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Fermented food consumption in wild non-human primates and its ecological drivers

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ABSTRACT

Objectives: Although fermented food use is ubiquitous in humans, the ecological and evolutionary factors contributing to its emergence are unclear. Here we investigated the ecological contexts surrounding consumption of fruits in the late stages of fermentation by wild primates to provide insight into its adaptive function. We hypothesized that climate, socio-ecological traits, and habitat patch size would influence the occurrence of this behavior due to effects on the environmental prevalence of late-stage fermented foods, the ability of primates to detect them, and potential nutritional benefits.

Materials and Methods: We compiled data from field studies lasting at least nine months to describe the contexts in which primates were observed consuming fruits in the late stages of fermentation. Using generalized linear mixed-effects models, we assessed the effects of 18 predictor variables on the occurrence of fermented food use in primates.

Results: Late-stage fermented foods were consumed by a wide taxonomic breadth of primates. However, they generally made up 0.01-3% of the annual diet and were limited to a subset of fruit species, many of which are reported to have mechanical and chemical defenses against herbivores when not fermented. Additionally, late-stage fermented food consumption was best predicted by climate and habitat patch size. It was more likely to occur in larger habitat patches with lower annual mean rainfall and higher annual mean maximum temperatures.

Discussion: We posit that primates capitalize on the natural fermentation of some fruits as part of a nutritional strategy to maximize periods of fruit exploitation and/or access a wider range of plant species. We speculate that these factors contributed to the evolutionary emergence of the human propensity for fermented foods.

Keywords: fermentation, feeding ecology, climate, herbivore defense, human evolution

Research Highlights

- Fruits in the late stages of fermentation are consumed by a wide range of primates but only a subset of available fruit species is consumed in this form.

- Primate late-stage fermented fruit consumption is more common in large habitat patches with lower annual mean rainfall and higher annual mean maximum temperatures.

- Consumption of late-stage fermented foods appears to be part of a primate nutritional strategy to increase dietary breadth both qualitatively and temporally.

1 INTRODUCTION

Food fermentation – the anaerobic microbial degradation of carbon compounds into ethanol and/or lactic acid – is a central part of human diet and culture (Tamang & Kailasapathy, 2010). Humans from many cultures regularly incite or direct microbial fermentation of a wide range of foods that include meat and dairy products, grains, fruits, and vegetables (Battcock & Azam-Ali, 1998; Campbell-Platt, 1994; Deshpande, 2000; Tamang, Holzapfel, Shin & Felis, 2017). Such foods make up 20 to 40% of the global food supply (Campbell-Platt, 1994). Although not all fermented foods contain ethanol, the majority of anthropological fermented food research to date targets ethanol as an indicator of fermentation (e.g. Dominy, 2015; Dudley, 2002; Garnier & Valamoti, 2016; Hayden, Canuel, & Shanse, 2013; Kuijt, 2009; Liu et al., 2018; Milton, 2004; Ross, Morgan, & Hill, 2002; Smalley et al., 2003).

Directed fermentation by humans has early origins. There is archaeological evidence that humans have engaged in directed fermentation of fruits and grains and stored the resulting ethanol in large quantities since ~4300 BC, although some suggest a date as early as 12,500 cal BP (Garnier & Valamoti, 2016; Hayden et al., 2013). Evolutionary changes in human genes for processing ethanol and for interacting with a major lineage of fermenting bacteria (Lactobacillales) are compatible with an even earlier association with fermented foods, dating back to the divergence of hominids from other primates at ~10 Mya (Carrigan et al., 2015; Janiak, Pinto, Duytschaever, Carrigan, & Melin, 2020; Peters et al., 2019). Limited technology for processing and storing food at this time makes it likely that our hominid ancestors relied more heavily on naturally occurring fermented foods. However, some simple forms of directed fermentation, such as burying food items or submerging them in water (Speth 2017), may have been possible.

Why humans have incorporated fermented products so prominently into their diet across their evolutionary history is unclear. Fermentation is an effective food preservative since it produces locally high concentrations of ethanol and lactic acid that ultimately prevent microbial growth and associated food spoilage (Boulton, Singleton, Bisson, & Kunkee, 1999; Pretorius, 2000; Skinner, Passmore, & Davenport, 1980; Thomson et al., 2005). Additionally, the physiological effects of consuming ethanol (i.e. intoxication) are believed to have facilitated social gatherings and rituals (Liu et al., 2018). Accordingly, the modern and ancient contexts in which fermented food use has been documented often suggest central roles of food preservation and socially motivated ethanol acquisition in driving the ubiquity of human fermented food use (Dominy, 2015; Dudley, 2002; Kuijt, 2009; Liu et al., 2018; Milton, 2004; Ross, et al., 2002; Smalley et al., 2003). However, given genetic evidence that human adaptations for fermented food consumption emerged before the technology associated with its directed production and storage (Carrigan et al., 2015; Janiak et al., 2020; Peters et al., 2019), fermented food consumption may have provided another selective advantage earlier in our evolutionary history.

Given their high sugar content, fruits often ferment naturally (Dominy, 2004; Duar et al., 2017; Dudley, 2002; Gorgus, Hittinger, & Schrenk, 2016; Martinson, Herre, Machado, & Arnold, 2012; Nyanga et al., 2007; Ruiz Rodriguez et al., 2019; Weaver, 2016) making it likely that all frugivorous animals consume some minimum amount of fermented foods. However, overripe fruits in late stages of fermentation commonly remain in food patches after other fruits have been depleted. As described above, fermentation is distinct from rot or decay in that it involves distinct microbes and precludes the production of most toxic microbial byproducts (except ethanol). Therefore, it has been suggested that fruits in the late stages of fermentation could have been a fallback food for increasingly terrestrial hominids during periods of low food availability in patchy woodland environments (Carrigan et al., 2015).

Foods in the late stages of fermentation could also convey nutritional benefits that provide a selective advantage to consumers year-round. Compared to unfermented foods, fermented foods have higher caloric, free amino acid, and vitamin content (NRC, 1998; Gobbetti et al., 1994; LeBlanc et al., 2013; Mitchell & Herlong, 1986; Tamang, Shin, Jung & Chae, 2016). In the wild, many fermented foods contain embedded insects, which provide an additional protein source (Barnett et al., 2017; Barnett et al., in press; Braham, 2015; Hodge & Arthur, 1996; Xiaoming, Ying, Hong, & Zhiyong, 2010). Also, fermentation improves digestibility of food by breaking down resistant starch, soluble fiber, toxins, and secondary plant metabolites (Binita & Khetarpaul, 1997; Chaves-López et al., 2014; Gupta, Gangoliya, & Singh, 2015; Rollan, Gerez & Leblanc, 2019). For example, some toxic foods, such as blowfish and cassava, can only be consumed after fermentation (Akinrele, 1964; Anraku et al., 2013). Together these properties not only directly affect consumer nutrient intake and balance but may also result in a more favorable balance among the nutrients of a food which in turn can play a critical role in food selection (Felton et al., 2009). Therefore, foods in the late stages of fermentation could have represented a critical nutritional resource to hominids, particularly as energetically expensive life history traits such as long juvenile periods, short interbirth intervals, and large brains emerged across evolutionary time (Aiello & Key, 2002; Antón, Potts, & Aiello, 2014; Leonard & Robertson, 1992, 1997). The consumption of other high quality diet items such as meat and cooked foods has also been hypothesized to have provided essential nutritional resources for the development and maintenance of these traits in hominids (Aiello & Wells, 2002;

DeCasien, Williams, & Higham, 2017; Wrangham, 2009; Wrangham & Conklin-Brittain, 2003).

Fermented foods contain live microbes, substrates for microbial metabolism, and microbial metabolites, which may affect consumer health and fitness either directly or indirectly through impacts on the microbiome (Jacobsen et al., 1999; Kim et al., 2016; Maldonado-Gómez et al., 2016; Marco et al., 2017). Given the broad effects of the microbiome on host metabolism (Oliphant & Allen-Vercoe, 2019; Visconti et al., 2019), immune function (Al Nabhani & Eberl, 2020), and neuroendocrine dynamics (Cryan et al., 2019; Sylvia & Demas, 2018), fermented foods have the potential to affect consumer physiology in many ways. Beyond intoxication caused by excessive consumption of fermented foods with high ethanol content, none of these documented physiological effects are negative. Therefore, fermented food consumption could have provided a selective advantage to hominids in addition to the nutritional advantages discussed above. Indeed, studies of human fermented food use consistently demonstrate a range of improved health outcomes (e.g. Bourrie, Willing, & Cotter, 2016; Burton et al., 2017; Yartey, Nkrumah, Hori, Harrison, & Armar, 1995). However, the wide variety of positive health effects that fermented foods can produce via the microbiome make it difficult to predict specific scenarios in which these properties would be most evolutionarily advantageous based on current knowledge.

Even in the context of nutrition, modern human technology and cultural practices complicate our ability to evaluate the potential fitness benefits of human fermented food consumption. As a result, comparative data from non-human primates (hereafter primates) are essential for exploring the adaptive function of this behavior. By determining how pervasive consumption of late-stage fermented foods by wild primates is and the ecological contexts in which it occurs, we can begin to more accurately assess the ecological and evolutionary forces that drive it and contextualize it within human evolutionary history. Nevertheless, few studies on this subject have incorporated primate data.

A handful of comparative genetic analyses of physiological adaptations for fermented food consumption integrate data from multiple primate species (Carrigan et al., 2015; Janiak et al., 2020; Peters et al., 2019). Additionally, some behavioral research has investigated primate ethanol affinity in response to the Drunken Monkey Hypothesis (Dudley, 2002, 2004). This hypothesis posits that humans direct the production of fermented foods and consume them as a result of our affinity for ethanol, which stems from our evolutionary past as frugivorous primates that used ethanol as an olfactory and/or gustatory signal for energy-rich fruit (Dudley, 2002, 2004). Therefore, data from other primates have been used to test the relationship between frugivory and ethanol affinity. The results indicate that primates across the Order prefer solutions of 2-5% ethanol over water (Dausch Ibañez, Hernandez Salazar, & Laska, 2019; Gochman, Brown, & Dominy, 2016; Hockings et al., 2015; Kornet, Goosen, Ribbens, & Van Ree, 1990; Mandillo, Titchen, & Miczek, 1998). However, data from spider monkeys (*Ateles geoffroyi*) indicate that sweet solutions are preferred over ethanol regardless of calorie content (Dausch Ibañez et al., 2019). Outside of this context, fermented food consumption is rarely mentioned in studies of primate feeding ecology, despite the fact that not all fermented foods contain ethanol but all of them likely confer a range of nutritional and health benefits to consumers.

As a first step to address this knowledge gap, we compiled qualitative data describing overripe fruit consumption from primate field studies around the world to estimate the minimum prevalence of late-stage fermented foods in wild primate diets, regardless of ethanol content, and the ecological contexts in which the consumption of these foods occurs. We hypothesized that local climate, primate socio-ecological traits, and habitat patch size (Table S1) would predict the prevalence of primate consumption of late-stage fermented foods. First, climate affects both the rate of fermentation and the rate of ethanol evaporation (Isu & Njoku, 1998), thereby influencing the local prevalence of late-stage fermented foods and the probability that primates will detect them via olfaction (Dominy, 2004; Nevo & Valenta, 2018; Melin et al., 2019). Therefore, we predicted that mean minimum annual temperature, mean maximum annual temperature, mean daily temperature, mean annual rainfall, elevation, and latitude and longitude would be associated with the occurrence of late-stage fermented food consumption in wild primates. Given that fruit ferments easily in nature (Dominy, 2004; Duar et al., 2017; Dudley, 2002; Gorgus, Hittinger, & Schrenk, 2016; Martinson, Herre, Machado, & Arnold, 2012; Nyanga et al., 2007; Ruiz Rodriguez et al., 2019; Weaver, 2016), we predicted that primate species and populations with high percentages of fruit in their diets and low percentages of leaves and invertebrates would be more likely to encounter and consume late-stage fermented food. Since home range, social group size, body size, and encephalization quotients are often correlated with diet (Clutton-Brock & Harvey, 1980; Dunbar & Shultz, 2007, 2017; Kudo & Dunbar, 2001), we also expected these variables to be associated with late-stage fermented food consumption. Finally, due to the relationship between habitat patch size and food availability more generally (Abbas et al., 2011; Fahrig, 2003; Laurance, Delamonica, Laurance, Vasconcelos, & Lovejoy, 2000), we predicted that habitat patch size would predict the prevalence of late-stage fermented foods and their consumption.

2 | MATERIALS AND METHODS

2.1 | Behavioral data collection

KRA, YZ, and TME identified a group of researchers who had completed a wild primate field study of at least nine consecutive months using multiple approaches. We searched two general online databases (https://scholar.google.com, http://xueshu.baidu.com) using specific key words such as “primate” and “diet” combined with primate family names one year at a time beginning with 2005. We also reviewed the literature cited in multiple primate ecology books (Brady & Carville, 2012; Campbell, Fuentes, MacKinnon, Bearder, & Stumpf, 2011; Davies & Oates, 1994; Dudley, 2014; NRC, 2003; Rowe & Myers, 2016; Strier, 2016). Finally, we flagged abstracts from the programs of primate conferences in 2018 and 2019, including the American Society of Primatologists and the American Association of Physical Anthropologists.

KRA asked 151 researchers with relevant field studies and current email contact information to report whether they had observed their study subjects consuming fermented foods (i.e., plant foods clearly overripe or fermenting based on their color, physical traits, smell, or other useful indicator traits). These food items could be found on the ground, but this was not necessary for a food to be deemed 'fermented.' Many fruits consumed by primates are likely to have undergone some degree of fermentation (Dominy, 2004), but only late stages of fermentation with higher concentrations of ethanol and other microbial products (Biale 1954) are likely to be identified using the conservative sensorial cues we employed here. For example, *Astrocaryum standleyanum* unripe and ripe fruits are reported to have 0% and 0.6% ethanol while fallen fruits have 0.9% ethanol and overripe fallen fruits have 4.5% ethanol (Dudley, 2004). Therefore, it is likely that we are excluding a substantial number of fermented foods from our analysis (e.g. floral nectar and fruits with other levels of maturity (Aleksey Maro, personal communication; Wiens et al., 2008; Weaver, 2016). However, our approach still represents an important contribution to this complex subject since foods that can be sensorially identified as being in the late stages of fermentation are more likely to have physiological effects on consumers as a result of higher concentrations of microbes and/or microbial by-products (Tamang et al., 2016). Systematic data describing chemical and microbial variables in wild fruits are necessary to more accurately quantify fermentation stages in wild food items and the probability of detection by foragers and observers. Because these traits likely vary across plant species, primate species, and environments, such an analysis is outside the scope of this study. Nevertheless, given that the ethanol content of the small number of ripe fruit species that have been measured in habitats occupied by wild primates is reported to range from 0.01-1.1% (Dominy, 2004; Dudley, 2004; Weaver, 2016), our conservative estimate is that late-stage fermented fruits in our study have an ethanol content >1%. No data exist to allow estimates of microbial biomass or concentrations of non-ethanol microbial by-products.

We collated data for 40 species of primates inhabiting 50 research sites (Table S1). While these data encompass a small percentage of all extant primate species (7.9%, 40 out of 504 recognized species; Estrada et al., 2017), 11 out of the 16 extant primate families were represented across all continents inhabited by primates, and we included both tropical and temperate environments. Therefore, we believe that our database fairly represents the phylogenetic and geographic diversity of the order Primates. Study duration ranged from 9 to 312 months (median = 15 months), and we used data from multiple social groups or communities of 18 species distributed across 13 sites.

We included data describing the location and length of their study, the elevation, mean annual maximum and minimum temperatures, mean daily temperature, and mean annual rainfall of the study site, the mean contribution of fruits, leaves, and invertebrates to the diet of the study species, the frequency with which any fermented foods were consumed relative to total observation time, and any other relevant details about the types of foods consumed or associated behavior, such as seasonality or specific handling behaviors (Table S1).

2.2 | Physical and chemical traits of the late-stage fermented foods consumed

For all late-stage fermented foods, we compiled data from each study site or the literature describing presence/absence of a tough husk or skin, relative fiber content, and presence/absence of secondary metabolites and their concentrations. We evaluated tough husks qualitatively. A relative assessment of fiber content compared to other fruits at the same site was possible for 35 fruits, and for 25 of these fruits the nutritional data were available for that study site specifically. Secondary metabolite data were more difficult to compile. Quantitative data were available for 11 fruit species at three sites. For the rest of the fruits, we searched the literature using the fruit species name combined with terms such as ‘toxin’ and ‘secondary metabolite.’ Because data describing secondary metabolite content in fruits is sparse, in many cases we had to rely on literature describing medicinal use that implied increased concentrations of identified or unidentified secondary metabolites. Using this approach, we were able to find evidence of the occurrence of secondary metabolites for 34 fruit species (Table 3).

2.3 | Data analysis

We assessed the influence of 18 predictor variables (Table 1) on the occurrence of late-stage fermented food consumption via generalized linear mixed-effects models (GLMM; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) with a binomial distribution and logit link function using the function 'lmer' of the R package lme4 (Bates et al., 2015). We specified the occurrence of late-stage fermented food consumption as a binary response variable, all the predictor variables as fixed factors, and study site as a random factor to account for data from repeated measures of the same species in different social groups at the same site. In addition to socio-ecological, climate, and habitat patch size variables, we included study length in all of our models to determine if shorter studies were biased against what we assumed would be a relatively rare behavior (Souza-Alves et al., 2019). To avoid overparameterization and problems of convergence with the global model, we did not consider variable interactions (see Grueber, Nakagawa, Laws, & Jamieson, 2011). We also did not include variables describing primate taxonomy because limited replication of species reduced the power of the analysis to assess the impact of these variables.

Given differences in scale among the predictor variables, we standardized them using the 'standardize' function of the package MuMIn (Barton, 2020) as recommended by Grueber et al. (2011). We avoided multicollinearity problems by only including those variables with Variance Inflation Factors (VIF) <3 into the models (Zuur et al., 2009) using the 'vifstep' function of the package usdm (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014). The seven variables with VIF >3 that we excluded from the global model were female body mass, male body mass, male relative encephalization quotient, percentage of leaves in the diet, percentage of invertebrates in the diet, mean daily temperature, and elevation.

We selected models with an ΔAICc <2 as the most parsimonious (Grueber et al., 2011). Given the occurrence of multiple equally parsimonious models, we also performed full-model averaging on all models with an ΔAICc <2 to account for model uncertainty and to identify the best predictors of patterns of late-stage fermented food consumption in our data set (Grueber et al., 2011). We used the 'model.avg' function of the R package MuMIn to identify the averaged model and the predictor weight ($\sum w_i$) of each variable. We determined the coefficient of determination for each model with ΔAICc <2 using the MuMIn 'r.squaredGLMM' function. We performed all statistical analyses in R 3.6.3 (R CoreTeam, 2020).

3 | RESULTS

3.1 | Occurrence of late-stage fermented food consumption in wild primates

Out of 40 species of wild primates studied at 50 sites, 15 species (37.5%) were reported to consume late-stage fermented foods at 23 sites in 12 countries across four continents. Overall, late-stage fermented food consumption occurred infrequently (Table 2, S1). We estimated that it constituted from 0.01% to 3% of the annual diet in most groups, although there were seasonal differences. For example, we found that late-stage fermented fruits could account for as much as 15% of the feeding records of *Cebus imitator* and *Alouatta guariba clamitans* during some seasons. For some primates, such as *A. guariba clamitans*, these seasons represented periods of low food availability (VBF personal observation), whereas for many others, such as *C. imitator*, they did not (EKM personal observation). While we recorded late-stage fermented food consumption in all our *Pan paniscus* and *C. imitator* social groups (three and seven, respectively), not all populations or social groups of the other species studied exhibited this behavior.

3.2 | Main sources of fermented foods and behavioral strategies used

Late-stage fermented food consumption was limited to fruits (Tables 2, 3, S1). The richness of late-stage fermented fruits exploited ranged from one to nine fruit species for a given primate species (Tables 2, 3, S1). *Pan paniscus* exhibited the highest richness of late-stage fermented fruit species in the diet (N=9 fruit species), followed by *Ateles geoffroyi* (N=8), *Alouatta guariba clamitans* (N=7), and *Cebus imitator* (N=5; Table 2). The remaining primate species exploited between one and three fruit species (Table 2).

At least 31 of the 44 fruit species that were consumed in late stages of fermentation have defenses in the form of difficult-to-break tough husks/skins (N=16) or secondary metabolites, such as alkaloids, acetogens, saponins, and tannins (N=25; Table 3). Almost all fruits (95%) were consumed both ripe/unfermented and overripe/fermented (Table 3). In some cases, late-stage fermented fruits were only consumed when the patch was depleted of ripe fruits (Table S1). We also reported cases in which very ripe or late-stage fermented fruits appeared to be preferred over semi-ripe and unripe fruits. Specifically, *Cebus imitator* at La Suerte, Costa Rica, was observed frequently knocking ripe *Dipteryx oleifera* (Fabaceae) fruits to the ground and returning up to two weeks later to consume them (up to 15% of feeding time seasonally, EKM personal observation). These fruits were never consumed unfermented by the capuchins. *Eulemur fulvus* at Ampijiroa, Madagascar (up to 5% of feeding time seasonally, PTR personal observation) and *Ateles geoffroyi* at Punta Laguna, Mexico (up to 1% of feeding time seasonally, BPG personal observation) were also reported to drop fruits to the ground and return to feed on them later. However, unlike the capuchins, both lemurs and spider monkeys consumed the target fruits in different stages of ripening, although the lemurs appeared to prefer fallen fruits over those on the trees since they would consume fallen fruits first when both were available.

3.3 | Main primate predictors of late-stage fermented fruit consumption

Only climate and habitat patch size were strong predictors of late-stage fermented food consumption in wild primates. Other socio-ecological traits did not contribute substantially to any of our top ranked models. We found six GLMMs equally parsimonious (**Δ**AIC <2) for explaining the observed patterns in late-stage fermented food consumption (Table 4). These models included mean maximum and minimum annual temperature, mean annual rainfall, habitat patch size, mean minimum annual temperature, longitude, home range size, and female relative encephalization quotient and explained approximately 99% of the observed variance (Table 4). However, only mean annual maximum temperature, rainfall, and habitat patch size were present in all six models. The model with the strongest empirical support (**Δ**AICc = 0.00) included these three variables and mean minimum annual temperature (Table 4). The averaged model explained 99% of the observed variance, and late-stage fermented food consumption was only strongly predicted by annual mean rainfall and mean annual minimum temperature, and positively influenced by mean annual maximum temperature and habitat patch size (Table 4).

4 | DISCUSSION

We found that wild primates from all major evolutionary lineages consume foods in the later stages of fermentation, although the behavior is relatively infrequent and limited to only a few species of fruits at the sites where we recorded it. Additionally, climatic and environmental variables generally predict the occurrence of late-stage fermented food consumption better than socioecological variables. Specifically, late-stage fermented food consumption is more common in hotter, drier environments and in larger, presumably less fragmented, habitats. As fermentation is a continuous process, future studies should analyze the chemical and microbial properties of the fermented fruits consumed at different stages by the primates to improve the resolution of these relationships. However, our findings provide an important foundation for understanding the ecological and evolutionary forces that drive fermented food consumption in primates and offer new insights into the emergence of this behavior in humans.

4.1 | Occurrence of fermented food consumption in wild primates

First, although reports of fermented food consumption are rare in most studies of wild primate feeding ecology, this behavior is probably pervasive across the Order. We observed late-stage fermented food consumption in more than one third of the primate species for which we received data. However, given that our data were biased toward late-stage fermentation and many fermented foods consumed by primates cannot be identified by researchers without chemical analyses, it is likely that the prevalence of fermented food consumption among wild primates is even higher. Fruits consumed by primates commonly ferment naturally despite no clear signs to observers that fermentation has occurred (Dominy, 2004; Dudley, 2002; Aleksey Maro, personal communication; Weaver, 2016). Given that most primates, even those considered leaf-eaters, rely heavily on fruit during at least part of the year (Campbell et al., 2011; Rowe, 2018; Sussman, 1991), it is likely that most primates regularly consume fermented foods. This scenario becomes more probable when we consider the fact that other foods such as nectar or gums may also often ferment despite being difficult to observe (e.g. Wiens et al., 2008). Because the relative concentrations of ethanol and other microbial products at different stages of fermentation -- and the likelihood of perception by foraging primates--are likely to vary by plant species, primate species, and habitat, quantitative data describing these variables for a range of food items are necessary to better define fermentation stages in wild foods, and to test the extent to which primate ecology varies with food fermentation stage. This area presents exciting opportunities for future research.

Nevertheless, we do not expect that all primates consume fermented fruits. For instance, primates of the subfamily Colobinae, which are physically unable to consume large amounts of ripe fruits as a result of their sacculated foregut (Davies & Oates, 1994), as well as immature fruit specialists, such as the Neotropical Pitheciinae, were not observed consuming fermented fruit (at least not clearly overripe fruits) in any context in this study. Additionally, the physical nature of some habitats can reduce access to fermented fruits. For example, while not represented in our data set, swamps and riverbank forests reduce opportunities for fruit fermentation on the ground, and fruits in these habitats are often water-dispersed and rarely fleshy and easily fermentable (López, 2001).

4.2 | Ecological contexts associated with late-stage fermented food consumption by wild primates

Despite how relatively common late-stage fermented fruit consumption appears to be throughout the Order Primates, we found that it is selectively employed in specific ecological contexts. Although most primates include many fruit species in their diets, in most cases only one or two fruit species were consumed in the late stages of fermentation by a given primate population or social group. In some cases, this pattern appeared to be a result of primates extending the utility of a fruit patch. For example, in the rare instances when *Pongo pygmaeus* was observed consuming late-stage fermented fruits, it was after the patch had been depleted by other frugivores (ERV personal observation). Alternatively, some primates, such as groups of *Alouatta guariba clamitans* in Santa Maria municipality, Southern Brazil, appeared to rely on late-stage fermented fruits during periods of low or altered food availability (VBF personal observation). Similarly, *Ateles geoffroyi* on Barro Colorado Island, Panama utilized late-stage fermented *Quararibea asterolepis* during a period of unusual fruiting patterns associated with the previous year's El Niño event, as did other frugivorous mammals and birds (Campbell, 2000). These potential uses of late-stage fermented foods as fallback foods are in line with previous hypotheses in other contexts (Carrigan et al., 2015).

Other primates appeared to use fermentation to increase fruit edibility. Many fruits contain secondary metabolites, and in some cases they may reach sufficient levels to have meaningful physiological effects if consumed in large quantities (Cipollini & Levey, 1997; Janzen, 1983). At least two-thirds of the fruit species consumed in the late stages of fermentation by wild primates in this study had mechanical or chemical herbivore defenses when unfermented. For seven of these species, primates were reported to reject fruits unless they were very ripe or fermented. *Pan troglodytes* has been previously shown to preferentially consume ripe fruits of plant species whose unripe fruits have high levels of tannins since ripening reduces tannin content (Wrangham & Waterman, 1983). Therefore, it is possible that fermentation was used by some of our study subjects in a similar way to break down plant herbivore defenses. For example, *Dipteryx oleifera*, has a hard husk that can only be breached by *Cebus imitator* when fermented (EKM personal observation).

Together, these patterns are compatible with the use of targeted consumption of late-stage fermented fruits in multiple ways by primates as part of a broader nutritional strategy to increase food availability and expand their dietary niches. We found preliminary support for this interpretation. As predicted, our models indicated that late-stage fermented food consumption was associated with climate and habitat patch size. In particular, late-stage fermented food consumption was more common in drier environments with more extreme mean annual maximum temperatures, as well as in larger habitat patches. Habitats with higher mean annual maximum temperatures and lower annual rainfall are potentially more nutritionally stressful for primates due to both chronic and seasonal reductions in food availability, as well as distinct plant growth strategies that result in increased mechanical and/or chemical defenses against herbivory (Coley & Barone, 1996; Onoda et al., 2011; Poorter & Kitajima, 2007; Zhao, Hartmann, Trumbore, Ziegler, & Zhang, 2013). In such environments, a primate foraging strategy that relied more heavily on late-stage fermented foods could well enhance survival during lean periods by both extending the utility of depleted food patches and increasing digestibility of heavily defended plant foods. We do not have quantitative data relating food availability or plant herbivore defenses to late-stage fermented food consumption across sites, precluding our ability to rigorously test this hypothesis here. However, future explorations of this relationship are warranted by our findings.

Our results also indicate other potentially important mechanisms driving patterns of primate late-stage fermented food consumption. To some extent, it appears that late-stage fermented food consumption occurs with more prevalence in habitats where primates are more likely to come into contact with fruit in the late stages of fermentation. Higher mean annual maximum temperatures are likely to result in more rapid rates of fermentation and ethanol evaporation (Isu & Njoku, 1998), increasing the local prevalence of late-stage fermented foods and the probability that primates will detect them via olfaction (Dominy, 2004; Nevo & Valenta, 2018; Melin et al., 2019). Furthermore, larger, potentially less fragmented, habitats are often associated with an increased abundance and diversity of fruiting trees (Abbas et al., 2011; Fahrig, 2003; Laurance, Delamonica, Laurance, Vasconcelos, & Lovejoy, 2000). Therefore, there may be a higher probability that primates in these habitats will encounter fermenting fruits. However, in our dataset, the effect of habitat patch size appears to be driven by two particularly large sites, Goualougo and Mandika in the Republic of Congo. As a result, it remains unclear whether factors influencing the availability of late-stage fermented foods to primates truly shape patterns of consumption more globally.

4.3 | Potential evolutionary benefits of late-stage fermented food consumption

The aforementioned relationships open up new perspectives on the emergence of food fermentation as an important component of the human diet. If late-stage fermented food consumption is part of an extant primate strategy for extending the time over which a particular type of fruit can be fed on and/or increasing the nutritional accessibility of foods, particularly in nutritionally harsh environments or environments with high levels of inter-specific feeding competition, it may have served a similar role for our hominin ancestors. As hominins diverged from other primates, they began to more consistently occupy a more terrestrial niche (Sponheimer et al., 2013). It has been suggested that fermented fruits may have emerged as a fallback food in this context (Carrigan et al., 2015), and the patterns we observed in extant non-human primates provide some support for this hypothesis.

Additionally, hominins including *Paranthropus* and *Australopithecus* are believed to have incorporated substantial amounts of hard and abrasive food items, as well as underground plant storage organs, in their diets (Dominy, 2012; Kay, 1985; Plummer, 2004; Teaford & Ungar, 2000). Underground plant storage organs are mechanically challenging, contain more starch and fiber compared to most ripe fruits, and expose foragers to potentially high amounts of diverse secondary plant metabolites that are toxic or can interfere with digestion (Buonocore & Silano, 1986; Dominy, Vogel, Yeakel, Constantino, & Lucas, 2008; Stahl et al., 1984; Waterman, 1984).

Fermentation could have reduced both the fiber and toxin levels in these food items. In fact, fermentation is commonly used to process tubers in modern human contexts (Akinrele, 1964; Ray & Sivakumar, 2009). While the transition to more settled, agrarian communities is often associated with the advent of human fermented food production for food preservation and ritual (Kuijt, 2009; Liu et al., 2018; Ross et al., 2002), the potential nutritional benefits of fermentation should not be underestimated. We found evidence that these benefits may be important drivers of late-stage fermented food consumption across the Order Primates.

Other nutritional and non-nutritional factors that we could not quantify should also be considered as proximate drivers of late-stage fermented food consumption in primates. First, the nutritional benefits of late-stage fermented fruits could be further improved by the presence of insects. Whilst generally composed of small individuals, insect assemblages in fermenting fruit can be diverse and abundant (Braham, 2015; Feinstein, Mori, & Berkov, 2007; Hodge & Arthur, 1996). Insects can provide fat, protein, vitamins and amino acids (Barnett et al., in press; Xiaoming et al., 2010), and fruit infested with them are known to be selected by some primate species in other contexts (Barnett et al., 2017). Additionally, fermentation is likely to alter food taste. Anecdotal researcher taste tests in our study indicated positive changes in taste with fruit fermentation. Fermentation is generally associated with sour or acid tastes, and humans tend to prefer sweet-sour tastes (Breslin, 2013; Katz, 2012). Little is known about sour taste receptors in primates and other animals—or even sour taste preference (Montell, 2018; Roper, 2007). However, it is likely that primates share an affinity for sour taste with humans. Taste has not been systematically examined in wild primate foods, but it will likely provide additional insight into primate food choices, both fermented and unfermented.

Finally, fermented foods are likely to provide health benefits to consumers as a result of probiotic and prebiotic properties (Bourrie et al., 2016; Burton et al., 2017; Löwenadler & Linberg, 1994; Marco et al., 2017; Summer et al., 2017; Tamang et al., 2016; Veiga et al., 2014; Yartey et al., 1995). These properties are likely to be stronger in late-stage fermented foods as a result of increased microbial activity, which may explain why these foods are targeted by some primates. Currently, without chemical and microbial data from primate foods as well as physiological and microbial data from primates, it is impossible to assess these potential relationships. However, rapidly emerging evidence of the importance of microbes for primate ecology and evolution (Amato, 2016; Amato, Jeyakumar, Poinar, & Gros, 2019; Davenport et al., 2017; Dunn et al., 2020; Gaulke et al., 2018) suggests that these interactions should not be overlooked.

Conclusion

We find that late-stage fermented fruits are consumed by a variety of non-human primates globally. This behavior generally targets a specific subset of fruit species, some of which contain herbivore defenses that are likely degraded by bacterial fermentation. It also occurs more often in hotter, drier environments, and in larger habitat patches. As a result, we suggest that primate late-stage fermented food consumption may be part of a nutritional strategy that increases food availability by increasing the duration across which a particular fruit patch can be used, and expands dietary niche space by degrading some toxins in ripe fruit and providing easily accessible nutrients. It is possible that the human propensity for fermented food consumption is rooted on this ancestral primate strategy, which was favored during the course of human evolution by periods of nutritional stress caused by climate change events and migration to unknown or unfavorable landscapes. Future studies should pair systematic assessments of spatial and temporal patterns of wild primate fermented food consumption with nutritional and microbial analyses of fermented and unfermented food items to further investigate these relationships.

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FIGURE LEGENDS

Figure 1. Wild primates consuming fermented fruits. (a) *Chlorocebus djamdjamensis* consuming *L. abyssinica* at Kokosa, Ethiopia; credit Addisu Mekonnen (b) *Cebus capucinus imitator* consuming *D. oleifera* at La Suerte Biological Field Station, Costa Rica; credit: Liz Rasheed (c) *Pan paniscus* consuming *A. mannii* at LuiKatole, Democratic Republic of Congo; credit Gottfried Hohmann (d) *Ateles geoffroyi* consuming *M. zapota* at Punta Laguna, Mexico; credit Fabrizio Dell'Anna (e) *Alouatta guariba clamitans* consuming *P. guajava* at Parque São Paulo, Brazil; credit Claudio Godoy (f) *Macaca assamensis* consuming *N. cadamba* at Phu Khieo Wildlife Sanctuary, Thailand; credit Oliver Schülke (g) *Hapalemur meridionalis* consuming *Uapaca* sp. at Mandena, Madagascar; credit Tim Eppley (h) *Callithrix jacchus* consuming *P. pachycladus* at Baracuhy Biological Field Station, Brazil; credit: Filipa Abreu.

Figure 2. Fruits consumed fermented by wild primates. (a) *Lagenaria abyssinica*, credit: Addisu Mekonnen (b) *Stemmadenia obovata*, credit: Amanda Melin (c) *Vangueria madagascariensis*, credit: Tojotanjona Razanaparany (d) *Spondias mombin,* credit: Amanda Melin (e) *Landolphia myrtifolia*, credit Tojotanjona Razanaparany (f) *Diospoyros kaki*, credit Bingua Sun.

Table 1 Potential predictors of fermented food consumption analyzed in this study.

Variable	Description
Socio-ecological traits	
1) Percent leaves in diet	Proportion of immature and mature leaves in diet
2) Percent fruit in diet	Proportion of immature and mature fruits in diet
3) Percent invertebrates in diet	Proportion of insects and other invertebrates in diet
4) Home range	Size of the home range for each study group (ha)
5) Group size	Number of members of each study group including adults, subadults, juveniles, and infants
6) Male body mass	Adult male body mass (kg) in each study species
7) Female body mass	Adult female body mass (kg) in each study species
8) Female relative encephalization quotient	Endocranial volume (cc) of the adult individuals divided by adult female body mass (kg)
9) Male relative encephalization quotient	Endocranial volume (cc) of the adult individuals divided by adult male body mass (kg)
Climate	
10) Latitude	Latitude (decimal degrees) in which each study site is located
11) Longitude	Longitude (decimal degrees) in which each study site is located
12) Mean annual rainfall	Annual mean rainfall (mm) in each study site according to the local meteorological stations
13) Mean annual maximum temperature	Annual mean maximum temperature (ºC) recorded by the local meteorological stations
14) Mean annual minimum temperature	Annual mean minimum temperature (ºC) recorded by the local meteorological stations
15) Mean daily temperature	Daily mean temperature (ºC) recorded by the local meteorological stations
16) Elevation	Representative elevation (m) of study site
Habitat quality	
17) Habitat size	Size of the habitat occupied by each study group (ha); proxy for fragmentation
Sampling Effort	
18) Study length	Number of months during which data were collected

Table 2. Wild primate species reported to consume fermented fruits.

Primate species	Family	Country	Study site[†]	# Groups	Fruits[‡]	%TFT[§]	Location[¶]
Alouatta caraya	Atelidae	Brazil	ECB	1	1	–	T
Alouatta guariba clamitans	Atelidae	Brazil	CISM, RE, PSP, PEI	7	1-7	<0.5-2	T, G
Ateles geoffroyi	Atelidae	Mexico, Panama	PL, RBMA, EPO, BCI	5	8-15	<0.5-1	T, G
Callithrix jacchus	Callitrichidae	Brazil	BBFS	1	16,17	0.5	G
Cebus imitator	Cebidae	Costa Rica	LSBFS, SSR	6	12, 18-21	<1	G
Macaca thibetana	Cercopithecidae	China	Huangshan	1	2	–	G
Chlorocebus djamdjamensis	Cercopithecidae	Ethiopia	Kokosa	1	22	<1	G
Macaca assamensis	Cercopithecidae	Thailand	PKWS	1	23,24	0.01	G
Papio anubis	Cercopithecidae	Uganda	KNP	1	25	<3	G
Pan troglodytes troglodytes	Hominidae	Republic of Congo	Goualougo	1	26-28	–	G
Pan paniscus	Hominidae	DRC	LuiKotale, Lomako	3	29-37	–	T
Gorilla gorilla	Hominidae	Republic of Congo	Goualougo, Mondika	3	26,36,38	–	G
Pongo pygmaeus wurmbii	Hominidae	Indonesia	Tuanan	1	39-41	<<0.01	T
Eulemur fulvus	Lemuridae	Madagascar	Ampijoroa	1	42,43	5	G
Hapalemur meridionalis	Lemuridae	Madagascar	Mandena	1	43,44	<0.01	T
Total = 15	**6**	**12**	**24**	**34**	**44**		

[†] Study sites: ECB = Estancia Casa Branca, CISM= Campo de Instrução de Santa Maria, RE= Reserva Econsciência, PSP = Parque São Paulo, PEI= Parque Estadual de Itapuã, PL= Punta Laguna, RBMA= Reserva de la Biósfera Montes Azules, EPO= Ejido Zamora Pico de Oro, BCI= Barro Colorado Island, BBFS= Baracuhy Biological Field Station, LSBFS = La Suerte Biological Field Station, SSR = Sector Santa Rosa, Area de Conservacion Guanacaste, PKWS = Phu Khieo Wildlife Sanctuary, KNP= Kibale National Park

[‡] Fruit species: 1=*Phytolacca dioica*, 2= *Diospyros kaki*, 3=*Citrus reticulata*, 4=*Campomanesia xanthocarpa*, 5= *Eugenia rostrifolia*, 6=*Enterolobium contortisiliquum*, 7 = *Psidium guajava*, 8=*Manilkara zapota*, 9=*Enterolobium cyclocarpum*, 10=*Spondias pupurea*, 11=*S. radlkoferi*, 12= *S. mombin*, 13= *Astrocaryum standleyanum,* 14= *Quararibea asterolepis,* 15= *Ampelocera hottlei*, 16=*Annona muricata*, 17= *Pilosocereus pachycladus*,18=*Dipteryx oleifera*, 19=*Manilkara chicle*, 20=*Stemmadenia obovata*, 21 = *Byrsonima crassifolia*, 22=*Lagenaria abyssinica*, 23=*Neolamarkia cadamba*, 24=*Gmelina arborea*, 25=*Mimusops* sp., 26= *Treculia Africana,* 27= *Gambeya lacourtiana ,* 28= *Detarium macrocarpum,* 29=*Parinari congensis*, 30=*Gilbertiodendron dewevrei*, 31=*Mammea africana*, 32=*Guibourtia demeusei*, 33=*Dialium angolense*, 34=*D. pachyphyllum*, 35=*D. corbisieri*, 36=*Anonidium mannii*, 37=*Pouteria* cf. *malaccensis*, 38= *Klainedoxa gabonensis*, 39=*Diospyros pseudomalabarica*, 40=*Ficus sundaica*, 41=*Landolphia myrtifolia*, 42=*Vangueria madagascariensis*, 43=*Uapaca* sp., 44=*Syzygium emirnense*

[§] Percentage of total feeding time. No available information is indicated with –

[¶] Location where food consumed: T = tree, G = ground

Table 3. Characteristics of fruit species consumed fermented.

Plant species	Family	GF‡	Fruit traits					References[ω]
			Type	Size (cm)	Tough husk	Secondary metabolites	Relative fiber content	
Ampelocera hottlei	Ulmaceae	T	Fleshy	2.5	no	–	–	
Annona muricata	Annonaceae	T	Fleshy	15-35	no	yes (alkaloids, acetogenins)	–	Badrie and Schauss 2010, Gajalakshmi et al. 2012, Boakye et al. 2015
Anonidium mannii¶	Annonaceae	T	Fleshy	25-40	yes	no§	moderate§	Masi et al. 2012, Djeussi et al. 2013
Astrocaryum standleyanum	Arecaceae	T	Dry	2-4	yes	–	moderate	
Byrsonima crassifolia	Malpighiaceae	T	Fleshy	2-3	no	–	moderate§	
Campomanesia xanthocarpa	Myrtaceae	T	Fleshy	1-2.5	no	yes (phenols)	–	Pereira et al. 2012, da Silva et al. 2016
Citrus reticulata	Rubiaceae	T	Fleshy	4-8	no	yes	–	Moravvej et al. 2010, Ezeabara et al. 2014
Detarium macrocarpum	Fabaceae	T	Dry	7-10	yes	yes (saponins)	moderate	Umaru et al. 2007
Dialium angolense†	Fabaceae	T	Dry	–	no	yes§	low§	
Dialium corbisieri†	Fabaceae	T	Dry	–	no	yes§	low§	Maloueki et al. 2015
Dialium pachyphyllum†	Fabaceae	T	Dry	–	no	yes§	low§	
Diospyros kaki¶	Ebenaceae	T	Fleshy	4-7	no	yes (proanthocyanogen)	low	Utsunomiya et al. 1998, Singh et al. 2011
Diospyros pseudo-malabarica	Ebenaceae	T	Fleshy	–	yes	yes (tannins)	moderate§	Maridass et al. 2008, Prasad and Raveendran 2011, Islam et al. 2019
Dipteryx oleifera#	Fabaceae	T	Dry	4-6	yes	–	–	
Enterolobium contortisiliquum¶	Fabaceae	T	Dry	4-10	yes	yes (saponins)	high	Bonel-Raposo et al. 2008, Matloub et al. 2015, Gamal

								El-Din et al. 2017, Machado et al. 2019, Abdel-Mageed et al. 2019
Enterolobium cyclocarpum	Fabaceae	T	Dry	7-15	yes	yes	moderate§	Hess et al. 2003, Babayemi 2006, Lopez-Escobar 2014, Gamal El-Din et al. 2017
Eugenia rostrifolia	Myrtaceae	T	Fleshy	1-2	no	—	—	
Ficus sundaica	Moraceae	T	Fleshy	—	no	no	moderate§	
Gambeya lacourtiana	Sapotaceae	T	Fleshy	9	no	yes (tannins, phenols)	low	Masi et al. 2012
Gilbertiodendron dewevrei†	Fabaceae	T	Dry	—	yes	yes§	low§	
Gmelina arborea	Lamiaceae	T	Fleshy	2-3	no	yes but low (tannins, phenols)	low§	Amata 2012, Nayak et al. 2012, 2013
Guibourtia demeusei†	Fabaceae	T	Dry	—	no	no§	low§	
Klainedoxa gabonensis	Irvingiaceae	T	Fleshy	6	yes	yes (tannins, phenols)	high	Masi et al. 2012
Lagenaria abyssinica#	Cucurbitaceae	V	Fleshy	5-18	yes	yes	low/moderate	Parker et al. 2007, Ragunathan and Solomon 2009, Amasalu et al. 2018
Landolphia myrtifolia¶	Apocynaceae	V	Fleshy	—	yes	no	moderate§	
Mammea africana	Clusiaceae	T	Fleshy	5-10	no	no§	low§	
Manilkara zapota	Sapotaceae	T	Fleshy	5-15	no	yes (tannins, saponins)	high§	Shui et al. 2044, Jamuna et al. 2011, Lopez-Escobar 2014
Manilkara chicle	Sapotaceae	T	Fleshy	—	yes	yes (tannins)	low§	Leonti et al. 2002
Mimusops sp.	Sapotaceae	T	Fleshy	—	no	no	low§	Baliga et al. 2011
Neolamarkia cadamba	Rubiaceae	T	Fleshy	5-7	no	yes (tannins, phenols)	moderate§	Masi et al. 2012, Djeussi et al. 2013, Islam et al. 2015
Parinari excelsa	Chrysobalanaceae	T	Fleshy	—	no	no§	low§	
Phytolacca dioica¶	Phytolaccaceae	T	Fleshy	1-1.5	no	yes (saponins)	low	Ashafa et al. 2010, Liberto et al. 2010
Pilosocereus pachycladus	Cactaceae	C	Fleshy	4-6	no (spikes)	—	—	
Pouteria cf *malaccensis*	Sapotaceae	T	Fleshy	—	yes	no	moderate§	
Psidium guajava	Myrtaceae	T	Fleshy	4-8	no	—	—	
Quararibea asterolepis¶	Malvaceae	T	Dry	1-2	no	—	high	

Spondias mombin	Anacardiaceae	T	Fleshy	2-4	no	yes	low§	Ayoka et al. 2005, Adediwura and Kio 2009, Ugadu et al. 2014
Spondias radlkoferi	Anacardiaceae	T	Fleshy	3-5	no	–	low	
Spondias purpurea	Anacardiaceae	T	Fleshy	2-3	no	yes (phenols)	–	Engels et al. 2012
Stemmadenia obovata	Apocynaceae	T	Dry	30-3-5	yes	–	moderate§	
Syzygium emirnense	Myrtaceae	T	Fleshy	1-2	no	yes§	moderate§	Razafindraibe et al. 2013
Treculia africana†	Moraceae	T	Fleshy	30-50	yes	yes§	high§	Ugwu and Oranye 2006, Ijeh et al. 2010
Uapaca spp.	Phyllanthaceae	T	Fleshy	2-4	no	no§	moderate§	Muchuweti et al. 2006
Vangueria madagascariensis¶	*Rubaceae*	T	Fleshy	3-5	yes	yes	low§	Mahomoodally 2014, Maroyi 2018

[†] Seed or seed and mesocarp consumed.

[¶] Never consumed unripe

#Never consumed unfermented

[‡] Growth form: T=tree, V=vine, C=cactus

§Data available for specific site where behavior was observed

–No available information

[ϖ] The entire list of references is available in the Supporting Information.

Table 4 Best linear mixed models ($\Delta AIC_c < 2$) and averaged-model that predict the consumption of fermented fruits in 40 wild primate species.

Predictor variables†	Parameters‡			
Best supported models				
	AIC_c	ΔAICc	w_i	R^2_c
1) habitat size+rainfall+tmax+tmin	84.5	0	0.11	1.00
2) habitat size+rainfall+tmax	84.5	0.02	0.10	0.99
3) habitat size+longitude+rainfall+tmax	85.5	0.96	0.07	0.99
4) habitat size+home range+rainfall+tmax	85.5	1.02	0.06	0.99
5) habitat size+home range+rainfall+tmax+tmin	86.5	1.96	0.04	0.99
6) female encephalization+habitat size+ rainfall+tmax	86.5	1.99	0.04	0.99
Averaged model (R^2_c =0.99)				
	β_i	SE	95% CI	$\sum w_i$
Intercept	-5.2	2.3	(-9.8, -0.6)	–
tmax	7.7	2.7	(2.3, 13.0)	1.00
rainfall	-5.7	2.4	(-10.5, -0.9)	1.00
habitat size	4.9	2.0	(1.0, 8.8)	1.00
tmin	-4.1	2.0	(-8.2, -0.1)	0.35
longitude	2.6	2.3	(-2.0, 7.2)	0.16
home range	1.4	1.1	(-0.8, 3.6)	0.25
female encephalization	-1.1	2.4	(-5.9, 3.8)	0.09

†Abbreviations of predictor variables: tmax= mean maximum ambient temperature, tmin= mean minimum ambient temperature, rainfall= mean annual rainfall.

‡Parameters shown are Akaike's Information Criterion (AICc) for small samples, difference in AICc (ΔAICc), model probability Akaike weights (w_i), Pseudo-R^2 (R^2_c) indicating the percentage of the variance explained by the fixed and random factors, partial regression coefficients of the averaged-model (β_i), standard errors that incorporate model uncertainty (SE), 95% confidence intervals for the parameter estimates, relative importance of each predictor variable ($\sum w_i$). The degrees of freedom of each model are equal to the number of variables in each model plus two. Significance level: * $P<0.05$