NEWS AND PERSPECTIVES

# Seed predation by bonobos (*Pan paniscus*) at Kokolopori, Democratic Republic of the Congo

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**Abstract** We compared the feeding ecology of the Hali–Hali community of bonobos (*Pan paniscus*) at Kokolopori, a new field site in the Democratic Republic of the Congo, between two periods 5 months apart. During the first study period (SP1), bonobos relied heavily on the dry seeds of *Guibourtia* (Caesalpiniaceae), mostly eaten from the ground. The second period (SP2) was characterized by high consumption of ripe tree fruit. Terrestrial herbaceous vegetation (THV) contributed little to the diet in either study period. The low amount of ripe fruit and the high reliance on seeds in the diet during SP1 were associated with high cortisol production and low levels of urinary C-peptide in females, suggesting nutritional stress. However, female gregariousness was not constrained during the fruit-poor period, probably because high seed abundance on the ground ameliorated scramble feeding competition. This is the first description of extensive seed predation by bonobos. It suggests that bonobo feeding ecology may be more similar to that of chimpanzees than previously recognized.

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## Introduction

Primates have two major types of relationship with tree seeds. First, they disperse them (Idani 1986; Tsuji et al. 2010; Lambert 2011). Second, they prey on them (Norconk et al. 1998). Seed predation by great apes is little studied. While its nutritional significance is not well known, some evidence suggests that among primates, tree seeds are principally eaten as part of a broadening of a mainly frugivorous diet during periods of fruit scarcity (e.g., *Ateles*: Wallace 2005). Despite similar patterns having been observed for some chimpanzee (*Pan troglodytes*) populations (Suzuki 1969), tree seeds need not necessarily be regarded as fallback foods (e.g., *Pongo*: Harrison and Marshall 2011), as their nutritional value may be high (Suzuki 1969; Rogers et al. 1990). For example, in Budongo, Uganda, during periods when chimpanzees fed on *Cynometra alexandrii* seeds, females tended to have high levels of ovarian hormones, suggestive of a positive energetic balance (Emery Thompson 2005). The significance of seed eating may therefore depend on the particular tree species and the ecological context of the period during which they are eaten. Here we report that bonobos at a new field site, at Kokolopori, Democratic Republic of the Congo, ate tree seeds extensively during a period when they ate few ripe fruits. Since bonobos have not been previously observed to rely on seeds for a major portion of their seasonal diet, we consider why Kokolopori bonobos ate seeds, and the socio-ecological consequences of seed eating.

We rely on direct observations to quantify dietary composition and gregariousness. To obtain preliminary data on

whether bonobos at Kokolopori experienced energetic stress as a result of changes in diet composition, we use urinary C-peptide of insulin. The level of this molecule, produced during the activation of pro-insulin, has been shown to correlate significantly with dietary quality and energy intake in wild chimpanzees, orangutans (*Pongo pygmaeus*), black-and-white colobus monkeys (*Colobus guereza*), and free-ranging rhesus macaques (*Macaca mulatta*), and with changes in body weight in captive bonobos and two macaque species (*M. mulatta* and *M. fascicularis*) (Sherry and Ellison 2007; Deschner et al. 2008; Emery Thompson and Knott 2008; Emery Thompson et al. 2009; Harris et al. 2010; Higham et al. 2011; Girard-Buttoz et al. 2011). It is therefore a promising new tool for assessing energetic condition in wild primates that fits the aims of our study. Since cortisol has often been used in primate field studies to evaluate levels of physiological stress brought about by ecological factors, social factors, or a combination of the two (e.g., Emery Thompson et al. 2010), we also use glucocorticoid production to determine whether physiological stress increased or decreased during a period of seed predation compared to a period of ripe fruit eating.

## Methods

### Study site and subjects

A.V.G. conducted field work at Kokolopori, Democratic Republic of the Congo, during two study periods: SP1 was 8th November to 20th December 2006; SP2 was 18th June to 26th July 2007. Observations were based at Nsondo Camp (0°12′N, 22°51′E), which was set up by A.L.L. and lies within Kokolopori Bonobo Reserve approximately 30 km to the east of the bonobo study site at Wamba. The study subjects were members of the Hali–Hali bonobo community. We observed and identified a total of eleven adult and adolescent members of the Hali–Hali community (3 males, 5 mothers, and 2 nulliparous females in both periods, plus one further nulliparous female in 2007). Additionally ca. 5 juveniles and 5 infants were seen on a regular basis although they were not fully identified. Long-term observations by A.L.L. suggest that the ca. 21 individuals seen in this study represent the entire Hali–Hali community, but this awaits confirmation.

### Data collection

#### Feeding behavior

We recorded the feeding of bonobos using instantaneous party scan sampling at 15-min intervals (Altmann 1974). If any food was eaten by any of the bonobos in sight on the sampling point, we noted the name of the food and the vegetative part eaten. For each feeding scan, we also noted whether party members fed on the ground, in the tree canopy, or both. We identified plants with the help of local field assistants and information from Wamba (Idani et al. 1994), and verified identities of the main food species against herbarium specimens at Royal Botanic Gardens, Kew and the Harvard University Herbaria. Daily diet composition was calculated as the percent of scans in which bonobos in the party fed on a particular food item from the total number of feeding scans recorded on that day. Dietary scores produced with this method were highly correlated with data on individual food intake obtained by the focal sampling of chimpanzee behavior at Kanyawara (Gilby et al. 2010). To maximize the sample size of observations lasting for at least half of the daylight hours, only observations ≥6 h in duration were used in this analysis (range 6–12.75 h). In SP1 we collected 16 observation days that satisfied this criterion (mean ± SEM hours per day: 10.2 ± 0.5 h/day). SP2 yielded 39 observation days (11.4 ± 0.2 h/day). The data-set on dietary intake thus comprises 608 observational hours spread over 55 days.

### Party composition

We noted party composition continuously, including all independent individuals leaving or joining parties. Party size refers to the number of adults and adolescents travelling together within 50 m of each other, or arriving at the same feeding location within 15 min. See the Electronic supplementary material (ESM) for details on defining a feeding location. We calculated mean daily party size using party counts made following all new fission or fusion events on days when we were confident that the entire party had been observed. There were 58 parties recorded in this way on 34 days (24 in SP1, 10 in SP2). Observation times on the days for which we report mean party size varied between 50 min and 12 h (mean ± SEM hours per day: 5.6 ± 0.6 h/day). We refer to the proportion of individuals in a given party from the total community as the relative party size (Boesch 1996).

### Urine sampling and analysis

We collected first-morning urine voids on disposable plastic bags or pipetted urine off vegetation when it was clear that only one individual contributed to that sample. Samples were stored on filter paper in the field and analyzed for C-peptide, cortisol and creatinine within 6 months of collection using standard laboratory protocols at the Primate Reproductive Ecology Laboratory at Harvard University. More details on sample collection, storage and urinalysis are provided in the ESM.

## Data analysis

We analyzed data on dietary composition and party size with Mann–Whitney $U$ tests using each observation day as a unit of analysis. We log-transformed all endocrine data and tested them for differences between study periods with a two-sample $t$ test assuming unequal variance. Since we collected urine very early in the morning while visibility was poor, we could not normally record individual identity, despite being able to assign to age–sex class. We therefore present our results for adults by sex. We conducted all tests using two-tailed probabilities in PASW Statistics 18 with a significance level of 0.05.

## Results

### Feeding ecology

Ripe fruit accounted for over half of all feeding observations (53.6%, Table 1). Terrestrial herbaceous vegetation (THV) and young arboreal leaves comprised only minor portions of the diet. Tree seeds were an important component of the diet, particularly during SP1 (57.3%; Tables 1, 2). Bonobos at Hali–Hali were also seen to feed on meliponine honey, dead wood, truffles, colonial spiders, and the tissue of a holoparasitic plant (*Chlamydophytum aphyllum*). They once attempted to catch a scaly-tailed flying squirrel (Anomaluridae), but we did not see meat consumption. To our knowledge, holoparasitic plants (Georgiev et al. 2010) and colonial spiders are new dietary records for bonobos.

Bonobos spent less time eating ripe fruit pulp in SP1 (28.5%) than in SP2 (71.3%, Mann–Whitney, $z = 4.9$, $N_1 = 16$, $N_2 = 39$ days, $p < 0.001$, Table 2). They also consumed a smaller number of different fruit species in SP1 (6) than in SP2 (24; Tables 1, 2). By contrast, the contribution of dry seeds to the diet was higher in SP1 (57.3%) than SP2 (18.5%; $z = -3.9$, $p < 0.001$). There were no significant differences between study periods in the dietary contribution of either THV ($z = -1.6$, $p = 0.12$) or young arboreal leaves ($z = -1.7$, $p = 0.09$).

Across all observation days, the daily dietary proportions of fruit and dry seeds were inversely correlated (Spearman $\rho = -0.8$; $N = 55$ days; $p < 0.001$). A weaker but similar correlation occurred between the daily dietary proportions of ripe fruit and THV (Spearman $\rho = -0.41$; $N = 55$; $p = 0.002$), whereas there was no correlation between the consumption of THV and young arboreal leaves (Spearman $\rho = 0.12$; $p = 0.4$) or between ripe fruit and young arboreal leaves (Spearman $\rho = -0.07$; $p = 0.6$).

One species of seed dominated the diet during SP1. *Guibourtia demeusei* is a swamp-forest upper-canopy tree

that produces seeds in dry dehiscent single-seed pods. In early November of SP1, *Guibourtia* seeds were available in trees, but few had fallen to the ground. At this time, bonobos ate *Guibourtia* seeds in the tree crowns. During November the seeds matured and fell in large numbers to the ground, where bonobos continued to eat them. As a result, ground foraging was much more common overall during SP1 than arboreal foraging for bonobos eating *Guibourtia* seeds (79.7% of 207 feeding observations with ground foraging vs. 20.3% for arboreal or mixed ground/ arboreal). During SP1, *Guibourtia* alone comprised 57% of all feeding observations. By contrast, during SP2, no *Guibourtia* seeds were recorded in the diet, though dry seeds of four other tree species still comprised 18.5% of the diet (Table 1).

### Gregariousness of Hali–Hali bonobos

The number of adults per party averaged 5.8–5.9 in both study periods (Table 2). There was no difference between study periods in mean party size (Mann–Whitney, $z = -0.4$, $N_1 = 24$, $N_2 = 10$ days, $p = 0.7$), relative party size ($z = -1.1$; $p = 0.3$), female party size ($z = 0.153$; $p = 0.9$), relative female party size ($z = -0.9$; $p = 0.4$), male party size ($z = -1.3$; $p = 0.2$) or relative male party size ($z = -1.4$; $p = 0.2$).

### Physiological status

Data from females indicated substantial differences in both C-peptide and cortisol status between study periods. In SP1, during the period of heavy seed consumption, C-peptide levels (624.2 pg/mg Cr) were relatively low, averaging 47.8% of those in SP2 (1306.2 pg/mg Cr, $t = -2.5$, $df = 36$, $N_1 = 17$, $N_2 = 26$ samples, $p = 0.02$, Table 2), indicating decreased energy balance in SP1. By contrast, cortisol levels in SP1 (213.3 ng/mg Cr) were relatively high, averaging 305.6% of those in SP2 (69.8 ng/mg Cr; $t = 3.9$, $df = 26$, $N_1 = 16$, $N_2 = 24$, $p = 0.0006$). Similar absolute differences occurred in male urines, but these were not statistically significant, presumably due to the small sample size (Table 2).

## Discussion

We observed bonobo behavior and physiology during two 2-month periods characterized by markedly distinct dietary composition. Yet, in both periods, tree seeds (mostly from Caesalpiniaceae) were an important part of the diet, occurring in between 15.9 and 67.7% of monthly scans. Tree seeds have not been reported to occupy such a large part of bonobo diets. Our study therefore extends the

**Table 1** Diet of the Hali–Hali bonobos during the four study months (Nov–Dec 2006 and June–July 2007)

| Food type/species | Family | Monthly dietary contribution (% of feeding observations) | | | | Total (%) |
|---|---|---|---|---|---|---|
| | | Nov 2006 | Dec 2006 | June 2007 | July 2007 | |
| Ripe fruit | | 27.4 | 30.1 | 55.7 | 76.5 | 53.6 |
| *Uapaca sp.* | Euphorbiaceae | 0.0 | 0.0 | 17.0 | 13.3 | 9.4 |
| *Sanitria trimera* | Burseraceae | 0.0 | 0.0 | 16.6 | 13.3 | 9.3 |
| *Pycnanthus marchalianus* | Myristicaceae | 0.0 | 0.0 | 12.6 | 11.3 | 7.6 |
| *Dialium sp. 1* | Caesalpiniaceae | 24.4 | 15.3 | 0.0 | 0.3 | 7.2 |
| *Annonidium mannii* | Annonaceae | 0.0 | 0.0 | 1.6 | 13.0 | 5.2 |
| *Oxyanthus unilocularis (*vine*)* | Rubiaceae | 0.0 | 0.0 | 0.4 | 5.9 | 2.3 |
| *Dialium sp. 2* | Caesalpiniaceae | 1.8 | 8.2 | 0.0 | 0.0 | 1.9 |
| *Garcinia punctata (?)* | Guttiferae | 0.0 | 0.0 | 0.8 | 3.1 | 1.4 |
| *Ficus spp. (2 spp.)* | Moraceae | 1.2 | 4.4 | 0.8 | 0.0 | 1.3 |
| Other 19 spp. | | 0.0 | 2.2 | 5.9 | 16.1 | 8.0 |
| Dry seeds | | 67.7 | 56.8 | 28.5 | 15.9 | 36.0 |
| *Guibourtia demeusei* | Caesalpiniaceae | 64.6 | 55.2 | 0.0 | 0.0 | 21.7 |
| *Leonardoxa romii* | Caesalpiniaceae | 0.0 | 0.0 | 26.1 | 7.6 | 9.8 |
| *Brachystegia laurentii* | Caesalpiniaceae | 2.4 | 1.1 | 1.2 | 3.1 | 2.1 |
| *Gilbertiodendron dewevrei* | Caesalpiniaceae | 0.0 | 0.0 | 0.4 | 3.1 | 1.3 |
| *Parkia bicolor* | Mimosaceae | 0.0 | 0.5 | 0.8 | 2.0 | 1.0 |
| *Acacia sp.* | Mimosaceae | 0.6 | 0.0 | 0.0 | 0.0 | 0.1 |
| Terrestrial herbaceous vegetation (5 spp. of herbs, 1 tree sapling; petioles and pith) | | 2.4 | 5.5 | 10.3 | 0.6 | 4.4 |
| Young arboreal leaves | | 1.2 | 7.7 | 1.2 | 3.1 | 3.2 |
| *Leonardoxa romii* | Caesalpiniaceae | 0.0 | 2.7 | 1.2 | 2.0 | 1.6 |
| *Scorodophloeus zenkeri* | Caesalpiniaceae | 0.0 | 4.9 | 0.0 | 0.6 | 1.2 |
| Other 3 spp. | | 1.2 | 0.0 | 0.0 | 0.6 | 0.4 |
| Fungi (truffles) | | 0.0 | 0.0 | 2.4 | 2.0 | 1.4 |
| Dead wood (vine) | | 0.6 | 0.0 | 0.8 | 1.7 | 0.9 |
| Unknown food item | | 0.0 | 0.0 | 1.2 | 0.0 | 0.3 |
| Honey (meliponine) | | 0.0 | 0.0 | 0.0 | 0.3 | 0.1 |
| Plant parasitic tissue (*Chlamydophytum aphyllum*) | Balanophoraceae | 0.6 | 0.0 | 0.0 | 0.0 | 0.1 |
| *N* 15-min feeding scans observed | | 164 | 183 | 253 | 353 | 953 |

Percent of feeding observations refers to the total number of 15-min scan points with feeding observed. Only days with ≥6 observation hours are included. Items that were seen eaten on days with <6 observation hours are not included in this table (e.g., colonial spiders). All named plants are trees unless noted otherwise

range of diet types known for bonobos. Chimpanzees have been previously recorded eating tree seeds (especially Caesalpiniaceae) at high concentrations in some months (Wrangham 1975; Goodall 1986; Reynolds 2005). At Budongo, the seeds of *Cynometra alexandrii* are described as being one of the "important foods" during a dry season lasting between December and March, a period characterized by a scarcity of fruiting figs (Sugiyama 1968). Sugiyama (1968) argued that the pattern of use of *C. alexandrii* seeds shown by the Budongo chimpanzees was similar to the reliance of savannah chimpanzees on the hard seeds of other Caesalpiniaceae trees during dry months (Suzuki 1969), and could thus be an important fallback food that buffers them against food shortages in

some years. This interpretation fits well with our observations of seed eating by the bonobos during the months of November and December at Kokolopori, and should be explored further when long-term data on feeding ecology at Hali–Hali become available. Another unexpected finding was that the consumption of tree fruit by the bonobos varied twofold between the two study periods. This raised the question of whether seasonal fruit shortages occur regularly at Hali–Hali, a topic that requires future phenological observations. In summary, our observations on seed eating and variance in ripe fruit intake between different months indicate a closer similarity in the plant diets of bonobos and chimpanzees then previously recognized.

**Table 2** Dietary quality, gregariousness and endocrine profiles of the Hali–Hali bonobos during the two study periods

| Measures | SP1 (Nov–Dec 2006) Mean (SEM) | SP2 (June–July 2007) Mean (SEM) |
|---|---|---|
| Dietary characteristics ($N_1 = 16$; $N_2 = 39$ days with more than 6 direct observational hours) | | |
| Number of ripe fruit species eaten | 6 | 24 |
| Mean daily ripe fruit consumption (%)* | 28.5 (5.1) | 71.3 (3.3) |
| Mean daily dry seed consumption (%)* | 57.3 (7.9) | 18.5 (2.3) |
| Mean daily THV consumption (%) | 5.9 (2.9) | 3.9 (1.5) |
| Mean daily arboreal leaf consumption (%) | 7.9 (3.0) | 2.3 (0.8) |
| Gregariousness measures ($N_1 = 24$; $N_2 = 10$ days with mean party size) | | |
| Mean adult party size | 5.9 (0.3) | 5.8 (0.6) |
| Mean female party size | 4.2 (0.2) | 4.4 (0.6) |
| Mean male party size | 1.7 (0.1) | 1.5 (0.1) |
| Mean relative adult party size (%) | 59.3 (2.8) | 53 (6.2) |
| Mean relative female party size (%) | 60.1 (3.1) | 54.7 (7.3) |
| Mean relative male party size (%) | 57.4 (3.8) | 48.3 (4.4) |
| Endocrine measures | | |
| Urinary C-peptide levels: males, females, unknown samples (pg/mg Cr), $N_1 = 43$; $N_2 = 44$ | 1049.0 (177.0) | 1603.6 (328.2) |
| Mean female C-peptide levels (pg/mg Cr)*, $N_1 = 17$; $N_2 = 26$ | 624.2 (84) | 1306.2 (254.2) |
| Mean male C-peptide levels (pg/mg Cr), $N_1 = 4$; $N_2 = 6$ | 594.7 (165.1) | 1657.1 (542.3) |
| Cortisol levels: males, females, juveniles and unknown samples (ng/mg Cr)*, $N_1 = 23$; $N_2 = 41$ | 196.2 (32.2) | 75.5 (6.5) |
| Mean adult female cortisol levels (ng/mg Cr)*, $N_1 = 16$; $N_2 = 24$ | 213.3 (41.1) | 69.8 (8.7) |
| Mean adult male cortisol levels (ng/mg Cr), $N_1 = 4$; $N_2 = 6$ | 157.2 (49.4) | 87.2 (10.7) |

$N_1$ and $N_2$ refer to the sample size for SP1 and SP2, respectively. Significant differences between study periods are indicated with an asterisk (*). See text for details on statistics

If either ripe fruit or seeds are preferred to the other, we expect that the preferred items should be more beneficial and associated with a more positive energy balance and less physiological stress. Our finding that ripe fruit diets were associated with high C-peptide and low cortisol therefore suggest that fruits were a more beneficial food item than tree seeds. The fact that our urine samples could not be identified to individual means the physiological data are preliminary, but our results clearly suggest that ripe fruits are preferred and that tree seeds are eaten when ripe fruits are scarce.

Bonobo females tend to be more gregarious than chimpanzee females (Furuichi 2009). One of the explanations proposed for this species difference is that bonobos have more seasonally stable and abundant fruit supplies than chimpanzees do (White and Wrangham 1988; Chapman et al. 1994; Hohmann et al. 2006). Another is that bonobos have greater access to THV than chimpanzees, allowing them to forage in a regime of low scramble competition (Wrangham 2000). The herbs available to bonobos have also been shown to be low in fiber and high in protein relative to similar plant foods in chimpanzee habitats (Sommer et al. 2010). Our data, however, show that even though ripe fruit was not eaten at uniformly high levels all year, and even though THV contributed little to

the diet, gregariousness in the study community did not change. None of the prior explanations is therefore easily applicable to Kokolopori bonobos. Nevertheless, because bonobos often fed on tree seeds collected from the ground, scramble competition was apparently low, allowing female gregariousness to remain high. Our observations thus suggest that the mechanisms allowing bonobos to forage in relatively stable parties are more variable than previously considered.

Despite the short duration of this investigation, the contrast in dietary composition between our two study periods, together with the fact that extensive seed eating has not yet been recorded at other sites, suggests that much ecological variation in bonobos remains to be described and explained. Establishing multiple conservation areas across the DRC where bonobos are protected by involving the local community, as is the case at Kokolopori, can be expected to improve not just the survival prospects for bonobos but also our ability to understand the range of their ecological and behavioral adaptations.

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