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Cite this article: Hirsch BT, Kays R, Alavi S, Caillaud D, Havmoller R, Mares R, Crofoot M. 2024 Smarter foragers do not forage smarter: a test of the diet hypothesis for brain expansion. *Proc. R. Soc. B* **291**: 20240138. https://doi.org/10.1098/rspb.2024.0138

Received: 18 January 2024 Accepted: 24 April 2024

Subject Category:

Behaviour

Subject Areas: behaviour, cognition, ecology

Keywords:

evolution, intelligence, brain size, foraging, mammal

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare. c.7241638.



Smarter foragers do not forage smarter: a test of the diet hypothesis for brain expansion

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A leading hypothesis for the evolution of large brains in humans and other species is that a feedback loop exists whereby intelligent animals forage more efficiently, which results in increased energy intake that fuels the growth and maintenance of large brains. We test this hypothesis for the first time with high-resolution tracking data from four sympatric, frugivorous rainforest mammal species (42 individuals) and drone-based maps of their predominant feeding trees. We found no evidence that larger-brained primates had more efficient foraging paths than smaller brained procyonids. This refutes a key assumption of the fruit-diet hypothesis for brain evolution, suggesting that other factors such as temporal cognition, extractive foraging or sociality have been more important for brain evolution.

1. Introduction

Brain size is assumed to be an important trait that impacts all aspects of animal behaviour, including movement, sociality, and foraging. While factors such as brain organization and relative neuronal investment can complicate assumptions linking brain size and cognitive performance [1–3], absolute and/or relative brain size is widely regarded as a proxy for animal intelligence [4–7]. Because brain tissue is metabolically expensive, animals may need to forage on high-energy, easily digestible foods such as fruit or cooked meat to sustain the growth and maintenance of large brains [8,9]. Some phylogenetic comparisons have supported this hypothesis with non-human primates [10,11], while others have linked increases in primate brain size to greater sociality [12]. Mixed results have also been reported in tests of this idea in non-primate taxa [13–15].

Milton [16] suggested that searching for fruit was a major selection pressure for the evolution of primate brain size because the spatiotemporal variance in the distribution of rainforest fruits creates a complex puzzle that frugivores must solve on a daily basis. A recent study has formalized this hypothesis, stating that 'primate brain evolution was primarily driven by selection on increased foraging efficiency' [11]. In this scenario, a positive feedback loop exists, whereby animals with relatively large brains make cognitively complex foraging decisions that increase nutrient intake, which in turn fuels the energetically expensive brain tissue that allows for greater foraging efficiency. A fundamental assumption of this hypothesis—that larger-brained animals exhibit greater foraging path efficiency—has never been tested.

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One of the difficulties of testing a hypothesis relating fruit foraging to brain size is that researchers typically do not know where food items are located in a field setting. In this study, we take advantage of a phenological phenomenon when a community of Central American frugivorous mammals predominantly feeds on one fruit species (Dipteryx oleifera). The Dipteryx fruit season is immediately preceded by a period of low fruit abundance, thus there is a strong pressure to maximize efficient consumption of this fruit [17]. Through the use of drones, we were able to create a map of almost all fruiting Dipteryx trees on Barro Colorado Island, Panama (electronic supplementary material, figure S1), which is effectively an accurate map of fruit resources available to these mammals. We then recorded high-resolution (4 min) GPS tracking data of four sympatric frugivores (two primates and two procyonids), listed in decreasing order based on their encephalization quotient: capuchin monkeys (Cebus capucinus) EQ = 4.16, spider monkeys (Ateles geoffroyi) EQ = 2.93, kinkajous (Potos flavus) EQ = 1.87, and coatis (Nasua narica) EQ = 1.16 [18]. While some authors have noted that EQ is not the best measure to compare brain size [19–21], these two primates also have larger overall brain sizes and larger deviations from their taxonomic specific brain/body size slopes than the two procyonids (capuchin monkeys: brain size (BS) = 70.14 g, brain residual (BR) = 0.61; spider monkeys: BS = 104.96, BR = 0.46, kinkajous: BS = 104.96, BR = 0.46, kinkajous: BS = 104.96, BR = 104.9633.08, BR = 0.27, coatis: BS = 44.17, BR = 0.06) [22]. Any within species variation in relative or total brain size is likely to be dwarfed by the large differences in primate-procyonid brain sizes. Because our study species' foraging choices were limited to the exact same fruiting trees, they all faced the same cognitive spatial puzzle to find food. If large-brained mammals forage more efficiently, we would expect the two primate species to find a more optimal solution to this spatial challenge and choose more efficient foraging paths than the two procyonids. We tested this hypothesis by comparing the path efficiency—the amount of time spent actively feeding in fruiting trees divided by the daily travel distance-for these four species.

2. Material and methods

(a) Study site

This research was conducted at the Smithsonian Tropical Research Institute on Barro Colorado Island (BCI) Panama, from December 2015 to March 2016 and from December 2017 to March 2018. BCI is a 1560 ha island covered by semi-deciduous tropical lowland forest and located within the Panama Canal. Average annual rainfall is 2600 mm per year, 90% of which falls between May and December [23]. Fruit availability is highest during the dry and early wet seasons, and lowest during the late wet season [24,25]. During our two study periods, the predominant fruit available to mammals was *Dipteryx oleifera* [26,27]. *Dipteryx* produce relatively large, 5 cm long fruits that mature between December and February (electronic supplementary material, figure S7).

(b) *Dipteryx* tree mapping

All flowering *Dipteryx* trees on the island were mapped during 2015 and 2017 using either a custom designed fixed wing (Penguin, FinWing, China) or multi-rotor UAV (Phantom 4 Pro, DJI, Shenzhen, China). Two sets of flights were conducted in each year of the study: the first was during, or a bit before, peak flowering and the second approximately two weeks later. Due to weather conditions and time constraints, flight altitude differed across the 4 sets of flights (but was held constant within each set), yielding imagery that ranged in resolution from 4–15 cm pixel. Photos were processed using the Agisoft Metashape program (Agisoft, St Petersburg, Russia), to create four georeferenced orthomosaic images of BCI, which were imported into ArcGIS (ESRI, Redlands, CA, USA). *Dipteryx* trees were identified by their distinctive pink/purple colour and polygons were manually delineated to cover the maximum visible extent of each tree crown [28]. We merged contiguous flowering tree crowns into larger polygons to create a final *Dipteryx* map (electronic supplementary material, figure S1), and we subsequently refer to merged and individual trees as *Dipteryx* patches. In addition to the combined map (electronic supplementary material, S1), separate 2015 and 2017 maps were created for use in the *Dipteryx* visitation analyses to account for year-to-year variation in fruit production.

(c) Animal tagging and accelerometry data

A total of 48 animals were fit with GPS/accelerometer collars (e-Obs GmbH, Gruenwald, Germany). Some animals were removed from the analyses due to being in the same social group as another collared animal, short periods of data collection (less than 7 weeks), or insufficient data collection per day (due to failed GPS fixes), resulting in a total of 42 animals used in the analysis (spider monkeys- 8, capuchins- 8, coatis- 15, kinkajous- 11). Two kinkajous (one male, one female) were followed during both study years, and thus the effective sample size of kinkajous is 13. Kinkajous and coatis were caught in cage traps baited with bananas, while the monkeys were immobilized via injectable darts [29]. No serious complications from animal capture occurred during this study, and animal handling methods were approved by the Institutional Animal Care and Use Committees (IACUC) at the Smithsonian Tropical Research Institute (protocol number 2014-1001-2017, 2017-0605-2020 and 2017-0912-2020) and the University of California, Davis (protocol number 18239). All GPS collars were activated by 15 December in each of the study years, and collected data until they ran out of battery (data recorded after 4–5 March were truncated). GPS collars were programmed to record a burst of six 1 Hz GPS locations every 4 min over the periods 18.00–6.30 for the nocturnal kinkajous, 6.00–18.30 for diurnal coatis, and 6.00–18.00 for diurnal capuchins and spider monkeys. The last fix of each burst consistently had the best horizontal accuracy measurement, therefore only the last fix of each burst was used for analyses.

GPS data were uploaded onto Movebank [30], and we used the Movebank data filter to remove duplicates and outliers by removing fixes with height above ellipsoid values less than or equal to 21 m or greater than 244 m. This corresponds to the first quartile minus twice the interquartile range and the third quartile plus twice the inter-quartile range respectively. Subsequent outlier detection was done using the ctmm package in R [31], using error information, straight line speeds, and distances from the median latitude and longitude to manually identify outliers via the outlie() function. GPS fixes that were located clearly outside the boundaries of the island (i.e. in water), were marked as outliers. Each collar recorded a 6 sec (12.5 Hz) burst of accelerometer (x,y,z axes) data every minute, 24 h per day. Accelerometry data were used to calculate vectors of the dynamic body acceleration (VeDBA) values, which are commonly used as a proxy measure of animal activity [32].

3

The number of *Dipteryx* patches within each animal's home range was calculated using the combined *Dipteryx* map and autocorrelated kernel density estimation (AKDE) home ranges. Home ranges, based on the utilization distribution, were estimated using the ctmm package in R [31]. All details regarding home range estimation methods and size are previously reported in [29,33].

(d) Determining foraging time

We used tracking data to quantify how much time animals were actively foraging in *Dipteryx* trees. For this analysis, we only included days when the percentage of fixes missing due to poor reception or excluded as outliers was less than 25% (daily samples excluded = 4.9%). To get a more precise estimate of when an animal entered or left a tree crown than possible with our 4 min fix schedule, we interpolated data between fixes to 1 sec. We then used the ctmm R package [31] to estimate the best fit movement models for each study animal, which allowed us to reconstruct movement trajectories to a 1 sec time scale. These fine scale movement trajectories were used to better estimate the time an animal entered or exited a *Dipteryx* patch, with biologically realistic parameters of speed and turning. If an animal left a *Dipteryx* patch but returned to the same patch within 12 min, we considered these visits as a single visit. This rule was used to account for GPS location error and animals carrying fruit back and forth to neighboring tree crowns for consumption.

To censor short tree visits, when it was unlikely that the animal was actively foraging, any *Dipteryx* visit shorter than 1 min was excluded from the analyses. Based on observed feeding rates [34], 1 min is unlikely to be enough time for an animal to enter a *Dipteryx* canopy and consume a single fruit. Finally, we used accelerometry data to determine what proportion of time in the tree crown was active versus resting using a VeDBA value of 35 as a cutoff to distinguish resting versus activity. This threshold was chosen after plotting the histogram of mean VeDBA values during *Dipteryx* visits for each species. All four species exhibited clearly bimodal distributions, and the threshold was chosen using the average trough values for all four species (electronic supplementary material, figure S5). To calculate the percentage of time animals were active (and possibly feeding) during *Dipteryx* visits, we multiplied the amount of time in the *Dipteryx* by the percentage of VeDBA values >35 during that time period.

Daily travel distances were calculated using the ctmm interpolated paths. We filtered the data such that only days when the Tau value was 2 (meaning we had enough data to reliably estimate a velocity autocorrelation parameter and therefore an OUF model) were retained in the dataset. Information from all *Dipteryx* patch visits was summarized into daily values of: number of *Dipteryx* patches visited, amount of time spent in *Dipteryx* patches, and the amount of active time spent in *Dipteryx* patches. From these values we calculated foraging efficiency as:

 $PathEfficiency = \frac{Timespentactive \in Dipteryx}{Dailytraveldistance}$

If animals with increased cognitive abilities are able to route themselves more efficiently in their environment, this could either result in the animal having a higher foraging efficiency over the course of the day, or they could use the extra time to engage in other activities such as resting, play, or socializing. If this latter scenario occurs, one would still expect that foraging during early hours of the active period (morning for capuchins, spider monkeys, and coatis; evening for kinkajous) would be as efficient as possible, due to higher hunger levels after a 12 h fast. To explore this possibility, we subset the *Dipteryx* patch visit data into periods representing the first 2 and 4 h of the day, thus calculating the amount of time spent active in *Dipteryx* trees, and the travel distance during these time periods. We then ran the same statistics with the full day, 4 h, and 2 h datasets.

(e) Use of non-*Dipteryx* foods

While *Dipteryx* trees were the primary source of fruit for all four species during our study, we determined the percentage of non-*Dipteryx* fruit in their diet based on a series of field 'trackbacks' (n = 39), whereby we followed the GPS route of an animal within three days of recording the data and looked for alternate foods. These trackbacks were carried out from Jan 17–Feb 23rd 2016, during the peak of *Dipteryx* ripeness. At any point where an animal's GPS track appeared to be clustered or stopped (defined here as three consecutive GPS fixes within 20 m), the observer searched the area within a 15 m radius of the center of the cluster of GPS points, and recorded any visible fruit in the area. We assumed that a cluster of GPS points in an area where fruit was found represented a foraging bout, and the number of *Dipteryx* patches divided by the total number of fruit patches (*Dipteryx* + other fruit species) found at these clusters was used to determine the proportion of *Dipteryx* in the fruit component of the species' diets. We then calculated trackback adjusted path efficiency measures using the following formula:

 $Adjusted Efficiency = \frac{Timespentactive \in Dipteryx}{Dailytraveldistance} x \frac{1}{\% Dipteryx \in diet}.$

(f) Statistical analyses

All statistical analyses were done in R v. 4.2.2 (R Core Team 2020). We built hierarchical Bayesian models in Stan via the brms package v. 2.18.8 [35]. All variables were standardized. We fit generalized additive mixed models (GAMMs). We compared five different combinations of predictor variables in our models, with increasing levels of model complexity (variables included: species, taxonomic group, individual ID, sex, and density of *Dipteryx* patches per home range) (electronic supplementary material, table S3). Model selection was implemented using leave-one-out cross validation. Results reported here were based on the winning models (electronic supplementary material, table S4). Pairwise comparisons among species were implemented using the method of estimated marginal means via the emmeans package [36]. We repeated these analyses using the 4 and 2 h subsets of data, as well as using both the standard path efficiency and the trackback adjusted path efficiency values.

(q) GAMM specifications

We determined the appropriate likelihood function for our models by estimating a best fit distribution using the 'fitdistrplus' package in R [37]. Path efficiency values followed a gamma distribution, therefore all models were gamma regression models. The random effect

 Table 1. Table of sample sizes, ecological measures, and variables used to determine daily path efficiency. These data were collected between 27 December 2015 and 5 March 2016, and between 25 December 2017 and 4 March 2018. Values reported are species means ± standard deviation.

| data | capuchin | spider monkey | kinkajou | coati |
|--|-------------|---------------|-------------|--------------|
| number of individuals | 8 | 8 | 11 | 15 |
| sex ratio of study subjects (F : M) | 4:4 | 4:4 | 4:7 | 9:6 |
| total tracking days | 477 | 449 | 493 | 571 |
| % Dipteryx in fruit portion of diet | 80% | 85% | 76% | 99% |
| home range size (ha) | 122 ± 51 | 770 ± 412 | 30 ± 12 | 151 ± 85 |
| daily distance travelled (m) | 3505 ± 608 | 3065 ± 993 | 2921 ± 743 | 3503 ± 989 |
| Dipteryx trees visited per day | 8.30 ± 4.43 | 9.95 ± 4.63 | 4.47 ± 2.73 | 11.59 ± 5.39 |
| daily time in <i>Dipteryx</i> (min) | 96 ± 119 | 215 ± 238 | 83 ± 84 | 185 ± 195 |
| daily time active in <i>Dipteryx</i> (min) | 83 ± 61 | 119 ± 80 | 76 ± 70 | 138 ± 81 |

structure was fully maximal [36] with random intercepts for each individual ID and random slopes on all continuous predictors. Priors were set to remain reasonably vague and to help with regularization. All models were run for 3000–6000 iterations over four MCMC chains. Initial parameter values for all models were set to 0. Visual inspection of the diagnostic plots showed stationarity and convergence, and all Rhat values were below 1.01. There were no divergent transitions after warm-up. Graphical posterior predictive checks indicated that our model structures appropriately reflected the distribution of our response variables.

(h) Evaluation of smooth terms in GAMMs

Inference on nonlinear effects in GAMMs are done using sums of smooth functions, which are penalized regression splines [38,39]. All splines in our models were thin-plate regression splines. To assist in interpretation of the splines, we used the 'method of finite differences' to estimate the first derivative of the spline, which allows for identification of periods of change along a fitted spline [40,41]. Previous implementations of the method of finite differences on GAMMs were done in a frequentist context [40,41]. We built on this approach by developing a fully Bayesian extension of this method (as in [42] code [43]). To accomplish this, we first used the 'posterior_smooths' function in 'brms' to obtain posterior predictions. Then we recomputed posterior predictions after adding or a small offset ($\varepsilon = 0.001$). The first derivative is estimated as $\Delta_{\varepsilon}[f](x)/\varepsilon$. With the first derivative approximation, we could identify regions of the spline where the rate of change in our response was non-zero. If 95% of the posterior uncertainty interval of the first derivative excluded 0, we interpreted this as reliable evidence for a non-zero rate of change. This conservative criterion allows us to identify areas of the regression line where we are confident the relationship to the predictor is biologically relevant. All data and code used for analyses in this paper are available from (https://doi.org/10.5281/zenodo.10059599) [44].

(i) Comparison of tree visit numbers per species

To determine if these species were moving in a manner that increased the likelihood of encountering *Dipteryx* trees, we compared observed frequency of *Dipteryx* encounters with the frequency of encounters generated by two random movement models: Ornstein–Uhlenbeck with foraging (OUF) and Brownian motion. We took the same OUF ctmm models used to reconstruct daily paths, and had these models generate random daily paths. We also fit Brownian movement models, and used those to simulate random daily paths. This allowed us to calculate the number of *Dipteryx* tree encounters under two types of random movement. We used the BRMS package in R to build a Bayesian multi-level model to compare the number of *Dipteryx* encountered in random versus observed paths. We used the method of estimated marginal means using the emmeans package in R [35] to do the pairwise comparisons between the OUF, Brownian and observed paths for the complete dataset. In all cases, the observed paths encountered more *Dipteryx* crows per day than the random models, for all four species.

3. Results

Combining high-resolution tracking data with drone-based fruit maps created a uniquely powerful dataset to test our hypothesis and provided important details on the foraging ecology of these species. We further validated these data on the ground by searching for available food at GPS point clusters, and confirmed that these species were primarily visiting *Dipteryx* for the fruit component of their diets (76–99%; table 1). The average daily travel distance was similar for all four species, while other measures such as home range size, number of *Dipteryx* visited per day, and average amount of time spent in *Dipteryx* trees were noticeably different (table 1).

Study species were observed to visit an average of 4 to 12 *Dipteryx* trees per day, far more than the values of less than 1 tree per day in both random movement models (OUF and Brownian motion; electronic supplementary material, figure S2). This result strongly supports the hypothesis that these species are traveling non-randomly and preferentially navigating to fruit trees (electronic supplementary material, figure S2, tables S1 and S2). Path efficiency—the percent of active time spent in *Dipteryx* fruit trees divided by the daily travel distance—was not significantly higher in the larger-brained primates, which is contrary to predictions of the fruit-diet hypothesis (figure 1; electronic supplementary material, tables S3 and S4). This pattern was the same after correcting for the proportion of non-*Dipteryx* fruit in the diets of each species (electronic supplementary material, figures S3 and S4, figures S3 and S4).



Figure 1. Raw path efficiency (active time spent in Dipteryx trees/daily travel distance) by species for the period 3 January–12 March. Primates = green, Procyonids = blue. Average values per individual indicated by grey \bigcirc = female, \triangle = males. Mean and standard deviation indicated by black point and lines. Brain images scaled to encephalization quotient size.

tables S3 and S4). More efficient foragers could conceivably exhibit more efficient routes during a portion of their day, become sated, and then use the excess time to rest, play or exhibit other fitness-maximizing behaviors. If this was the case, we would predict that the larger-brained species would exhibit greater path efficiency in the early morning, when hunger is the greatest. This was not the case, as primates did not exhibit greater path efficiency than procyonids during the first 2 or 4 h of the day (electronic supplementary material, figures S3 and S4, tables S3 and S4).

4. Discussion

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Our results align well with studies such as that of Janson *et al.* [45], who found that large-brained capuchin monkeys did not exhibit cognitively advanced path planning, but instead used simple decision rules to generate relatively efficient foraging paths. Our results are also consistent with the observation that brain expansion in higher primates has primarily occurred in the neocortex and cerebellum regions, while navigational abilities that could lead to greater path efficiency are primarily controlled by the hippocampus, which has not expanded in larger-brained primates [46–48]. These lines of evidence suggest that increased brain size in primates did not lead to better spatial routing decisions. An alternate explanation may be that, during the *Dipteryx* season, fruits are sufficiently plentiful that there is no large selection pressure for choosing more efficient travel paths (i.e. satisficing). This alternate hypothesis is not supported by our results that path efficiency was higher during the first 2 and 4 h of the day (increased hunger = better path efficiency), and we observed far greater efficiency than predicted by random encounter models. In a similar manner, even if satiation limits the maximum possible path efficiency that a species could achieve, the pre-satiation 2 and 4 h results also do not support the hypothesis that primates exhibit greater efficiency than procyonids (electronic supplementary material, figure S3).

Rather than affecting route planning and path efficiency, it is feasible that increased brain size could lead to better temporal cognition (or episodic memory), which could lead to animals timing their fruit tree visits in a manner that increases food intake [49–51]. While there is evidence that brown capuchin monkeys (*Sapajus nigritus*) use memory to anticipate future fruit rewards [52], this hypothesis that temporal cognition is a major driver of brain size evolution is untested. Some authors have linked increased brain size to extractive foraging and tool use, which could lead to greater nutrient uptake in more intelligent species regardless of their spatial cognition [53–55]. Intriguingly, capuchin monkeys have the highest relative brain size of our four study species and are also the only species in our study observed to use tools in the wild and regularly engage in extractive foraging [56,57].

There are several caveats to this study. Little is known about potential handling cost differences between these species, and some species may consume more fruit per unit of time than others. It's also possible that these species differ in their ability to extract nutrients from food. Primates are able to use structural polysaccharides through the fermentation of structural fibers, so they may have greater nutritional benefits per fruit eaten compared to the fruit-eating carnivores [58]. There could also be significant differences in travel costs between the four species. We assume that coati terrestrial locomotion expends less energy than arboreal movements of capuchins, which include substantial vertical leaping and climbing [59], although arboreal species can reduce locomotor costs in hilly areas by traveling at consistent altitudes within the canopy [60]. How these differences in locomotor costs affect foraging efficiency is not known. While prior knowledge of *Dipteryx* tree locations probably plays a major role in routing decisions, if this was the primary mechanism driving differences in path efficiency, we would predict that the social, longer-lived species (capuchins and spider monkeys) should exhibit greater path efficiency, which is not what we observed. Taking these caveats into account doesn't lead to any clear support for the diet hypothesis for brain evolution since they do not change the fact that all four species need to solve the same spatial puzzle of navigating between fruit patches. Our results do not support a strict correlation between the complexities of finding fruit and increased brain size [61]. While brain size in different clades has probably been shaped by different evolutionary forces [21], we suggest that increases in primate brain size were driven by factors unrelated to locating fruit trees and choosing efficient routes between them.

Ethics. Animal capture and handling methods were approved by the Institutional Animal Care and Use Committees (IACUC) at the Smithsonian Tropical Research Institute (protocol number 2014-1001-2017, 2017-0605-2020 and 2017-0912-2020) and the University of California, Davis (protocol number 18239).

Data accessibility. Code used for analyses in this paper is available from Github [62] and Zenodo [43]. GPS and accelerometry data are available from the Movebank Data Repository [63]. Additional information is provided in the electronic supplementary material [64].

Declaration of Al use. We have not used AI-assisted technologies in creating this article.

Authors' Contributions. B.T.H.: conceptualization, funding acquisition, investigation, methodology, writing—original draft, writing—review and editing; R.K.: conceptualization, data curation, funding acquisition, investigation, methodology, writing—review and editing; S.A.: conceptualization, formal analysis, methodology, writing—review and editing; D.C.: conceptualization, funding acquisition, investigation, methodology, writing—review and editing; R.H.: investigation, methodology, writing—review and editing; M.C.: conceptualization, funding acquisition, investigation, methodology, project administration, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This project received funding from the Smithsonian Tropical Research Institute, the National Science Foundation (BCS-1440755), a Packard Foundation Fellowship (2016-65130) and the Alexander von Humboldt Foundation in the framework of the Alexander von Humboldt Professorship endowed by the Federal Ministry of Education and Research awarded to M.C. Further support for the project was also provided by the Center for the Advanced Study of Collective Behaviour at the University of Konstanz, Deutsche Forschungsgemeinschaft Centre of Excellence 2117 (ID: 422037984).

Acknowledgments. Special thanks to Melissa Cano, Rafael Batista, Oris Acevedo and Adriana Bilgray from the Smithsonian Tropical Research Institute for assistance on logistics. We thank Diorene Smith DVM, at the Parque Municipal Summit and Suzan Murray from the Smithsonian Conservation Biology Institute for veterinary support and consultation. For drone photography we thank Jonathan Dandois, Ryan Nolin, Helene Muller-Landau, Milton Garcia, Andreas Schuerkmann and Matt Jones. For assistance during animal capture, downloading of GPS data and fruit collection, we thank Robert Lessnau, Anthony Di Fiore, Linnea Worsøe Havmøller, Ninon Meyer, Grace Davis, Brianna Pinto, Alexis Moreno, Josue Ortega, Cesar Gutierrez, Yessenia Guadalupe, Allie Davis, Dan Marsh, Megan O'Keefe, Michelle Faehr, Aimee Owen, April Pitman, Michelle Kuchle, Devin Lindsley, Gregg Cohen, Jean Hirwa, Kevin McLean, Lucia Torrez, Alexander Vining and Claudio Monteza. We would like to thank Sarah Brosnan and two anonymous reviewers for their insightful comments on an earlier draft of this paper.

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