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Fruit-feeding and activity patterns of mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda

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Abstract

Objectives: Availability of fruit is an important factor influencing variation in great ape foraging strategies and activity patterns. This study aims to quantify how frugivory influences activity budgets across age-sex classes of mountain gorillas in Bwindi Impenetrable National Park, Uganda.

Materials and methods: Daily proportions of fruit-feeding and activity budgets were calculated using 6 years of observational data on four habituated groups. We fitted generalized linear mixed models to test for age-sex differences in the amount of fruit-feeding, and to test whether these factors influence the proportion of time spent feeding, resting, and traveling.

Results: Bwindi mountain gorillas spent on average 15% of feeding time consuming fruit, with monthly variation ranging from 0 to 70%. Greater amounts of fruit-feeding were associated with more time feeding and traveling, and less time resting. Immatures tended to spend more feeding time on fruit than adults, but less overall time feeding and more time traveling. There were no significant differences in the amount of fruit-feeding and overall feeding time between adult females and silverback males, despite differences in body size.

Discussion: This study confirms that gorillas are frugivorous, and only the Virunga mountain gorilla population can be characterized as highly folivorous. Along with other frugivorous great apes, Bwindi mountain gorillas alter their activity patterns in response to varying amounts of fruit in their diet. A better understanding of how variable ecological conditions can drive diversity even within a subspecies has important implications for understanding relationships between ecology, body size, and foraging strategies in great apes.

KEYWORDS
activity budget, ape, frugivory, mountain gorilla

1 | INTRODUCTION

Food availability, which varies in time and space, influences the activity budgets of primates. Because fruit is usually more patchily distributed than leaves or herbs, frugivorous primates tend to have longer daily travel distances than more folivorous species (Chapman, Wrangham, & Chapman, 1995; Clutton-Brock & Harvey, 1977; Janson & Goldsmith, 1995; van Schaik, van Noordwijk, de Boer, & den Tonkelaar, 1983). Furthermore, seasonal variation in fruit availability results in many primates altering their ranging patterns, activity budget, and/or showing dietary flexibility in response to the availability of preferred and fallback foods (reviewed in Hemingway & Bynum, 2005; Knott, 2005).

Body size differences can also influence activity patterns across age-sex classes. Because animals with smaller body mass have higher metabolic rates (e.g., Kleiber, 1961; McNab, 1978), immature individuals tend to have relatively higher energetic requirements (per unit of body mass) compared to adults (Altmann, 1980). Among adults, a large degree of size dimorphism can lead to significant energetic consequences (e.g., Altmann, 1980; Clutton-Brock, 1977; Key & Ross, 1999; Mitani, 1989). In many primate species, the energetic demands of lactation, pregnancy, and infant carrying in females as well as increased nutritional requirements for growth in immatures may lead to more time spent feeding than adult males, despite males often being much larger (Altmann & Samuels, 1992; Fox, van Schaik, Sitompul, & Wright, 2004; Key & Ross, 1999; Mitani, 1989).

Great apes are a diverse taxon with wide variation in body size (Smith & Jungers, 1997), degree of sexual dimorphism (Susman, Stern, & Jungers, 1984), patterns of sociality (Meder, 2015), foraging strategies (Conklin-Brittain, Knott, & Wrangham, 2001; Knott, 2005), and activity budgets (e.g., Masi, Cipolletta, & Robbins, 2009; Morrogh-Bernard et al., 2009; Pruetz & McGrew, 2001; White, 1992; Wright et al., 2015). They are generally considered selective in their fruit choice, preferring ripe fruits when they are available (e.g., Doran-Sheehy, Mongo, Lodwick, & Conklin-Brittain, 2009; Knott, 1999, 2005; Remis, Dierenfeld, Mowry, & Carroll, 2001; Remis & Kerr, 2002; Rogers et al., 2004; Wrangham, Conklin-Brittain, & Hunt, 1998), although the quantity of fruit in ape diets varies substantially between taxa, as well as within and between years, and within and between sites (e.g., Cipolletta, 2004; Doran-Sheehy et al., 2009; Doran-Sheehy, Shah, & Heimbauer, 2006; Ganas, Ortmann, & Robbins, 2008; Ganas, Robbins, Nkurunungi, Kaplin, & McNeilage, 2004; Knott, 2005; Masi et al., 2009; Morrogh-Bernard et al., 2009; Robbins, Nkurunungi, & McNeilage, 2006; Rothman, Plumptre, Dierenfeld, & Pell, 2007; Tutin & Fernandez, 1985; Wrangham et al., 1998). Even within a species, primate populations may inhabit a wide ecological range, leading to variation in feeding ecology and behavior (e.g., Chapman & Chapman, 1999; Ganas et al., 2004; Harris & Chapman, 2007; Potts, Watts, & Wrangham, 2011). Investigating the range of inter- and intraspecific variation in great apes builds our understanding of the different ways apes have adapted to varying ecological conditions.

Given that gorillas (*Gorilla* spp) exhibit a large degree of ecological and behavioral diversity (e.g., Harcourt & Stewart, 2007; Robbins & Robbins, 2018), they are important for understanding variation in large-bodied, closely related taxa. Eastern (*Gorilla beringei*) and western (*Gorilla gorilla*) gorillas live in a wide range of habitats with varying densities of herbaceous vegetation and abundances of fruiting trees (e.g., Doran et al., 2002; Robbins et al., 2006; Rogers et al., 2004). Fruit availability and the degree of frugivory across gorilla populations tends to increase as altitude decreases, leading to variation in foraging strategies and activity patterns across populations (Robbins, 2011). Furthermore, as gorillas show a large degree of sexual dimorphism with respect to body size (Jungers & Susman, 1984; Smith & Jungers, 1997), there may be differences in activity budgets across age-sex classes.

Gorillas have historically been viewed as largely folivorous, based on the long-term research on the Virunga population of mountain gorillas (*Gorilla beringei beringei*) studied by the Karisoke Research Center. These mountain gorillas live on an extreme end of the ecological spectrum inhabited by gorillas, feeding on perennially available and abundant terrestrial herbaceous vegetation, and almost no fruit (Vedder, 1984; Watts, 1984). With minimal food items available arboreally in the high-altitude montane forest, mountain gorillas have been characterized as highly terrestrial, spending little time in trees (females 7%, males 2%) (Doran, 1996, 1997b; Tuttle & Watts, 1985). In comparison to the more arboreal and frugivorous pattern seen in other great apes, namely, chimpanzees and orangutans (e.g., Knott, 2005; Morgan & Sanz, 2006; Morrogh-Bernard et al., 2009; Newton-Fisher, 1999; Potts et al., 2011; Wrangham, 1977), this terrestriality and folivory of mountain gorillas was traditionally viewed as a consequence of their large body size. However, despite their large body size, lowland gorilla populations are distinct from the Virunga mountain gorillas, inhabiting lowland tropical forests where fruit is seasonally abundant, and high-quality terrestrial herbaceous vegetation is less abundant and more sparsely distributed than in montane habitats (e.g., Rogers et al., 2004; Tutin, 1996; Williamson, Tutin, Rogers, & Fernandez, 1990). In contrast to the less than 1% of foraging time spent on fruit in Virunga mountain gorillas, western lowland gorillas spend approximately 30% of their foraging time consuming fruit, accounting for up to 70% of feeding time during peak fruit season (Doran-Sheehy et al., 2009; Masi et al., 2009; Masi et al., 2015). Most studies of western gorilla diet have not found age or sex differences in frugivory (Doran et al., 2002; Doran-Sheehy et al., 2009; Rogers et al., 2004), despite the large size of silverback males potentially limiting their access to terminal branch foods (e.g., Remis, 1995, 1999).

Western lowland gorillas have longer daily travel distances than mountain gorillas, and travel distances are longer when they consume fruit (e.g., Cipolletta, 2004; Doran & McNeilage, 2001; Doran-Sheehy, Greer, Mongo, & Schwindt, 2004; Tutin, 1996). With respect to the activity budget, during high-fruit periods, western gorillas spend more time traveling and less time feeding than in low-fruit periods (Masi et al., 2009; Masi et al., 2015). In general, compared to Virunga mountain gorillas, western lowland gorillas spend more time feeding and traveling, and less time resting (Masi et al., 2009; Watts, 1988). Although there is limited information considering sex differences, the available data indicate that for the Virunga mountain gorillas in the Karisoke study area, silverbacks spend slightly more time feeding and less time traveling than adult females (Watts, 1988). For western lowland gorillas, it is unclear if there are consistent sex differences, as both studies examining activity patterns only included one silverback, and had contradicting results: at Bai Hokou, the silverback traveled and rested more and fed less than both adult females and immatures (Masi et al., 2009), while at Mondika Research Center, there were no sex differences in time spent feeding (Doran-Sheehy et al., 2009).

Despite our knowledge of gorillas living on opposite ends of the continuum of their ecological niche, namely, the Virunga mountain gorillas and western lowland gorillas, we know little about patterns of frugivory and activity budgets in populations occupying intermediate habitats. Specifically, the other population of mountain gorillas in Bwindi Impenetrable National Park, Uganda, located only 25 km north of the well-known Virunga Volcanoes, represents the same subspecies

(Roy et al., 2014) but inhabits lower altitudes with differences in food availability and feeding ecology compared to the Virungas (Ganas et al., 2004; Ganas & Robbins, 2005; Goldsmith, 2003; Robbins et al., 2006; Wright et al., 2015). While both populations rely heavily on evenly distributed and highly abundant herbaceous vegetation, Bwindi mountain gorillas also incorporate fruit into their diet when it is available (Ganas et al., 2004; Robbins et al., 2006). They appear to have an intermediate level of frugivory between western gorillas and Virunga mountain gorillas, with on average 10% of feeding time spent on fruit (Robbins, 2008; Wright & Robbins, 2014). Based on wet-weight proportion of food, the proportion of fruit eaten by mountain gorillas is close to 15% at Bwindi, and 0.2% in the Virungas (Rothman et al., 2007; Watts, 1984). Furthermore, Bwindi mountain gorillas have been observed to spend a substantial amount of time in trees foraging, resting, and playing (e.g., Goldsmith, 2003; Sarmiento, Butynski, & Kalina, 1996; Wright et al., 2015). They also have longer daily travel distances compared to Virunga mountain gorillas, and show similar patterns to western gorillas in that less time is spent feeding and daily travel distances are longer when fruit consumption is high (Ganas & Robbins, 2005; Seiler et al., 2018; Wright et al., 2015; Wright & Robbins, 2014). However, previous studies have not examined the influence of fruit-feeding on the overall activity budget, and either cover only a 1-year time interval, include only one social group, or use indirect measures of frugivory.

The aim of this study is to determine the degree of frugivory and its influence on activity budgets of Bwindi mountain gorillas, to gain a more complete understanding of inter- and intraspecific variation in gorillas. First, we predicted no differences in the degree of frugivory across age and sex classes, as previous studies of western gorillas have not found age-sex differences in fruit-feeding (Doran et al., 2002; Doran-Sheehy et al., 2009; Rogers et al., 2004). Prior studies of other great apes show that when fruit is patchily distributed, they will increase daily travel distance as fruit consumption increases (e.g., Cipolletta, 2004; Doran, 1997a; Doran-Sheehy et al., 2004; Galdikas & Teleki, 1981; Tutin, 1996; Wrangham et al., 1998; Yamagiwa & Mwanza, 1994). For the African apes, where relatively higher quality fallback foods are available and daily energy intake does not vary considerably throughout the year, the available studies indicate that when fruit consumption is high, less time is spent feeding (e.g., Conklin-Brittain, Wrangham, & Hunt, 1998; Doran, 1997a; Knott, 2005; Masi et al., 2009; Masi et al., 2015). Therefore, we next predicted that during periods of higher frugivory, Bwindi mountain gorillas spend less time feeding and more time traveling, compared to periods of less fruit-eating. We also predicted that they spend more time resting during lower fruit-eating periods, when there is greater reliance on more abundant and densely distributed herbaceous vegetation, which would require relatively more time to digest the more highly fibrous foods (e.g., Dunbar, 1988; Knott, 2005; Williamson & Dunbar, 1999). Lastly, although there is not yet a clear pattern established for age-sex differences in gorilla activity patterns (Doran-Sheehy et al., 2009; Masi et al., 2009; Watts, 1988), we examined age-sex differences in activity budgets of Bwindi mountain gorillas.

2 | MATERIALS AND METHODS

2.1 | Study population and data collection

This study was conducted in Bwindi Impenetrable National Park, Uganda. Bwindi is a medium-altitude to afro-montane forest with two rainy (March–May, September–November) and two dry seasons (June–August, December–February) per year. Data were collected from four groups habituated for research and tourism that range near Ruhija, which ranges in altitude between 2,100 and 2,500 m above sea level. All four groups have overlapping home ranges within this higher-altitude southeastern section of the park (e.g., see Seiler, Boesch, Mundry, Stephens, & Robbins, 2017).

Data collection for Kyagurilo (KYA) group extended from March 2012 to March 2016, and included 19–20 individuals. The dominant silverback died in April 2015, and in March 2016 the group fissioned into Mukiza (MUK) and Rukara (RUK) groups. Thus, data collection for MUK and RUK extended from March 2016 to February 2018, and included 10–11 and 8–10 individuals, respectively. For analysis, these are treated as three separate groups. Data for the fourth group, Bitukura (BIT) group, extended from January 2015 to December 2017, and included 10–13 individuals. (Details on group compositions throughout the study period can be found in Table S1.) The study period included a total of 2,113 observation days. Groups were observed daily for approximately 4 hr per day, the maximum allowable by national park authorities. Initial contact times were typically between 07:45 and 10:00 hr (range: 07:25 to 13:20 hr).

Age-sex categories used here are similar to those used for Virunga mountain gorillas (Williamson and Gerald-Steklis, 2003; Robbins, Gray, Kagoda, & Robbins, 2009). For each observation day, an age-sex category was assigned to each individual based on known or estimated birth dates (Table S1). Distinctions based on sex were not used for immatures (including infants, juveniles, and subadults), as significant sex differences in body size do not emerge until early adulthood (Galbany et al., 2017), and thus energetic demands of males and females are not likely to differ for immatures. Given that individuals matured into different age categories and/or emigrated out of or joined one of the study groups, the total composition of study groups varied slightly throughout the study period (Table S1).

Instantaneous scan sampling (Altmann, 1974) was conducted every 5 min from the start of the study until May 21, 2015 for KYA group and January 8, 2016 for BIT group, after which the protocol was changed to 10-min intervals for the rest of the study period. The observer recorded the activity of each individual in view (feeding, resting, and traveling). Feeding included foraging, food processing, and chewing. When feeding, the type of food item was recorded to the genus or species level when it could be identified, and minimally was recorded as a fruit or nonfruit food item. For analysis, all recorded food items were simplified to fruit or nonfruit. Resting included affiliative activities such as grooming and play, though it should be noted that other studies have included social behaviors such as grooming in a separate activity (e.g., Doran, 1997a; Huffman, 1990; Masi et al., 2009; Sanz, 2004; Teleki, 1981; Watts, 1988; White, 1992). Traveling included walking, running, and climbing not related directly with foraging. If an individual was not visible and clearly identified when the group was traveling, no activity was recorded for that individual.

Proportion of scans spent in each activity (F, R, and T) was calculated for each individual for each day. For each individual, days for which less than five total scans were recorded were excluded from analysis. To investigate the amount of time spent feeding on fruit, the proportion of total feeding scans that were spent feeding on fruit was also calculated for each individual per day. Thus for all statistical analyses, we considered the daily proportion of each activity per individual as an independent data point. Previous studies have shown wide interannual variability in frugivory patterns of Bwindi mountain gorillas (Robbins, 2008; Robbins et al., 2006), so the intra- and inter-annual variation in feeding time spent on fruit was quantified over the 6 year study period for comparison. We determined monthly mean time in each behavior by averaging daily percentages for each month, for each age category.

2.2 | Models used in the analysis

2.2.1 | Fruit-feeding model

To test whether there are age-sex differences in the amount of fruit-feeding, we fitted a generalized linear mixed model (GLMM, Baayen, 2008) with beta error distribution and logit link function (Bolker, 2008; McCullagh & Nelder, 1989). The response variable was the daily proportion of fruit-feeding scans, and as fixed effects we included the age-sex category (factor with levels: Infant, Juvenile, Subadult, Adult female, Blackback, Silverback), our main predictor of interest, as well as social group (factor with levels: Bitukura (BIT), Kyagurilo (KYA), Mukiza (MUK), Rukara (RUK)) to control for its effects. We included random intercept effects for the individual ID and the day (nested in group). To keep type I error rates at the nominal level of 0.05, we included random slope terms (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009) to allow for the fixed-effects terms to randomly vary among the levels of the random-effects variables, that is, social group to vary within ID, and age class within day. The number of scans per day per individual was added as weights to the model to account for stochastic variation in the proportion of fruit-feeding likely varying with decreasing number of behavioral scans per day. Since the daily proportion of fruit-feeding for each individual was considered an independent data point, the full dataset for this model included a total of 29,352 daily proportions determined on 2,791 days for 35 individuals.

2.2.2 | Activity budget models

To test whether the amount of fruit-feeding and age-sex category influenced the proportions of time spent feeding, resting, and traveling, we fitted three GLMMs (Baayen, 2008) with beta error distribution and logit link function (Bolker, 2008; McCullagh & Nelder, 1989). The three models, with response variables of proportion of time spent feeding, resting, and traveling, were identical with regard to the fixed and random effects included. As fixed effects, we included the daily proportion of fruit-feeding scans, age-sex category, and their interaction as our main predictors of interest, and social group to control for its effects. We again included random intercept effects for the individual ID and the day (nested in group), as well as random slopes of the daily proportion of fruit-feeding scans within individual and day; of social group within individual; and of age class within day. (Other random slope components were unidentifiable because of a lack of variation of the respective fixed effect within the levels of the random effect.) Overall sample sizes included a total of 29,352 proportions on 2,791 days for 35 individuals for the activity budget models.

2.2.3 | Data analysis

We utilized likelihood ratio tests to compare each of the full models as described above with respective null models lacking the main predictors of interest, but otherwise identical (Dobson, 2002; Forstmeier & Schielzeth, 2011). To obtain the significance of individual predictors, we used likelihood ratio tests comparing the full model with reduced models lacking the predictor in question (Barr et al., 2013; Dobson, 2002). For the activity budget models, nonsignificant interactions were removed.

All models were fitted in R (version 3.4.4; R Core Team, 2018), using the function glmmTMB of the package *glmmTMB* (version 0.2.2.0, Brooks et al., 2017). Prior to fitting the models, where fruit-feeding was included as a fixed effect, the daily proportion of fruit-feeding scans was z-transformed to a mean of zero and *SD* of one to avoid model fitting problems. For all models, in order to include categorical variables (i.e., age-sex category and social group) as random slopes, we manually dummy coded their levels (except the reference level), then centered the resulting dummy variables to a mean of zero, and included these into the random effects part of the model. We did not include estimates assessing the correlations among random intercepts and slopes to avoid model fitting problems, and neglecting such correlation parameters does not seem to compromise type I error rates (Barr et al., 2013). Pairwise post-hoc comparisons between age-sex classes and between social groups were conducted using the function glht of the package *multcomp* (version 1.4-12, Hothorn, Bretz, & Westfall, 2008).

None of the models were overdispersed (range of dispersion parameters: 0.462 to 0.721). We tested for collinearity by calculating variance inflation factors (VIF) (Fox & Monette, 1992; Quinn & Keough, 2002) using the package *car* (Fox, Weisberg, & Price, 2018) for the equivalent linear models only including the fixed effects from each model and lacking the random effects and interaction. Collinearity was not an issue in any of the models (maximum VIF: 1.049). We assessed model stability by excluding individuals one at a time, which revealed the models to be of moderate to good stability (Figure S1). We also checked for each model whether the residuals were autocorrelated by first extracting the residuals of a given model and then determining, separately for each individual, the degree of autocorrelation (using Spearman's rho) for each of the lags from 1 to

100 days. We then determined the average autocorrelation coefficient per lag. It appeared there was hardly any autocorrelation in the residuals (Figure S2).

3 | RESULTS

3.1 | Fruit-feeding

All age-sex categories exhibited significant monthly variation in time spent feeding on fruit, with mean monthly time ranging from approximately 0 to 70% (Figure 1, Table 1). For the fruit-feeding model, the full-null model comparison revealed significance (χ^2 = 73.016, *df* = 5, *p* < .001). Age category had a significant effect on the response, though post-hoc pairwise comparisons of the model results indicated that differences were due to greater fruit-feeding by infants and subadults compared to adult females and silverbacks (Table 2, Figure 1; Table S2). In particular, silverbacks had relatively low fruit-feeding compared to younger age-sex categories, but were not significantly different from adult females (Table 2, Figure 1; Table S2).

3.2 | Activity patterns

The full-null model comparisons for the three models examining if fruit-feeding and age-sex class influenced activity patterns (time spent feeding, resting, and traveling) revealed significance in all cases (likelihood ratio tests: proportion time feeding: χ^2 = 360.282, *df* = 11, *p* < .001; proportion time resting: χ^2 = 188.411, *df* = 6, *p* < .001; proportion time traveling: χ^2 = 131.849, *df* = 11, *p* < .001). The control variable social group appeared significant in all models (Table 3, Figure S3).

3.2.1 | Feeding

The interaction between fruit-feeding and age-sex class was significant for the feeding model (Table 3). The proportion time feeding

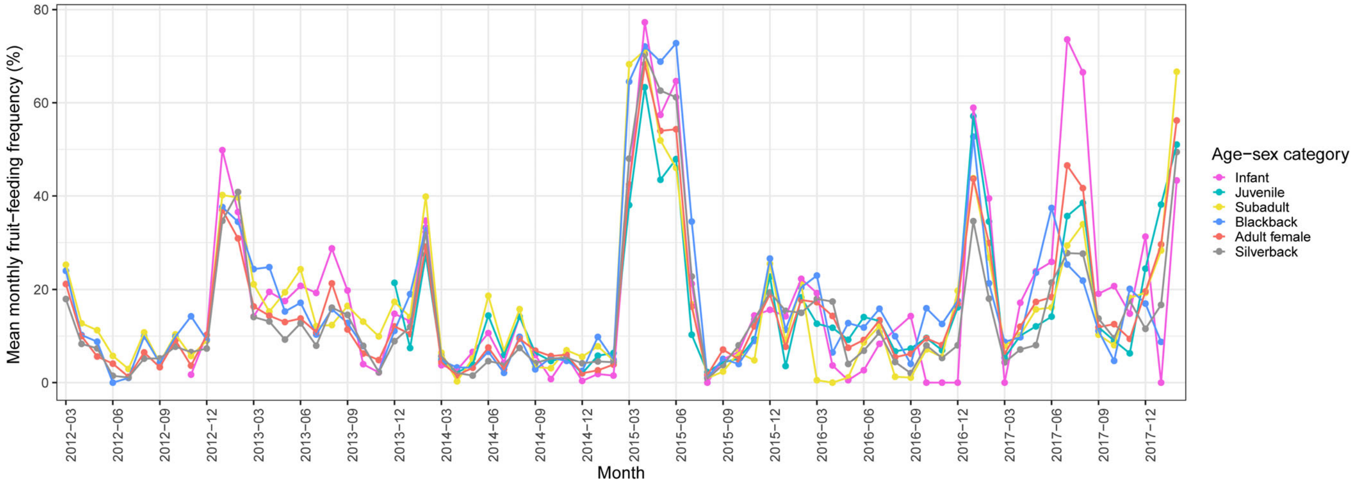

FIGURE 1 Mean monthly fruit-feeding frequency for each age-sex category throughout the study period. Dots indicate the monthly mean of daily percentages for feeding time spent on fruit for each age-sex category

TABLE 1 Mean monthly percent time spent in each behavior for all age-sex categories

	Infant	Juvenile	Subadult	Blackback	Adult female	Silverback
Feeding	21.5 (10.4)	41.4 (6.2)	44.2 (7.7)	44.2 (6.3)	48.2 (6.0)	44.2 (6.7)
Resting	56.9 (10.2)	40.8 (6.2)	40.4 (7.3)	41.5 (6.0)	39.0 (6.8)	43.2 (7.3)
Traveling	21.6 (5.6)	17.7 (3.4)	15.4 (3.8)	14.2 (2.8)	12.7 (2.4)	12.5 (2.7)
Fruit-feeding	18.9 (19.8)	16.8 (15.6)	16.5 (16.0)	16.9 (16.6)	15.8 (14.9)	14.5 (14.9)
Min	0.0	2.0	0.0	0.0	1.3	0.9
Max	77.3	63.3	71.2	72.8	68.3	70.4
KW χ^2	547.8	1,029.6	542.4	571.8	2,349.4	1,069.5
p	<.001	<.001	<.001	<.001	<.001	<.001
Months	63	51	72	71	72	72

Note: Values are from monthly means of daily percentages for each age-sex category. Data include mean (*SD*) for percent time feeding, resting, traveling, and fruit-feeding, and minimum and maximum monthly means for percent time fruit-feeding. Results of the Kruskal-Wallis rank sum test show there is significant variation in fruit-feeding across months for all age-sex categories.

TABLE 2 The influence of age-sex category and social group on the proportion of feeding time spent on fruit

	Fruit-feeding model				
Term	Estimate	*SE*	χ^2	*df*	*p*
Intercept	−1.136	0.077			
Age category—Blackback[a]	0.106	0.059	73.016	5	**<.001**
Age category—Infant	0.201	0.061			
Age category—Juvenile	0.108	0.057			
Age category—Silverback	−0.130	0.058			
Age category—Subadult	0.191	0.055			
Group—KYA[b]	−0.789	0.083	68.703	3	**<.001**
Group—MUK	−0.730	0.099			
Group—RUK	−0.867	0.098			

Note: Comparison of the full model versus the null model that excluded the test predictors revealed significance. We show the estimate, *SE*, χ^2 value, *df*, and *p*-values from the likelihood ratio tests of individual predictors. Significant *p*-values ($p < .05$) are indicated in bold; *p*-values not shown have a very limited interpretation.

[a] Age-sex category was dummy coded with adult female being the reference category, i.e., the age category terms are in relation to adult females. The indicated test indicates the significance of the comparison of the full model with one lacking age-sex category.

[b] Social group was dummy coded with group BIT being the reference category, i.e., the group terms are in relation to BIT group. The indicated test indicates the significance of the comparison of the full model with one lacking group.

was generally positively correlated with the proportion of fruit-feeding, and the effect was strongest in adults and weakest in infants, juveniles, and subadults (Table 3, Figure 2). On average, infants had the lowest proportion of time feeding, but other age-sex categories spent similar amounts of time feeding, accounting for approximately 45% of the activity budget, though it was slightly lower for juveniles and slightly higher for adult females (Table 1; Table S3).

3.2.2 | Resting

The interaction between age-sex class and proportion time fruit-feeding was nonsignificant and was removed from the resting model; in the model without the interaction, all fixed effects revealed significance (Table 3). With increasing time spent feeding on fruit, the proportion time resting decreased. For age-sex class, infants rested the most, and adult females rested the least (Table 3, Figure 3; Table S4).

3.2.3 | Traveling

The interaction between age-sex category and proportion time fruit-feeding revealed significance for the traveling model. The proportion time spent traveling was generally low, and its correlation with the proportion of fruit-feeding varied among age-sex categories. While in silverbacks the correlation was very slightly negative, it was slightly positive in all other age classes, and the relationship was steepest in juveniles (Table 3, Figure 4). Results also indicate that infants spent the most time traveling, while adult females and silverbacks spent the least (Tables 1 and 3; Table S5).

4 | DISCUSSION

4.1 | Fruit-feeding

Our results confirm that Bwindi gorillas incorporate a substantial amount of fruit into their diet. The proportion of feeding time spent on fruit, on average approximately 15%, is intermediate between that of Virunga mountain gorillas (almost none; Watts, 1988) and western lowland gorillas (approx. 35%; Masi et al., 2009), with yearly means ranging from ~7 to 27% at Bwindi. The significant monthly variation in fruit-feeding, ranging from 0 to 70% of daily feeding scans each month, is consistent with previous studies indicating wide intra- and interannual variability in frugivory of Bwindi mountain gorillas (e.g., Robbins, 2008; Robbins et al., 2006). This is still considerably less fruit-feeding compared to chimpanzees and orangutans (Table 4). For chimpanzees, while time spent feeding on fruits varies across populations, fruit-feeding comprises over half of feeding time at all sites (Hladik, 1977; Morgan & Sanz, 2006; Newton-Fisher, 1999; Nishida & Uehara, 1983; Wrangham, 1977; Wrangham et al., 1996). Orangutans are also primarily frugivores, on average spending a majority of their feeding time on fruit, though depending on whether they live in a masting forest, may have some months where fruit is a minor part of the diet (Knott, 2005; Morrogh-Bernard et al., 2009; Wich et al., 2006). While there are many months at Bwindi where the proportion of feeding time on fruit may be relatively small, the fact that they do regularly incorporate fruit into their diet, and in some months devote a majority of their feeding time to it (Figure 1), is an important distinction from the Virunga mountain gorillas that should be taken into account when characterizing this subspecies that has long been considered highly folivorous.

Regarding fruit-feeding behavior across age-sex classes, our prediction that there would be no significant differences in the level of frugivory across age-sex classes was not fully supported. Infants and

TABLE 3 Influence of fruit-feeding, age-sex category, and social group on the proportion of time spent feeding, resting, and traveling

	Feeding model					Resting model					Traveling model				
Term	Estimate	*SE*	χ^2	*df*	*p*	Estimate	*SE*	χ^2	*df*	*p*	Estimate	*SE*	χ^2	*df*	*p*
Intercept	0.131	0.067				−0.880	0.075				−2.341	0.044			
propFruitFeed[a]	0.101	0.019				−0.087	0.014	32.278	1	**<0.001**	0.019	0.017			
Age category—Blackback[b]	−0.228	0.065				0.284	0.072	155.746	5	**<0.001**	0.236	0.045			
Age category—Infant	−0.895	0.068				0.731	0.074				0.607	0.043			
Age category—Juvenile	−0.339	0.064				0.290	0.069				0.327	0.038			
Age category—Silverback	−0.282	0.066				0.453	0.074				0.110	0.041			
Age category—Subadult	−0.161	0.062				0.168	0.068				0.295	0.040			
Group—KYA[c]	−0.053	0.062	16.952	3	**<0.001**	0.066	0.075	15.337	3	**0.002**	0.056	0.046	17.596	3	**<0.001**
Group—MUK	−0.080	0.074				−0.113	0.087				0.391	0.069			
Group—RUK	0.248	0.080				−0.247	0.101				0.014	0.057			
Interaction of propFruitFeed, age cat—Blackback[d]	−0.021	0.033	12.997	5	**0.023**						0.011	0.033	17.811	5	**0.003**
Interaction of propFruitFeed, age cat—Infant	−0.065	0.028									0.022	0.029			
Interaction of propFruitFeed, age cat—Juvenile	−0.047	0.026									0.081	0.027			
Interaction of propFruitFeed, age cat—Silverback	0.014	0.030									−0.049	0.028			
Interaction of propFruitFeed, age cat—Subadult	−0.080	0.028									−0.017	0.029			

Note: For all models, comparisons of the full model versus the null model that excluded the test predictors revealed significance. We show the estimate, *SE*, χ^2 value, *df*, and *p*-values from the likelihood ratio tests of individual predictors. Significant *p*-values ($p < .05$) are indicated in bold; *p*-values not shown have a very limited interpretation.

[a] Daily proportion of fruit-feeding (propFruitFeed) was z-transformed to a mean of zero and a *SD* of one; mean and *SD* of the original predictor were 0.158 and 0.304, respectively.

[b] Age-sex category was dummy coded with adult female being the reference category, i.e., the age category terms are in relation to adult females.

[c] Social group was dummy coded with group BIT being the reference category, i.e., the group terms are in relation to BIT group. The indicated test indicates the significance of the comparison of the full model with one lacking group.

[d] The indicated test indicates the significance of the comparison of the full model with one lacking the interaction between age-sex class and the proportion time spent feeding on fruits.

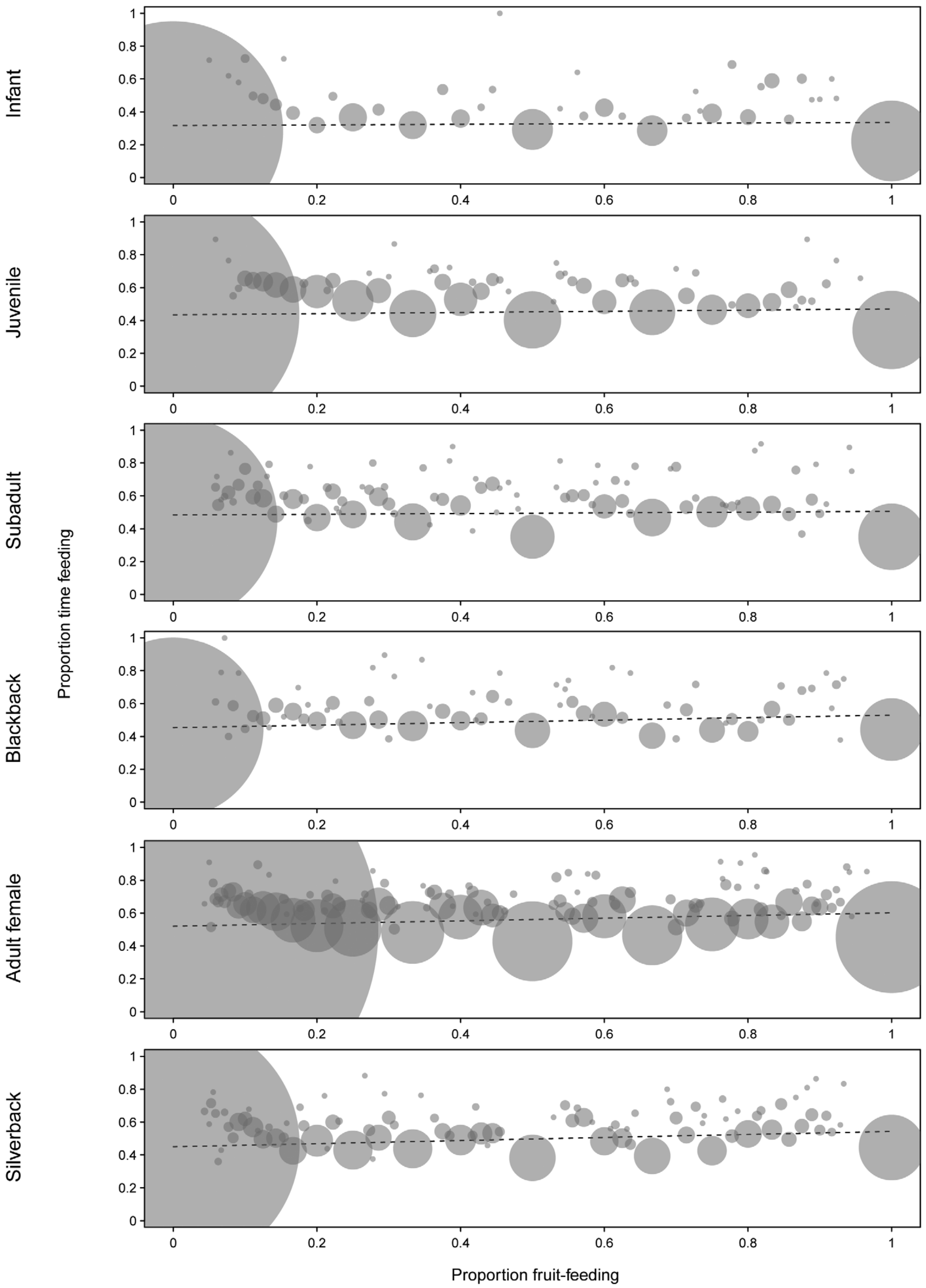

FIGURE 2 Effects of the proportion of fruit-feeding on the proportions of time spent feeding. Dashed lines indicate the fitted model for each age-sex category, with the average response (proportion time feeding) per bin of the predictor (proportion fruit-feeding). The area of the dots depicts the number of days per binned value of the predictor (*N*: 1–8,598)

subadults spent a greater proportion of feeding time on fruit than adult females and silverbacks, and silverbacks in particular had a lower level of fruit-eating than immatures. Fruit is easy to process and digest; thus, if younger individuals are not yet as efficient as adults at processing and digesting some of the terrestrial herbaceous vegetation, they may spend a greater proportion of their feeding time on fruit, from which it is easier to gain energy. Most great ape studies have not examined variation in fruit-feeding across all age-sex classes, though comparisons between adult males and adult females have not revealed differences in feeding time spent on fruit for western lowland gorillas (Doran-Sheehy et al., 2009), chimpanzees (Doran, 1997a; Hunt, 1989), or in orangutans (Fox et al., 2004). Similarly, we found no significant differences in the degree of frugivory between adult females and silverbacks, which is also consistent with a nutritional study at Bwindi that found no sex differences in fruit-feeding (Rothman, Dierenfeld, Hintz, & Pell, 2008).

4.2 | Activity patterns

As found in other primates, Bwindi mountain gorillas respond to variation in resource availability by adjusting their diet and activity patterns

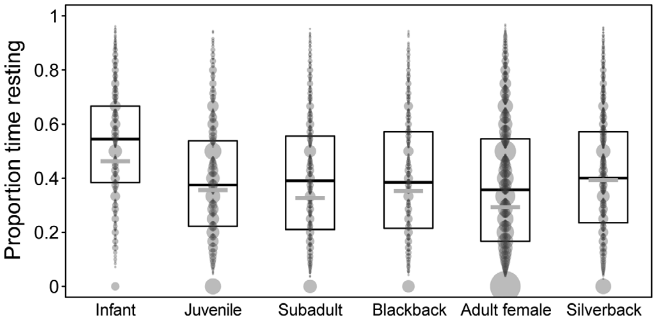

FIGURE 3 Differences in proportion of time spent resting across age-sex categories. Boxes and black horizontal lines depict medians and quartiles, and gray horizontal lines the fitted model estimates given average levels of fruit-feeding for each age-sex category. The area of the dots represents the number of days (*N*: 1–1,280) with a given proportion time resting per age-sex category

(Ganas & Robbins, 2005; Seiler et al., 2018; Wright et al., 2015; Wright & Robbins, 2014). However, our predictions that during periods of high frugivory, Bwindi gorillas would spend less time feeding and more time traveling—as has been shown for western lowland gorillas (Masi et al., 2009)—and less time resting, were not fully supported. While they did spend less time resting and more time traveling during periods of higher fruit-eating, they spent more time feeding (Table 3, Figures 2 and 3). Previous studies on African apes have shown that during periods of greater fruit consumption, there is typically a decrease in time spent feeding (Doran, 1997a; Masi et al., 2009), associated with fruit-feeding having a positive influence on energy intake rates and thus the expectation that individuals can meet their nutritional needs faster (Conklin-Brittain, Knott, & Wrangham, 2006; Harrison, Morrogh-Bernard, & Chivers, 2010; Knott, 2005; Masi et al., 2015). The results here go against this expectation and are also in contrast to those of a previous study at Bwindi, which indicated that the proportion of time spent feeding decreased during periods of greater food availability, that is, in this case, fruit availability (Wright et al., 2015). The same study also showed that similarly, at Karisoke, Virunga mountain gorillas spent less time feeding during periods of greater food availability, associated with the bamboo shoot season (Wright et al., 2015). It is difficult to determine the reason for the discrepancy in the results between the two studies, as the methods differ. Wright et al. (2015) used different measures for level of frugivory and for proportion of time spent feeding than those used here. In particular, they used monthly averages for the proportion of time spent feeding based on scans of group activity, and food availability was an estimated monthly value representing the energy density of important gorilla foods. At Bwindi, food availability increased substantially during periods of peak fruit consumption (Wright et al., 2015). Their models indicated a negative relationship between food availability and time spent feeding. Our models used daily proportions of feeding time and the daily proportion of fruit-feeding per individual, and showed a positive relationship between them.

Still, it is unclear why the proportion of time spent feeding increased during periods of greater fruit-feeding, contra expectations. A study of the nutritional quality of the Bwindi gorilla diet showed that overall energy intake does not vary throughout the year, despite seasonality in fruit-feeding, as the energy content of some of the herbaceous vegetation commonly eaten by gorillas were similar to those of fruits (Rothman et al., 2008). This pattern of relatively constant daily energy intake throughout the year despite seasonal variation in fruit availability has been shown for western lowland gorillas and chimpanzees as well (Conklin-Brittain et al., 1998; Masi et al., 2015). However, even if fruits are not of higher energetic value than some of the herbaceous vegetation at Bwindi, it would still be expected that increases in fruit-feeding would either lead to no change in the amount of feeding time, or if fruits have higher ingestion rates, a decrease in the amount of feeding time. Since previous studies indicate that energy intake per hour is higher during high fruit consumption months, as fruit has the highest intake rate per hour compared to other food items (Wright & Robbins, 2014; Wright, Robbins, & Robbins, 2014), this means that feeding time would be expected to decrease. It is possible that the results from the nutritional study do not reflect potential daily fluctuations in energy intake during periods of increased fruit consumption, as they calculated an average nutritional intake over a two-month period, which was then averaged over the study period (Rothman et al., 2008). It is also possible that these discrepancies are due to differences in methods, and the fact that previous studies at Bwindi included one year of observation for one group, while the current study includes observations of four groups over a six-year period.

An alternative explanation for the increased proportion of time spent feeding during periods of greater frugivory is that the less fibrous diet requires less time for digesting foods during resting periods, that is, they are less constrained by time needed for digestion ("enforced resting"; e.g., Dunbar et al., 2009), allowing for more feeding time. Additionally, Bwindi gorillas may simply be taking advantage of fruit when it is available and consuming as much as possible. Apes in habitats where fruit availability is more variable and unpredictable may need to maximize energy intake during periods of high fruit availability, as in the more extreme case of orangutans (Knott, 2005). Unpredictability of fruiting patterns, particularly in masting forests in Borneo, leads to orangutans increasing time spent feeding when fruit is abundant, gaining weight and storing fat for use during times of fruit scarcity and extended periods of energy deficits (Harrison et al., 2010; Knott, 1998, 1999, 2005; Leighton, 1993; Morrogh-Bernard et al., 2009). Mountain gorillas never have a period of low food availability, and previous studies suggest their diet provides similar energy throughout the year, with or without fruit (Rothman et al., 2008; Wright et al., 2015). Further study of nutrition, energy intake, and energy expenditure may be needed to resolve the discrepancies between studies.

In terms of the proportion of time spent traveling, as expected, traveling increased during periods of high fruit-feeding for most age-sex categories (Table 3, Figure 4). However, this relationship was not strong, but time spent traveling may have been underestimated due to the sampling methods because individuals may not all be in view while the group is traveling. Scan sampling also does not take into

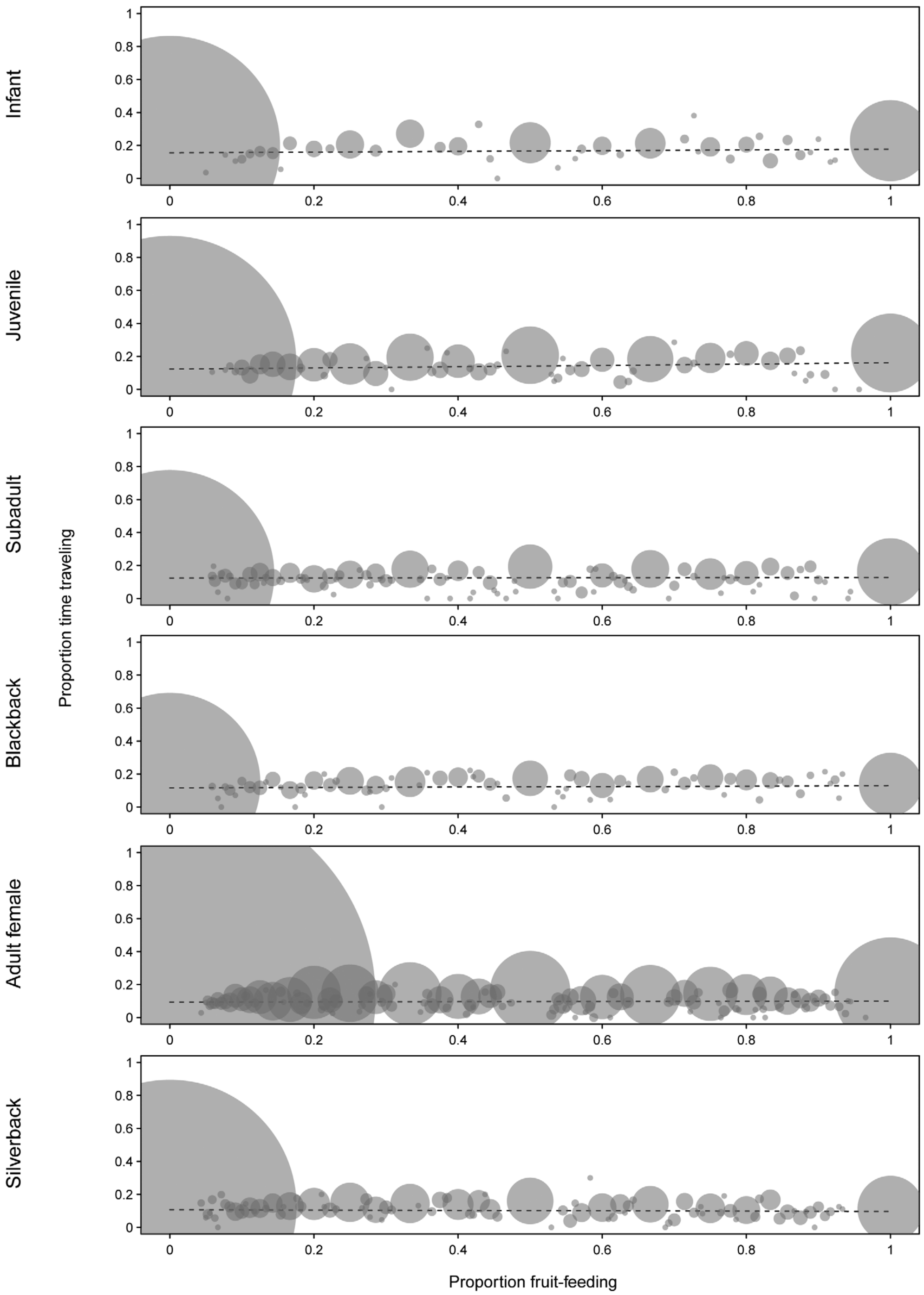

FIGURE 4 Effects of the proportion of fruit-feeding on the proportions of time spent traveling. Dashed lines indicate the fitted model for each age-sex category, with the average response (proportion time traveling) per bin of the predictor (proportion fruit-feeding). The area of the dots depicts the number of days per binned value of the predictor (*N*: 1–8,598)

account speed or total duration of travel, and may not always reflect the total distance traveled (Altmann, 1974). Given the way activity budget was calculated for the models, since we found only a small increase in time spent traveling during higher fruit-eating and a relatively larger decrease in time spent resting, an underestimation of travel time could also be contributing to the result of increased feeding time. Nonetheless, increased frugivory has been shown to have a positive influence on daily travel distance at Bwindi, which is likely due to fruit being sparser and more dispersed than herbaceous vegetation (Ganas & Robbins, 2005; Seiler et al., 2018; Wright et al., 2015). Similar patterns of increased travel distance associated with periods of high-fruit consumption have been shown for other eastern gorillas (Wright et al., 2015; Yamagiwa, Kahekwa, & Basabose, 2003; Yamagiwa & Mwanza, 1994), western lowland gorillas (e.g., Cipolletta, 2004; Doran-Sheehy et al., 2004; Goldsmith, 1999; Masi et al., 2009), as well as chimpanzees (Doran, 1997a; Wrangham, 1977; Wrangham et al., 1998) and Bornean orangutans (Galdikas & Teleki, 1981; Knott, 1999).

When examining the overall activity budget, it is difficult to make direct comparisons across study sites because methods differ, and differences in size of study groups and different definitions for activities may lead to changes in results (e.g., Dunbar, 1988). However, Bwindi

TABLE 4 Comparison of fruit-feeding and activity budgets for great apes

		Fruit-feeding		Activity budget			
Taxon	**Study site**	**Avg**	**Monthly range**	**Feed**	**Rest**	**Travel**	**Social/other**
Gorilla gorilla gorilla	Bai Hokou[a]	34	~5–70	67.1	21	11.7	0.5
	Bai Hokou[b]	51		54.5	28	13	0
	Mondika[c]	36	9–70	43.5	—	—	—
	Maya Nord[d]			72	0	16.5	11.5
	Loango[e]	35		—	—	—	—
Gorilla beringei beringei	Karisoke[f]	<1		55.4	34.4	6.5	3.6
	Karisoke[g]			49	—	—	—
	Bwindi[h]	14.3	0–70	46.3	41.1	12.6	—
	Bwindi[g,i]	11	0–65	51	—	—	—
Pongo abelii	Suaq Balimbing[j]	66.2	62.7–69.6	55	25	17	3
	Ketambe[k,l]	67.5	57.5–71.5	53.9	34	11.5	—
Pongo pygmaeus wurmbii	Tuanan[l]	68.6	26.3–88.0	50.6	30.9	16.8	—
	Sabangau[l]	73.8	24.4–91.9	61.3	19.7	15.9	—
	Tanjung Puting[l,m]	60.9	16.4–96.1	55.9	25.5	16.4	—
	Gunung Palung[l,n]	70	25.8–99.0	36.1	52.8	9.9	—
Pongo pygmaeus morio	Kinabatangan[l]	68		34.1	53.6	10.3	—
	Ulu Segama[o]	62	7.7–90.8	32.3	51.4	16.4	—
	Mentoko[n,p,q]	53.8	25.7–89.0	43.9	45.9	9.5	1
Pan troglodytes verus	Tai[r]	80.9	~45–90	43	39	12	6
	Tai[s,t]	85		54	22	22	—
Pan troglodytes troglodytes	Goualougo Triangle[u,v]	57		22.1	50.8	12.8	14.3
Pan troglodytes schweinfurthii	Budongo[w]	63.8		52.7	25	7.5	14.3
	Budongo[x]	64.5		48.8	—	—	—
	Gombe[y]	59.4		55.6	23.5	14.2	6.2
	Gombe[z]			42.8	18.9	13.4	24.9
	Mahale[aa,ab]	64.5		29.7	38.6	19.5	12
	Ngogo[ac]	80.5		47	34	14	5
	Ngogo[ad]	72.1	36.2–94.1	—	—	—	—
	Kanyawara[ac]	64.4		44	11	45	0
	Kanyawara[ae]	79		54.3	—	—	—
Pan paniscus	Lomako[af]	72.1		40.4	31.9	16.1	6.3

Note: Summary of published data on fruit-feeding and activity budgets of great apes from previous studies, including the average percent fruit-feeding, monthly range of percent fruit-feeding, and percent of time spent in feeding, resting, traveling, and social/other. Note that methods differed across studies in terms of number of individuals and/or study groups, duration of study, definition of activities, and calculation of monthly averages, as well as the level of habituation of study groups.

[a] Masi et al. (2009).

[b] Remis (1994); activity budget percentages are mean of females and group males; note that observations were biased towards arboreal sightings.

[c] Doran-Sheehy et al. (2009).

[d] Magliocca and Gautier-Hion (2002); observations were all taken from a single location; social/other includes visual surveillance, social behavior, miscellaneous, and water consumption.

[e] Robbins, unpublished data. Fruit-feeding is average daily percentage of feeding time spent on fruit.

[f] Watts (1984; 1988).

[g] Wright et al. (2015); presented model estimate for proportion of time spent feeding.

[h] This study; averages include adults only. Fruit-feeding is average of monthly means, calculated from daily percentages of feeding time spent on fruit; activity budget is average of monthly means, calculated from daily percentages of overall time spent in each activity.

[i] Robbins (2008).

[j] Fox et al. (2004).

[k] Wich, Utami-Atmoko, Mitra Setia, Djoyosudharmo, and Geurts (2006).

[l] Morrogh-Bernard et al. (2009); activity budget percentages are averages of age-sex classes in Table 8.2.

[m] Galdikas (1988).

[n] Rodman (1988).
[o] MacKinnon (1974), estimated.
[p] Mitani (1989).
[q] Rodman (1977).
[r] Doran (1997a; 1997b); monthly averages estimated from Figure 4.
[s] Boesch and Boesch-Achermann (2000): feeding includes meat-eating; social interactions are included in resting.
[t] Porter, Garber, Boesch, and Janmaat (2020).
[u] Sanz (2004).
[v] Morgan and Sanz (2006).
[w] Fawcett (2000).
[x] Newton-Fisher (1999).
[y] Wrangham (1977).
[z] Teleki (1981).
[aa] Huffman (1990): activity budget percentages are means across age-sex classes; social/other includes grooming only.
[ab] Matsumoto-Oda and Hayashi (1999).
[ac] Potts et al. (2011); fruit-feeding is proportion of feeding time on ripe fruit.
[ad] Watts, Potts, Lwanga, and Mitani (2012).
[ae] Wrangham, Chapman, Clark-Arcadi, and Isabirye-Basuta (1996).
[af] White (1992); not fully habituated.

gorillas appear to spend a greater proportion of time traveling compared to Virunga gorillas (Table 4), as would be expected given the greater amount of frugivory. The two mountain gorilla populations appear to spend relatively similar proportions of time feeding, as was also found in a previous study directly comparing the two (Virunga 0.49, Bwindi 0.51; Wright et al., 2015), with the average for Bwindi approximately 45–50% for adults and the estimate for Virungas close to 55% (Watts, 1988). Rothman et al. (2008) also estimated the proportion of feeding time to be 55% for Bwindi mountain gorillas.

Compared to western lowland gorillas, Bwindi gorillas spend less time feeding, and substantially more time resting (Table 4). Given that the diet of Bwindi mountain gorillas includes relatively more fibrous foods, it would be expected that that they would require more time for resting to digest and extract nutrients from the more fibrous diet (Dunbar, 1988; Knott, 2005; Williamson & Dunbar, 1999). Although it would be expected for western gorillas to spend more time traveling than Bwindi mountain gorillas because their daily travel distances are larger (Doran & McNeilage, 2001), the proportion of time spent traveling appears to be similar (Table 4), but this may be due to differing methodologies used (Masi et al., 2009).

With respect to age-sex differences in activity budgets, the larger-bodied and more sexually dimorphic great apes show some sex differences (e.g., Doran-Sheehy et al., 2009; Masi et al., 2009; Morrogh-Bernard et al., 2009; Watts, 1988), while for chimpanzees, no significant sex differences have been found in adult activity budgets (Doran, 1997a). Results from Bwindi suggest differences from both the Virunga population as well as western lowland gorillas. The proportion of time spent feeding at Bwindi was generally similar for all age-sex categories, except for infants, for which it was particularly low. There may be some differences in feeding time between gestating and lactating females which were not taken into account here, as reproductive state has been shown to affect time spent feeding both in Bwindi and Karisoke mountain gorillas (Watts, 1988; Wright et al., 2014). The proportion of time spent feeding was similar between Bwindi adult females and silverback males, though female feeding time was slightly higher (Table 1). This pattern may be more similar to western lowland gorillas, where adult females spent more time feeding than silverbacks (Masi et al., 2009; Remis, 1994), in contrast to Karisoke mountain gorillas, where silverbacks spent more time feeding than adult females (Watts, 1988). When comparing across sites for orangutans, generally nonsexually active females spent the most time feeding compared to sexually active females, flanged, and unflanged males (Morrogh-Bernard et al., 2009). For Bwindi gorillas, given their large body size, although silverback males do not spend more time feeding, Rothman et al. (2008) showed that silverbacks eat more food per day, with greater absolute energy intake than adult females and subadults (note that the age category “juveniles” in that study was age 6–11 years, which more closely corresponds to subadults here). This suggests higher food intake rates for silverbacks, though it is unclear if this is achieved by consuming larger food items, increasing feeding rate, spending more time in each food patch, and/or having access to better food patches. Given that dominant silverback males have the highest social rank and displace other individuals at a much higher rate than others (Robbins, 2008), access to better food patches is likely to be a contributing factor. Dominance rank has been shown to have an effect between females at Bwindi, as higher-ranking females had higher ingestion rates compared to lower-ranking females, leading to greater energy intake rates (Wright et al., 2014). Still, for their given body mass, both females and subadults had relatively higher daily energy intake, which may be due to the increased metabolic requirements for reproduction in females and for growth in immatures (Altmann & Samuels, 1992; Key & Ross, 1999; Rothman et al., 2008).

For resting, Bwindi silverbacks spent more time resting than adult females, which was also the case for western lowland gorillas at Bai Hokou, where the silverback spent more time resting than adult females and immatures (Masi et al., 2009). Similarly, for orangutans, flanged males spent the most time resting compared to unflanged males and females, and nonsexually active females rested the least (Morrogh-Bernard et al., 2009). For Virunga mountain gorillas at Karisoke, there did not seem to be age-sex differences in the proportion of time spent resting (Watts, 1988). Given the varying methods across taxa and study sites, it is uncertain why this pattern differs between the mountain gorilla populations, but is perhaps related to the lack of fruit in the Virunga diet. While infants have not been included in other studies of ape activity budgets, at Bwindi infants rested more than any other age-sex category (Table 1).

The proportion of time spent traveling was similar between adult females and silverbacks at Bwindi, with immatures, especially infants, spending a greater proportion of time traveling. For adults, this again differs from both Virunga mountain gorillas, where travel time was greater for adult females compared to silverbacks (Watts, 1988), and western lowland gorillas at Bai Hokou, where travel time was greater for the silverback compared to adult females as well as immatures (Masi et al., 2009). However, at Bwindi, lower-ranking females spend more time traveling than higher-ranking females (Wright et al., 2014), which was not taken into account here, and may have revealed a different pattern between adult females and silverbacks. For orangutans, flanged males spend the least time traveling, and travel time tends to be greater for unflanged males, with females in between (Morrogh-Bernard et al., 2009). The overall pattern shown here for infants, including the relatively high proportion of time traveling and resting and low feeding, is likely in part due to the fact that infants are still nursing, and that observations of infant travel may also incorporate some movement that was classified as traveling during self-play.

5 | CONCLUSIONS

This study provides another example of how variation in ecology can drive diversity in behavioral patterns within a species (e.g., Chapman & Chapman, 1999; Potts et al., 2011; Wright et al., 2015), expanding what we know about the relationship between fruit-feeding and activity budgets of mountain gorillas. While difficult to directly compare across studies, Bwindi gorillas seem to spend a similar proportion of time feeding to western gorillas, as well as chimpanzees and Bornean orangutans, though spend a greater proportion of time resting and less time traveling compared to these more frugivorous apes (Table 4). Compared to the more folivorous Virunga mountain gorillas, the Bwindi population spends a greater proportion of time traveling.

Because resource availability, foraging strategies, and activity patterns differ among gorillas found in lowland and montane habitats (reviewed in Robbins, 2011), it is not surprising that Bwindi mountain gorillas, which live in intermediate ecological conditions, show intermediate levels of frugivory, and share some aspects of their activity patterns with the more frugivorous western lowland gorillas. Recent studies comparing mountain and western lowland gorillas have pointed to ecological differences as driving forces for differences in social organization, behavior, brain development, and life history traits between the species (e.g., Barks et al., 2015; Breuer, Hockemba, Olejniczak, Parnell, & Stokes, 2009; McFarlin et al., 2013; Robbins et al., 2004; Robbins & Robbins, 2018; Stoinski, Perdue, Breuer, & Hoff, 2013). Such differences also exist between the Bwindi and Virunga populations, such as delayed life history events in the more frugivorous population (e.g., Robbins et al., 2009; Robbins & Robbins, 2018; Wright et al., 2015).

It is clear that Bwindi mountain gorillas incorporate substantially more fruit into their diets than Virunga mountain gorillas do, and variation in fruit-feeding influences their activity patterns. Although previous studies suggest that greater fruit availability is associated with less time feeding, results here indicate that with increased fruit consumption, Bwindi mountain gorillas spend a greater proportion of their time feeding and traveling, with less time needed for resting. This pattern of increased feeding time during higher fruit availability is more expected when food availability is highly variable and less predictable, and when high-quality fallback foods are not available during times of fruit scarcity, such as for orangutans in masting forests (Harrison et al., 2010; Knott, 2005). Given the general abundance of herbaceous vegetation at Bwindi, some of which has energy content similar to that of fruits (Ganas, Nkurunungi, & Robbins, 2009; Nkurunungi, Ganas, Robbins, & Stanford, 2004; Rothman et al., 2007; Rothman et al., 2008; Wright et al., 2015), further study is warranted to determine why Bwindi gorillas seem to increase the proportion of time spent feeding and whether it possibly influences daily energy intake on a smaller time scale than examined in previous studies (e.g., Rothman et al., 2008).

More complete information regarding the degree of frugivory in different ape populations has important implications for understanding relationships between ecology, body size, and foraging strategies. These results show that Bwindi gorillas do not conform to the traditional view of mountain gorillas as large-bodied folivores (e.g., Fossey & Harcourt, 1977; Watts, 1990, 1996), but instead fit within a range of ecological and behavioral diversity within the genus *Gorilla*. The abundance of terrestrial herbaceous vegetation and their large body size do not restrict the Bwindi mountain gorillas' diet to one of persistent folivory or restrict their access to arboreal food resources. As with western lowland gorillas, their large body size is associated with related gut adaptions, including a relatively long colon, a large surface area of the colon and cecum with a high number of cellulose-digesting ciliates (Chivers & Hladik, 1980; Collet, Bourreau, Cooper, Tutin, & Fernandez, 1984; Milton, 1984), and relatively long gut retention times (Remis, 2000; Remis & Dierenfeld, 2004), which together should allow for greater absorption of nutrients (Chivers & Langer, 1994; Kay & Davies, 1994; Lambert, 1998). An enlarged hindgut associated with colocecal fermentation, in addition to the presence of fiber-digesting intestinal bacteria, likely help to digest a diet high in fiber and tolerate tannin-rich foods (e.g., Cork & Foley, 1992; Frey et al., 2006; Rogers, Maisels, Williamson, Fernandez, & Tutin, 1990; Rothman et al., 2007; Simmen, Josseaume, & Atramentowicz, 1999). This allows gorillas to be more flexible in their diet compared to more frugivorous apes, by eating fruit when it is available and having the ability to digest large amounts of more fibrous foods when it is not (Doran-Sheehy et al., 2009; Masi et al., 2015; Remis, 2000; Remis, 2003; Remis et al., 2001).

Ecological differences that influence frugivory and activity patterns within mountain gorillas are expected to also contribute to differences in arboreality and locomotor behavior, as Bwindi mountain gorillas will spend relatively more time climbing and navigating arboreal supports to feed on fruit. While locomotor behavior of Virunga mountain gorillas is characterized as predominantly quadrupedal walking (Doran, 1997b), the locomotor repertoire of Bwindi mountain gorillas is likely to be more diverse. Future studies examining differences in gorilla energy expenditure and skeletal morphology will have to take into account this intraspecific variation, though further study is needed to understand the extent of this variation in arboreality and the amount of time spent in arboreal locomotor behaviors.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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