collected data on 10 adult males and nine adult females, drawing on those individuals that were sufficiently habituated to human observation. We deliberately selected males (from within each community) to provide variation in age and social dominance rank, while for females we selected individuals that were not cycling at the time: four of the five focal Sonso females were lactating and travelled with at least one infant during the study, while the remaining individual was not lactating but travelled with her juvenile offspring. One of the nine focal Waibira females was a noncycling mother of a weaned infant, while the others were lactating, travelling with unweaned infants and in some cases a socially dependent juvenile (Table A1). We also conducted a handful of focal samples on additional individuals, two females and one male in each of the two communities, before settling on the 11 for Sonso and 19 for Waibira; these individuals contributed 26 patch choice decisions (ca. 6% of our data set).

During focal follows, activity of the focal individual was recorded continuously (Altmann, 1974). All behaviours related to food handling, the entire process of picking and ingesting food items, were categorized as 'feeding'. A feeding 'patch' was defined as an aggregation of food items that allowed uninterrupted foraging movements by the focal animal (Chapman et al., 1994; Pruetz & Isbell, 2000; White & Wrangham, 1988). All food patches visited by a focal animal were assigned a unique 'patch number', to identify revisits and novel patches, and we recorded the location of each food patch using a handheld GPS (Garmin GPSMAP 64). We recorded diameter at breast height (DBH) for each feeding tree, to the nearest centimetre, as an index of patch size. When chimpanzees foraged on the fruit or leaves of lianas, the DBH measurements of all supporting trees were measured and summed. In those cases where it was not possible to measure DBH, for example when a feeding tree was surrounded by dense vegetation or the tree was so small that it could not be approached without interfering with the foraging animal, DBH of the food patch was estimated visually with reference to known (measured) trees. While in most cases a patch



was equivalent to an individual feeding tree, for certain tree species (for example, *B. papyrifera*, *Drypetes gerrardii*) a patch could consist of multiple trees with overlapping crowns, in which case we summed the DBH measurements. *Broussonetia papyrifera* occurred in spatially restricted groves, and individual chimpanzees within a single party often distributed themselves across a large area within such groves. To adequately capture foraging events in these groves, we distinguished seven spatially separated groves, within each of which we determined the total number of trees. We multiplied this number by 30 cm, the average DBH of trees of this species in which chimpanzees were observed feeding, to generate an index of patch size for this species.

We distinguished five different food types: (1) ripe fruit, (2) unripe fruit, (3) young leaves, (4) flowers and (5) seeds. These were the most common food items for chimpanzees in both communities (Villioth, 2018). Other food types, such as bark and soil, were eaten only occasionally and excluded from our analysis due to small sample sizes. We also excluded data from food patches when the foraging activities and travel were influenced by an intercommunity encounter, crop foraging (Sonso only), hunting or travel to waterholes.

#### Data Analysis

We analysed foraging decisions in the following manner: each time a focal forager left a food patch, it could choose from among a discrete set of further patches (trees providing one of the food types listed above) as its destination. It is in this sense that we use the word 'choice': the selection by the forager from the particular array of options presented by the environment at any given time. To identify this array (i.e. the set of 'option trees') for each patch choice decision, we identified all the food patches that chimpanzees were recorded (within our data set) as visiting during the previous 3 days, and all patches visited by the focal animal and its party during the day of that focal follow. This limit of 3 days prior was based on the average interval between visits to the same food patch (Sonso: 3.57 days; Waibira: 3.09 days), and is in line with the revisit rate to food trees by both chimpanzees (Normand et al., 2009) and other frugivorous primates (Cunningham & Janson, 2007; Hopkins, 2016; Suarez, 2014). Although chimpanzees are able to remember the location of fruit trees, and thus the locations where food patches will appear, over much longer periods (Janmaat et al., 2013), this average interval between visits provides a conservative estimate of patch depletion.

We analysed a set of 419 foraging decisions across both communities (Sonso: 205, Waibira: 214, drawn from 594 h and 491 h of focal sampling, respectively), with a mean number of option trees per decision of six (SD 4, range 2–19). For each foraging decision, we determined seven variables for each option tree in that decision set: (1) 'patch size', as indexed by DBH; (2) 'food type', as categorized above; (3) 'travel distance', the straight-line distance (m) that the forager would have to travel to reach each of the available options from a given starting point, established using GPS data and Garmin BaseCamp software, which we considered a measure of the cost of choosing each particular patch. We used straight-line distance as it was not possible to record a forager's travel path (i.e. the distance in fact travelled) for an option tree to which it did not travel. This habitat is relatively flat and so, while minor terrain differences may have differentially impacted the length of an actual travel path compared to straight-line distance, we have no reason to think that deviations from straight-line distance would generate anything other than random noise.

We also determined (4) 'feeding bout length', which, for patches visited only once by a specific forager, was simply the total amount of time which that individual spent feeding in a patch (see Potts

et al., 2011). For cases where patches were visited several times by a specific forager, we summed all feeding bouts by that individual within that particular patch. Thus, at each foraging decision, each of the option trees that the forager could in principle choose had a subject-determined measure of patch quality. However, long bout lengths might reflect foraging within a depleted patch rather than extensive exploitation of a large or high-value patch, so past a certain bout length any relationship between increased bout length and patch value should change sign with long bouts at some point indicating low value (Marshall et al., 2012; Suarez, 2014). To check for this, we also determined (5) the 'square of feeding bout length'. To control for the state of the foraging animal (e.g. level of hunger or energy) we calculated (6) its 'recent foraging', that is, the number of food patches visited that day by that animal, prior to each patch choice decision. To test whether chimpanzees biased their choices towards recently visited food patches, we scored each patch by (7) the number of previous 'visits' that the forager had made to that specific patch. While we initially coded this on a five-point scale, results from both communities were similar and indicated that the largest difference occurred between no visits and one visit. Thus, we considered only the contrast between previously visited and newly visited, or novel, food patches (binary: 0/1). Logistical constraints prevented us from monitoring all individuals at all times and thus it is possible that some patches labelled by us as 'novel' had indeed been visited by a focal forager prior to first appearance in our data set. However, between ourselves and the resident research team at this study site (which continually monitors the two study groups) we were aware of all major food sources exploited by our study animals across this study. This awareness, together with the typically ephemeral nature of food patches in this habitat, allowed us to be confident that most, if not all, patches recorded by us as novel were not revisits and we consider the qualitative distinction between 'novel' and 'previously visited' to be meaningful.

We used nonparametric Wilcoxon rank sum tests in R 3.4.3 (R Core Team, 2017) to compare these seven variables across our study communities prior to running discrete-choice models to identify which of these variables predicted the choice of food patch by foraging chimpanzees.

For our discrete-choice analysis, we used mixed logit regression (Hole, 2007) in preference to multinomial (e.g. Marshall et al., 2012) or conditional (e.g. Hopkins, 2016) logit regression, as this approach allows for different preferences (random coefficients) across individuals, rather than applying fixed coefficients to all decision makers (Train, 2009). This allowed us to analyse multiple foraging decisions by the same individuals, and to combine our analysis across these individuals, across two social groups and both sexes. To predict patch choice, we entered travel distance, patch size, feeding bout length and recent foraging as continuous variables, while food type and visits were dummy coded. We included the identity of each focal animal to allow for the repeated measures and separate choices of each individual subject. We also entered, as additional terms, the interaction of each of these variables with either community (Sonso or Waibira) or sex (male or female), as noted below. We were not able to include tree species as a variable due to the large number of possible species and the small sample size for many of them. We ran the regression model first for all 419 patch choice decisions across both communities (i.e. Sonso versus Waibira), and then separately by sex across communities (i.e. Sonso males versus Waibira males; Sonso females versus Waibira females), and between sexes within each community (i.e. Sonso males versus Sonso females; Waibira males versus Waibira females). We took this approach because we were interested in understanding how our ecological variables predicted patch choice, taking both ecological variation (between communities) and

potential sex differences in patch choice decisions into account. All discrete-choice models were run in Stata 15 (StataCorp, 2017).

### Ethical Note

This research complied with regulations set by the Ethics Committee of the University of Kent, the protocols of the Budongo Conservation Field Station (BCFS) and the legal requirements of Uganda, with permission granted by both the Ugandan Wildlife Authority (UWA) and the Ugandan National Council for Science and Technology (UNCST). All fieldwork was observational, did not interfere with the chimpanzees, and followed disease transmission prevention protocols established by BCFS. All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

## RESULTS

### Foraging Variables

Travel distance to all option trees across both communities varied from 10 m to 3800 m (median = 520 m, mean = 654.12 ± 556.70 m). For the Sonso chimpanzees, median distance was 730 m (mean = 840.51 ± 597.43 m) whereas for Waibira it was 380 m (mean = 494.14 ± 462.91 m). The distance to food patches chosen from each set of options varied between 10 m and 1800 m (median = 210 m), with a mean of 304.17 m ± 304.46 m. Sonso chimpanzees travelled on average further to food patches than did Waibira chimpanzees (Sonso: 369.05 m ± 323.41 m, median = 300 m; Waibira: 241.92 ± 271.64 m, median = 150 m; Wilcoxon rank sum test:  $W = 28522$ ,  $P < 0.001$ ).

Patch size (as indexed by DBH) of all option trees varied from 10 cm to 4200 cm (median = 60 cm), with a mean of 106.08 ± 325.40 cm (Sonso: 161.63 ± 471.26 cm, median = 70 cm; Waibira: 58.40 ± 35.88 cm, median = 60 cm). The size of food patches chosen from each set of options averaged 304.17 ± 304.46 cm (Sonso: 327.53 ± 793.74 cm; Waibira: 59.69 ± 36.66 cm), although excluding the large *B. papyrifera* patches reduced this average to 64.25 cm ± 37.70 cm across communities, and the mean value for patches selected by Sonso chimpanzees to 69.68 ± 38.29 cm (median = 70 cm versus 60 cm for Waibira). Sonso chimpanzees chose larger patches than did those in Waibira (Wilcoxon rank sum test:  $W = 22552$ ,  $P = 0.003$ ).

Across all option trees, patches of ripe fruit accounted for the largest share (51.3%), followed by young leaves (19.9%) and seeds (15.1%). Within the Sonso community, patches of ripe fruit and young leaves were chosen most frequently (Table 1). Chimpanzees of the Waibira community visited a greater proportion of ripe fruit patches but also fed frequently in patches of young leaves (Table 1).

**Table 1**

Percentage of different food types in the diets of two chimpanzee communities, Sonso and Waibira, in the Budongo forest, Uganda

	Sonso		Waibira	
	Options (%)	Chosen (%)	Options (%)	Chosen (%)
Ripe fruit	41.3	40.0	59.9	54.7
Unripe fruit	14.3	12.2	4.3	6.1
Flowers	7.8	10.2	1.6	1.9
Seeds	20.9	17.6	10.1	8.4
Young leaves	15.1	19.0	24.1	29.0
Other	0.6	1.0	0.0	0.0

Data are presented across all option trees ( $N = 4095$ ) and chosen feeding trees ( $N = 419$ ). Option trees are those foraged in by any chimpanzee in the previous 3 days or during the observation day (for any given foraging decision), while chosen trees are those that an individual forager selects (for any given foraging decision).

Most feeding patches were visited only once (Sonso: 76%; Waibira: 89%). Two visits to the same patch accounted for 11% of the patches chosen from the set of options within the Sonso community and for 7% within the Waibira community. Patches that were visited more than twice accounted for 13% (Sonso: range 3–14) and 4% (Waibira: range 3–6), respectively.

Feeding bout length across all food patches ranged from 1 min to 875 min (median 20 min), with a mean of 36.6 ± 54.2 min. By community, mean bout length was 44.7 ± 59.7 min (median 22 min) for Sonso, and 29.6 ± 47.9 min (median 20 min) for Waibira. Mean feeding bout length for the patch selected from the set of options was 46.2 ± 92.1 min (median 20 min), although Sonso chimpanzees fed for longer than did Waibira chimpanzees (Sonso: 54.69 ± 79.10 min, median 23 min; Waibira: 38.02 ± 102.60 min, median 19 min; Wilcoxon rank sum test:  $W = 26020$ ,  $P < 0.001$ ).

### Discrete-choice Foraging Models

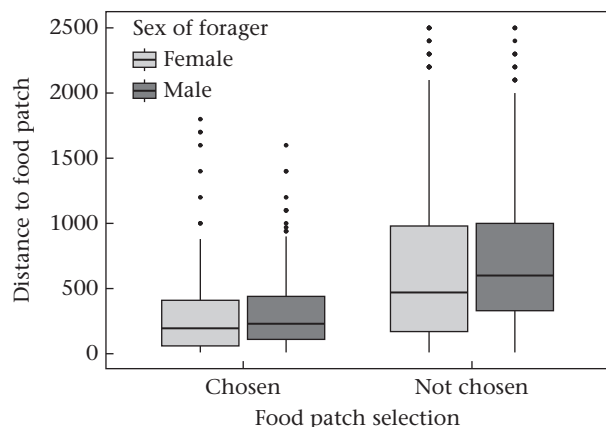
Across the two communities, foraging choices were predicted by (1) interpatch travel distance, (2) whether the patch had been visited previously (visits), (3) food type and (4) feeding bout length (Table 2), with our specified regression model a better predictor of choice than the null model (Akaike information criterion, AIC: 789.76 versus 1743.43). As the interpatch travel distance increased, patches were less likely to be chosen by foragers (Table 2, Fig. 1), supporting Prediction 1. This effect was stronger for the Waibira community and, as separate models for males and females showed, Waibira males selected closer trees than did Sonso males (Table 3) whereas, across communities, females did not differ in this respect (Table 4). Prediction 2 was not supported: patch size did not influence choice when considering both males and females from both communities (Table 2), although it did influence patch choice by Waibira community males (Table 3). A distinct choice of novel food patches over patches that had been visited before was shown by chimpanzees of both communities (Fig. 2). Prediction 3 was therefore supported. The size of this effect differed between communities (Table 2) since females of the Waibira community selected novel food patches more often than did Sonso females.

**Table 2**

Predictors of food patch choice as determined by a discrete-choice model across two chimpanzee communities

Variable	$\beta$	$z$	$P$
Interpatch distance (S)	<b>-0.004</b>	<b>-9.12</b>	<b>&lt;0.001</b>
Interpatch distance (W)	<b>-0.003</b>	<b>-3.30</b>	<b>0.001</b>
Patch size (S)	0.000	0.54	0.586
Patch size (W)	0.008	1.79	0.073
Food type: flowers (S)	-0.300	-0.64	0.525
Food type: flowers (W)	-0.141	-0.16	0.877
Food type: seeds (S)	<b>-0.927</b>	<b>-2.76</b>	<b>0.006</b>
Food type: seeds (W)	-0.202	-0.35	0.728
Food type: unripe fruit (S)	<b>-0.787</b>	<b>-2.40</b>	<b>0.016</b>
Food type: unripe fruit (W)	<b>1.496</b>	<b>2.52</b>	<b>0.012</b>
Food type: young leaves (S)	-0.223	-0.70	0.487
Food type: young leaves (W)	0.140	0.32	0.749
Visits (S)	<b>-3.576</b>	<b>-11.73</b>	<b>&lt;0.001</b>
Visits (W)	<b>-1.295</b>	<b>-2.38</b>	<b>0.017</b>
Feeding bout length (S)	<b>0.017</b>	<b>3.74</b>	<b>&lt;0.001</b>
Feeding bout length (W)	-0.003	-0.39	0.698
Feeding bout length squared (S)	0.000	-1.82	0.069
Feeding bout length squared (W)	0.000	0.99	0.323
Recent foraging (S)	13.819	0.01	0.993

S: Sonso community. W: Waibira community. Bold values indicate statistical significance at  $\alpha = 0.05$ . Coefficients for Waibira indicate differences between the two communities.



**Figure 1.** Choice of food patches by foraging chimpanzees as a function of distance to that patch. Box and whisker plots show median (solid line), 25th and 75th percentiles (hinges) and whiskers to  $1.5 \times$  the interquartile range. Circles are outliers. Data from both study groups are combined.

The influence of food type did not follow Prediction 4: while patches of ripe fruit were chosen over those of both seeds and unripe fruit, they were not chosen over patches of flowers or of young leaves (Table 2). While the sample size for flowers was rather small (Sonso:  $N = 21$ ; Waibira:  $N = 4$ ), it was sufficiently large for young leaves to conclude that those results were statistically meaningful. While the overall model suggested that the effect of unripe fruit on patch choice might differ between communities, single-community models (Tables 5 and 6) revealed that this difference was driven by an apparent preference for unripe over ripe fruit by Waibira females (Table 6), but this is probably an artefact of the small sample size ( $N = 6$ ) for patches of unripe fruit chosen by females in that community.

Across both communities (Table 2) and in both sexes (Tables 3 and 4), patches associated with longer feeding bouts were chosen significantly more frequently over other option trees within any given decision set, supporting Prediction 5. The quadratic term of feeding bout length was not significant (Table 2), although the negative trend suggests that future work should investigate whether very long bout lengths might be the consequence of depletion, which could explain why such patches might be less

**Table 3**  
Predictors of food patch choice as determined by a discrete-choice model across two chimpanzee communities, for male foragers only

Variable	$\beta$	$z$	$P$
Interpatch distance (S)	<b>-0.004</b>	<b>-6.56</b>	<b>&lt;0.001</b>
Interpatch distance (W)	<b>-0.003</b>	<b>-2.43</b>	<b>0.015</b>
Patch size (S)	0.000	0.99	0.324
Patch size (W)	<b>0.012</b>	<b>1.99</b>	<b>0.047</b>
Food type: flowers (S)	-1.352	-1.58	0.114
Food type: flowers (W)	-0.536	-0.33	0.740
Food type: seeds (S)	-0.650	-1.52	0.127
Food type: seeds (W)	-0.521	-0.66	0.507
Food type: unripe fruit (S)	-0.727	-1.49	0.137
Food type: unripe fruit (W)	0.688	0.85	0.395
Food type: young leaves (S)	-0.052	-0.10	0.922
Food type: young leaves (W)	0.160	0.24	0.808
Visits (S)	<b>-3.980</b>	<b>-7.50</b>	<b>&lt;0.001</b>
Visits (W)	-0.460	-0.60	0.546
Feeding bout length (S)	<b>0.020</b>	<b>2.95</b>	<b>0.003</b>
Feeding bout length (W)	-0.006	-0.40	0.688
Feeding bout length squared (S)	0.000	-1.29	0.198
Feeding bout length squared (W)	0.000	0.06	0.953

S: Sonso community. W: Waibira community. Bold values indicate statistical significance at  $\alpha = 0.05$ . Coefficients for Waibira indicate differences between the two communities.

**Table 4**  
Predictors of food patch choice as determined by a discrete-choice model across two chimpanzee communities, for female foragers only

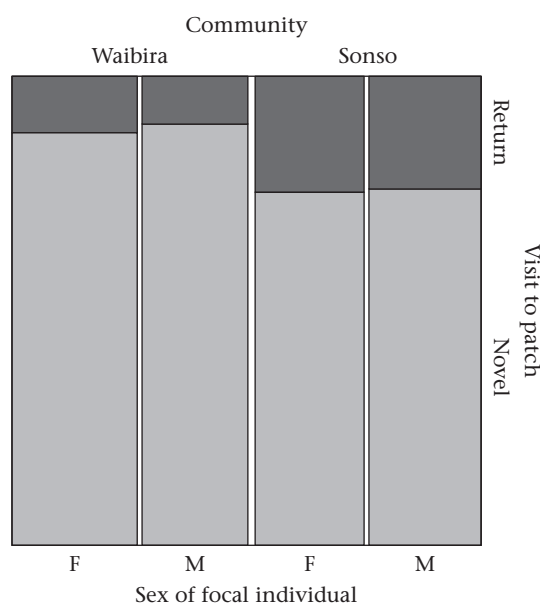
Variable	$\beta$	$z$	$P$
Interpatch distance (S)	<b>-0.004</b>	<b>-6.15</b>	<b>&lt;0.001</b>
Interpatch distance (W)	-0.002	-1.92	0.055
Patch size (S)	0.000	0.34	0.732
Patch size (W)	0.001	0.1	0.918
Food type: flowers (S)	0.150	0.25	0.800
Food type: flowers (W)	0.262	0.22	0.830
Food type: seeds (S)	<b>-1.385</b>	<b>-2.39</b>	<b>0.017</b>
Food type: seeds (W)	0.153	0.17	0.866
Food type: unripe fruit (S)	-0.790	-1.74	0.082
Food type: unripe fruit (W)	<b>2.775</b>	<b>2.8</b>	<b>0.005</b>
Food type: young leaves (S)	-0.313	-0.72	0.474
Food type: young leaves (W)	0.150	0.22	0.827
Visits (S)	<b>-3.539</b>	<b>-8.75</b>	<b>&lt;0.001</b>
Visits (W)	<b>-2.155</b>	<b>-2.34</b>	<b>0.019</b>
Feeding bout length (S)	<b>0.021</b>	<b>2.65</b>	<b>0.008</b>
Feeding bout length (W)	-0.002	-0.14	0.887
Feeding bout length squared (S)	0.000	-1.73	0.083
Feeding bout length squared (W)	0.000	1.13	0.258

S: Sonso community. W: Waibira community. Bold values indicate statistical significance at  $\alpha = 0.05$ . Coefficients for Waibira indicate differences between the two communities.

preferred. Data on intake rates and how these change during a feeding bout, which we were unable to collect during this study, would help quantify depletion. The variable 'recent foraging' showed no predictive power for patch selection, suggesting that foraging strategies of chimpanzees were stable across the course of the day.

## DISCUSSION

Discrete-choice models proved here to be a valuable tool for gaining insight into foraging decisions. Our models were successful in identifying the effects of several ecological variables on patch choice, our focus in this study, broadly supporting our hypothesis of a trade-off between the value of a particular patch and the travel costs to reach it. For all foraging variables for which we had



**Figure 2.** Mosaic plot showing chosen patches according to three categorical variables: visits to the patch, with revisits in dark grey and novel visits in light grey; community (i.e. social group); and sex of the focal individual.

**Table 5**

Predictors of food patch choice as determined by a discrete-choice model for the Sonso community

Variable	$\beta$	$z$	$P$
<b>Males</b>			
Interpatch distance	<b>-0.004</b>	<b>-6.55</b>	<b>&lt;0.001</b>
Patch size	0.000	0.98	0.326
Food type: flowers	-1.351	-1.57	0.115
Food type: seeds	-0.649	-1.52	0.127
Food type: unripe fruit	-0.727	-1.49	0.137
Food type: young leaves	-0.052	-0.1	0.922
Visits	<b>-3.980</b>	<b>-7.49</b>	<b>&lt;0.001</b>
Feeding bout length	<b>0.020</b>	<b>2.95</b>	<b>0.003</b>
Feeding bout length squared	0.000	-1.29	0.198
<b>Females</b>			
Interpatch distance	<b>-0.004</b>	<b>-6.15</b>	<b>&lt;0.001</b>
Patch size	0.000	0.34	0.732
Food type: flowers	0.150	0.25	0.800
Food type: seeds	<b>-1.385</b>	<b>-2.39</b>	<b>0.017</b>
Food type: unripe fruit	-0.790	-1.74	0.082
Food type: young leaves	-0.313	-0.72	0.474
Visits	<b>-3.539</b>	<b>-8.75</b>	<b>&lt;0.001</b>
Feeding bout length	<b>0.021</b>	<b>2.65</b>	<b>0.008</b>
Feeding bout length squared	0.000	-1.73	0.083

Bold values indicate statistical significance at  $\alpha = 0.05$ .

sufficient sample size (i.e. all those we tested, with the exception of the food types flowers and unripe fruit for Waibira community females), the discrete-choice (mixed logit regression) models reported comparable effects on food patch choice in both communities: across sexes and communities, chimpanzees exhibited a clear preference for closer and unvisited food patches.

Travel distance has been identified as a strong predictive variable in patch choice across several small-bodied primates (*Cebus apella*: Janson, 1998; *Ateles belzebuth*: Suarez, 2014; *A. palliata*: Hopkins, 2016). For large-bodied chimpanzees, travel is expected to be energetically more costly than for smaller foragers (Garland, 1983) and so it is unsurprising, although not previously demonstrated, that chimpanzees aim to minimize distance between consecutive feeding patches. What is more intriguing, however, is that travel costs had broadly the same impact on both adult males and adult females: if anything, the consideration of distance was of greatest impact for the males of one of the two communities. Although travel costs are assumed to fall more heavily on females with dependent offspring (Wrangham, 2000), so reducing the length of their day range, we see no evidence of that in these data: all our focal females were mothers with such offspring, who should show the greatest differences when compared to adult males (the sex difference we tested) if this general assumption were true. While there is the possibility that our focal females were pursuing a suboptimal foraging strategy, accepting additional energy costs in order to travel in mixed-sex parties, the benefits of such a strategy are not clear and our sample contained a high proportion (11/14) of lactating females, at least some of whom might be expected to reduce association with males to reduce infanticide risk (Lowe et al., 2019, 2020). Thus, in the absence of contrary data, we conclude that energetic constraints of travel appear to be an important cost for foraging chimpanzees, but not one that is sex differentiated.

The preference for previously unvisited, or novel, food patches is likely to be linked to chimpanzees' fluid, fission–fusion social organization. Chimpanzees in our study tended to avoid former foraging sites, presumably because such patches could have been depleted by other chimpanzees travelling independently of the focal animal since the focal animal's last visit, and our results suggest that scheduling revisits to food patches is not a particularly profitable option in animals characterized by fission–fusion dynamics (where patch depletion is likely to occur unseen by a given

forager). While Bates and Byrne (2009) suggested that female chimpanzees were more likely to revisit previous feeding patches than males, drawing on data from one of our two study communities (Sonso), we found that both males and females exhibited a strong preference for novel food patches. This effect was stronger for females than for males of the Sonso community, while the reverse was true for the Waibira community chimpanzees. Where patches deplete slowly or are replenished, the resultant predictability of resources should favour repeated visits to food patches (Hall-McMaster et al., 2021) at least while a patch offers marginal gains over the expected average returns (Charnov, 1976; cf. Hall-McMaster et al., 2021); that we do not, in general, see such repeated visits for these chimpanzees emphasizes the ephemerality of food patches in this habitat.

Much of the forest of the Waibira community's home range (Villioth et al., n.d.) is more fragmented when compared to the Sonso range, at least in part due to the differences in logging history (Plumptre, 1996) as noted above, and option trees in Waibira were more clumped than those in Sonso. Thus, differences existed between the two communities both in their ecology and in their observed foraging behaviour: the size of chosen patches and the distances travelled between them, with Sonso community chimpanzees travelling further between patches and the Waibira chimpanzees foraging in more restricted areas at any particular point in time, moving between these areas across the duration of the study. Yet, despite differing constraints on the patches available, with greater food abundance and larger and more dispersed food patches on average for Sonso than for Waibira, chimpanzees in the two communities shared a common foraging strategy, at least with regard to patch choice decisions, with the observed differences in foraging behaviour an accommodation to the availability of resources: in both communities, chimpanzees pursued a strategy of reducing travel distance (and so costs) and reducing time spent in depleted patches by exploring novel opportunities. An unexploited, or barely exploited, patch not only contains more food than a depleted patch, but provides a higher rate of return on the time invested in foraging (Charnov, 1976; Stephens & Krebs, 1986). Thus, this foraging strategy would seem an optimized response to the problems created by distributed and ephemeral patches. The degree to which our findings can be generalized, however, remains to be determined. Some of the differences observed between communities might be attributable to variation in the degree of habituation: some Waibira females showed a preference for more arboreal travel (Villioth et al., 2022), which might exaggerate sex or community differences in, for example, the distance animals were willing to travel between patches. But what remains striking in our findings is the lack of difference between both communities and sexes, despite factors such as varied habituation levels and differing resource supply. This increases our confidence that we have identified a common, underlying, strategy. Further work, drawing comparisons across more disparate ecologies, will be needed to confirm that this strategy is common to all chimpanzees, and such work might identify switch points where foraging decisions become governed by different sets of variables to those shaping the foraging behaviour of these forest-dwelling chimpanzees. Testing for this possibility, and identifying such distinct foraging strategies should they exist, is thus an important task for future studies of foraging ecology in this species, and indeed for any species that successfully exploits a range of ecological conditions.

Our finding that the size of food patches did not predict foraging decisions was particularly surprising, given both our own finding that feeding party size was significantly and positively associated with patch size in this data set (Villioth et al., 2022), and the



**Table 6**  
Predictors of food patch choice as determined by a discrete-choice model for the Waibira community

Variable	$\beta$	z	P
<b>Males</b>			
Interpatch distance	-0.006	-7.19	<0.001
Patch size	<b>0.012</b>	<b>2.04</b>	<b>0.042</b>
Food type: flowers	-1.889	-1.38	0.168
Food type: seeds	-1.172	-1.77	0.077
Food type: unripe fruit	-0.041	-0.06	0.949
Food type: young leaves	0.106	0.27	0.784
Visits	<b>-4.441</b>	<b>-8.11</b>	<b>&lt;0.001</b>
Feeding bout length	0.014	0.99	0.321
Feeding bout length squared	-0.000	-0.20	0.840
<b>Females</b>			
Interpatch distance	-0.006	-5.52	<0.001
Patch size	0.001	0.12	0.907
Food type: flowers	0.412	0.39	0.699
Food type: seeds	<b>-1.232</b>	<b>-1.75</b>	<b>0.080</b>
Food type: unripe fruit	<b>1.985</b>	<b>2.26</b>	<b>0.024</b>
Food type: young leaves	-0.167	-0.33	0.741
Visits	<b>-5.694</b>	<b>-6.87</b>	<b>&lt;0.001</b>
Feeding bout length	<b>0.019</b>	<b>2.50</b>	<b>0.012</b>
Feeding bout length squared	-0.000	-1.52	0.129

Bold values indicate statistical significance at  $\alpha = 0.05$ .

considerable body of research linking the size of foraging groups to patch size (Chapman, 1990; Chapman et al., 1995; Chapman & Chapman, 2000; Ghiglieri, 1984; Isabirye-Basuta, 1988; Janson, 1988; Newton-Fisher et al., 2000; Snaith & Chapman, 2005; White & Wrangham, 1988; but see Fashing, 2001; Pengfei et al., 2014). While it might be expected that patch choice decisions would be influenced by the number of co-feeders expected at each of the available patches if foragers seek to minimize competition, we were unable to test this directly: given the dispersal of patches and distances between them, we were unable to count individuals present at all option trees for each foraging decision. However, in the absence of other information, a foraging chimpanzee is likely to be faced with the same problem: they have no knowledge of the number of potential competitors at each of the possible food patches. Foraging chimpanzees will at times give loud distinctive calls, pant-hoots, on arrival at food patches and while feeding (Bouchard & Zuberbühler, 2022; Notman & Rendall, 2005; Uhlenbroek, 1995), but not all foragers vocalize and any information gained this way would be incomplete at best if relied upon to guide patch choice decisions to minimize competition for food (although such calls may provide useful information about the location of particular individuals: Bouchard & Zuberbühler, 2022). The persistent correlation between party size and patch size across multiple studies of chimpanzee foraging (see above for citations) in fact suggests that there is no foraging benefit to preferring larger patches, because the level of competition scales with patch size. Our analysis, therefore, considers a scenario of patch choice where the selecting individual expects to encounter the same level of foraging competition in all destination patches, which may be a useful rule of thumb for individual animals making foraging decisions. The extent to which this is true remains a topic for future work. It was only among male chimpanzees of the Waibira community that we found a preference for larger patches, which may have been a consequence of the relative scarcity of such patches within the Waibira home range. Given that large patches should attract greater numbers of foragers (evidenced by the strong correlation between the two), such patches may allow males to associate with one another for reasons unrelated to foraging, so Waibira males may therefore have chosen such patches when they were available to benefit from associations with other males, potentially leveraging interactions with specific individuals through coalitions, meat sharing, grooming and joint border patrols, to increase social status and mating

opportunities (Duffy et al., 2007; Kaburu & Newton-Fisher, 2015; Newton-Fisher, 1997, 1999a; Nishida & Hosaka, 1996; Watts & Mitani, 2002).

Our study demonstrates that choices made by multiple independent foragers can be analysed in a meaningful manner through the application of mixed logit models. For chimpanzees, we have shown that foraging decisions are driven by a trade-off between minimizing travel costs and the need to reach novel food patches, suggesting that chimpanzees operate on a rule of thumb that such patches will be less depleted than those they have visited previously. It also appears that chimpanzees expect levels of foraging competition to be consistent across food patches, and thus this does not impact their choice of foraging locations. Our results confirm the importance of explicitly considering presumed sex differences in foraging behaviour when testing theories of foraging strategy (Pokempner, 2009), given our contrary-to-expectation findings, and demonstrate the usefulness of investigating foraging strategies through direct consideration of the behaviour of individual foraging animals.

The discrete-choice approach allowed us to evaluate simultaneously salient ecological parameters, as identified by previous work, across multiple foraging decisions for each individual forager rather than averaging across multiple decisions and/or foragers. Compared to other statistical approaches, the focus on discrete foraging decisions and the shifting array of options at each decision point adds an important element of realism for foragers that have imperfect knowledge of their current environment and available foraging options (Marshall et al., 2012). By considering each foraging choice, this approach can avoid arbitrarily drawing a distinction between a destination food patch and opportunistic foraging en route. Apparently opportunistic foraging contributes to an individual's diet and nutritional needs, and it is biologically more meaningful to be guided in the identification of food patches by the foraging behaviour of the animal itself, and to quantify the foraging efforts therein, than to subjectively distinguish what seem to observers to be 'real patches' of food. Discrete-choice modelling has broad applicability across taxa as a powerful individual-focused approach to tackling questions regarding why animals select the foraging patches that they do or, more broadly, select from any limited array of options.

#### Author Contributions

**Jakob Villioth:** Conceptualization, Data collection and curation, Formal analysis, Investigation, Methodology, Writing - Original draft; **Klaus Zuberbühler:** Conceptualization, Funding acquisition, Resources, Supervision. **Nicholas E. Newton-Fisher:** Conceptualization, Formal Analysis, Funding acquisition, Project administration, Supervision, Writing - Review & editing.

#### Data Availability

Data used in this study are uploaded as [Supplementary material](#).

#### Declaration of Interest

None.

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## Supplementary Material

Supplementary material associated with this article is available in the online version at <https://doi.org/10.1016/j.anbehav.2023.04.003>.

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## APPENDIX

**Table A1**  
Demographic details for focal subjects from each of the two study communities

Focal ID	Sex	Age (years)	Rank (males only)	Dependent offspring (females only)
<b>Sonso community (2015–2016)</b>				
HW	Male	ca. 22	High	–
FK	Male	ca. 16	High	–
NK	Male	ca. 33	Mid	–
SQ	Male	ca. 24	Mid	–
SM	Male	ca. 23	Mid	–
KZ	Male	ca. 20	Low	–
KU	Female	ca. 36	–	Juvenile (7) + infant (1)
KL	Female	ca. 36	–	Infant (1)
KW	Female	ca. 34	–	Juvenile (8) + infant (2)
JN	Female	ca. 31	–	Juvenile (9)
OK	Female	ca. 19	–	Infant (1)
<b>Waibira community (2016–2017)</b>				
TAL	Male	ca. 40	High	–
KEV	Male	ca. 35	High	–
URS	Male	ca. 29	High	–
BEN	Male	ca. 24	High	–
DOU	Male	ca. 40	Mid	–
GER	Male	ca. 23	Low	–
MAC	Male	ca. 18	Low	–
SAM	Male	ca. 17	Low	–
KID	Female	ca. 38	–	Juvenile (7) + infant (<1)
LIR	Female	ca. 35	–	Juvenile (6) + infant (1)
LOT	Female	ca. 32	–	Infant (5)
NEV	Female	ca. 32	–	Juvenile (6) + infant (1)
PEN	Female	ca. 29	–	Juvenile (8) + infant (3)
AKI	Female	ca. 28	–	Infant (1)
BAH	Female	ca. 22	–	Infant (1)
NOR	Female	ca. 20	–	Infant (3)
KIP	Female	ca. 19	–	Infant (2)

Individuals are listed by community, with males ordered by rank class and age, and females ordered by age. Rank classes were estimated using prior knowledge of the study communities and within-patch aggression observed during this study. The age (years) of dependent offspring is given in parentheses. For demographic data see: <http://www.budongo.org/about/documents-and-guidelines>.