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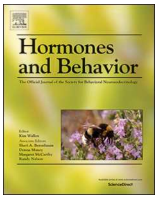

Non-invasive estimation of the costs of feeding competition in a neotropical primate

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ABSTRACT

A key goal in behavioral ecology is to investigate the factors influencing the access to food resources and energetic condition of females, which are strong predictors of their reproductive success. We aimed to investigate how ecological factors, social factors, and reproductive state are associated with energetic condition in a wild neotropical primate using non-invasive measures. We first assessed and compared urinary C-peptide levels (*uCP*), the presence of urinary ketones (*uKet*), and behaviorally assessed energy balance (*bEB*) in female white-faced capuchin monkeys (*Cebus imitator*) living in Santa Rosa, Costa Rica. Then, we assessed how these measures were associated with feeding competition, dominance rank, and reproductive state. As predicted, *uCP* and *bEB* were positively associated with each other, and *bEB* was negatively associated with *uKet*. However, we did not find a relationship between *uCP* and *uKet*. Females showed lower *uCP* and *bEB* values during periods of intense feeding competition, but this relationship was not dependent on dominance rank. Furthermore, rank was not directly associated with *uCP* and *bEB*. Urinary ketones, on the other hand, were only produced in the most adverse conditions: by low-ranking, lactating females during periods of intense feeding competition. Behavioral strategies are assumed to maximize reproductive success and not energetic condition per se, which might explain why rank was not generally associated with energetic condition in our study population. This highlights the importance of considering potential differences between reproductive success and proxies of reproductive success, such as energetic condition or food intake, when investigating predictions of socioecological models.

1. Introduction

A key goal in behavioral ecology is to understand the behavioral and physiological mechanisms underlying variation in reproductive fitness. While numerous social and ecological factors contribute to an individual's reproductive success, proximate access to resources, subsequent nutritional gain, energetic expenditure and resulting energetic condition play a central role in reproductive performance (Altmann and Alberts, 2003; Ellison and Valeggia, 2003; Emery Thompson, 2017, 2013; McCabe et al., 2013; Willis et al., 1996). In mammals, food is crucial for the survival of both males and females, but food resources are predicted to limit the reproductive success of females in particular (Trivers, 1972). Accordingly, documenting the energetic condition of females provides key physiological information that may help to reveal social and ecological influences on overall fitness.

Variation in the availability of food resources is considered a key factor affecting energetic condition of mammals (Goldizen et al., 1988; Jeanniard du Dot et al., 2008; Knott, 1998; Koenig et al., 1997). However, individuals within a population also compete with each other over available resources, and the energetic condition of different individuals might therefore be affected to varying degrees. Given the importance of feeding competition on energetic condition, and therefore fitness, feeding competition has been considered a major factor in theories trying to explain animal social behavior [*i.e.*, socioecological theory; *e.g.*, (Sterck et al., 1997; Van Schaik, 1989; Wrangham, 1980)]. For example, in addition to vulnerability to predation, the need to

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defend food resources against conspecifics is assumed to be one of the major drivers of social grouping in mammals [*e.g.*, (Ebensperger et al., 2012; Markham and Gesquiere, 2017)]. Despite the advantages of group living, it also comes with the cost of intragroup competition over food resources. Generally, larger groups will deplete available food resources at faster rates, and on average, individuals within a group may therefore devote more time to foraging, travel farther distances, or change their dietary strategies [(Chapman and Chapman, 2000; Janson and Goldsmith, 1995; Terborgh and Janson, 1986; Wrangham et al., 1996); but see (Markham et al., 2015)]. As a consequence, the energetic condition of females within a group is predicted to be related to the density of food resources and also to the number of individuals feeding on those available resources. For example, when few individuals forage in a home range with a high density of food resources (*i.e.*, periods of low feeding competition), the energetic condition of those females is expected to be higher compared to periods when many individuals forage in an area with a low density of food resources (*i.e.*, periods of high feeding competition).

Feeding competition might not have equal consequences for all females within a group if some individuals are able to monopolize spatially concentrated food resources, and therefore benefit more from available food than others. Under these conditions, females are often observed to form dominance hierarchies, and the rank position of a female is predicted to determine the priority of access to such clumped food resources (Koenig et al., 2013; Koenig and Borries, 2006; Sterck et al., 1997; Van Schaik, 1989). Indeed, previous studies have shown that access to food resources and/or energy gain varied according to dominance rank [*e.g.*, (Barrette and Vandal, 1986; Holand et al., 2004; Koenig and Borries, 2006)]. Consequently, relative to low-ranking females, the energetic condition of high-ranking females is expected to be less affected by feeding competition, which we define as the availability of food relative to the size of a group. In addition to these ecological and social factors, the energetic condition of individuals can also be affected by reproductive condition. For example, in mammals, gestation and lactation require considerable amounts of energy, and, therefore, reproductive state may impact the energetic condition of females (Gesquiere et al., 2018; Lochmiller et al., 1986; McCabe et al., 2013). Consequently, the energetic condition of gestating and lactating females is expected to be lower than that of cycling females.

While behavioral responses to feeding competition have frequently been studied, fewer data are available on the impacts of competition on individual energetic condition (Emery Thompson et al., 2014; Gómez-Espinosa et al., 2014; Grueter et al., 2014; Harris et al., 2010). These data are essential for understanding how different ecologies shape feeding competition and constrain sociality, and for explaining how these effects may impact fitness. The main goal of our study was to assess the effects of feeding competition on energetic condition among adult females in a population of wild white-faced capuchin monkeys (*Cebus imitator*) in Santa Rosa, Costa Rica, by examining social factors, ecological factors, and reproductive state as potential predictors of energetic condition. This population of capuchins lives in a habitat with extreme intra- and inter-annual variability in rainfall (Campos, 2018; Fedigan and Jack, 2012), leading to considerable variability in the availability of ripe fruit, the main diet of capuchins (Bergstrom et al., 2018; Melin et al., 2014). Furthermore, female white-faced capuchin monkeys form linear dominance hierarchies (Bergstrom and Fedigan, 2010), in which the rank position of a female determines the priority of access to valuable food resources (Vogel, 2005). This makes this population a valuable model to investigate the dynamics of feeding competition and its effects on the energetic condition of mammalian females.

Non-invasive measures of the energetic condition of wild animals are invaluable, since capture and sedation or even baiting and weighing, interfere with normal activity and physiological processes. Estimations of changes in physical condition can be obtained via qualitative visual assessment measures such as rating physical condition along a scale based on the visibility of bones (Berman and Schwartz, 1988; Johnson and Kapsalis, 1995; Koenig and Borries, 2006; Perryman and Lynn, 2002; Pettis et al., 2004; Schulte-Hostedde et al., 2001; Zucca et al., 2011), or the use of photography or parallel lasers (Kurita et al., 2012; Rothman et al., 2008). However, these measures may be difficult to apply in some study systems because of species-specific morphology or poor observation conditions. A second approach is to calculate energetic condition noninvasively through nutritional analysis, combined with behavioral estimates of energy intake and energy expenditure [*e.g.*, (Heesen et al., 2013)]. This method ideally includes estimates of the energetic demands of physical activity and reproductive state in addition to basal metabolic costs. However, this approach is labor intensive and may not provide accurate estimation due to the number of variables that may affect energetic condition, assumptions that must be made to calculate energy intake or expenditure, and the high density of observational data required. A third approach is the direct measurement of biomarkers that reflect energetic condition from non-invasively collected samples, such as urine or fecal samples. One such measure is urinary C-peptide (*uCP*), a proxy for insulin secretion that has been validated and used extensively to investigate energetic condition in primates (Deschner et al., 2008; Dias et al., 2018; Emery Thompson, 2017; Emery Thompson et al., 2009; Emery Thompson and Knott, 2008; Girard-Buttoz et al., 2014, 2011; Grueter et al., 2014; Harris et al., 2010; Lodge, 2012; McCabe et al., 2013; Sherry and Ellison, 2007). Other studies have assessed urinary ketones (*uKet*), which can be performed easily in the field with urinary dipsticks. Ketones are produced and expected to be present in urine when individuals are severely metabolically stressed and metabolizing fat stores, most specifically during nutritional deficit and severe carbohydrate shortages (Laffel, 1999; Soskin and Levine, 1944). Indeed, some studies of apes have correlated the presence of *uKet* with periods in which energy intake and *uCP* levels were low, providing support for the use of this biomarker to identify periods of metabolic stress and fat metabolism (Deschner et al., 2008; Emery Thompson and Knott, 2008; Sherry and Ellison, 2007).

The first aim of our study was to assess and compare three different measures of energetic condition in capuchins: *uCP*, *uKet*, and energy balance estimated from behavioral observations (*bEB*; note that *uCP* and *uKet* are proxies for energy balance, as well, but to avoid confusion, hereafter, the use of “energy balance” refers only to the calculated behavioral measure). We predicted that *uCP* and *bEB* would be positively related to each other, whereas *uKet* would be negatively related to the other two indicators. The second aim was to assess the degree to which feeding competition, dominance rank, and reproductive state were associated with these three measures of energetic condition. For the degree of feeding competition, we calculated a composite variable reflecting the monthly density of fruit biomass within the home range of each group in relation to the biomass of the group. We included group biomass because the available fruit biomass per female, and hence the potential for feeding competition, depends on the number of individuals in a group feeding on available food resources. We predicted that a higher density of ripe fruit biomass in relation to group body mass would result in higher energetic condition of females. However, we also predicted that this association would be dependent on individual dominance rank. More specifically, we expected that the energetic condition of high-ranking females would be less affected by the intensity of feeding competition whereas low-ranking females would show a greater decline in energetic condition during periods of intense competition. With regard to reproductive state, we predicted that lactating females would have lower energetic condition than pregnant females, and cycling females would have the highest energetic condition (Key and Ross, 1999), although insulin sensitivity associated with pregnancy and lactation may influence this predicted pattern for *uCP* levels (Hadden and McLaughlin, 2009; Tigas et al., 2002; Vernon, 1989). Finally, because *bEB* was based on the behavioral assessment of energy intake (*bEI*) and energy expenditure (*bEE*), this offered us the opportunity to test whether a potential drop in *bEB* during periods of intense feeding competition was linked to reduced energy intake, increased energy expenditure (because of increased foraging effort), or both.

2. Material and methods

2.1. Data collection

We studied three groups (LV, CP and GN) of wild white-faced capuchin monkeys living in the seasonal tropical dry forest of Sector Santa Rosa (SSR), Área de Conservación Guanacaste, Costa Rica. Average annual rainfall in SSR between 1980 and 2018 was ~1700 mm, which accumulates almost exclusively between mid-May and early November (Campos, 2018; Fedigan and Jack, 2012). Our study groups are part of a long-term study population habituated to researcher presence (CP group since 1983, LV group since 1990, and GN group since 2005). Data collection took place over three four-month periods between September 2009 and May 2011 (Sep–Dec 2009, May–Aug 2010, and Jan–Apr 2011) to sample across seasonal variation. We followed the groups from dawn until dusk for four-to-six-day periods per group per month (in total 2124 h of observational contact with the groups). During these group follows, we conducted 10-min focal animal follows to record general state behaviors of focal females (*e.g.*, travel, forage, rest, feed, or social), detailed social behaviors, and feeding events to calculate ingestion rates (in total 575 focal hours: LV = 120 h, CP = 227 h, GN = 228 h). During the study period, each group included between 20 and 37 individually known subjects in total (LV: 20-23; CP: 26-33; GN: 33-37; for the number of adult and subadult individuals in each group see Table S1, Supplementary information). We considered all females as adult that were 6 years or older (the average age of first conception in our population), or that had conceived at an earlier age, and included all adult females that did not disappear or die during the study. The number of sampled subjects per month ranged from 24 to 25 (LV = 5, CP = 10, GN = 9–10; for the number of adult females in each group and year see Table S1).

2.2. Estimation of energy intake (bEI), energy expenditure (bEE), and energy balance (bEB) using behavioral data

We calculated monthly *bEB* values based on behavioral data as detailed in Method S1 (SI) and Bergstrom et al. (2018). In brief, we calculated energy intake (*bEI*) based on the rate of food item ingestion recorded during individual focal data collection, and the nutritional value of the ingested items. We calculated energy expenditure (*bEE*) based on estimated basal metabolic costs of females in addition to the estimated costs of different activities for which we recorded the rates during focal observations, and the costs of reproductive state (lactating > gestation > cycling; see the section on the Determination of Reproductive State and Rank below). We then calculated *bEB* values per month and female as the difference between the mean of *bEE* and the mean of *bEI*.

2.3. Assessment of urinary C-peptide levels (uCP) and presence of urinary Ketone bodies (uKet)

We collected urine samples opportunistically from all female study subjects either by catching urine on plastic bags attached to extended hoops or by pipetting it from vegetation (Emery Thompson and Knott, 2008). Samples were then placed on ice and frozen within 6–8 h of collection. On average, we collected 1–3 urine samples per female and month, spaced as equally as possible over each observation period. This yielded 825 urine samples that contained sufficient volume for the C-peptide analysis. Due to variation in the dilution of samples, urinary C-peptide concentrations were determined for 534 out of 825 examined urine samples. Furthermore, we determined the presence or absence of ketone bodies for 424 of these urine samples (we did not have sufficient volume for the other samples to perform the urinalysis test).

Samples were transported on dry ice to the Hominoid Reproductive Ecology Laboratory at the University of New Mexico, where hormone assays were conducted between October and December 2011. To measure *uCP*, we used commercially available human radioimmunoassay kits with a sensitivity range of 100 pg/ml to 5000 pg/ml (RIA Human C-peptide Kit, Millipore Corporation, Billerica, MA). While marketed for use in humans, the assay exhibits 90% cross-reactivity with monkey C-peptide and it has been validated for use in a range of primate species [*Colobus guereza*, (Harris et al., 2010); *Cercocebus sanjei*, (McCabe et al., 2013); *Aotus spp.*, (Fernandez-Duque et al., 2011); *Pongo pygmaeus*, (Emery Thompson and Knott, 2008); *Pan troglodytes*, (Emery Thompson et al., 2009; Sherry and Ellison, 2007); *Gorilla beringei*, *Cercopithecus spp.*, *Ateles geoffroyi*, unpublished data, Comparative Human & Primate Physiology Center, University of New Mexico]. We assayed each sample for *uCP* levels in duplicate (Method S2). We reassayed samples if the coefficient of variation (CV) of duplicate samples exceeded 15% for sample concentrations > 250 pg/ml and 25% for sample concentrations ≤250 pg/ml due to the smaller margin of error at lower values. The intra-assay CVs, based on the mean CV of duplicates were 11.9% for low (≤250 pg/ml) and 7.1% for high (> 250 pg/ml) samples, respectively. The inter-assay CVs were 10.8% and 9.4% for low and high controls, respectively. To avoid artificially excluding samples with low *uCP* values, if a sample value fell below assay sensitivity but had a sufficient creatinine level (Cr ≥ 0.100 mg/ml, indicating that the sample was not low because it was too dilute), we assigned it the value of minimum assay sensitivity of 100 pg/ml [(Deschner et al., 2008; Girard-Buttoz et al., 2011); for details on the measurement of creatinine, see (Bergstrom et al., 2018)]. All *uCP* results were standardized to specific gravity to adjust for urine concentration (see Method S3). An exploratory analysis confirmed that sample storage duration had no effect on *uCP* levels (see Method S4).

We determined the presence or absence of ketone bodies for each urine sample by using urinalysis reagent strips (Siemens Multistix 10 SG, Siemens Healthineers, formerly Siemens Healthcare, Erlangen, Germany) either immediately upon sample collection or after data collection finished the same day the sample was collected. We pipetted a small amount of urine onto the test site of the reagent strip to measure the level of ketone bodies present as a broad indication of the degree of ketosis (produced in the process of fat metabolism). Because ketone strips can only measure the presence of ketone bodies rather than their concentration, they may yield false negative readings if ketones are diluted by high water content of the sample. This problem was unlikely to bias our results because we had few dilute samples (only one urine sample yielded a specific gravity of < 1.004) and specific gravity values did not vary significantly across reproductive states (see Method S5).

2.4. Determination of Reproductive State and Rank

We assigned monthly reproductive states to females, as one of three distinct categories: gestation, lactation, and cycling. Gestation was inferred based on infant birth dates and the mean gestation time for this population, 158 days (Carnegie et al., 2011). We based the duration of lactation on infant nursing rates. Specifically, we classified female as lactating from parturition until the infant stopped nursing completely, or infant nursing rates dropped below one bout per hour based on the observation that when nursing did occur during pregnancy, it was below this rate. Finally, we also considered females who were neither gestating nor lactating to be cycling. Since the energy requirements of gestation and lactation may change over time, we further split up these categories into more detailed reproductive states and then performed a parallel analysis using these more fine-grained categories (see below). For gestation, which takes 158 days on average, we considered the first 79 days as early, and the remaining days as late gestation. For lactation, we considered the first 14 weeks as early, and the remaining weeks as late lactation since the mother's rates of nursing, infant carrying, and energy intake drop considerably after 14 weeks (McCabe and Fedigan, 2007).

We assigned ordinal dominance ranks to all female subjects based on agonistic interactions that we recorded during focal and *ad libitum* observations. Using directional agonistic interactions, we minimized the number and strength of inconsistencies in dominance matrices (*i.e.*, the *I&SI* method) as described in Bergstrom and Fedigan (2010). Dominance hierarchies among female capuchins are highly linear. We then scaled the ranks from 0 (lowest rank) to 1 (highest rank) for each group and data collection period.

2.5. Determination of the potential degree of Feeding Competition

The composite variable *Feeding Competition* was derived from two other resource-related factors: ripe fruit biomass density within each home range in kg per hectare, and group adult body mass in kg. We divided fruit biomass density in the home range by group adult body mass to obtain a value that reflects how much ripe fruit biomass was available per unit of area and kg of adult body mass. We then used the reciprocal of this variable so that high values reflect low levels of fruit biomass per area considering the size of the group, corresponding to high levels of *Feeding Competition*.

The first step to calculate the density of ripe fruit biomass within each home range was to determine home ranges for each group during each of the three study periods. The methods are described in detail in Campos et al. (2014). In brief, we collected location data on each group approximately every 30 min using a handheld Garmin GPS device (models 70Cx and GPSmap 62 s; Garmin, Kansas, US) while following the groups during the day. We estimated home ranges as the 95% isopleth for each group and for each of the three four-month data collection periods by using a movement-based kernel method that is based on biased random bridges (Benhamou, 2011; Benhamou and Cornélis, 2010). The advantage of this method (and other movement-based methods) over more commonly used location-based methods is that the utilization distribution is estimated from a time-ordered movement path rather than from unlinked points, thereby accounting for autocorrelation and increasing biological realism (Benhamou, 2011; Horne et al., 2007; Kranstauber et al., 2012). We implemented the biased random bridge method using the packages adehabitatHR v0.4.15 and adehabitatLT v0.3.23 (Calenge, 2006) in R v3.5.2 (R Core Team, 2018). Home range sizes ranged from 116 ha to 261 ha (see Table S1 and Fig. S1, for details and an example of the shape and size of home ranges).

As a next step to estimate monthly fruit biomass density in each home range, we used plant transect and plant phenology data as detailed in Method S6. In brief, we used information on abundance and size of trees commonly eaten by capuchins collected on 423 plant transects, each with a length of 100 m, within the entire study area. To estimate the maximum ripe fruit biomass within each home range, we used all transects that intersected with that home range (see Fig. S1, for the design of the plant transects and an example of home ranges). Then, we estimated the mean monthly tree coverage and maturity of ripe fruit for each species using monthly phenological data collected from approximately eight different individual trees per species. We multiplied this monthly availability index by the maximum available ripe fruit biomass per species within each home range, and then summed this value for all included species. The resulting monthly value of ripe fruit biomass was then divided by the included transect area to obtain a density of ripe fruit (in kg/ha) for each home range.

Following Campos et al. (2014), we estimated adult group body mass by multiplying the number of adult and subadult individuals of different age and sex classes present in the group by the mean body mass reported for the respective age/sex class in white-faced capuchins (Smith and Jungers, 1997). We used 2.54 kg for adult females and 3.68 kg for adult males. We also used 2.54 kg for subadult males, which are similar in size to adult females. We did not include immature animals in the calculation of group body mass, but the number of immatures is strongly correlated with the number of sexually mature animals (Campos et al., 2014), thus our (relative) estimates of group body mass should be comparable across groups and time.

2.6. Statistical analysis

We used linear mixed models and generalized linear mixed models to investigate the relationship between the three different estimates of energetic condition (*uCP*, *uKet*, *bEB*), and to investigate potential factors associated with these three estimates plus the two components of *bEB*, namely *bEI* and *bEE*. To fit the models, we used the R package lme4 v.1.1-17 (Bates et al., 2015) following the procedures described in Method S7.

To investigate which factors were related to variation in energetic condition of females, we built three models, each with one of the three estimates of energetic condition as the outcome variable and *Reproductive State*, *Feeding Competition*, *Rank*, and the interaction *Feeding Competition*Rank* as predictor variables. For *Reproductive State*, we only included the three categories (gestation, lactation, cycling) in our main models to keep the model complexity at a reasonable level, but we also fit an additional model for *uCP* using the five categories described above. For the model with *bEB* as outcome variable, we did not include the variable *Reproductive State* because *bEB* was defined as ‘energy expenditure – energy income’, where energy expenditure was calculated partly based on *Reproductive State* (see Method S1). Thus, testing the effect of *Reproductive State* on *bEB* would have been partly circular. Furthermore, to distinguish between the effects of *Feeding Competition* and *Rank* on energy intake and expenditure, we fit two more models with *bEI* and *bEE* as outcome variables. In addition to the fixed effects, we included the identity of females as a random intercept. Because only eight out of 25 females were observed in all three reproductive states and individual dominance rank positions were highly stable over time, we did not include the random slopes for these variables. Furthermore, the number of groups was fairly small (three groups), and we therefore included the identity of groups as a (categorical) fixed effect rather than a random effect and used sum-to-zero contrasts. This means that the sum of the coefficients for the included groups always had a sum of zero. Thus, the intercepts of the models indicate the predicted values for ‘average’ groups, and the coefficients for each of the groups indicate how much the predicted value for this group differs from the average value. Because *uCP* levels have been shown to be affected by the time of the day [*e.g.*, in chimpanzees, *Pan troglodytes*, (Georgiev, 2012)], we included the time of sample collection (*Collection Time*) as a control variable in all of our models with *uCP* as outcome variable.

Before running the models, *uCP* values were log-transformed to improve the normality of residual distribution. Furthermore, to improve homoscedasticity of residuals, we transformed *bEB* values using the following formula:

$$EB_{transformed} = \sqrt{EB - min(EB) + 1}$$

We applied this transformation because some of the original *bEB* values were negative. Since *bEI* and *bEE* were always positive numbers, we simply used a square-root transformation for these two variables. Similarly, we log-transformed the predictor variable *Feeding Competition* to improve the homoscedasticity of residuals of our calculated models. Before running each model, we calculated z-scores for all numerical variables to improve model convergence and because two of the numerical variables (*Rank*, *Feeding Competition*) were included in an interaction. As detailed in Method S7, all models were checked for respective assumptions.

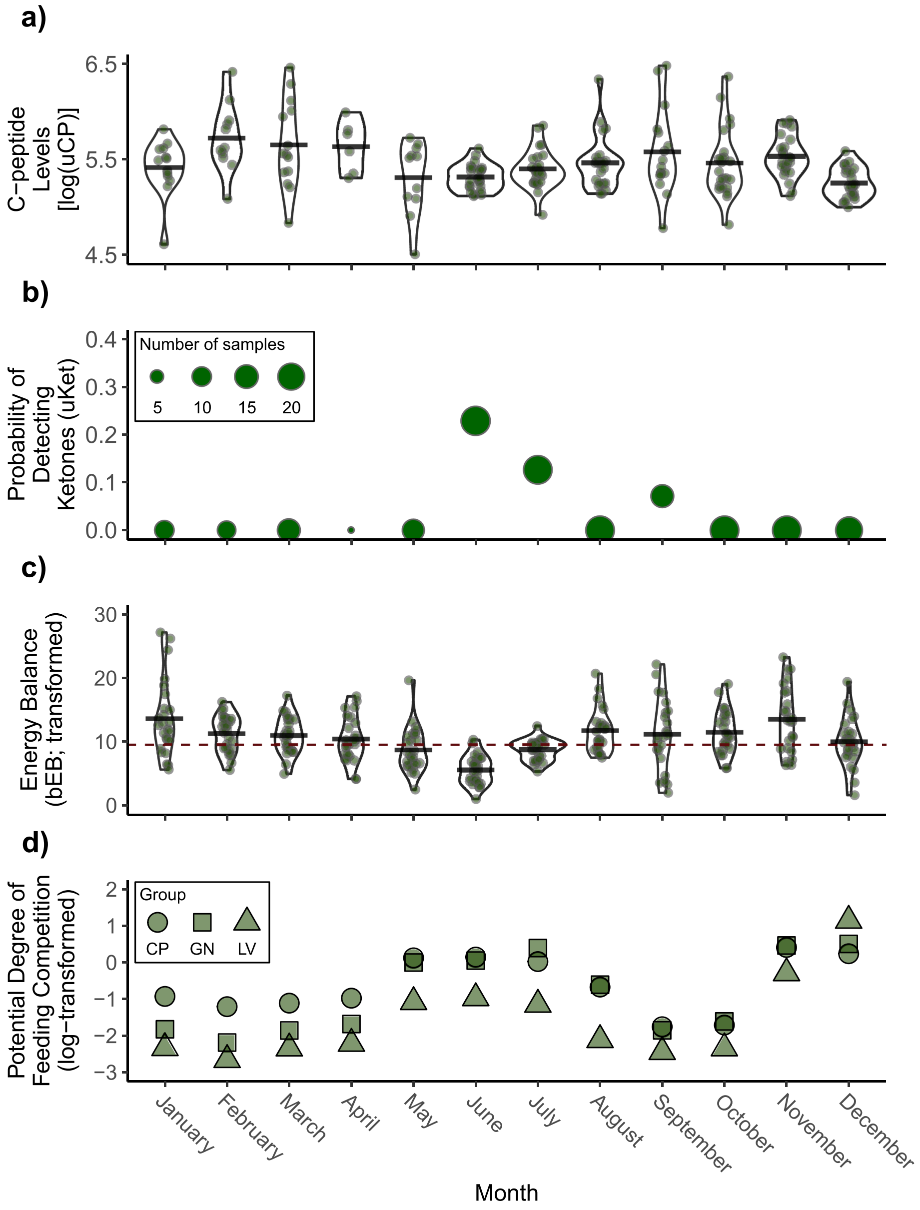

Fig. 1. Temporal variation for the three measurements of energetic condition and potential degree of *Feeding Competition* in female white-faced capuchins: a) urinary C-peptide levels (*uCP*; log-transformed), averaged per female and month; b) the proportion of urine samples with ketone bodies (*uKet*; the area of the circles is proportional to the number of samples); c) energy balance calculated based on behavioral observations (*bEB*), and transformed as described in the methods (the dashed, horizontal line indicates the original zero-value, where energy income and expenditure were balanced); and d) potential degree of *Feeding Competition* (log-transformed) for each group and month. The violin plots in a) and c) illustrate the probability density of values and the horizontal black lines indicate the monthly mean values. For individuals who provided more than one sample per month, values were averaged for each month so that each dot in a) and c) represents a monthly value per female and the number of samples in b) is the number of females per month included.

3. Results

3.1. Relationships between different estimates of energetic condition

Each female contributed between 7 and 32 *uCP* samples (mean ± sd = 21.4 ± 5.96 samples), and between 7 and 24 *uKet* samples (mean ± sd = 17.0 ± 4.98). For *bEB*, we calculated one value per female and month (with the exception of one female who was included in 2010 and 2011, but not in 2009). Each of these three variables showed variation over the duration of our study (Fig. 1).

Although none of these differences were significant, the LV group had, on average, the highest *uCP* concentrations, and ketone bodies were not present in any of the samples from this group. The GN group had intermediate *uCP* levels, and ketones were present in 9 out of 163 samples (or 5.5%). For the CP group, with the lowest *uCP* levels, ketones were present in 29 out of 178 samples (16.3%). Furthermore, we found that the presence of *uKet* was not significantly related to *uCP* levels (Table 1, Model a). In contrast, both *uCP* and *uKet* were significantly related to *bEB* in the predicted direction (Table 1, models b and c). On average, when individuals had a higher *bEB*, they had higher *uCP* values, and individuals that had ketone bodies in their urine had lower *bEB* levels. Collection time of samples, which we included as control variable in models with *uCP* as outcome variable, was significantly and negatively associated with *uCP* levels (Table 1, model a and b).

3.2. Predictors of uCP

In contrast to our prediction, the interaction *Feeding Competition*Rank* was not significantly related to urinary C-peptide levels (Table 2). However, *uCP* was significantly related to *Feeding Competition* (Table 2). During periods of more intense food resource competition, females generally showed lower energetic condition as assessed by *uCP* levels. Furthermore, *uCP* levels were significantly related to *Collection Time*, and *uCP* levels decreased over the course of the day. *Reproductive State* was not associated with *uCP* levels (Table 2), and this result did not change when we included the five more detailed reproductive states instead of our three broader reproductive states into the model (see Results S2).

Table 1
Relationships between the three estimates of energetic condition based on mixed models. For model a), we included 408 data points from 25 females. For model b), we included 534 data points from 25 females. For model c) we used 424 data points from 25 females. See Results S1 (SI) for original means and standard deviations for all variables before transformation. P-values < 0.05 are shown in boldface.

Model	Outcome variable	Term	Estimate (SE)	CI (95%)	Df	χ^2	P
a)	C-peptide *(uCP)*	(Intercept)	0.053 (0.055)	[−0.053, 0.155]	–	–	–
		Ketone *(uKet)* - Present	−0.265 (0.172)	[−0.600, 0.070]	1	2.412	0.120
		Collection Time	**−0.182 (0.049)**	**[−0.279, −0.086]**	**1**	**13.521**	**< 0.001**
		Group (CP)	−0.097 (0.072)	[−0.230, 0.039]	2	3.114	0.211
		Group (GN)	−0.046 (0.072)	[−0.182, 0.087]			
b)	C-peptide *(uCP)*	(Intercept)	0.030 (0.047)	[−0.064, 0.127]	–	–	–
		Energy balance *(bEB)*	**0.186 (0.043)**	**[0.102, 0.270]**	**1**	**18.390**	**< 0.001**
		Collection Time	**−0.187 (0.042)**	**[−0.269, −0.105]**	**1**	**19.809**	**< 0.001**
		Group (CP)	−0.057 (0.062)	[−0.183, 0.069]	2	2.822	0.244
		Group (GN)	−0.073 (0.063)	[−0.200, 0.056]			
c)	Energy balance *(bEB)*	(Intercept)	0.103 (0.072)	[−0.046, 0.250]	–	–	–
		Ketone *(uKet)* - Present	**−0.864 (0.165)**	**[−1.190, −0.539]**	**1**	**26.355**	**< 0.001**
		Group (CP)	−0.228 (0.095)	[−0.421, −0.031]	2	5.101	0.078
		Group (GN)	0.095 (0.095)	[−0.101, 0.288]			

3.3. Predictors of uKet

Presence of *uKet* was only observed in samples from lactating females, and only in females from the GN and CP groups (see above). To prevent issues with model stability and overfitting due to complete separation, we had to exclude samples from all cycling and pregnant females in addition to excluding samples from the LV group in general. As a consequence, we were not able to include *Reproductive State* as a predictor variable. The resulting model indicated that the interaction *Feeding Competition*Rank* was significantly related to the presence of *uKet* (Table 3; despite modelling issues, results were qualitatively similar in a model including all *uKet* data points; see Results S5). During periods of low and intermediate levels of feeding competition, none of the lactating females had ketone bodies in their urine samples. However, during periods of intense resource competition, low-ranking lactating females were more likely than high-ranking lactating females to show *uKet* presence (Fig. 2).

3.4. Predictors of bEB

Behaviorally assessed energy balance (*bEB*) was significantly related to *Feeding Competition* but not to the other variables (Table 4). During periods of more intense food resource competition, females showed lower energy balance. To investigate whether this pattern was due to variability in energy intake, energy expenditure, or both, we fit two more models with *bEI* and *bEE* (the two components of *bEB*), as outcome variables respectively (Table 5). The results indicated that energy intake was lower during periods of intense feeding competition but that there was no significant association between energy expenditure and feeding competition. *Rank* was not significantly related to either outcome variable.

4. Discussion

We examined and compared the effects of feeding competition, dominance rank, and reproductive state on three different estimates of energetic condition: urinary ketones, C-peptide levels, and behavioral measures of energy balance in white-faced capuchin monkeys. Our principal results are fourfold: 1) Both *uCP* and *uKet* correlate with behavioral and nutritional estimates of energy balance, confirming that both are useful biomarkers of energetic condition in capuchins, although *uKet* are only excreted under conditions of drastic negative energy balance; 2) lactating females are more likely to be energetically stressed, as indicated by the presence of *uKet*, than are pregnant or cycling females; 3) female energetic condition as measured by *uCP* and *bEB* is greater during times when there was less potential competition over available food resources; 4) dominance rank had relatively little effect on energetic condition, though under the most extreme conditions, *i.e.*, when lactating under conditions of high feeding competition, low ranking females were more likely to excrete *uKet*. We discuss these results below in more detail and their implications for understanding how individuals are affected by temporal variation in food availability (Emery Thompson et al., 2009; Emery Thompson and Knott, 2008; Sherry and Ellison, 2007), reproductive costs (Harris et al., 2010), and the differential effects of resource competition (McCabe et al., 2013).

Table 2
Linear mixed model testing for potential predictors of *uCP*. The full model, including the interaction *Feeding Competition*Rank* in addition to *Feeding Competition*, *Rank*, *Reproductive State*, *Collection Time*, and *Group* was significantly better than null model (χ^2 = 40.703, df = 6, P < 0.001). However, *Feeding Competition*Rank* was not significantly related to *uCP* (χ^2 = 1.143, df = 1, P = 0.2320). Therefore, we removed this interaction from the model to establish P-values for main-effect terms using chi-square tests (for the model including the interaction, see Results S3). The model was calculated including 534 *uCP* value from 25 females. See Results S4 for original means and standard deviations for all variables before transformations. P-values < 0.05 are shown in boldface.

Term	Estimate (SE)	CI (95%)	Df	χ^2	P
(Intercept)	0.236 (0.152)	[−0.069, 0.536]	–	–	–
Feeding Competition	**−0.182 (0.043)**	**[−0.267, −0.097]**	**1**	**17.425**	**< 0.001**
Rank	0.001 (0.044)	[−0.087, 0.092]	1	0.001	0.982
Reproductive State (Lactation)	−0.241 (0.159)	[−0.554, 0.081]	2	2.300	0.317
Reproductive State (Gestation)	−0.175 (0.185)	[−0.538, 0.191]			
Collection Time	**−0.193 (0.042)**	**[−0.275, −0.111]**	**1**	**21.032**	**< 0.001**
Group (CP)	−0.064 (0.061)	[−0.190, 0.060]	2	2.223	0.329
Group (GN)	−0.052 (0.065)	[−0.181, 0.083]			

Table 3

Generalized linear mixed model testing for potential predictors of *uKet*. The full model, including *Feeding Competition***Rank*, *Feeding Competition*, *Rank*, and *Group* as predictor variables was significantly better than the null model (χ^2 = 28.221, df = 3, P < 0.001). The model was calculated including 259 *uKet* values from 19 females (only lactating females from CP and GN group were included). See Results S5 for the model results including all values, and Results S6 for original means and standard deviations for all variables before transformation. *P-values for main-effect terms are not reported because of the significant interaction term. P-values < 0.05 are shown in boldface.

Term	Estimate (SE)	CI (95%)	Df	χ^2	P
(Intercept)	−3.200 (0.582)	[−4.626, −2.263]	–	–	–
Feeding Competition	1.869 (0.571)	[0.928, 3.203]	–	–	–*
Rank	0.082 (0.382)	[−0.754, 0.868]	–	–	–*
***Group* (CP)**	**0.908 (0.355)**	**[0.263, 1.794]**	**1**	**7.141**	**0.008**
Feeding Competition*Rank	**−1.056 (0.447)**	**[−2.051, −0.246]**	**1**	**6.641**	**0.010**

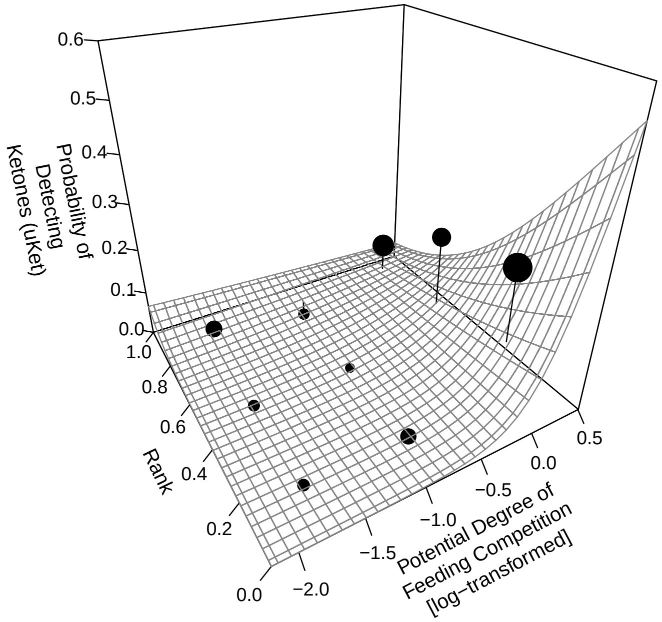

Fig. 2. Illustration of the effects of *Feeding Competition* and *Rank* on the probability of the presence of *uKet* for lactating females. The grid shows the predicted values based on the model coefficients in Table 3 and assuming an average group. The black circles illustrate the observed proportion of samples with positive *uKet* values for 9 different areas of the plane. The area of circles is proportional to number of included values. Rank and log-transformed competition values were scaled to a mean of 0 and sd of 1 before running the models but are here shown on their original scales. For details see Table 3.

Table 4

Linear mixed model testing for potential predictors of *bEB*. The full model, including *Feeding Competition***Rank*, *Feeding Competition*, *Rank*, and *Group* as predictor variables was significantly better than the null model (χ^2 = 12.694, df = 3, P < 0.005). However, *Feeding Competition***Rank* was not significantly related to *bEB* (χ^2 = 3.0965, df = 1, P = 0.078). Therefore, we removed this interaction from the model to establish P-values for main-effect terms (for the model including the interaction, see Results S7). The model was calculated including 296 *bEB* values from 25 females. See Results S8 for original means and standard deviations for all variables before transformation. P-values < 0.05 are shown in boldface.

Term	Estimate (SE)	CI (95%)	Df	χ^2	P
(Intercept)	10.503 (0.260)	[9.991, 11.015]		NA	NA
Feeding Competition	**−0.769 (0.263)**	[−1.287, −0.252]	**1**	**8.415**	**0.004**
Rank	−0.274 (0.247)	[−0.759, 0.211]	1	1.231	0.267
Group (CP)	−0.237 (0.357)	[−0.940, 0.466]	2	5.070	0.079
Group (GN)	0.783 (0.347)	[0.101, 1.465]			

4.1. Interrelationships among biomarkers

As predicted, the concentration of urinary C-peptides (*uCP*) and energy balance (*bEB*) were positively related to each other (Fig. 3), indicating that the insulin physiology in capuchins aligns with our measurements of estimated energy gained from food intake minus the estimated energy expenditure during observed activity. While both methods appear to lead to similar conclusions, the choice of best method is dependent on the research question, study species and other circumstances. For example, if the collection of urine samples is possible without much effort, the assessment of C-peptide levels appears to be easier than collecting many hours of behavioral observations to estimate energetic condition of animals. Furthermore, the assessment of *uCP* does not require the various assumptions regarding energetic costs of different behavioral activities and the assessment of energy content of different food items. On the other hand, using a behavioral assessment of energetic condition allows researchers to disentangle energy intake and expenditure, which can provide important insights as to how individuals balance these two parameters over time (see below). This also means that it is possible to determine periods with positive and negative energy balance. With regard to *uKet*, urine samples with ketone bodies were associated with lower *bEB* level. Although we expected to observe lower *uCP* levels in such samples as well, we did not detect a significant relationship between *uKet* and *uCP*. Production of ketones may only reflect the most extreme instances of fat metabolism rather than a reliable indicator of smaller, short-term changes in energetic condition. The presence of *uKet* may also be specific to the restriction of certain nutrients such as carbohydrates (Weinhouse, 1952; Werk et al., 1955). Indeed, wild orangutans only show ketones when *uCP* levels are extremely low (Emery Thompson and Knott, 2008; Knott, 1998), and ketones are very rarely detected in the urine of wild chimpanzees (Kelly et al., 2004; Leendertz et al., 2010).

4.2. Impact of feeding competition

Low potential degree of feeding competition (*i.e.*, high density of ripe fruit biomass per adult body mass) led to greater *uCP* and *bEB* values. Conversely, *uCP* and *bEB* levels dropped during the months of highest potential degree of feeding competition, May through July and December (Fig. 1). A similar relationship between food abundance and female *uCP* levels has also been found in wild chimpanzees, orangutans, and colobus monkeys (Emery Thompson et al., 2009; Emery Thompson and Knott, 2008; Harris et al., 2010), and was therefore expected among these highly frugivorous capuchins. When less fruit is available per individual, we expected that energy intake would decrease, as shown in other primate species [*e.g.*, (Heesen et al., 2013)]. On the other hand, in some mammals, such as Antarctic fur seals (*Arctocephalus gazelle*), foraging effort and energy expenditure has been shown to be higher during periods of low food availability compared to periods of high food availability (Costa et al., 1989). Therefore, we expected that

Table 5

Linear mixed models testing for the relationship between *Feeding Competition*, *Rank*, and the two components of *bEB*, energy income (*bEI*) and energy expenditure (*bEE*). For *bEI*, the full model was significantly better than the null model ($\chi^2 = 8.758$, df = 2, $P < 0.013$). However, for *bEE*, the full model was not significantly better ($\chi^2 = 2.210$, df = 2, P0.332). For details, see Table 4. P-values < 0.05 are shown in boldface.

Outcome variable	Term	Estimate (SE)	CI (95%)	Df	χ^2	P
Energy intake (*bEI*)	(Intercept)	38.325 (0.872)	[36.605, 40.044]	–	–	–
	Feeding Competition	**−2.279 (0.882)**	**[−4.013, −0.545]**	**1**	**6.602**	**0.010**
	Rank	−1.233 (0.826)	[−2.863, 0.393]	1	2.219	0.136
	Group (CP)	−0.436 (1.197)	[−2.791, 1.922]	2	4.146	0.126
	Group (GN)	2.378 (1.161)	[0.087, 4.664]			
Energy expenditure (*bEE*)	(Intercept)	34.833 (0.253)	[34.318, 35.347]	–	–	–
	Feeding Competition	0.149 (0.136)	[−0.117, 0.416]	1	1.210	0.271
	Rank	−0.241 (0.238)	[−0.720, 0.248]	1	0.998	0.318
	Group (CP)	0.363 (0.338)	[−0.323, 1.050]	2	1.324	0.516
	Group (GN)	−0.243 (0.335)	[−0.926, 0.438]			

the energy decrease during periods of intense feeding competition represented both a reduction in caloric intake as well as an increase in energy expenditure through search effort and travel to find the more limited fruit sources among other food types. However, an examination of the relationship between the degree of feeding competition and energy income and energy expenditure separately indicated that females consumed less energy during periods of intense feeding competition, but that their energy expenditure did not change during these periods. This suggests that female capuchins store fat during periods of food abundance for periods of food scarcity. Furthermore, this illustrates that it is important to take into account different pathways (through energy intake and expenditure) leading to a specific energetic condition.

June and July were the only months during which we found a high probability of ketone production, a more extreme response to low energy balance. However, only lactating females ever showed urinary ketone bodies, and for these females the relationship between degree of feeding competition and the probability of *uKet* was mediated by dominance rank. Even when ketones are produced, they are often metabolized and do not appear in the urine; it is only under hypoglycemic conditions that the body switches to fat stores and produces ketones in such high concentrations that some are excreted in the urine (Laffel, 1999). Interestingly, at our study site some months of low relative fruit abundance coincide with the seasonal outbreak of Lepidopteran larvae (*i.e.*, caterpillars), which are high in fat and protein but low in carbohydrates per unit dry mass (Bergstrom et al., 2019, 2018). During a second period of low ripe fruit energy density in December, the capuchins exploited seasonally available flowers, which served as an alternate source of carbohydrates (Hogan et al., 2016). Thus, while *uCP* levels and calculated energy balance were similar during June–July and December, ketones were only excreted in June–July, the caterpillar season. This is consistent with the physiology of these markers: insulin responds to both protein and carbohydrate intake, while ketones are excreted specifically during carbohydrate restriction (Emery Thompson, 2017).

4.3. Impact of rank

Female white-faced capuchins exhibit matrilineal, linear, and stable hierarchies, and a large proportion of dominance interactions occur over food resources, over which they exhibit contest competition (Bergstrom and Fedigan, 2010; Vogel, 2005). Accordingly, we predicted that higher-ranking females would have better access to higher quality resources or maintain control over optimal foraging positions within food trees for longer periods of time, and would therefore show higher energy balance, *uCP*, and fewer ketones than lower-ranking females. Furthermore, we expected that this rank effect would be most

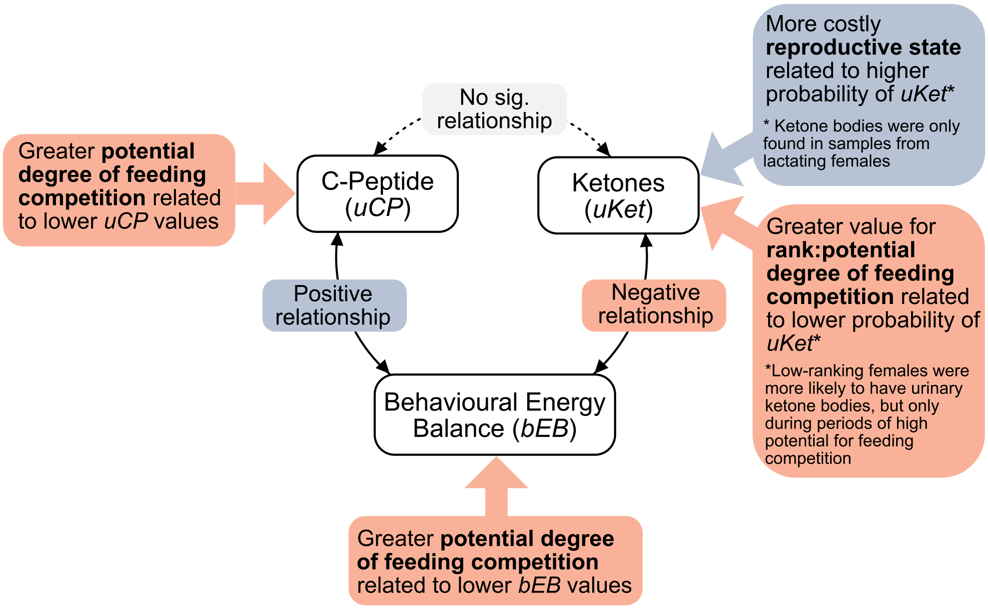

Fig. 3. Illustration of the detected relationships between different measures of energetic condition and factors related to these measures. For details, see the Results section.

pronounced during periods of intense food resource competition. Only our results for *uKet* supported this prediction. Ketones were only produced by lactating females during months in which our analyses indicate competition was the greatest, and under these conditions, low-ranking females were more likely to produce ketones than high-ranking females.

Why did we not detect a similar rank effect dependent on feeding competition on *uCP* or *bEB* levels? One interpretation is that fallback foods are usually of sufficient availability that low-ranking females can reach equity with high-ranking females, though perhaps with enhanced foraging effort. Such an interpretation is supported by observations in Assamese macaques (*Macaca assamensis*), a primate with a similar diet, where high ranking females did not seem to have a higher energy intake during periods of food scarcity than low-ranking females (Heesen et al., 2013). It is also possible that dominant females immediately reinvest the additional energy that they gain from having priority of access to high quality food resources. As suggested for bonobos [*Pan paniscus*; (Nurmi et al., 2018)], high-ranking females might invest more energy into reproductive effort than low-ranking females. For example, females may provide larger quantities of milk per time to reduce the duration they have to nurse their infants and therefore reproduce more rapidly. While high rank is linked to faster reproductive rates in many primates [*e.g.*, (Altmann and Alberts, 2003; Gesquiere et al., 2018; Pusey, 2012; Pusey et al., 1997)], such an effect was not found among capuchins in an earlier examination of this population (Fedigan et al., 2008). High-ranking mothers may also invest more total energy into each single infant. Such a pattern has been observed in baboons (*Papio* spp.), where offspring of high-ranking females show a faster growth rate than offspring of low-ranking females, but only in energy-limited environments (Alberts, 2019). Such a higher investment might also explain the positive effect of maternal dominance rank on infant survival probability in some primates (Majolo et al., 2012), a pattern which we have also observed during stable periods in our study population (Kalbitzer et al., 2017). Instead of gaining and then reinvestigating additional energy, high-ranking females may also leverage their preferential access to resources by spending less time of their day foraging and more time socializing. This could be crucial for their social integration, which has been shown to be positively related to fitness components, such infant survival and longevity, in our study population (Kalbitzer et al., 2017), and many other mammals (Brent et al., 2013; Cameron et al., 2009; Frère et al., 2010; Silk et al., 2010, 2003; Stanton and Mann, 2012). Finally, the lack of a rank effect on energetic condition may also indicate that female contest competition over food resources is not as important as predicted in capuchins. These different explanations can be tested in future studies by integrating measures of energetic condition and feeding competition into examinations of the effects of dominance rank on social behavior and reproductive investment—including nursing rates, weaning age, interbirth-intervals, and infant growth rate. We expect that the ways that feeding competition constrains female condition, and in turn reproductive success, may vary across species, and the analysis of data targeting these interactions has the potential to greatly increase the power of socioecological models.

4.4. Impact of reproductive state

Metabolic costs are expected to be highest in mammals during early lactation when an infant is still growing and is highly dependent on the mother for energy, and lowest during the cycling stage when females are free from the energetic demands of offspring (Clutton-Brock et al., 1989; Key and Ross, 1999). The presence of ketones was detected only among low-ranking, lactating females during fruit-poor months. A previous study of the feeding behavior and nutritional intake of females in this population indicated that lactating females consumed significantly more energy per unit time by eating food at faster rates than other females (McCabe and Fedigan, 2007). Our study indicates that despite these potential modifications to feeding and foraging behavior, lactating females endure a cost to their energetic condition, leaving them particularly vulnerable to extreme dips in food abundance and/or high levels of resource competition. In contrast to low-ranking females, however, high-ranking females seem better able to compensate for energetic stress during these periods of extreme requirements, as we would expect based on socioecological theory.

5. Conclusion

We show that temporal variability in feeding competition is related to non-invasive measures of energetic condition in female white-faced capuchin monkeys in the wild. We were able to do this by measuring *uCP* and *uKet* levels in combination with analyzing behavioral observations and plant ecological data. Despite the difficulty of collecting urine samples, they are an effective medium to monitor energetic condition in highly active arboreal animals such as capuchins and may represent a valuable alternative to the labor-intensive assessment of energetic conditions based on behavioral observations. Comparing our two biological markers of energetic condition, *uCP* appears to be better adapted to monitor subtle variation over time, whereas *uKet* is an easily applied method in the field for studies aiming to identify the most critical drops in energetic condition. Perhaps the most surprising result of our study was that dominance rank was not associated with energetic condition as assessed through *uCP* or *bEB*. Possibly, high-ranking females have advantages during feeding competition, but they reinvest additional energy into reproductive efforts to either reduce the duration of inter-birth intervals or into their offspring to improve the survival probability of these infants. Alternatively, high-ranking females might show *uCP* and *bEB* levels similar to those of low-ranking females because they spend less time foraging and more time in other activities, such as socializing, which has been shown to be associated with better fitness. Also, it is possible that contest competition is not as important as previously assumed in our study population. Our study highlights the importance to carefully consider potential differences between reproductive success and proxies often used for reproductive success, such as energetic condition or food intake, when investigating predictions of socioecological models.

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Declaration of competing interest

None.

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