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ORIGINAL ARTICLE

Patch choice decisions by a fission–fusion forager as a test of the ecological constraints model

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Abstract

Chapman et al.'s (Behav Ecol Sociobiol 36:59–70, 1995) ecological constraints model posits that the size and distribution of food patches place restrictions upon foraging group size. Larger groups incur increased travel costs for any given array of patches, and thus, to fulfil individual energetic and nutritional requirements, foragers should adjust group sizes to balance energy obtained against that spent on travelling. Support for this model comes from both comparative and species-specific studies but findings are contradictory, and the utility of the model has been questioned. This study provides a rigorous test, analysing measurements from distinct food patches and individual inter-patch movements, on an appropriately shorter temporal scale. Using data drawn from two social groups of a species characterised by a high degree of fission–fusion dynamics, the chimpanzee (*Pan troglodytes*), we show that larger parties foraged in larger food patches and for longer durations, and that larger parties were associated with further travel between patches. Overt contest competition over food increased with party size. We found no evidence of distinct sex differences in either party size or travel distances: the predictive power of forager sex was low compared to that of ecological variables. We propose that analysis at the patch level is more appropriate than a daily averaging approach that may smooth out the very variation being investigated. Our findings suggest that, despite certain limitations, Chapman et al.'s (Behav Ecol Sociobiol 36:59–70, 1995) model of ecological constraints remains a useful tool. Ecology does indeed constrain grouping patterns, and the impact of this is not necessarily differentiated by sex.

Significance statement

Foraging animals face the 'more mouths to feed' problem: as the numbers in a group increase, the group must travel further to find enough food, using up energy. Hence, foragers should adjust numbers to minimise these costs, but tests of this idea have proved inconclusive. We investigated the foraging behaviour of chimpanzees, a species with highly flexible grouping, considering their travel between specific patches of food. We found clear support for this proposition, with larger patches of food hosting larger numbers of foragers, and such groups having to travel further to find food. Although it is often thought that female animals should respond more strongly to foraging costs, we found little evidence of sex differences. Our results show that ecology does indeed constrain grouping patterns, and that the impact is felt equally by males and females.

Keywords Foraging · Patch size · Travel distance · Party size · *Pan troglodytes* · Chimpanzee

Introduction

Optimal foraging theory, the dominant approach in behavioural ecology for understanding how animals search for food, emphasises the importance of constraints, often imposed by the environment and thus external to the forager, on shaping the strategies employed (MacArthur and Pianka 1966; Charnov 1976; Stephens and Krebs 1986). Chapman et al. (1995) proposed that the size and spatial arrangement of depletable food patches generate constraints on the size of groups of co-foraging individuals, primarily

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through costs associated with travel between patches. This ecological constraints model assumes that intra-group competition increases with group size, and so larger groups experience faster patch depletion, forcing them to travel to greater numbers of additional patches. Such inter-patch travel incurs energy, time, and opportunity costs, and potentially also costs associated with predation risk if this increases relative to that experienced within patches. For gregarious species that are obligate group foragers, the constraint is thus to the size of the social group. Under the assumption that such species will attempt to maximise group size (and associated benefits), the model provides an explanation for realised variation in group size, grounded in ecology.

The fundamental logic of Chapman et al.'s (1995) ecological constraints model is that, all else being equal, foragers should minimise their inter-patch travel costs: large adjacent patches will support larger groups than would the same quantity of food arranged in small dispersed patches due to substantially lower costs of travelling between such patches. This follows from optimal foraging theory and Charnov's (1976) marginal value theorem. For any given patch depletion rate (the rate of gain for the forager is the rate of depletion for the patch), animals are predicted to forage for longer in patches with a greater associated travel time, i.e. those that are further apart. Efficient foraging—maximising energy gain per unit time—therefore involves minimising travel time in order to maximise time spent feeding in non-depleted patches (i.e. those that provide greater than average returns: Charnov 1976; Stephens and Krebs 1986).

Testing Chapman et al.'s (1995) ecological constraints model in species with stable social groups, and which are thus obligate group foragers, is logistically challenging as the necessary variation in group size and ecology accumulates slowly (Chapman and Chapman 2000). In consequence, opportunities offered by species with pronounced fission–fusion dynamics (Aureli et al. 2008), whereby individuals travel and forage in small subgroups that frequently change in size and composition throughout the day (Sugiyama 1968) have proved attractive to researchers (Chapman and Chapman 2000). Such societies are rare and found only in a few mammal species, e.g. dolphins *Turliops truncatus* (Connor et al. 2000), sperm whales *Physeter macrocephalus* (Whitehead et al. 1991), elephants *Loxodonta africana* (Wittemyer et al. 2005), spotted hyenas *Crocuta crocuta* (Holekamp et al. 1997), lions *Panthera leo* (Schaller 1972), and several taxa of non-humans primates, including spider monkeys *Ateles* spp. (Symington 1990; Chapman et al. 1995; Wallace 2008) and chimpanzees *Pan troglodytes* (Goodall 1986; Nishida and Hiraiwa-Hasegawa 1987). Such 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 and Boesch 2004). The resultant variation in foraging group size presents an ideal opportunity with which to test increasingly complex socio-ecological models (Janson 2000), and Chapman et al.'s (1995) ecological constraints model in particular.

The results of such tests have been mixed, however. Mbizah et al. (2019) found no effect of mean prey herd size (i.e. average patch size) on the size of either prides or subgroups thereof of lions. By contrast, Smith et al. (2008) reported that spotted hyena adjust grouping patterns to variation in prey abundance, and the energy available (essentially, patch size), as predicted by this ecological constraints model. While some studies of spider monkeys report a strong positive relationship between food abundance and either monthly or daily subgroup size (Symington 1990; Chapman et al. 1995; Shimooka 2003; Asensio et al. 2009), others find only weak (Ospina 2011) or no (Stevenson et al. 1998; Ramos-Fernandez 2001; Weghorst 2007) relationship. Similarly, findings for chimpanzees are inconsistent. Many studies report that foraging parties increase in size with the size of food patches (Ghiglieri 1984; Isabirye-Basuta 1988; White and Wrangham 1988; Newton-Fisher et al. 2000) and that foragers typically spend longer periods in larger patches (Janson 1988; White and Wrangham 1988; Chapman et al. 1995; Snaith and Chapman 2005; Wallace 2008), but Potts et al. (2011) found that while patch size explained 80% of the variance in feeding party size in the Ngogo community (Kibale, Uganda), it explained only 23% of the variance in party size in the nearby Kanyawara community, with Pokempner (Pokempner 2009) reporting no increase in party size with mean daily fruit patch size for the same Kanyawara community. The relationship between party size and travel distances (Chapman et al. 1995) and between travel distance and patch productivity (Normand et al. 2009; Pokempner 2009) tend in general terms to correspond well to predictions of the ecological constraints model, but when separating individuals by sex, findings are similarly less conclusive. While adult female chimpanzees tend to travel shorter distances and move in a more linear way in between feeding trees (Bates and Byrne 2009; Normand and Boesch 2009; Pokempner 2009), in line with theories of sex differences in foraging effort (Schoener 1971; Trivers 1972), these differences apparently disappear when either all food patches (Pokempner 2009) or individual movement phases rather than daily averages (Bates and Byrne 2009) are analysed.

While the variation in foraging strategies and group size seen across species of non-human primates have made these taxa particularly attractive for tests of the ecological constraints model and its proposed effects of increased feeding competition (Majolo et al. 2008), it is now widely acknowledged that social organisation and group size in non-human primates are more flexible than once thought (Harris and Chapman 2007; Chapman and Rothman 2009; Strier et al. 2009). Multiple additional factors, such as dominance styles

(Isbell 1991), phylogeny and terrestrially (Janson and Goldsmith 1995), nutrient balancing (Felton et al. 2009; Hohmann et al. 2010), demography (Lehmann and Boesch 2004; Struhsaker 2008), and other social factors (Sterck et al. 1997; Isbell and Young 2002), appear to colour the relationship between feeding competition and group size. Travel costs alone do not seem to be the only factor constraining group size (Struhsaker and Leland 1988; Bronikowski and Altmann 1996; Fashing 2001; Pengfei et al. 2014) and the perceived importance of the distribution and abundance of food resources for understanding group size has been questioned (Koenig and Borries 2006; Thierry 2008; Clutton-Brock and Janson 2012).

Here, we address the relevance of foraging ecology through testing the predictions of Chapman et al.'s (1995) ecological constraints model with an analysis of individual inter-patch movements of foragers and the parameters of individual food patches, rather than broad averages that risk smoothing out the very variation that makes fission–fusion species an attractive model system. We investigate the foraging behaviour of both adult males and adult females across two adjacent chimpanzee communities with differing patterns and levels of resource availability to allow for a rigorous test of the model. We predict that (1) feeding party size increases with patch size, (2) inter-patch travel distance increases with party size, and (3) following from theories of sex differences in foraging effort, these relationships are more pronounced for adult females than they are for adult males. Overt agonism within feeding patches offers a reliable indicator of levels of feeding competition (Saito 1996; Vogel and Janson 2007; Hanya 2009; Heesen 2014), and so we predict further that (4) direct contest competition over food increases with feeding party size, and (5) is more frequent in smaller patches. Finally, we predict that (6) food-related agonism in patches increases with the number of female foragers rather than the number of male foragers.

Methods

Study site and subjects

Research was conducted within the Budongo Forest Reserve (1°35′–1°55′ N, 31°08′–31°42′ E). We collected data over a period of 16 months from two neighbouring chimpanzee communities, Sonso (October 2015 to June 2016) and Waibira (October 2016 to June 2017). The Sonso community has been observed continuously since 1990 (Newton-Fisher 1997; Reynolds 2005). All members of this community were individually recognized and could be observed at close quarters on the ground. During the study period, the Sonso community consisted of 71 individuals in total and, following age classifications by Goodall (1986), included 12 adult males (≥ 16 years old) and 24 adult females (≥ 14 years old). Habituation of the Waibira community started in 2011 (Samuni et al. 2014) and almost all adult members could be individually recognized at the time of this study; observation distances permitted the study foraging behaviour at a sufficiently close range (Hobaiter et al. 2017). The Waibira community consisted of at least 88 known individuals, including 17 adult males and 29 adult females.

The home ranges of these two communities differed floristically (Villioth 2018). The Budongo Forest, 428 km^2 of moist semi-deciduous tropical forest in western Uganda, is a mosaic of forest types (Reynolds 1992; Plumptre 1996) as a consequence of forest dynamics and management history (Eggeling 1947; Plumptre 1996). Much of the forest has been selectively logged, with this more recent (1963–1964 vs 1947–1952) for forest within the Waibira home range than within the Sonso home range (Plumptre 1996), with Waibira additionally suffering illegal pitsawying in recent decades. Food availability was greater for Sonso chimpanzees during our study, for whom 11–30% of trees provided food each month, whereas only 11–17% did so for Waibira (Villioth 2018), while data on dietary diversity (standardized Shannon–Wiener index: 0.67 (Sonso) vs. 0.76 (Waibira): Villioth 2018) similarly suggested greater food abundance for Sonso chimpanzees (cf. Wrangham et al. 1998; Fawcett 2000).

Data collection

We aimed to conduct full-day nest-to-nest follows of individual chimpanzees in both communities to obtain a complete record of that individual's foraging behaviour, as well as travel between feeding patches. During such focal follows, activity of the focal individual was recorded continuously (Altmann 1974). This approach meant that it was not possible to record data blindly. All behaviours related to food handling—the entire process of picking and ingesting food items—were categorised as feeding. Each morning, we selected one focal from a randomised list, with focal follows starting at the night nest and continuing for as long as conditions allowed. If we lost contact with the initial focal individual, we attempted to increase the number of focal samples from individuals that were still underrepresented in the overall dataset to maintain a balanced sampling regime. Sonso community chimpanzees engage in crop-foraging (Tweheyo et al. 2005) and focal follows had to be suspended when the designated focal left the forest to forage on field crops (duration (mean ± SD) of Sonso follows: 5.6 ± 3.1 h, range: 1–12 h, median: 5 h). The ongoing habituation of the Waibira community and their denser habitat also restricted our ability to consistently conduct full-day nest-to-nest follows of individual chimpanzees (duration (mean ± SD) of Waibira follows: 4.1 ± 2.6 h, range: 1–12 h median: 4 h).

We collected data from six adult males and five adult females from the Sonso community, and ten adult males and nine adult females from the Waibira community (we sampled a larger number in Waibira since the community was larger in size and it was not always possible to find a predetermined focal individual). Males from both communities were of different ages and represented different rank categories (high-, mid-, and low-ranking). Of the Sonso females, four were lactating and travelled with at least one dependent infant and one juvenile; the fifth female was not lactating and travelled with her juvenile offspring. In the Waibira community, seven of the focal females were lactating while the other two females, each travelling with a single juvenile offspring, were not lactating.

We defined a food patch as an aggregation of food items that allowed uninterrupted foraging movements by the focal animal (White and Wrangham 1988; Chapman et al. 1994; Pruetz and Isbell 2000). While in most cases a patch was equivalent to an individual feeding tree, for certain tree species (e.g. *Broussonetia papyrifera*, *Putranjivace gerrandi*), a patch could consist of multiple trees with overlapping crowns. If the focal animal was able to feed consecutively in such contiguous crowns without extensive travel, we considered all of these trees to form one patch and so patch size measurements (such as diameter at breast height (DBH) and bout length) of all visited trees were summed. Non-overlapping crowns, such that the focal animal travelled either along the ground, or through the crown of a non-feeding tree, to reach another feeding location, delineated separate patches. We excluded from subsequent analysis those food patches where the chimpanzees' foraging was influenced by an inter-community encounter, crop-foraging, hunting, or travel to waterholes. For each food patch, the type (fruit, leaves, flowers, seeds), species, and where relevant the phytophase (ripe, unripe; young, mature) of food items were identified and recorded.

We used the DBH of the feeding tree to index patch size. DBH may not always capture the dynamic nature of fruit availability within trees (Suarez 2014), but it is the most widely used method for estimating fruit abundance and thus allows comparison of results across study sites and species (Chapman et al. 1992). Measurements were obtained using a tape measure and were accurate to the nearest centimetre. When chimpanzees foraged on fruits or leaves of lianas, the DBH measurements of all supporting trees were measured and summed (following Strier 1989). Where it was not possible to measure DBH, for example when a feeding tree was surrounded by dense vegetation or when the tree was small and could not be approached without disturbing the foraging animal, we estimated DBH visually with reference to measured trees.

We obtained inter-patch travel distance by following the focal animal's travel path on the ground as closely as possible and recording the distance to the next feeding patch with the help of the track-log function of a handheld GPS (Garmin GPSMAP 64). We manually removed all GPS locations recorded during resting/grooming bouts as the track-log function can erroneously record small movements when subjects remain stationary for longer periods (Janmaat et al. 2013). To investigate the accuracy of locations recorded by the GPS device within the forest, we kept the device in a fixed position for 5 h under forest canopy (Asensio et al. 2009; Bates and Byrne 2009). Setting the recording interval to 'normal' resulted in $n = 499$ locations recorded over this duration, with the device recording its position on average 1.66 times per minute (interval between recordings: 31–50 s). The average error (distance recorded while being in the same place) was 3.97 m (St. Dev. = 2.58 m, range = 0–23 m). We also recorded GPS locations for all food patches visited by each focal animal. Chimpanzees typically travelled between food patches terrestrially, and previous work (using data drawn from one of our two study communities: Bates and Byrne 2009) has shown that adult chimpanzees, both male and female, travel at a speed of approximately 2 km h^{-1} when moving between food patches in this habitat (Bates and Byrne 2009). While chimpanzees will accelerate as they approach (or flee) socially salient activities such as agonistic interactions, or immediately prior to entering food patches (personal observations), we know of no evidence to suggest that chimpanzees adjust their travel speed to compensate for the distances between patches, and so greater inter-patch distances are associated with greater travel times. Thus, it is at least a reasonable working assumption that the distance between patches provides a good proxy for the costs associated with traversing that distance.

We defined party size as the maximum number of individuals that simultaneously occupied a food patch (Strier 1989), achieved by noting changes in feeding party membership as individuals entered or left the patch during each feeding bout. We only included adult and adolescent individuals in this count; independent individuals below age of adolescence were not included (cf. Pokempner 2009). This approach assumed that food removed from a patch by these individuals had negligible impact on adult chimpanzees' foraging decisions. In support of this position, adult chimpanzees did not seem to view such individuals as competitors for food: none of the cases of high-intensity agonistic competition (see definition below) that we observed targeted a young independent chimpanzee.

We defined feeding bout length as the total amount of time that the focal animal spent feeding in a patch, from entering until leaving (Potts et al. 2011). The fission–fusion nature of chimpanzee society renders attempts to record occupancy of all foragers within a patch (Snaith and Chapman 2005; Vogel and Janson 2007) impractical, as a focal

animal can join an already occupied patch or leave a patch while others are still foraging. Focusing our data collection on patches (Vogel and Janson 2007; Heesen 2014) rather than individuals—which would allow such data to be collected—would have precluded collection of other foraging data, such as previous/subsequent patches visited by a forager and travel distance between such patches.

To investigate contest competition over food, we recorded all agonistic interactions between adult individuals during focal follows using all-occurrence sampling (Altmann 1974). Six types of aggression were distinguished and classified by intensity (Goodall 1986; Newton-Fisher 2017). Furthermore, different contexts were defined, based on the identity and sex of the aggressor and victim, the apparent cause of aggression, and the chronological sequence of events. We categorised feeding (contest) competition as that subset of aggressive interactions occurring within a feeding patch over either food items or position (feeding site) within a feeding tree, and which were not associated with direct competition over mating opportunities.

Data analysis

Prior work on other chimpanzee populations has shown striking contrasts between communities located within the same forest. For example, Potts et al. (2011) highlight significant differences in foraging ecology between the communities of Ngogo and Kanyawara, both of which are located within the Kibale National Park. Given such findings, together with the contrasts in history of habitat disturbance and food availability for our study communities, our a priori assumption for this study is that data drawn from these communities constitute distinct datasets.

We compared foraging variables (party size, travel distance between patches, feeding bout length, contest competition) across communities using mixed-effects models. These models tested solely whether community identity (Sonso vs Waibira) predicted a difference in the relevant foraging variable, controlling for the repeated observations of focal individuals and for between-subject variation (Bolker et al. 2009). We analysed data across patches, with foraging variables describing each patch visited by a focal forager: maximum party size within the patch, travel distance to the patch by the focal, the duration for which the focal fed, and any contest competition within that patch while the focal was present. This mixed-models approach allowed us to use data from several feeding patches, whether collected over the course of a day when following the same individual, or from the same individual across multiple days. For inter-community comparison of the foraging variable patch size, we used the non-parametric Wilcoxon rank sum test, as patch size is independent of the identity of the forager.

As it is unknown to what extent chimpanzees are able to adjust the size of foraging parties to their individual needs, we designed two models (GLMM and LMM, below) to explore the relationship between party size, patch size, and travel distance. Both models included the identity of the focal as a random effect (as above), and a count of feeding bouts by each focal per day as a second random effect to account for data (consecutive food patches) that could stem from following the same individual over the course of a day. Both models also included the interactions between main predictors and a community identity term to investigate whether the effects of fixed and random factors on the dependent variable differed between communities. We used a likelihood ratio test to determine the statistical significance of each of these models (Dobson 2002) in comparison to a null model that included only the intercept, random effects, and the two variables which we wanted to control (feeding bout length and food type).

We used a generalized linear mixed model (GLMM) with a negative binomial error structure implemented by the function glmer.nb (Venables and Ripley 2013), and the function r.squaredLR (Nagelkerke 1991) to calculate effect size, to examine the effect of multiple predictors (fixed factors) on feeding party size: patch size (continuous, measured in centimetres), travel distance (continuous, measured in metres), feeding bout length (continuous, measured in minutes), food type (categorical: ripe fruit, unripe fruit, young leaves, flowers, seeds), and sex of the focal chimpanzee (binary: male or female).

We used a linear mixed model (LMM) implemented by the function 'lmer' (Bates et al. 2015) to explore the predictors of inter-patch travel distance: feeding party size, patch size, feeding bout length, food type, and sex of the focal chimpanzee.

We used a generalized linear model (GLM) with binomial error structure (McCullagh and Nelder 1989) to model contest competition as a binary dependent variable, with patch size, feeding party size, and the proportion of either males or females within the party as fixed factors. This model also included the interactions between main predictors and community identity. We restricted this analysis to the subset of our contest competition data that including only those food patches with a known measure of size, and at least two foragers (Sonso: 311 patches, 59 aggressive interactions; Waibira: 258 patches, 69 aggressive interactions). We were unable to model rates of contest competition due to the scarcity of agonistic interactions within food patches, with very few of these involving a current focal individual.

In all models, data met the assumptions of normality and homoscedasticity of residuals, as determined by visual inspection of diagnostic plots. Continuous variables were centred before running the models to achieve a mean of zero and a standard deviation of one. We inspected variance

inflation factors (VIF) (Quinn and Keough 2002) using the function 'VIF' (Fox et al. 2012) to check for collinearity between predictors. All analyses were conducted in R 3.4.3 (R Core Team 2017).

Results

Table 1 summarizes the tests of our predictions arising from Chapman et al.'s (1995) ecological constraints model. Below, we present detailed comparisons between the two study communities for each foraging variable in turn, together with the details of the tests of these predictions. For reference, the Sonso community is the smaller of the two (36 vs > 46 adults), inhabiting forest less recently and less intensively disturbed.

Food patches

Small feeding patches (10–30 cm DBH) made up 24% of patches in Waibira, but only 12% in the Sonso community. Large patches (DBH > 70 cm) were, in contrast, more common in the Sonso community (50% vs. 36%). Perhaps unsurprisingly, therefore, Sonso (Sn) chimpanzees foraged in significantly larger food patches than did Waibira (Wb) chimpanzees (Sn med.: 70 cm, range: 10–260 cm; Wb med.: 63 cm, range: 10–200 cm; Wilcoxon rank sum test $W = 89{,}282$, $p < 0.001$). This difference remained significant even when excluding the larger proportion of lone foragers (see below) within the Waibira community (Sn med.: 80 cm, range:10–260 cm; Wb med.: 70 cm, range: 10–260 cm; $W = 46{,}372$, $p = 0.029$). Feeding patches of ripe fruit made up a larger proportion of all patches for the Waibira community (Fig. 1) with these mostly tree species with smaller fruits (*Ficus sur*: 19%, *Putranjivace gerrandi*: 16%); in Sonso, the largest share of ripe fruit came from a tree species with large fleshy fruits (*Ficus mucoso*: 18%). While Waibira chimpanzees rarely foraged on flowers, these provided a larger share of the diet of the Sonso community.

Table 1 Summary of predictions tested for each of two communities of East African chimpanzees, Sonso (smaller, less disturbed) and Waibira (larger, more disturbed) from the Budongo Forest, Uganda

Prediction	Sonso	Waibira
Feeding party size increases with patch size	Yes	Yes
Inter-patch travel distance increases with party size	Yes	Yes
Sex difference in the impact of foraging variables	No	No
Contest competition increases with party size	Yes	Yes
Contest competition more frequent in smaller patches	No	No
Contests increase with proportion of female foragers	No	Unclear

Especially during October and November 2015, flowers and young leaves of *Broussonetia papyrifera* made up a substantial part of the Sonso community's diet, and we pooled foraging data on flowers and young leaves for patches of this species as chimpanzees often consumed both food types during the same bout. Overall, young leaves of *Celtis mildbraedii* were the most important food item of the Waibira community (Villioth 2018; JV et al., unpubl. data).

Patch occupancy

Chimpanzees from the two communities occupied feeding patches for broadly similar durations (mean ± SD: Sn: 33.45 ± 31.46 min; Wb: 27.38 ± 25.91 min), although slightly and significantly longer for Sonso than for Waibira (LMM: $\beta \pm \text{SE} = 0.188 \pm 0.077$, $X^2 = 5.99$, $p < 0.014$; pseudo-*R*-squared: marginal 0.010, conditional 0.071).

Party size

Mean feeding party size was significantly higher within the Sonso community than within the Waibira community (mean ± SD: Sn: 7.3 ± 5.9; Wb: 4.4 ± 4.0; GLMM: $\beta \pm \text{SE} = 0.509 \pm 0.096$, $z = 5.34$, $p < 0.001$, adjusted $R^2 = 0.126$). Large parties (more than 10 individuals) accounted for 32% of feeding parties in Sonso, but only for 12% in Waibira, while small feeding parties (1–3 individuals) made up more than half of all observations in the Waibira community (55%), but only one-third (34%) in Sonso. Lone foragers were more common in Waibira (33% of all feeding bouts) than in Sonso (18% of all bouts), and in both communities, these were more often female than male (Sn: 63% of lone foragers; Wb: 60%).

Inter-patch travel distance

Chimpanzees of the Sonso community travelled further between feeding patches than did those of the Waibira community (mean ± SD: Sn: 503 ± 422 m; Wb: 307 ± 368 m; LMM: $\beta \pm \text{SE} = 0.805 \pm 0.235$, $X^2 = 11.74$, $p < 0.001$; pseudo-*R*-squared: marginal 0.092, conditional 0.285). There was no significant sex difference in travel distance for the Sonso community (male: 510 ± 413 m; female: 471 ± 389 m; LMM: $\beta \pm \text{SE} = -0.006 \pm 0.186$, $X^2 = 0.001$, $p = 0.97$; Fig. 2), whereas in the Waibira community, males tended to travel further than females (male: 354.52 ± 377.19 m, female: 254.57 m ± 352.81 m; LMM: $\beta \pm \text{SE} = 0.615 \pm 0.337$, $X^2 = 3.324$, $p = 0.068$; pseudo-*R*-squared: marginal 0.0508, conditional 0.2804; Fig. 2). Within the Waibira community, focal animals often travelled between patches arboreally, especially females (females: 46% of travel bouts, males: 13%), while arboreal travel was rare in the Sonso community (females: 5% of travel bouts, males 1%). When considering

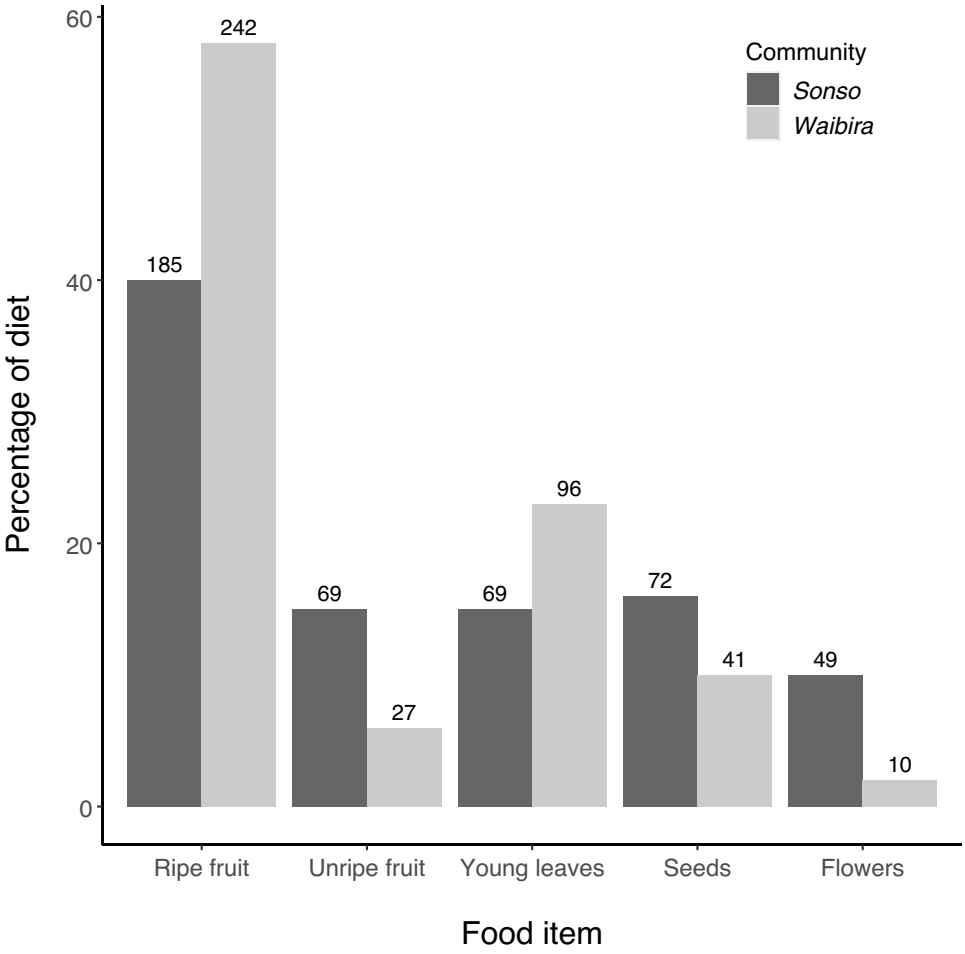

Fig. 1 Proportion (%) of food types in the diets of each of two communities of East African chimpanzees (Sonso, Waibira) from the Budongo Forest, Uganda. The food type 'seeds' refers to the targeting and consumption of these to the exclusion of other parts of the fruit

only terrestrial travel ($n = 455$), there were no significant differences in travel distance either at a community level (mean ± SD: Sn: 517 ± 420 m; Wb: 415 ± 389 m; LMM: $\beta \pm \text{SE} = 0.121 \pm 0.143$, $X^2 = 0.71$, $p = 0.398$); or between sexes (Table 2). Sonso community chimpanzees travelled farthest for patches of ripe fruit (602 ± 474 m), whereas Waibira chimpanzees travelled furthest for patches of seeds (397 ± 408 m). When considering only terrestrial travel, this difference across communities remained the same. Terrestrial travel distances to patches of young leaves (Sn: 351 ± 285; Wb: 331 ± 356 m) and, to an extent, seeds (Sn: 576 ± 377 m; Wb: 510 ± 413 m) were comparable across communities (Table 3).

Predictors of party size and travel distance

We found variation in feeding party size was better explained by our model (GLMM) that included patch size, travel distance, and sex of the focal than it was by the null model that included only feeding bout length and food type (likelihood ratio test: $X^2 = 164.17$, df = 12, $p < 0.001$). For both communities, larger feeding parties were found in larger patches (Sn: $\beta \pm \text{SE} = 0.817 \pm 0.099$, $z = 8.212$, $p < 0.001$; Wb: $\beta \pm \text{SE} = 0.576 \pm 0.101$, $z = 5.691$, $p < 0.001$; Fig. 3), and with increased travel distance between patches (Sn: $\beta \pm \text{SE} = 0.128 \pm 0.048$ $z = 2.678$, $p = 0.007$; Wb: $\beta \pm \text{SE} = 0.143 \pm 0.046$, $z = 3.102$, $p = 0.002$). Larger parties also fed for longer within a patch (Sn: $\beta \pm \text{SE} = 0.153 \pm 0.064$, $z = 2.390$, $p = 0.017$; Wb: $\beta \pm \text{SE} = 0.190 \pm 0.068$, $z = 2.79$, $p = 0.005$). We found no significant effect of sex on feeding party size. Patches of the food type 'seeds' were associated with larger feeding parties for the Sonso community ($\beta \pm \text{SE} = 0.564 \pm 0.198$, $z = 2.853$, $p = 0.004$) but not for the Waibira community ($\beta \pm \text{SE} = -0.481 \pm 0.386$, $z = -1.246$, $p = 0.213$; Table 4). Patches of this food type were of a similar size in both communities (mean ± SD: Sn: 80.49 ± 11.71 cm, Wb: 88.61 ± 5.85 cm), suggesting that these larger parties in Sonso were not a simple consequence of patch size.

We found variation in inter-patch travel distance was better explained by our model (LMM) that included patch size, feeding party size, and sex of the focal, than it was by the null model that included only feeding bout length and food type (likelihood ratio test: $X^2 = 50.75$, df = 6, $p < 0.001$).

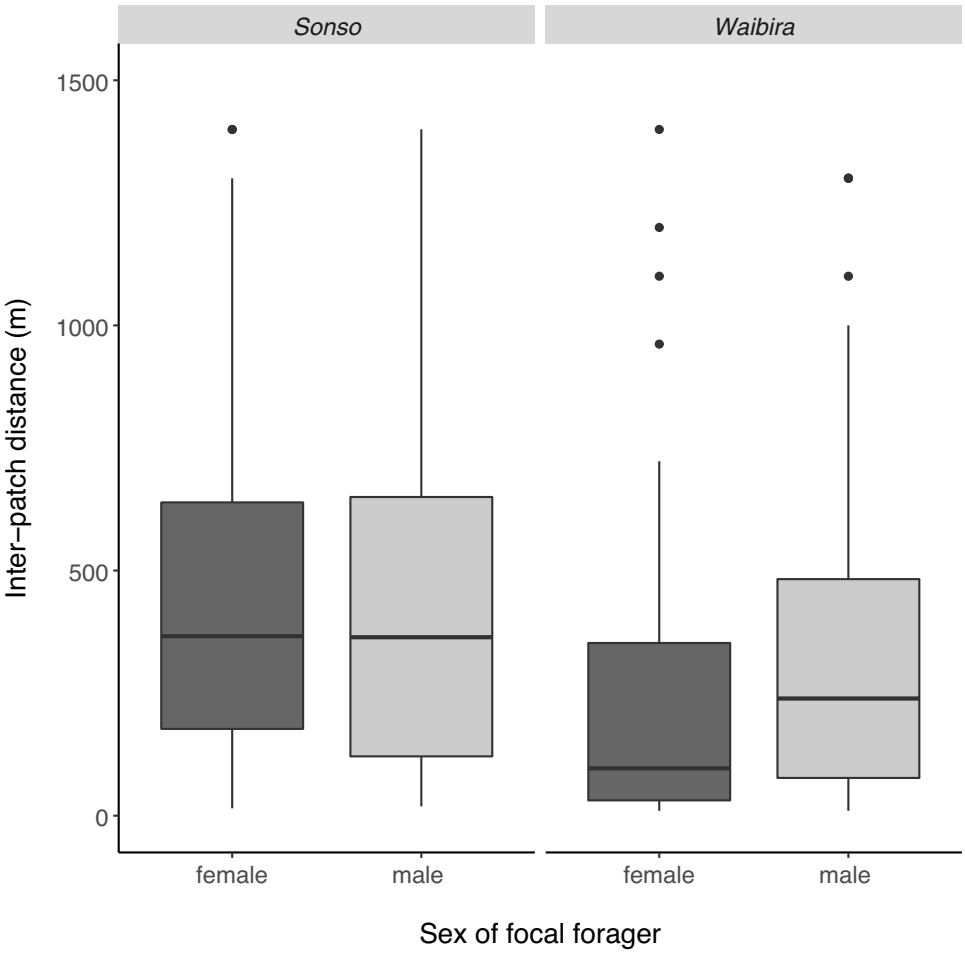

Fig. 2 Sex and inter-community differences in distance travelled between food patches for two communities of East African chimpanzees. Boxes show the inter-quartile range (IQR), with the median indicated by the dark internal line. Whiskers extend to 1.5 times the IQR. Solid circles represent outliers, with those beyond 1500 m travel distance not shown. NB: possible sex difference for Waibira community chimpanzees may an artefact of lower habituation of these females, as this disappears when considering terrestrial travel alone

Table 2 Inter-patch travel distances (mean ± SD) for (adult) male and female chimpanzees from each of two communities of East African chimpanzees (Sonso, Waibira) from the Budongo Forest, Uganda, as arboreal and terrestrial travel combined, and terrestrial alone

	n	All travel (m)	*n*	Terrestrial only (m)
Sonso				
Males	146	525 ± 441	144	532 ± 439
Females	134	479 ± 401	128	500 ± 398
Total	280	503 ± 422	272	517 ± 420
Waibira				
Males	135	355 ± 377	116	405 ± 381
Females	124	255 ± 353	67	434 ± 405
Total	259	307 ± 368	183	415 ± 389

Travel distance between patches were greater when the destination patch hosted a larger party, in both communities (Sn: $\beta \pm \text{SE} = 0.024 \pm 0.012$, $z = 2.10$, $p = 0.036$; Wb: $\beta \pm \text{SE} = 0.034 \pm 0.017$, $z = 2.06$, $p = 0.040$; Table 5). The effect of patch size on travel distance differed between communities (interaction between community and patch size: $X^2 = 5.98$, df = 1, $p = 0.015$) as did the effect of food type

Table 3 Inter-patch travel distances (mean ± SD) to patches of six different food types for each of two communities of East African chimpanzees (Sonso, Waibira) from the Budongo Forest, Uganda, as arboreal and terrestrial travel combined, and terrestrial alone

	n	All travel (m)	*n*	Terrestrial only (m)
Sonso				
Ripe fruit	109	602 ± 474	107	612 ± 472
Unripe fruit	38	574 ± 467	37	588 ± 465
Young leaves	54	339 ± 286	52	351 ± 285
Flowers	25	223 ± 167	25	223 ± 167
Seeds	42	537 ± 390	39	576 ± 377
Other	12	582 ± 348	12	582 ± 348
Total	280	503 ± 422	272	517 ± 420
Waibira				
Ripe fruit	145	339 ± 392	106	448 ± 407
Unripe fruit	13	274 ± 213	9	365 ± 192
Young leaves	71	222 ± 313	44	331 ± 356
Flowers	6	389 ± 518	5	465 ± 541
Seeds	20	397 ± 408	15	510 ± 413
Other	4	174 ± 86	4	174 ± 86
Total	259	307 ± 368	183	415 ± 389

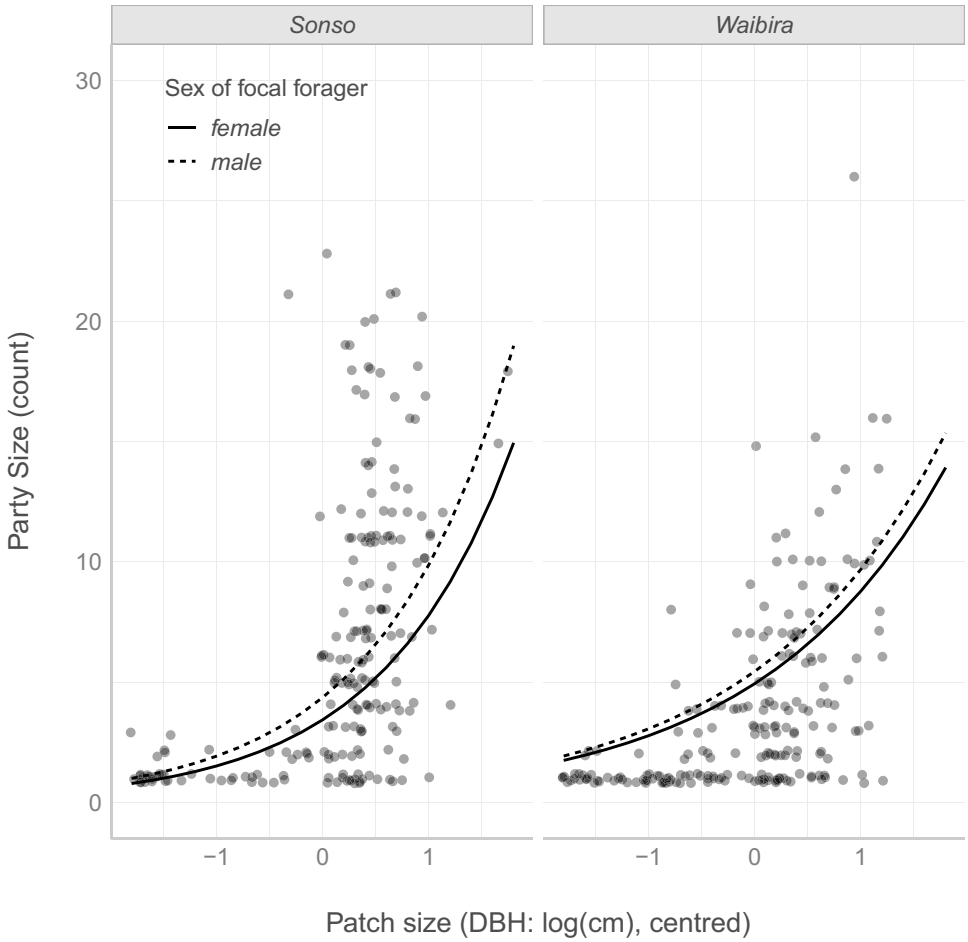

Fig. 3 Relationship between patch size and party size for two communities of East African chimpanzees (Sonso, Waibira), as predicted using generalized linear mixed modelling. In both communities, party size is strongly predicted by the size of foraging patches

($X^2 = 10.51$, df = 4, $p = 0.033$). Patch size was predictive of inter-patch travel distance only for the Waibira community. Travel distance increased with feeding bout length in both communities (Sn: $\beta \pm \text{SE} = 0.402 \pm 0.198$, $z = 2.03$, $p = 0.043$; Wb: $\beta \pm \text{SE} = 0.503 \pm 0.215$, $z = 2.34$, $p = 0.020$; Fig. 4). The sex of focal chimpanzees had no significant effect on travel distances in either community in this model.

Feeding competition

We observed 64 agonistic interactions over food within 447 food patches for the Sonso chimpanzees and 69 interactions within 421 food patches for the Waibira chimpanzees. Occurrence of contest competition did not differ significantly between communities (LMM: $\beta \pm \text{SE} = 0.355 \pm 0.183$, $X^2 = 3.77$, $p = 0.052$). In both communities, the aggressor was more likely to be male (Sn: 80%, Wb: 59%) than female (Sn: 16%, Wb: 22%; unknown: Sn: 5%, Wb: 19%). High-intensity competition (charges, chases, and attacks) made up 58% of events in Sonso and 51% in Waibira, while low-intensity competition (non-directed displays within the food patch, threats, and displacements) accounted for 42% of events in Sonso and 33% in Waibira (interactions for which we had no data on intensity of competition: Sn: 0%, Wb: 16%).

We found that the occurrence of contest competition over food was better explained by our model that included patch size, feeding party size, and the proportion of males within the party, than it was by the intercept-only null model (likelihood ratio test: $X^2 = 107.61$, df = 9, $p < 0.001$). For both communities, contest competition over food was more likely to occur within larger feeding parties (Sn: $\beta \pm \text{SE} = 1.905 \pm 0.720$, $z = 2.65$, $p = 0.008$, Wb: $\beta \pm \text{SE} = 2.599 \pm 0.794$, $z = 3.28$, $p = 0.001$; Table 6), but patch size was not predictive of aggression for either community. The proportion of males within feeding parties also had no significant effect on the occurrence of aggression. When we ran the model using the proportion of females in place of the proportion of males, we found that this had a stronger effect on contest competition within the Waibira community (interaction between community and proportion of females: $X^2 = 3.96$, df = 1, $p = 0.047$). However, our analysis also suggested a possible interaction between total party size and the proportion of females ($p = 0.083$), so this finding is not conclusive.

Table 4 Variables in and results of a generalized linear mixed model (GLMM) explaining feeding party size in two communities of chimpanzees (Sonso, Waibira) in the Budongo Forest, Uganda. Bold text highlights statistical significance (at $\alpha = 0.05$)

	β	SE	z	p
Dataset: Sonso				
Intercept	1.235	0.177	6.985	< 0.001
Patch size	0.817	0.099	8.212	**< 0.001**
Travel distance	0.128	0.048	2.678	**0.007**
Sex (male)	0.239	0.128	1.873	0.061
Feeding bout length	0.153	0.064	2.390	**0.017**
Food type: ripe fruit	0.023	0.177	0.131	0.896
Food type: seeds	0.564	0.198	2.853	**0.004**
Food type: unripe fruit	0.092	0.189	0.487	0.626
Food type: young leaves	-0.003	0.197	-0.016	0.987
Dataset: Waibira				
Intercept	1.597	0.330	4.840	< 0.001
Patch size	0.576	0.101	5.691	**< 0.001**
Travel distance	0.143	0.046	3.102	**0.002**
Sex (male)	0.098	0.124	0.792	0.429
Feeding bout length	0.190	0.068	2.790	**0.005**
Food type: ripe fruit	− 0.415	0.345	− 1.204	0.229
Food type: seeds	− 0.481	0.386	− 1.246	0.213
Food type: unripe fruit	− 0.492	0.403	− 1.219	0.223
Food type: young leaves	− 0.489	0.361	− 1.355	0.175

Intercept represents the food type 'flower' and the focal sex 'female'. Datasets were analysed in a single model, with results for the Waibira community indicating the nature and extent of any differences between the two datasets

Table 5 Variables in and results of a linear mixed model (LMM) explaining inter-patch travel distances for two communities of chimpanzees (Sonso, Waibira) in the Budongo Forest, Uganda. Bold text highlights statistical significance (at $\alpha = 0.05$)

	β	SE	t	p
Dataset: Sonso				
Intercept	0.710	0.206	3.441	< 0.001
Feeding party size	0.024	0.012	2.104	**0.036**
Sex (male)	− 0.121	0.155	− 0.782	0.442
Feeding bout length	0.402	0.198	2.033	**0.043**
Dataset: Waibira				
Intercept	1.209	0.376	3.215	0.001
Feeding party size	0.034	0.017	2.062	**0.040**
Sex (male)	0.276	0.148	1.871	0.071
Feeding bout length	0.503	0.215	2.340	**0.020**

Results from the variables 'patch size' and food types could not be interpreted in the same manner as those for feeding party size, sex, and feeding bout length, due to their interaction with community and are therefore omitted from the table. Datasets were analysed in a single model, with results for the Waibira community indicating the nature and extent of any differences between the two datasets

Discussion

Across both our study communities, we found strong support for the key predictions of Chapman et al.'s (1995) ecological constraints model: larger parties foraged in larger patches, and the formation of larger parties required chimpanzees to travel further between patches. Our results stand in contrast to previous studies of fission–fusion foragers in which the relationship between party size and patch characteristics did not follow predictions of this model (Stevenson et al. 1998; Pokempner 2009; Ospina 2011; Busia et al. 2016). The difference is likely to be down to our use of a shorter temporal scale and of the foragers' behaviour to quantify resources.

In species with fluid or fission–fusion social systems, foragers are able to readily adjust party size to patch size and, in consequence, daily averages will have little meaning. Previous studies which failed to find predicted correlations between food abundance and daily subgroup size (Stevenson et al. 1998; Pokempner 2009; Ospina 2011) might have simply eliminated all meaningful variation from their samples. Our approach shows that an analysis at the patch level is more appropriate, at least for chimpanzees. Even though our two study communities differed in the floristic composition of their home ranges and food availability (Villioth, 2018; JV et al., unpubl. data), the relationship between party size and patch size was strongly linked to individual patches. Moving beyond daily averages and exploring inter-patch variation in party size, patch size, and travel distance is thus clearly a promising approach that deserves broader application. As it is now possible to consider non-systematic (random) variation of individual foragers within their groups through the use of mixed models (Bolker et al. 2009), this offers a promising approach with which to investigate the dynamic responses of foragers to their changing environments.

Distinct sex differences in party size and travel distances, as reported from other chimpanzee communities (Kibale National Park: Wrangham 2000; Pokempner 2009; Gombe: Williams et al. 2002; Taï forest: Normand and Boesch 2009), were not present for these Budongo Forest chimpanzees. While adult female chimpanzees foraged slightly more often on their own, and in smaller food patches, than did adult males, when these females joined parties, they fed in patches of comparable size to those fed in by males. In the Waibira community, travel distances to food patches tended to differ between males and females but this difference appeared to be driven by particular females who travelled only arboreally during some days of observation, which itself may have been an artefact of lower levels of habituation to human observers. The predictive power of forager sex was low compared to that of

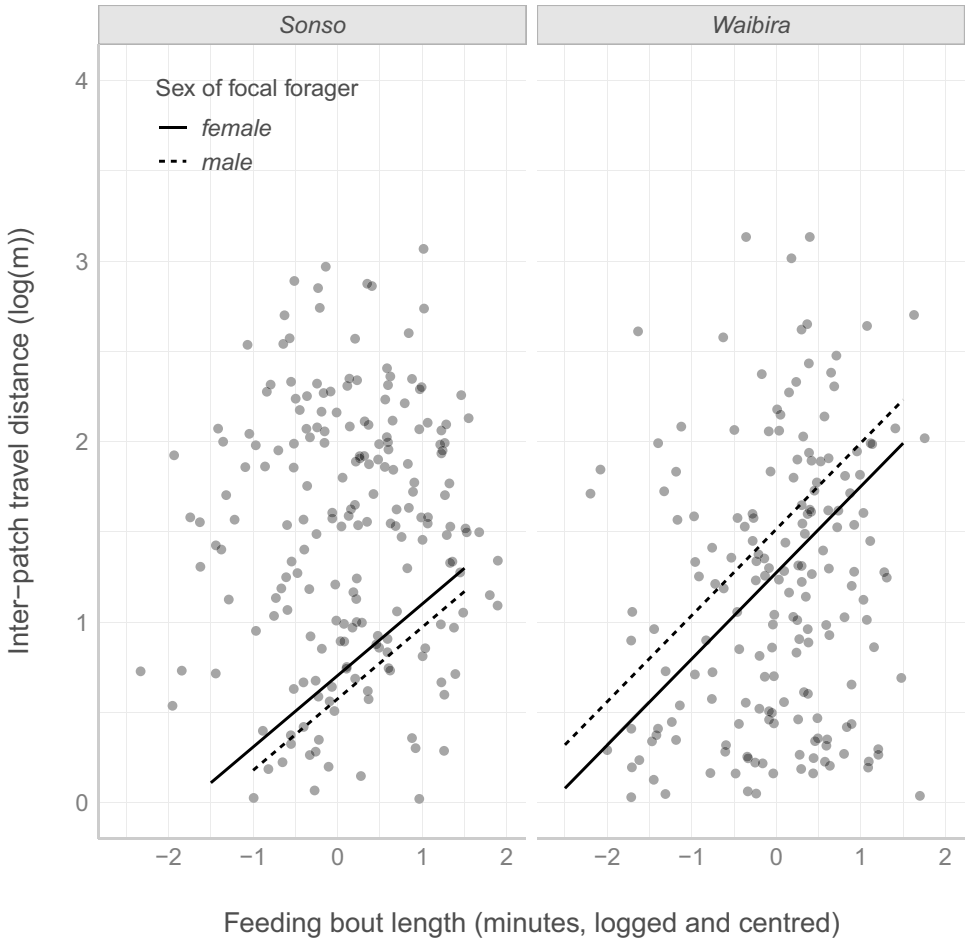

Fig. 4 Relationship between feeding bout length and inter-patch travel for two communities of East African chimpanzees (Sonso, Waibira), as predicted using linear mixed modelling. In both communities, chimpanzees feed for longer in patches that they travelled greater distances to reach

ecological variables in our models of party size and travel distance: male and female chimpanzees foraged in similar ways. This contrast to other studies may reflect differences in food abundance and distribution across chimpanzee communities.

Table 6 Variables in and results of a generalized linear model (GLM) accounting for the occurrence of foraging contest competition in two communities of chimpanzees (Sonso, Waibira) in the Budongo Forest, Uganda. Bold text highlights statistical significance (at $\alpha = 0.05$)

	β	SE	z	p
Dataset: Sonso				
Intercept	−7.924	2.408	−3.291	0.001
Feeding party size	1.905	0.720	2.649	**0.008**
Proportion of males	4.290	3.361	1.276	0.202
Patch size	−0.163	0.425	−0.383	0.701
Dataset: Waibira				
Intercept	−6.828	2.013	−3.391	<0.001
Feeding party size	2.599	0.794	3.275	**0.001**
Proportion of males	3.535	2.948	1.199	0.231
Patch size	−0.412	0.353	−1.166	0.244

Datasets were analysed in a single model, with results for the Waibira community indicating the nature and extent of any differences between the two datasets

Bates and Byrne (2009), examining travel distance and direction between halts of 20 + mins for Sonso community chimpanzees in 2003, found no significant sex differences in the distance travelled between such halts. While Bates and Byrne (2009) did not consider inter-patch distance directly, their findings are broadly congruent with ours, with their 'halts' corresponding in duration to mean patch occupancy in this study (20 + vs ~ 33 and 27 min, Sonso and Waibira respectively). However, we did not replicate their finding that lactating females were significantly more 'food orientated' in their travel than males (84% of 'halts' at feeding locations for lactating females, vs. 68% for males: Bates and Byrne 2009). In our study, 11 of 13 focal females were lactating, yet we found no evidence that this influenced their foraging behaviour differentially from that of males. In part, this difference might be ascribed to the different methods and questions in the two studies, but it may also reflect variation in food supply between the two study periods (with this potentially more restricted for Sonso chimpanzees in 2003). Peripheral females of the Sonso community are more gregarious than in other East African populations

(Reynolds 2005; Emery Thompson and Wrangham 2006) and resources have been characterised as typically abundant (Newton-Fisher et al. 2000), which supports a view that costs of grouping for Budongo Forest chimpanzees are typically lower than elsewhere. Female chimpanzees in this forest might thus in general be less constrained by resource availability and not required, any more than males, to maximise foraging efficiency (as tends to be assumed following Trivers 1972; Wrangham and Smuts 1980). Our data, drawn from two chimpanzee communities with differing resource supplies, indicate that foraging efforts by male and female chimpanzees in this forest are less divergent than has been reported for other chimpanzee populations. Further inter-community comparison, capturing a greater range of ecological conditions (e.g. across multiple study sites), should help elucidate the conditions under which sex-differentiated foraging strategies emerge.

Food-related agonism was observed in a minority of food patches for both of our study communities, but its occurrence increased, as predicted, with party size. In common with other work, we interpret this as evidence for more intense feeding competition in larger parties (Saito 1996; Vogel and Janson 2007; Hanya 2009; Wheeler et al. 2013; Heesen 2014). However, patch size was not predictive of the occurrence of agonism over food, despite a positive relationship between patch size and party size. Thus, it appears that foraging chimpanzees were only partially successful at adjusting the size of their foraging parties to the availability of food, reducing, but not eliminating, consequent contest competition.

Perhaps contrary to expectation, aggressors in food patches were much more likely to be male rather than females for whom feeding competition is typically considered to be more significant: while male chimpanzees are generally the more aggressive (Wrangham and Peterson 1996; Muller 2002; Muller et al. 2007), such aggression usually takes place in the context of male dominance interactions or sexual competition, whereas aggression in female chimpanzees is more frequently related to competition over food (Muller 2002). Although we restricted our analysis to agonistic interactions clearly linked to competition over food, we cannot exclude the possibility that males used feeding-related aggression to reinforce social dominance. However, given that none of our models revealed greater foraging efforts by females, we should acknowledge that male chimpanzees may in fact be more concerned with food acquisition than the current theory suggests. Male ranging and association patterns are not always explained by the search for fertile females but might also reflect the need for male-male interactions (Newton-Fisher 1999, 2014) or efficient foraging in familiar areas (Murray et al. 2008).

This is the first study to test the predictions of Chapman et al.'s (1995) ecological constraints model across two neighbouring chimpanzee communities. Despite differences in vegetation composition, food availability, and overall community size, interactions between party size and patch characteristics followed the predictions of this model for both communities. Our results support the applicability of Chapman et al.'s (1995) ecological constraints model in the study of feeding competition and demonstrate that analysing individual inter-patch movements and parameters of individual food patches is a more appropriate approach for species with high levels of fission–fusion dynamics than the use of daily averages. While the incorporation of new research areas such as nutrient balancing may be beneficial, complete abandonment of socio-ecological models (Thierry 2008) seems misguided. Despite certain limitations (Janson 2000; Koenig and Borries 2006), Chapman et al.'s (1995) ecological constraints model clearly remains a useful tool with which to investigate the impact of foraging competition for socially foraging animals.

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Data availability The datasets generated and analysed during the current study are included in this published article (and its supplementary information).

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval This research complied with regulations set by the Ethics Committee of the University of Kent, the protocols of the Budongo Conservation Field Station, and the legal requirements of Uganda, with permission for fieldwork granted by the Ugandan Wildlife Authority (UWA) and the Ugandan National Council for Science and Technology (UNCST). All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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