



Elevated activity in adult mountain gorillas is related to consumption of bamboo shoots

CYRIL C. GRUETER,* MARTHA M. ROBBINS, DIDIER ABAVANDIMWE, SYLVIA ORTMANN,
ANTOINE MUDAKIKWA, FELIX NDAGIJIMANA, VERONICA VECELLIO, AND TARA S. STOINSKI

School of Anatomy, Physiology and Human Biology, The University of Western Australia, Crawley, Western Australia 6009, Australia (CCG)

Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany (CCG, MMR)

The Dian Fossey Gorilla Fund International, Atlanta, GA 30315, USA (CCG, DA, FN, VV, TSS)

Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, 10315 Berlin, Germany (SO)

Department of Tourism and Conservation, Rwanda Development Board (RDB), Kigali, Rwanda (AM)

Zoo Atlanta, Atlanta, GA 30315, USA (TSS)

* Correspondent: cyril.grueter@uwa.edu.au

Eastern gorillas (*Gorilla beringei*) are among the few mammal species that seasonally consume large quantities of young bamboo shoots, which are a rich source of energy. Here, we document how the consumption of bamboo shoots coincides with changes in behavior of adult mountain gorillas (*Gorilla beringei beringei*) monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center in Volcanoes National Park, Rwanda. We offer a preliminary analysis of possible mechanisms underlying this behavioral change by measuring energy intake rates and the presence of cyanide and alcohol—ingredients potentially associated with increased activity levels—in fresh bamboo shoots. The percentage of bamboo shoots in the diet of gorillas was correlated positively with the rate of play behavior shown by adults in 2 of the 3 study groups. Play behavior was not the result of better weather conditions and also did not reflect the availability of spare time. Rather, there is some, but not consistent, evidence for a link between energy intake rates and play behavior of adults. Cyanide was not detected in young bamboo shoots, and the presence of alcohol remains inconclusive, albeit unlikely. In sum, our results show that consumption of a high-quality food can have a direct influence on the activity budget (and by extrapolation energy expenditure) of mountain gorillas through increased rates of play behavior. However, the physiological aspects underlying this elevated activity warrant further investigation.

Key words: bamboo, energy intake, *Gorilla beringei*, play behavior, Volcanoes National Park

Food selection has direct consequences on the nutritional status of animals and indirectly affects their health and fitness (Altmann 1998). Food choices thus reflect attempts to balance nutritional gains versus potential costs (antifeedants, high fiber, etc.) from particular plants (Raubenheimer and Simpson 1997). Bamboo shoots (Poaceae, subfamily Bambusoideae) are a potentially beneficial dietary item because they are rich in several macro- and micronutrients including protein (amino acids), carbohydrate, minerals, and several vitamins; they also have a low fiber and tannin/phenol content (Waterman et al. 1983; Chongtham et al. 2011; C. C. Grueter, pers. obs.). They also contain potentially toxic cyanogenic glycosides (Haque and

Bradbury 2002; Ballhorn et al. 2009), which break down upon disruption of plant cells to form hydrogen cyanide (Møller and Seigler 1999). Release of cyanide may well be an adaptive response on part of the plant to deter herbivory (see Nahrstedt 1988).

Bamboo shoots constitute an important food resource for humans (Satya et al. 2010) and also are used as fodder for livestock (Mekuriaw et al. 2011). There are a few mammal species that are specialized in eating bamboo (shoots), including giant pandas (*Ailuropoda melanoleuca*—Schaller et al. 1985) and bamboo rats (*Dactylornys dactylinus*—Emmons 1981); among primates, bamboo shoots feature importantly on the menu of

eastern gorillas (*Gorilla beringei*—Casimir 1975; Fossey and Harcourt 1977; Yamagiwa et al. 2005), bamboo lemurs (*Hapalemur* spp.—Glander et al. 1989), snub-nosed monkeys (*Rhinopithecus bieti*—Grueter et al. 2009), golden monkeys (golden guenons, *Cercopithecus mitis kandti*—Twinomugisha and Chapman 2008), Bale monkeys (*Chlorocebus djamdjamenensis*—Mekonnen et al. 2010), a population of Assamese macaques (*Macaca assamensis*—Huang et al. 2015), and to a lesser degree, golden langurs (*Trachypithecus geei*—Chetry et al. 2010) and owl-faced monkeys (*Cercopithecus hamlyni*—Kaplin et al. 2014). How primates alleviate the potentially toxic effects of cyanide ingestion is unknown.

Mountain gorillas (*Gorilla beringei beringei*) in the Virunga Volcanoes are almost exclusively herbivorous and their diet does not vary seasonally with the single exception of bamboo shoots which are available only a few months per year (Fossey and Harcourt 1977; Vedder 1984; Grueter et al. 2014). The local bamboo plant (*Yushania alpina*) is geographically restricted to the bamboo zone, which is generally concentrated along the park boundary at lower altitudes than other vegetation types. Bamboo usually produces new shoots during 2 seasons that coincide with periods of high rainfall, October to early January and March to late May to early June (Fossey and Harcourt 1977; Vedder 1984; McNeilage 1995; Grueter et al. 2014), but it may sometimes skip shoot production seasons (Watts 1998). The seasonal presence of bamboo shoots affects habitat use of virtually all gorilla groups whose home ranges encompass the bamboo zone, including groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center, with some groups spending up to 90% of their time in the bamboo zone during peak productivity and feeding almost exclusively on shoots (Watts 1998; Grueter et al. 2014).

There have been anecdotal observations of gorillas “getting drunk on bamboo” (e.g., Moulard 2009), which could more scientifically be referred to as an increased level of playfulness and activity, influencing their energy budget through increased energy expenditure. Here, we aim to empirically substantiate a link between the frequency of bamboo shoots in the diet of gorillas and rates of a particular social behavior, specifically play. We use play involving adult individuals (adult–adult or adult–immature play)—a generally rare behavior in mountain gorillas (C. C. Grueter and M. M. Robbins, pers. obs.; Watts and Pusey 1993)—as a surrogate for the manifestation of elevated activity. The relationship between play behavior and bamboo eating could be mediated by the high energy content of bamboo shoots. Levels of energy balance derived from measurements of urinary C-peptides are higher in months when the Virunga gorillas heavily use the bamboo zone and subsist largely on bamboo shoots (Grueter et al. 2014). Western gorillas (*Gorilla gorilla*) increase their playing activity during the high fruit season when they feed heavily on energy-rich fruit (Masi et al. 2009), and this includes even adult individuals (S. Masi, Muséum National d'Histoire Naturelle & Musée de l'Homme, Paris, pers. comm.). In other primates and non-primates, seasonality in resource availability has been shown to impact play behavior. For example, Stone (2008) showed that play behavior

in immature squirrel monkeys (*Saimiri sciureus*) was reduced in times of low fruit availability, and Sommer and Mendoza-Granados (1995) reported for male bands of Hanuman langurs (*Semnopithecus* sp.) a dramatic increase in play rates during periods of increased food availability in the monsoon season. In immature vervet monkeys (*Chlorocebus pygerythrus*), play was entirely absent from the immature social repertoire during the energetically demanding dry season (Lee 1984). In meerkats (*Suricata suricatta*) and ground squirrels (*Urocitellus beldingi*), food supplementation led to elevated rates of play (Nunes et al. 1999; Sharpe et al. 2002). We therefore test if play behavior in adult mountain gorillas is related to the high levels of energy they derive from bamboo consumption. The alternatives—that intoxication through increased levels of cyanide and/or alcohol found in bamboo consumption triggers behavioral changes—cannot be directly addressed here, but we do provide preliminary data on alcohol and cyanide content in bamboo shoot samples collected in the field.

A comprehensive assessment of the correlates of play behavior also needs to rule out the effects of possible confounds. Weather conditions can have an influence on play behavior. For example, in golden snub-nosed monkeys (*Rhinopithecus roxellana*), the time infants spent playing was correlated positively with ambient temperature (Li et al. 2011). Although temperature does not vary much across the year in the Virungas, rainfall does; given that social behavior in primates often has been shown to decrease with rainy weather (e.g., Majolo et al. 2013), we predict that play behavior by adults will be correlated negatively with rainfall. Activity budgets also can constrain play behavior. Dunbar et al. (2009) proposed that once primates have fulfilled their time commitments to essential activities, some of the remaining time represents “free resting time” that can be allocated to activities such as socializing. Play behavior may thus reflect the availability of free resting or spare time, so we expect more play behavior by adults in times of decreased feeding and traveling activity, indicating satiation and lack of nutritional stress; such a trade-off between foraging demands and play behavior has been documented in western gorillas and squirrel monkeys (Stone 2008; Masi et al. 2009). We predict a negative correlation between play behavior of adults and combined time spent feeding and traveling.

In the following, we assess whether rates of occurrence of an unusual and energetically costly behavior in the repertoire of mountain gorillas—play involving adults—vary as a function of intake of an ephemeral resource—bamboo shoots. We also explore possible mechanisms underlying this behavioral change by measuring energy intake rates and the presence of cyanide and alcohol—ingredients potentially associated with increased activity levels—in this food resource.

MATERIALS AND METHODS

Study site and subjects.—We evaluated play behavior of adult gorillas in Volcanoes National Park in northwest Rwanda, a high-altitude site (approximately 2,500–4,500 m.a.s.l.) that is characterized by a mosaic of vegetation communities including

bamboo forest, *Hagenia*-dominated woodlands, and afroalpine vegetation, as described by Grueter et al. (2013), McNeillage (2001), and Plumtre (1991). Annual rainfall in 2010 amounted to 2,076 mm (rainfall data were collected at the field station in Bisate in the vicinity of the park). We collected behavioral data between January and December 2010; 2010 was a year with a single massive season of bamboo growth lasting from October to December. At the beginning of the year, there also were some leftover bamboo shoots from the previous season (i.e., end of 2009).

We collected data in 3 gorilla groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center (Pablo, Bwenge, Ntambara). Pablo and Ntambara were multimale groups (with 6 silverbacks in Pablo and 3 silverbacks in Ntambara), while Bwenge was a single-male group. The number of weaned individuals across the study period averaged 38 in Pablo, 7 in Bwenge, and 9 in Ntambara. The number of adult females (> 8 years of age) averaged 12 in Pablo, 6 in Bwenge, and 4 in Ntambara (see Supplementary Data SD1 for a list of all individuals present in the 3 groups at the time of the study). No major changes in the composition of the study groups occurred during the study period.

Behavioral observations.—We conducted focal animal sampling using 2 different protocols. The first protocol consisted of 30-min sessions during which we recorded all food intake of adult females (aged 8 years or more; details below). The second protocol included 50-min focal observation sessions of individuals of all age–sex classes (except infants) during which we recorded all instances of dyadic play bouts involving at least 1 adult individual on an opportunistic basis, i.e., the focal animal was not always one of the play partners. We operationally defined play as an individual engaging in wrestling, chasing, or mock-biting with another individual. Play can be distinguished from display behavior (i.e., giving an excited directional or nondirectional performance of chest beating, hooting, smashing/dragging plants, pounding the ground, symbolic feeding, or some combination of these activities) by the affiliative manner of the interaction: a play face (open mouth, not displaying teeth) and soft play chuckle vocalizations (Fossey 1972; Harcourt et al. 1993). As part of the second protocol, we also took instantaneous scans of the focal individual at 10-min intervals during which the activity (feed, rest, travel, groom, etc.) of the focal animal and any food items being consumed by that individual were recorded. The mean observation time per individual using the first protocol was 28.5 h. The mean observation time per individual using the second protocol was 40.4 h.

Energy intake.—We estimated food intake by counting the number of predefined food units consumed by a focal animal during a timed feeding bout, which we defined as the time when the individual commenced and terminated feeding. A food unit refers to a certain dimension of a plant part such as 1 whole blackberry or a 20-cm segment of a thistle stem or a handful of *Galium* vines. We transformed intake of units to energy intake by multiplying the item-specific energy value (see below) with number of units eaten. We collected, dried, and weighed 50

samples of each food unit, and based on these weights calculated the mean weight for each food unit.

For energy content analyses, we collected about 400 g (wet mass) of all major food plants in areas used by the gorillas for feeding. We processed the samples in a manner similar to the feeding behavior of the gorillas (Rothman et al. 2006) and collected only the consumed parts of the plant. We weighed all items instantly after collection and dried them overnight at 40–45°C using a fruit dryer. We stored samples in paper bags within small jars or Ziploc bags filled with silica gel.

We determined macronutrient content of all samples at the Nutritional Lab of the Leibniz Institute for Zoo and Wildlife Research (Berlin, Germany). Prior to analysis, we ground all samples with an IKA A11 basic mill (IKA-Werke GmbH and Co. KG, Staufen, Germany) and determined dry matter content (DM) by drying a subsample at 105°C overnight. All nutrient data are expressed as % dry matter. We used subsamples of each sample to determine (in duplicate) macronutrient contents using standard techniques. We determined crude ash by burning a subsample at 550°C for 6 h in a muffle furnace. We extracted lipids with ethyl ether using a fully automatic Soxhlet system (Soxtherm; Gerhardt Laboratory Systems, Königswinter, Germany). Following Van Soest et al. (1991), we determined neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) sequentially from each sample using an Ankom Fiber Analyser 220 (Ankom Technology, Macedon, New York). We determined nitrogen by complete combustion (Dumas combustion) at high temperature (about 950°C) in pure oxygen with a Rapid N III analyzer (Elementar Analyser Systeme GmbH, Hanau, Germany). For conversion to protein, we used the Kjeldahl determination: crude protein (%DM) = 6.25 × N (%DM).

We quantified total energy content of foods by estimating the amount of energy assimilated from the nutrient contents of forage (Stacey 1986; Conklin-Brittain et al. 2006; Ortmann et al. 2006). We calculated the metabolizable energy of foods with the following standard conversion factors (or physiological fuel values). Based on dry matter, we used 4 kcal/g for crude protein (CP) and total nonstructural carbohydrates (TNC) and 9 kcal/g for lipids (L—National Research Council 2003), and 1.6 kcal/g for NDF (Conklin-Brittain et al. 2006). For each food item, we calculated predicted metabolic energy (PME) per gram of dry matter following N'guessan et al. (2009):

$$\text{PME(kcal / g)} = (4 \times \% \text{CP} + 4 \times \% \text{TNC} + 9 \times \% \text{L} + 1.6 \times \% \text{NDF}) / 100$$

For subsequent calculations, we transformed kilocalories (kcal) into kilojoules (kJ). We determined TNC, i.e., digestible carbohydrates, as follows (Conklin-Brittain et al. 2006):

$$100\% \text{TNC} = 100 - \% \text{L} - \% \text{CP} - \% \text{total ash} - \% \text{NDF}$$

We obtained intake of each food item (in grams) in each bout by multiplying the number of specific food units consumed by their respective dry weight. We then derived energy intake per bout for each diet item from the energy content (kJ/g) of specific plant parts. We divided total kJ consumed for each female

and month by total time spent feeding (in min) in that month. We then averaged values across females to yield a monthly mean.

Alcohol and cyanide analyses.—On 13 May 2015, we collected 7 young bamboo shoots (*Y. alpina*) in 1 area of the bamboo zone of Volcanoes National Park, which is frequented by the gorilla groups monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center. The shoots were of more-or-less equal length (approximately 80 cm). We used a commercial test strip, Cyantesmo (Macherey-Nagel, Dueren, Germany), to provide a semiquantitative assessment of the amount of hydrogen cyanide present (Rella et al. 2004; Yamashita et al. 2010). We cut bamboo shoots into small pieces and placed them in Ziploc bags or plastic tubes. Within 1 h of collection, we added 2–3 drops of distilled white vinegar to the sample to precipitate detection of hydrogen cyanide. Vinegar (a medium-strong acid) has been proven to be a good substitute for sulfuric acid (Yamashita et al. 2010) recommended by the manufacturer. We then added strips of test paper to the sample and recoded changes in paper color, indicative of the amount of cyanide in the sample, after 5 min, 1 h, 5 h, and 24 h by comparing the test strips against a control strip. We repeated the testing procedure with 4 different shoots.

We determined the presence of alcohol in bamboo sap with Chematics ALCO-Screen test strips. ALCO-Screen will react with methyl, ethyl, and other short-chain alcohols. We wetted test pads with bamboo juice and recorded the resulting color of the pad after 2 min. According to the manufacturer, when testing a beverage for alcohol (as opposed to saliva), the color chart provided does not apply and only strong color change to very dark brown or black should be used as evidence for the presence of alcohol. We repeated the testing procedure with 7 different shoots. We confirmed proper performance of the test by testing a mixture of 4 drops of 80 proof distilled spirits in 237 ml of water. The result was equal or higher than the 0.04% color block.

Statistics.—We calculated the percentage of bamboo shoots in the diet and the percentage of time spent feeding and moving on a monthly basis from instantaneous scans based on the total number of feeding and bamboo feeding records, respectively, for all individuals combined in month *i* divided by total number of scans in month *i*. We computed play rates in 2 ways. First, we calculated individual-based monthly rates of play by dividing the number of play bouts for each adult individual in any given month by the focal observation time for that individual in that month. Here, only play bouts observed during focal sampling were used. For subsequent analysis, we averaged monthly rates across individuals in each group. Second, we obtained monthly rates of play by dividing the total number of play bouts involving adults observed in a month by the total group observation time in that month. The second approach allows the inclusion of opportunistic observations (those in addition to data collected during focal sessions), thus rendering the sample size larger. Both methods produced similar results.

We refrained from conducting multiple regressions or other similar forms of analysis because we had numerous predictor

variables but only 12 cases (months), which would lead to elevated type I error rates (sensu Green 1991). Instead, we performed Spearman rank correlations between variables as well as a Wilcoxon signed rank test. All tests were 2-tailed and we considered *P*-values ≤ 0.05 significant.

RESULTS

Correlates of play.—The total number of play bouts recorded was 76 in group Pablo, 31 in group Bwenge, and 58 in group Ntambara (Table 1). Ten of 12 adult females participated in play bouts in group Pablo, 5 of 6 in group Bwenge, and 2 of 4 in group Ntambara. One of 6 silverbacks was observed playing in group Pablo, 1 of 1 in group Bwenge, and 2 of 3 in group Ntambara (see Supplementary Data SD2). Group-based monthly rates of play were 0.07 bouts/h in group Pablo, 0.09 bouts/h in group Bwenge, and 0.13 bouts/h in group Ntambara.

In all 3 groups, monthly rate of play behavior was correlated positively with the monthly percentage of bamboo shoots in the diet, and in groups Pablo and Bwenge, the correlation reached statistical significance (Table 2). In group Ntambara, rate of play was correlated positively with energy gain/min (Table 2). The individual-based results indicated that for individuals in groups Pablo and Bwenge, the proportional importance of bamboo in the diet was associated positively with monthly play behavior (Table 3). For all 3 groups combined, play rates on the individual level were significantly higher when bamboo shoots were available than when they were not available (Wilcoxon signed rank, $V = 160$, $P = 0.001$). None of the other investigated explanatory variables (time spent feeding and moving and rainfall) were significantly correlated with monthly rates of play behavior.

Alcohol and cyanide analyses.—Immediately after processing (cutting and crushing) the bamboo shoots, the ALCO-Screen test pad exhibited no color change; after 5–10 min the test pad showed a color change to light green-gray; and

Table 1.—Number of play bouts involving adults in 3 mountain gorilla groups (Pablo, Bwenge, Ntambara) in Volcanoes National Park, Rwanda, separated into age–sex class combinations. The data cover the period January–December 2010.

| Age–sex class ^a | Pablo | Ntambara | Bwenge |
|----------------------------|-------|----------|--------|
| SB-SB | 0 | 13 | 0 |
| SB-AF | 0 | 2 | 0 |
| SB-SAF | 4 | 3 | 0 |
| SB-I | 0 | 0 | 1 |
| AF-AF | 5 | 13 | 1 |
| AF-SAF | 4 | 27 | 0 |
| AF-I | 4 | 0 | 29 |
| AF-BB | 10 | 0 | 0 |
| AF-SAM | 26 | 0 | 0 |
| AF-J | 23 | 0 | 0 |
| Total | 76 | 58 | 31 |

^aSB = silverback (age > 12 years); AF = adult female (> 8 years); SAF = subadult female (6–8 years); I = infant (0–3.5 years); BB = blackback (8–12 years); SAM = subadult male (6–8 years); J = juvenile (3.5–6 years).

Table 2.—Group-based rates of play involving adult individuals calculated from both opportunistic and focal data on mountain gorillas in Volcanoes National Park, Rwanda. Correlations between monthly rates of play and rainfall, time spent feeding and moving, bamboo in diet, and energy intake rate in the 3 study groups Pablo, Ntambara, and Bwenge. $N = 12$ months (January–December 2010). R_s = Spearman correlation coefficient; $P = P$ -value. Significant correlations are depicted in italics.

| Variable | Pablo | | Ntambara | | Bwenge | |
|---------------------------|--------------|--------------|--------------|--------------|--------------|--------------|
| | R_s | P | R_s | P | R_s | P |
| Rainfall | 0.477 | 0.194 | -0.214 | 0.505 | -0.531 | 0.075 |
| % time feeding and moving | -0.287 | 0.366 | -0.182 | 0.571 | 0.000 | 1.000 |
| Bamboo in diet | <i>0.602</i> | <i>0.038</i> | 0.471 | 0.122 | <i>0.674</i> | <i>0.016</i> |
| Energy intake rate | -0.120 | 0.726 | <i>0.581</i> | <i>0.047</i> | 0.147 | 0.649 |

Table 3.—Individual-based rates of play for all adult individuals in 3 study groups (Pablo, Ntambara, Bwenge) of mountain gorillas in Volcanoes National Park, Rwanda. Rates were calculated from focal data only. Correlations between monthly rates of play and rainfall, time spent feeding and moving, and bamboo in diet. $N = 12$ months (January–December 2010). R_s = Spearman correlation coefficient; $P = P$ -value. Significant correlations are depicted in italics.

| Variable | Pablo | | Ntambara | | Bwenge | |
|---------------------------|--------------|--------------|----------|-------|--------------|--------------|
| | R_s | P | R_s | P | R_s | P |
| Rainfall | 0.479 | 0.115 | -0.312 | 0.324 | -0.347 | 0.269 |
| % time feeding and moving | -0.112 | 0.510 | -0.231 | 0.470 | 0.014 | 0.966 |
| Bamboo in diet | <i>0.592</i> | <i>0.047</i> | 0.479 | 0.115 | <i>0.629</i> | <i>0.028</i> |

after 1 h the color changed to dark green-gray. Results were consistent across all 4 trials and point to an absence or very small concentrations of alcohol. No cyanide was detected in the samples, judging from a lack of color change of the Cyantesmo test strips; this result was consistent across all 4 trials.

DISCUSSION

A significant correlation between rate of play and bamboo consumption per month in 2 of the 3 mountain gorilla groups supports an influence of this seasonal resource on the levels of playfulness in gorillas. The mechanism behind the bamboo–“hyperactivity” relationship, however, has thus far remained elusive. A plausible explanation is that increased play activity is related to a strong, positive energy balance derived from consumption of energy-rich bamboo. Correlations between availability of high-quality food and play behavior have been reported for western gorillas (Masi et al. 2009) and a number of other primates and non-primates (Lee 1984; Sommer and Mendoza-Granados 1995; Nunes et al. 1999; Sharpe et al. 2002; Stone 2008). We have shown previously that urinary C-peptide levels indicate energy balance is higher in months when gorillas move to the bamboo zone and rely heavily on bamboo shoots (Grueter et al. 2014). Our results using energy intake rates are inconsistent across groups and only partly in concordance with previous findings (Grueter et al. 2014; see also Wright et al. 2015), which we suspect might be attributed to the complexities of applying different methods for estimating energy that animals have at their disposal to expend in energetically costly activities such as play. Lack of a relationship between energy intake and play rates in 1 of the 3 groups might be because of our response variable. The average observation time of energy intake per female gorilla per month may not be

sufficient to detect a relationship, and play and energy intake data were not collected simultaneously in all instances.

An alternative or complementary explanation to heightened play behavior following bamboo consumption is that play by adults is a manifestation of being mildly intoxicated; bamboo shoots in general are known to contain high levels of cyanogenic glycosides which can be toxic. There are many documented examples of deaths and serious illness from consumption of cyanogenic plants in humans (Cardoso et al. 1998), livestock (Robinson 1930; Webber et al. 1985), and other grazing animals (Saucy et al. 1999). Nevertheless, we failed to detect cyanide in the samples collected. Although the possibility of test malfunction cannot be ruled out completely (Yamashita et al. 2010), it is possible that cyanide concentrations in the lower parts of young shoots are too low to be detected (Egan et al. 1998; Sarangthem et al. 2010). Also, cyanide content is reported to decrease substantially following harvesting (Food Standards Australia New Zealand 2004). Furthermore, we have documented habitual co-ingestion of bamboo shoots with leaves of 2 herbaceous plants (*Droguetia iners* and *Laportea alatipes*; C. C. Grueter, pers. obs.), both of which are extremely rich in tannins and phenols (C. C. Grueter, pers. obs.), and there is evidence that tannins can reduce the toxicity of cyanide by inhibiting cyanogenesis (Goldstein and Spencer 1985).

According to popular beliefs, alcohol is responsible for the exaggerated play and display behavior of the gorillas; however, bamboo shoots would probably have to be left to rot for fermentation to occur. In parts of East Africa, “ulanzi” (bamboo wine) is obtained by tapping young bamboo shoots and letting the sap ferment naturally (Stewart 2013; see also www.fao.org/docrep/x0560e/x0560e09.htm). Bamboo shoots also are commonly fermented by indigenous peoples in northeastern India (Das and Deka 2012). Our crude tests indicate either a complete absence or only minimal concentrations of alcohol in

fresh bamboo shoots. The color changes of the ALCO-Screen test pads recorded over time may be indicative of initiation of fermentation. More quantitative tests of alcohol content using refractometers–hydrometers (Hockings et al. 2015) or amperometric biosensors (Wiens et al. 2008) are needed to gain more robust evidence. Some behavior observed may be suggestive of gorillas getting mildly intoxicated. For example, we have an anecdotal observation from 16 November 2010 of an adult female placing her 5-month-old infant on the ground to join other individuals in rambunctious play bouts, which is rather incompatible with the high levels of maternal solicitude typically shown by parous gorilla females; infants are usually in constant physical contact with their mothers for the first 6 months of life, irrespective of group activity (Fletcher 2001).

Our explanations for play behavior in adult gorillas are couched on a more proximate explanatory level and thus remain silent about the adaptive significance of elevated play behavior. The possible consequences of increased play for immature development and within-group social dynamics merit brief attention. Animal social play in general appears to fulfill different functions depending on species and the age–sex of playing individuals. Play involving immature individuals may help develop their motor skills and foster cognitive development and behavioral flexibility (Fagen 1981; Chiszar 1985; Byers and Walker 1995; Špinka et al. 2001). Play between adults may serve a social assessment function, especially in loosely organized and fluid social organizations (Pellis and Iwaniuk 2000). However, this explanation is tempered by the fact that gorillas live in cohesive social groups with high levels of familiarity. Play also may provide another opportunity for individuals to strengthen their social relationships (e.g., Mancini and Palagi 2009).

In sum, our results have shown that behavioral changes do occur in gorillas as a result of consumption of bamboo shoots, but the physiological processes involved are still unclear. While a surplus in energy appears the most parsimonious explanation for these changes, intoxication cannot yet be completely ruled out.

ACKNOWLEDGMENTS

We thank Rwanda Development Board (RDB) for permission to conduct this research, Prosper Uwingeli for facilitating research in Volcanoes National Park, the Karisoke trackers and data technicians for help with data collection under often difficult conditions, H. Barleben for the nutritional analyses, and S. Masi for useful comments on this manuscript. Funding for this study was provided by the Max Planck Society, the Dian Fossey Gorilla Fund International, and the Swiss National Science Foundation/Schweizerischer Nationalfonds (PBZHP3-128152). The research conducted adhered to the legal requirements of Rwanda.

SUPPLEMENTARY DATA

Supplementary Data SD1.—Group composition: list of all individuals present in the 3 study groups at the time of the study. **Supplementary Data SD2.**—Information on all play bouts observed in this study.

LITERATURE CITED

- ALTMANN, S. 1998. Foraging for survival: yearling baboons in Africa. Chicago University Press, Chicago, Illinois.
- BALLHORN, D. J., S. KAUTZ, AND F. P. RAKOTOARIVELO. 2009. Quantitative variability of cyanogenesis in *Cathariostachys madagascariensis*—the main food plant of bamboo lemurs in southeastern Madagascar. *American Journal of Primatology* 71:305–315.
- BYERS, J. A., AND C. B. WALKER. 1995. Refining the motor training hypothesis for the evolution of play. *American Naturalist* 146:25–40.
- CARDOSO, A. P., M. ERNESTO, J. CLIFF, S. V. EGAN, AND J. H. BRADBURY. 1998. Cyanogenic potential of cassava flour: field trial in Mozambique of a simple kit. *International Journal of Food Sciences and Nutrition* 49:93–99.
- CASIMIR, M. J. 1975. Feeding ecology and nutrition of an eastern gorilla group in the Mt. Kahuzi region (République du Zaïre). *Folia Primatologica* 24:1–36.
- CHETRY, D., R. CHETRY, K. GHOSH, AND P. C. BHATTACHARJEE. 2010. Status and conservation of golden langur in Chakrashila Wildlife Sanctuary, Assam, India. *Primate Conservation* 25:81–86.
- CHISZAR, D. 1985. Ontogeny of communicative behaviors. Pp. 207–238 in *The comparative development of adaptive skills: evolutionary implications* (E. S. Gollin, ed.). Lawrence Erlbaum, Hillsdale, New Jersey.
- CHONGTHAM, N., M. S. BISHT, AND S. HAORONGBAM. 2011. Nutritional properties of bamboo shoots: potential and prospects for utilization as a health food. *Comprehensive Reviews in Food Science and Food Safety* 10:153–169.
- CONKLIN-BRITAIN, N. L., C. D. KNOTT, AND R. W. WRANGHAM. 2006. Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. Pp. 445–471 in *Feeding ecology in apes and other primates: ecological, physical and behavioral aspects* (G. Hohmann, M. M. Robbins, and C. Boesch, eds.). Cambridge University Press, New York.
- DAS, A. J., AND S. C. DEKA. 2012. Fermented foods and beverages of the North-East India. *International Food Research Journal* 19:377–392.
- DUNBAR, R. I. M., A. H. KORSTJENS, AND J. LEHMANN. 2009. Time as an ecological constraint. *Biological Reviews* 84:413–429.
- EGAN, S. V., H. H. YEOH, AND J. H. BRADBURY. 1998. Simple picrate paper kit for determination of the cyanogenic potential of cassava flour. *Journal of the Science of Food and Agriculture* 76:39–48.
- EMMONS, L. H. 1981. Morphological, ecological, and behavioral adaptations for arboreal browsing in *Dactylopsilus dactylinus* (Rodentia, Echimyidae). *Journal of Mammalogy* 62:183–189.
- FAGEN, R. 1981. *Animal play behavior*. Oxford University Press, New York.
- FLETCHER, A. 2001. Development of infant independence from the mother in wild mountain gorillas. Pp. 153–182 in *Mountain gorillas: three decades of research at Karisoke* (M. M. Robbins, P. Sicotte, and K. J. Stewart, eds.). Cambridge University Press, Cambridge, United Kingdom.
- FOOD STANDARDS AUSTRALIA NEW ZEALAND. 2004. Cyanogenic glycosides in cassava and bamboo shoots: a human health risk assessment. www.foodstandards.gov.au/publications. Accessed 10 May 2015.
- FOSSEY, D. 1972. Vocalizations of the mountain gorilla (*Gorilla gorilla beringei*). *Animal Behaviour* 20:36–53.
- FOSSEY, D., AND A. H. HARCOURT. 1977. Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). Pp. 415–447 in *Primate ecology: studies of feeding and ranging behaviour in*

- lemurs, monkeys and apes (T. H. Clutton-Brock, ed.). Academic Press, New York.
- GLANDER, K. E., P. C. WRIGHT, D. S. SEIGLER, V. RANDRIANASOLO, AND B. RANDRIANASOLO. 1989. Consumption of cyanogenic bamboo by a newly discovered species of bamboo lemur. *American Journal of Primatology* 19:119–124.
- GOLDSTEIN, W. S., AND K. C. SPENCER. 1985. Inhibition of cyanogenesis by tannins. *Journal of Chemical Ecology* 11:847–858.
- GREEN, S. B. 1991. How many subjects does it take to do a regression analysis? *Multivariate Behavioral Research* 26:499–510.
- GRUETER, C. C., T. DESCHNER, V. BEHRINGER, K. FAWCETT, AND M. M. ROBBINS. 2014. Socioecological correlates of energy balance using urinary C-peptide measurements in wild female mountain gorillas. *Physiology & Behavior* 127:13–19.
- GRUETER, C. C., D. LI, B. REN, F. WEI, AND C. P. VAN SCHAIK. 2009. Dietary profile of *Rhinopithecus bieti* and its socioecological implications. *International Journal of Primatology* 30:601–624.
- GRUETER, C. C., F. NDAMIYABO, A. J. PLUMPTRE, D. ABAVADIMWE, K. A. FAWCETT, AND M. M. ROBBINS. 2013. Long-term temporal and spatial dynamics of food availability for endangered mountain gorillas in Volcanoes National Park, Rwanda. *American Journal of Primatology* 75:267–280.
- HAQUE, M. R., AND J. H. BRADBURY. 2002. Total cyanide determination of plants and foods using the picrate and acid hydrolysis methods. *Food Chemistry* 77:107–114.
- HARCOURT, A., K. STEWART, AND M. HAUSER. 1993. Functions of wild gorilla ‘close’ calls. I. Repertoire, context, and interspecific comparison. *Behaviour* 124:89–122.
- HOCKINGS, K. J., ET AL. 2015. Tools to tipple: ethanol ingestion by wild chimpanzees using leaf-sponges. *Royal Society Open Science* 2:150150.
- HUANG, Z., ET AL. 2015. Dietary adaptations of Assamese macaques (*Macaca assamensis*) in limestone forests in Southwest China. *American Journal of Primatology* 77:171–185.
- KAPLIN, B. A., N. NTARE, C. WESOLEK, F. MULINDAHABI, AND A. GASOGO. 2014. Use of bamboo forest by the owl-faced monkey *Cercopithecus hamlyni* in Nyungwe National Park, Rwanda. Abstract #585 in 25th Congress of the International Primatological Society, August 2014, Hanoi, Vietnam.
- LEE, P. 1984. Ecological constraints on the social development of vervet monkeys. *Behaviour* 91:245–261.
- LI, Y., S. GUO, W. JI, G. HE, X. WANG, AND B. LI. 2011. Social play behavior in infant Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Qinling Mountains, China. *American Journal of Primatology* 73:845–851.
- MAJOLO, B., R. MCFARLAND, C. YOUNG, AND M. QARRO. 2013. The effect of climatic factors on the activity budgets of Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology* 34:500–514.
- MANCINI, G., AND E. PALAGI. 2009. Play and social dynamics in a captive herd of gelada baboons (*Theropithecus gelada*). *Behavioural Processes* 82:286–92.
- MASI, S., C. CIPOLLETTA, AND M. M. ROBBINS. 2009. Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *American Journal of Primatology* 71:91–100.
- MCNEILAGE, A. 2001. Diet and habitat use of two mountain gorilla groups in contrasting habitats in the Virungas. Pp. 265–292 in *Mountain gorillas: three decades of research at Karisoke* (M. M. Robbins, P. Sicotte, and K. J. Stewart, eds.). Cambridge University Press, Cambridge, United Kingdom.
- MCNEILAGE, A. R. 1995. Mountain gorillas in the Virunga Volcanoes: feeding ecology and carrying capacity. Ph.D. dissertation, University of Bristol, United Kingdom.
- MEKONNEN, A., A. BEKELE, AND P. J. H. FASHING, G. 2010. Diet, activity patterns, and ranging ecology of the Bale monkey (*Chlorocebus djambjambensis*) in Odobullu Forest, Ethiopia. *International Journal of Primatology* 31:339–362.
- MEKURIAW, Y., M. URGE, AND G. ANIMUT. 2011. Role of indigenous bamboo species (*Yushania alpina* and *Oxytenanthera abyssinica*) as ruminant feed in northwestern Ethiopia. *Livestock Research for Rural Development* 23:9.
- MØLLER, B. L., AND D. S. SEIGLER. 1999. Biosynthesis of cyanogenic glucosides, cyanolipids, and related compounds. Pp. 563–609 in *Plant amino acids, biochemistry and biotechnology* (B. K. Singh, ed.). Marcel Dekker, New York.
- MOULAND, B. 2009. Bamboozled! Amazing pictures of a 30 stone Silverback gorilla who has one too many - and ends up with a sore head. <http://www.dailymail.co.uk/sciencetech/article-1163991/Bamboozled-Amazing-pictures-30-stone-Silverback-gorilla-ends-sore-head.html>. Accessed 10 May 2015.
- N’GUESSAN, A. K., S. ORTMANN, AND C. BOESCH. 2009. Daily energy balance and protein gain among *Pan troglodytes verus* in the Taï National Park, Côte d’Ivoire. *International Journal of Primatology* 30:481–496.
- NAHRSTEDT, A. 1988. Cyanogenic compounds as protecting agents for organisms. Pp. 31–150 in *Cyanide compounds in biology* (D. Evered and S. Harnett, eds.). John Wiley & Sons, Chichester, United Kingdom.
- NATIONAL RESEARCH COUNCIL. 2003. Nutrient requirements of nonhuman primates. National Academy Press, Washington, D.C.
- NUNES, S., E. MUECKE, J. A. ANTHONY, AND A. S. BATTERBEE. 1999. Endocrine and energetic mediation of play behavior in free-living Belding’s ground squirrels. *Hormones and Behavior* 36:153–165.
- ORTMANN, S., B. J. BRADLEY, C. STOLTER, AND J. U. GANZHORN. 2006. Estimating the quality and composition of wild animal diets: a critical survey of methods. Pp. 397–420 in *Feeding ecology in apes and other primates: ecological, physical and behavioral aspects* (G. Hohmann, M. M. Robbins, and C. Boesch, eds.). Cambridge University Press, New York.
- PELLIS, S. M., AND A. N. IWANIUK. 2000. Adult–adult play in primates: comparative analyses of its origin, distribution and evolution. *Ethology* 106:1083–1104.
- PLUMPTRE, A. J. 1991. Plant-herbivore dynamics in the Birungas. Ph.D. dissertation, University of Bristol, United Kingdom.
- RAUBENHEIMER, D., AND S. J. SIMPSON. 1997. Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition Research Reviews* 10:151–179.
- RELLA, J., S. MARCUS, AND B. J. WAGNER. 2004. Rapid cyanide detection using the Cyantesmo kit. *Journal of Toxicology* 42:897–900.
- ROBINSON, M. E. 1930. Cyanogenesis in plants. *Biological Reviews* 5:126–142.
- ROTHMAN, J. M., E. S. DIERENFELD, D. O. MOLINA, A. V. SHAW, H. F. HINTZ, AND A. N. PELL. 2006. Nutritional chemistry of foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology* 68:675–691.
- SARANGTHEM, K., T. HOIKHOKIM, N. SINGH, AND G. SHANTIBALA. 2010. Cyanogenic glycosides in bamboo plants grown in Manipur, India. P. 2 in VIII World Bamboo Congress Proceedings, 2010.
- SATYA, S., L. M. BAL, P. SINGHAL, AND S. N. NAIK. 2010. Bamboo shoot processing: food quality and safety aspect (a review). *Trends in Food Science & Technology* 21:181–189.
- SAUCY, F., J. STUDER, AND V. S. AERNI, B. 1999. Preference for acyanogenic white clover (*Trifolium repens*) in the vole *Arvicola terrestris*:

- I. Experiments with two varieties. *Journal of Chemical Ecology* 25:1441–1454.
- SCHALLER, G. B., J. HU, W. PAN, AND J. ZHU. 1985. The giant pandas of Wolong. University of Chicago Press, Chicago, Illinois.
- SHARPE, L. L., T. H. CLUTTON-BROCK, P. N. M. BROTHERTON, E. Z. CAMERON, AND M. I. CHERRY. 2002. Experimental provisioning increases play in free-ranging meerkats. *Animal Behaviour* 64:113–121.
- SOMMER, V., AND D. MENDOZA-GRANADOS. 1995. Play as indicator of habitat quality: a field study of langur monkeys (*Presbytis entellus*). *Ethology* 99:177–192.
- ŠPINKA, M., R. C. NEWBERRY, AND M. BEKOFF. 2001. Mammalian play: training for the unexpected. *Quarterly Review of Biology* 76:141–168.
- STACEY, P. B. 1986. Group size and foraging efficiency in yellow baboons. *Behavioral Ecology and Sociobiology* 18:175–187.
- STEWART, A. 2013. The drunken botanist: the plants that create the world's great drinks. Algonquin Books, Chapel Hill, North Carolina.
- STONE, A. I. 2008. Seasonal effects on play behavior in immature *Saimiri sciureus* in eastern Amazonia. *International Journal of Primatology* 29:195–205.
- TWINOMUGISHA, D., AND C. A. CHAPMAN. 2008. Golden monkey ranging in relation to spatial and temporal variation in food availability. *African Journal of Ecology* 46:585–593.
- VAN SOEST, P. J., J. B. ROBERTSON, AND B. A. LEWIS. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* 74:3583–3597.
- VEDDER, A. L. 1984. Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. *American Journal of Primatology* 7:73–88.
- WATERMAN, P., G. CHOO, A. L. VEDDER, AND D. P. WATTS. 1983. Digestibility, digestion inhibitors, and nutrients from herbaceous foliage from an Afromontane flora and its comparison with other tropical flora. *Oecologia* 60:244–249.
- WATTS, D. P. 1998. Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*). *International Journal of Primatology* 19:929–948.
- WATTS, D. P., AND A. E. PUSEY. 1993. Behavior of juvenile and adolescent great apes. Pp. 148–167 in *Juvenile primates: life history, development, and behavior* (M. E. Pereira and L. A. Fairbanks, eds.). Oxford University Press, Oxford.
- WEBBER, J. J., C. R. ROYCROFT, AND J. D. CALLINAN. 1985. Cyanide poisoning of goats from sugar gums (*Eucalyptus cladocalyx*). *Australian Veterinary Journal* 62:28.
- WIENS, F., ET AL. 2008. Chronic intake of fermented floral nectar by wild treeshrews. *Proceedings of the National Academy of Sciences* 105:10426–10431.
- WRIGHT, E., ET AL. 2015. Energetic responses to variation in food availability in the two mountain gorilla populations (*Gorilla beringei beringei*). *American Journal of Physical Anthropology* 158:487–500.
- YAMAGIWA, J., A. K. BASABOSE, K. KALEME, AND T. YUMOTO. 2005. Diet of Grauer's gorillas in the montane forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology* 26:1345–1373.
- YAMASHITA, N., C. L. TAN, C. J. VINYARD, AND C. WILLIAMS. 2010. Semi-quantitative tests of cyanide in foods and excreta of three *Hapalemur* species in Madagascar. *American Journal of Primatology* 72:56–61.

Submitted 27 October 2015. Accepted 25 July 2016.

Associate Editor was Kevin Monteith.