



Arboreal monkeys facilitate foraging of terrestrial frugivores

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Abstract

Terrestrial animals feed on fruit dropped by arboreal frugivores in tropical forests around the world, but it remains unknown whether the resulting spatial associations of these animals are coincidental or intentionally maintained. On Barro Colorado Island, Panama, we used a combination of acoustic playback experiments, remote camera monitoring, and GPS tracking to quantify the frequency of such interactions, determine who initiates and maintains spatial associations, and test whether terrestrial animals adopt a strategy of acoustic eavesdropping to locate fruit patches created by foraging primates. Indeed, 90% of fruits collected in fruit fall traps had tooth marks of arboreal frugivores, and terrestrial frugivores visited fruit trees sooner following visits by GPS-collared monkeys. While our play back experiments were insufficient to support the hypothesis that terrestrial frugivores use auditory cues to locate food dropped by arboreal primates, analyses of movement paths of capuchin monkeys (*Cebus capucinus*), spider monkeys (*Ateles geoffroyi*), and coatis (*Nasua narica*) reveal that observed patterns of interspecific attraction are not merely a byproduct of mutual attraction to shared resources. Coatis were significantly more likely to initiate close encounters with arboreal primates than *vice versa* and maintained these associations by spending significantly longer periods at fruiting trees when collared primates were present. Our results demonstrate that terrestrial frugivores are attracted to arboreal primates, likely because they increase local resource availability.

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Primates are often among the first species in a habitat to be extirpated by hunting; our results suggest that their loss may have unanticipated consequences for the frugivore community.

Abstract in Spanish is available with online material.

KEYWORDS

attraction, camera trapping, eavesdropping, GPS tracking, interspecific associations, Panama, tropical forest

1 | INTRODUCTION

Tropical rainforests are complex ecosystems where diverse communities of plants and animals are connected by networks of interspecific interactions (Miura et al., 1997). Fruit-producing trees are important sources of food for many rainforest animals (Howe, 1986). Animals can act both as seed predators and seed dispersers playing an important role in the dynamics of forest regeneration and maintenance of biodiversity (Howe, 1990). Fruiting trees are typically aggregated (Condit et al., 2000), and fruit production is ephemeral and seasonal (van Schaik et al., 1993). Frugivores, therefore, must constantly search for new food resources and experience annual seasons of food scarcity which, in some years, result in famine and widespread starvation (Foster, 1982; Wright et al., 1999).

Animals can acquire information about the location of resources either directly, by sensing the food, or indirectly, by using signals obtained from conspecifics or heterospecifics (Danchin et al., 2004). Obtaining information through eavesdropping on other animals is a relatively cost-effective strategy (Danchin et al., 2004; Valone, 2007). Animals have been shown to eavesdrop to detect predators (Lea et al., 2008), locate nest sites (Doligez et al., 2003) and discover resources (Coolen et al., 2003). Eavesdropping may be an important strategy animals use to adjust their movement and foraging behavior, helping them to locate rich resources or avoid areas where cues suggest resources have been depleted (Goodale et al., 2010). Finding food via eavesdropping could increase direct feeding competition if the cues are coming from other feeding animals, or if they attract several animals simultaneously. Accordingly, eavesdropping should be most beneficial for species that differ in their foraging niche and thus do not compete directly with one another (Gautier-Hion et al., 1983; Goodale et al., 2010).

Interspecific associations where animals of different species forage together can involve commensalism, parasitism, or mutualism (Danchin et al., 2004), with varying degrees of behavioral interactions from passive associations with no direct interactions, to coordinated activities (Stensland et al., 2003). These associations may be the result of species selecting similar habitats because they are attracted to the same resources (Arita & Vargas, 1995), or because they are attracted to one another for anti-predator benefits (Fitzgibbon, 1990) and increased foraging efficiency (Stensland et al., 2003). For example, seabirds benefit from marine mammals

forcing fish towards the surface (Bräger, 1998) and birds follow monkeys that flush insects (Stott & Selsor, 1961). Associations between primates and non-primates generally appear to be related to food acquisition (but see e.g. (Morgan-Davies, 1960) for antipredator associations), and multiple species of arboreal primates are known to drop food, which is later eaten by terrestrial species (Heymann & Hsia, 2015). Although commonly remarked upon, few studies have quantified how these associations are established, who initiates them, or whether they are simply random encounters resulting from the mutual attraction to shared resources (Heymann & Hsia, 2015; Koda, 2012).

In this study, we investigate interspecific associations in a Neotropical frugivore community. We test the hypothesis that terrestrial frugivores alter their movement in response to the foraging behavior of arboreal primates. Specifically, we test if (a) arboreal primates increase the availability of fruit for terrestrial frugivores, (b) terrestrial frugivores spend more time with arboreal primates than would be expected by chance, (c) terrestrial frugivores eavesdrop on cues made by arboreal primates to locate ephemeral food sources and they are attracted to these auditory cues, and (d) terrestrial frugivores stay longer and/or revisit fruit trees more frequently when arboreal primates are present.

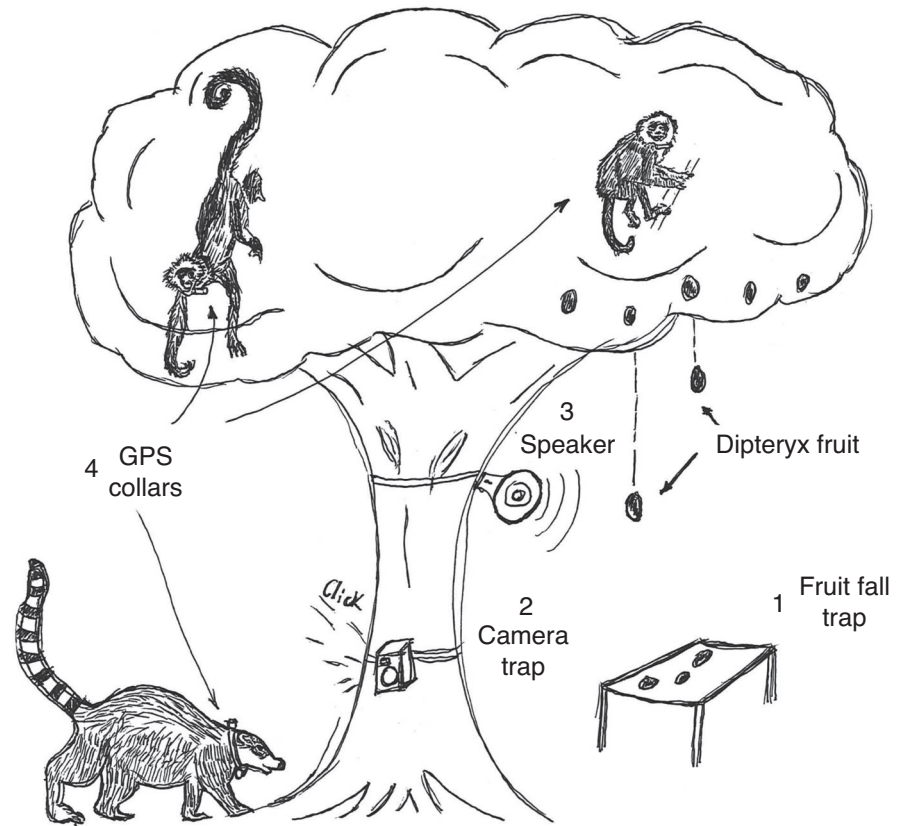
2 | METHODS

We used a combination of acoustic playback experiments, camera trapping, GPS tracking, and phenological monitoring to test our hypotheses. Methods are summarized in Figure 1. All animal handling followed the practice of the Code of Best Practice for Field Primatology (Riley et al., 2014). 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) approved all animal handling and collaring procedures.

2.1 | Study site and study species

We studied the movement and foraging of a Neotropical frugivore guild on Barro Colorado Island (BCI) in Panama. BCI is a 1560 ha island

FIGURE 1 Schematic of methods used (1) Fruit fall traps: What percentage of fruits are partially eaten by arboreal frugivores? (2) Camera traps: Do terrestrial frugivores stay longer at fruit trees when monkeys are overhead? (3) Acoustic playback experiments: Are terrestrial frugivores attracted to monkey sounds? (4) GPS collars: Who initiates interactions? Do coatis spend more time near fruit trees when monkeys present? Do monkeys and coatis meet more than expected by chance?



of semi-deciduous tropical lowland forest located in the Panama Canal (9°09'N, 79°51'W; for a full description see (Leigh, 1999). The study took place over two seasons from June 2015 to April 2016 and June 2017 to April 2018. During the period December–March a single tree species, *Dipteryx oleifera* (hereafter *Dipteryx*), produces the majority of the food resources available to the frugivore community (Wright & Calderón, 2006; De Steven and Putz 1984).

Sixteen species of mammals have been recorded to eat *Dipteryx* fruits at this study site, with the majority being arboreal or aerial (Bonaccorso et al., 1980). Great fruit-eating bats (*Artibeus lituratus*) and other large fruit bats are thought to be the main dispersers of *Dipteryx*, carrying fruits up to hundreds of meters away from the parent tree (Bonaccorso et al., 1980). Collared peccaries (*Pecari tajacu*) and several species of rodents (e.g., red-tailed squirrel [*Sciurus granatensis*], Central American agouti [*Dasyprocta punctata*], and Tome's spiny rat [*Proechimys semispinosus*]) have been recorded feeding on *Dipteryx* seeds, primarily after they have fallen to the ground (Bonaccorso et al., 1980). In contrast, primates (white-faced capuchins [*Cebus capucinus*], black-handed spider monkeys [*Ateles geoffroyi*] and mantled howler monkeys [*Alouatta palliata*]) are arboreal and feed exclusively on the pulp of *Dipteryx* fruit (Bonaccorso et al., 1980). Kinkajous (*Potus flavus*) and white-nosed coati (*Nasua narica*) also only feed on the pulp, with kinkajous feeding arboreally (Bonaccorso et al., 1980) while coatis mainly feed on the ground (Kaufmann, 1962).

In this study we focused on four species of frugivores that rely heavily on seasonally available *Dipteryx* fruit, which has been found

to constitute more than 75% of feeding times for these four species during this period: two species of arboreal frugivores—capuchin and spider monkeys—and two species of terrestrial frugivores—agoutis and coatis (unpublished data from Davis, Crofoot, Kays, Hirsh; Gompper, 1996; Kaufmann, 1962). The importance of this resource is illustrated by the fact that they experience die-offs during years where *Dipteryx* fails to produce fruit (De Steven and Putz 1984; Wright et al., 1999). Three of our study species are social with capuchin monkeys living in stable social groups that travel together as a cohesive unit. We tracked a single capuchin per group (eight groups over the two years, six unique groups) and considered the movements of these individuals as representative of their entire social unit following (Crofoot et al., 2008). A single community of spider monkeys inhabits our study site, and members of this community engage in highly dynamic and flexible patterns of subgrouping (Campbell, 2004). The movements of the eight spider monkeys we tracked were treated as independent, although due to their fission-fusion dynamics, these individuals sometimes travelled together. Finally, coati males and females differ in their social behavior with females travelling as part of stable and cohesive social groups and males living solitarily through most of the annual cycle, but joining groups during the mating season (Gompper & Krinsley, 1992; Hirsch & Gompper, 2017). We tracked 6 male and 10 female coatis belonging to seven unique groups. As with capuchins, the movements of collared female coatis were considered as representative of their group. Agoutis live in pairs with varying degrees of social interactions depending on season and food

availability (Smythe, 1978). We did not track their movements in this study, but instead used camera traps to record visits to fruiting *Dipteryx* trees.

2.2 | Mapping of *Dipteryx oleifera* trees

Dipteryx are 25–40 m tall trees that produce distinctive pink flowers during May–July, when few other trees are flowering (Bonaccorso et al., 1980). We mapped the location of every flowering *Dipteryx* from June–July in 2015 and 2017 using drone-based aerial photography (Phantom 4 Pro, DJI, Shenzhen, China, and a custom designed fix-winged drone) following (Caillaud et al., 2010). We processed photographs using Agisoft Metashape (Agisoft LLC, St. Petersburg, Russia) to create georeferenced orthomosaic images for each year. Flowering *Dipteryx* in the orthomosaics were visually identified, and crowns were delineated by hand in ArcGIS (ESRI, Redlands, CA). A subset of the mapped *Dipteryx* trees ($N = 30$) were checked again in January; all 30 trees had fruit. We then used this *Dipteryx* map produced in ArcGIS to determine when and where collared animals were in fruiting trees.

2.3 | Phenological monitoring

We monitored *Dipteryx* availability using fruit fall traps placed below 30 fruiting *Dipteryx* selected based on being accessible via the trail system and within the area where we focused our animal capture effort. Fruit traps were monitored for the duration of the fruiting season from December–March in both years of the study. We visually assessed fruit that was collected from the traps for tooth marks to evaluate the proportion which had been dropped by arboreal frugivores. Eight 1×1 m fruit traps were placed per tree (covering an average of 12% of the crown): four within 25% distance from trunk to edge of crown, and four within 75–100% distance to edge of crown. Traps were placed facing north, east, south and west using the tree trunk as central point. Traps were emptied every week and fruits were classified as intact, <25% eaten, and >25% eaten.

2.4 | Animal capture

Between August to December 2015 and September to December 2017, we captured and fitted a total of 32 neotropical frugivores—8 capuchins, 16 coatis, and 8 spider monkeys—with GPS collars (e-Obs GmbH, Gruenwald, Germany). We chemically immobilized primates using 15 mg/kg Zoletil® (see (Crofoot et al., 2009) for description of capture methods) using a DanInject™ JM Standard and 14-gauge Pneu Dart™ Type P RDD device (Pneu-Dart). We trapped coatis in Tomahawk Live Traps™ (Tomahawk Live Trap) and chemically immobilized them using 5 mg/kg Zoletil® (Di Blanco & Hirsch, 2006). All collars had built-in cotton weak-links

designed to make the collars break off within a year. We successfully recaptured 10 out of 16 coatis at the end of the study and removed their collars.

2.5 | GPS-settings

The GPS tags were set to collect GPS-locations every four minutes during the animal's active periods: 0600–1800 h for capuchins and spider monkey and 0600–1830 h for white-nosed coatis. This sampling schedule allowed two intensive monitoring periods of these three neotropical frugivore species from December 2015 to April 2016 and December 2017 to April 2018 during the fruiting season of *Dipteryx* in lowland Panamanian forests.

2.6 | Ground activity based on camera-traps

From December 2017–March 2018, we deployed camera-traps (HC500 Hyperfire Reconyx Inc.) underneath 23 fruiting *Dipteryx* for periods of 15–30 days, resulting in a total of 458 camera-trap days and 11,658 detections of terrestrial frugivores. To determine whether primates were in the tree overhead at the time of each of these detections, we matched the timestamps on the camera trap photos with the timestamps from GPS data on capuchin and spider monkey visits to these *Dipteryx*. If arboreal primates make resources available to terrestrial frugivores, we expect to see increased activity at the base of *Dipteryx* trees when primates are known to be present: detections of animals under fruiting trees should be more frequent and the interval between animals' visits to the tree should be shorter. Because only a small subset of the monkeys at the study site were GPS tracked, we cannot know whether or not monkeys were absent from a *Dipteryx*. However, false negatives (i.e., our failure to detect un-tagged primates in focal *Dipteryx*) should bias the data against, rather than for, our prediction.

Defining what constitutes a visit can be challenging, as foraging animals may frequently leave the field of view of our cameras without actually leaving the patch of food beneath the fruiting tree. To accommodate this behavior without making an arbitrary decision about what constitutes a unique visit, we allowed the distribution of inter-visit intervals to have two modes; one potentially corresponding to recaptures of an individual as it moves around the patch searching for food in one continuous foraging bout (within patch movement), and the other corresponding to behaviorally distinct visits. We assume that log-transformed inter-visit intervals followed a Gaussian mixture distribution, where the average inter-visit interval of within patch movement is the same whether or not monkeys are present, but the average inter-visit interval of the unique visit component is potentially different under the two conditions. We further assume that individual trees have characteristic average inter-visit interval between unique visits; thus, the model includes random effects for trees. We assume that the standard deviation of the log-inter-visit interval is shared across all components and the two conditions. A

computational Bayesian approach implemented in the Stan modelling language (Gelman et al., 2015) makes inference straightforward by providing specific functions for Gaussian mixture models, and through the availability of relevant case studies (Betancourt, 2017), (see Supplementary Information for model details). Although several species of terrestrial frugivores visited *Dipteryx* trees during our study, the number of visits by most species was inadequate for analysis (see Table S1 for species detections).

2.7 | Detecting if terrestrial frugivores eavesdrop on arboreal primates

We ran acoustic playback experiments between December 2017 and February 2018 during mornings (0700–1000 h) and afternoons (1400–1700 h), corresponding to peaks in activity for most diurnal terrestrial frugivores including agoutis and coatis (see Table S1) (Rowcliffe et al., 2014). Experiments were located in a grid system with a randomized treatment order and repeated 10 times. Simultaneous experiments were at least 500 m apart to eliminate the chance of animals hearing both speakers. In subsequent trials, speakers were moved to a new site at least 200 m away from the previous experimental location. To minimize disturbance to the area, all treatments consisted of a one-hour pre-treatment, where the speaker was on but emitting no sound, followed by a 30 min treatment. The four treatments consisted of four sounds (1) Fruit dropping; (2) Capuchin monkey non-feeding vocalizing; (3) Capuchin feeding vocalization, no fruit dropping, and (4) Capuchin feeding vocalizing with fruit dropping. We also had two controls (1) Speaker on but no sound and (2) Sound of cicadas. At the site of each experiment, we placed four Reconyx HC500 Hyperfire camera-traps (Reconyx Inc.) strapped around a tree pointing north, south, east and west. At the same tree, we placed a waterproof plastic box containing a mp3-player (SanDisk 16GB Clip Sport Plus MP3 Player; Western Digital Corporation) and a waterproof speaker (Fugoo Tough XL; Fugoo LLC) 1.5 m above ground level.

Visits by terrestrial frugivores of the same species with multiple consecutive photos separated by less than 60 s were regarded as belonging to the same event (Sollmann, 2018). The experiments take the form of paired comparisons of a given treatment with a pre-treatment baseline at each location at a given time of day. In order to account for likely time-lag effects on foraging behavior of the 30 min playback, we included terrestrial frugivore visits that occurred during subsequent 3.5 h after playback ended as part of the treatment period. The total duration of acoustic playback periods, as well as acoustic control periods, was therefore 4 h. The dependent variable was the number of events (unique visits encompassing all terrestrial frugivores) recorded during a trial phase (either pre-treatment or treatment), modelled as a Poisson-distributed variable with effects for treatment (controls 1–2, sounds 1–4) and time of day. Unique location effects were modelled as random intercepts because these adjust for location-to-location differences and allow

for sharper estimates of event rates during treatment phases versus pre-treatment. This Generalized Linear Mixed-Effects Model was fitted using the package 'lme4' (Bates et al., 2014) in R version 3.5.1. We examined a scatterplot of Pearson residuals versus predicted values to check that the fit of the model was adequate.

2.8 | Quantifying behavioral interactions

In this study, we defined encounters as instances when a coati and a primate (capuchin or spider monkey) came within 20 m of each other for at least two sampling periods (i.e., minimum duration of 4 min). To ensure independence of interactions, we only included the first interaction per dyad per day in the analysis. A total of 114 encounters were used to create short animations which were then used to characterize the encounter (see Videos S1 and S2. Individuals in the animations were given anonymous ID numbers to minimize reviewer bias when scoring the initiator of an encounter. All three species show a high degree of directional travel (coati: 0.011° , $SD = \pm 2.4^\circ$; spider monkeys: 0.013° , $SD = \pm 2.5^\circ$; capuchin: 0.035° , $SD = \pm 3.4^\circ$). We can therefore use these turning angles to look at who initiated the interactions. Turning angles ($45\text{--}180^\circ$) were recorded when individuals clearly changed direction in order to approach a *Dipteryx* tree, and whether the encounters occurred inside or outside a *Dipteryx* crown.

To determine whether coatis spend more time at feeding locations in the presence of monkeys, we extracted the duration of visits to *Dipteryx* by coatis with and without the presence of a GPS-collared monkeys. As not all primates at the study site were fitted with tracking devices, coati visits to *Dipteryx* categorized as 'without the presence of a collared primate' include a combination of visits where no monkeys were present (i.e., true negatives) and visits where uncollared monkeys were present (i.e., false negatives). Only visits between 0700 h and 1800 h were used, and thus sleeping trees were excluded. We used the 'recurse' package (Bracis et al., 2018) in R (version 3.5.1) in combination with the spatial layer with all known flowering *Dipteryx* to determine when an individual entered and left a *Dipteryx*.

2.9 | Detecting attraction

All three of our study species are social, but differ in their patterns of grouping in ways that had to be accounted for in the design of our data collection and analysis (see Figure S1 for *Dipteryx* distribution and home range estimates using the ctm package (Fleming & Calabrese, 2021)). Spider monkeys have fission–fusion dynamics but by only considering the first interaction of a dyad each day, we avoided possible pseudoreplication due to this joint travel.

For every dyad comprised of a monkey (capuchin or spider monkey) and a coati, we calculated the Euclidean distance between the pair at each four-minute timestep. When the dyadic distance between the two animals fell below our given threshold of 20 m, we

defined the animals as being in association at that particular time. These instances of association were subdivided into foraging associations and non-foraging associations. An association was defined as a foraging association if at least one individual in the dyad was within 20 m of the perimeter of a known fruiting *Dipteryx* tree. We based this threshold of 20 m to separate foraging and non-foraging interactions while taking the mean GPS error of 9 m into account and potential scattering of fruits when dropped to the ground. We calculated the probability of association in a foraging context between monkeys and coatis as the number of instances of foraging association summed across all monkey-coati dyads, divided by the total number of simultaneous GPS locations summed across all monkey-coati dyads. These are joint probabilities of the event that a dyad is in association and the event that at least one member of the dyad is in (or not in) a *Dipteryx* tree. Similarly, we calculated the probability of non-foraging association between monkeys and coatis as the number of instances of non-foraging association divided by the total number of simultaneous GPS locations, again summing values across all monkey-coati dyads.

We compared foraging association and non-foraging association probabilities from the empirical data to theoretical distributions of these probabilities produced by 1000 randomizations of each dyad's movement paths. In order to ensure that random travel paths had the same characteristics of the true travel paths, and to account for mutual attraction to resources, each randomization compared one animal's true travel path to the other dyad member's true travel path shifted in time (Alba-Mejia et al., 2013; Spiegel et al., 2016). We shifted travel paths by whole days to account for diel patterns in space and resource use. Randomized paths separated by weeks or months reflect the use of a different resource base, due to ripening and depletion of *Dipteryx* crops, and might therefore underestimate the frequency of chance associations. We therefore constrained time-shifted and real travel paths to be at most seven days apart, as our phenological monitoring showed that food resources did not change markedly within this timeframe.

We tested the null hypotheses that monkeys and coatis do not associate more than expected by chance against the alternative hypothesis that they positively associate, which is indicative of at least one member of the dyad being attracted to the other. We tested this hypothesis in both a foraging and non-foraging context. For each context, we calculated a one-sided simulated p-value as the proportion of probabilities of association that resulted from the movement path randomizations that were as great or greater than the observed probability of association.

3 | RESULTS

3.1 | Fruit fall data results

A total of 1123 *Dipteryx* fruits were collected in 2016, and 805 in 2018. In 2016 only 86 (7.7%) of the collected fruits were intact, 1037 (92.3%) were partly eaten with 429 (38%) <25% eaten and 608

(54%) >25% eaten. In 2018 a total of 76 fruits (9.4%) were intact with 729 fruits (90.6%) partly eaten of which 260 fruits (32%) were <25% eaten and 469 (58%) were >25% eaten.

3.2 | Agouti activity in the presence versus absence of GPS-collared monkeys

Monitoring of activity under fruiting *Dipteryx* resulted in a total of 11,658 animal detections, of which 241 occurred in the presence of collared monkeys. Although, several species of terrestrial frugivores were recorded in camera traps to visit *Dipteryx* trees, agoutis accounted for 64% of all detections in the presence of collared monkeys. Because the topic of eavesdropping in a foraging context between mammals is not well established, we chose a statistically conservative approach to ensure confidence of our results. Consequently, only agoutis had a sufficient sample size for our statistical approach (see Table S1). In the model we see a slight shift towards shorter inter-visit intervals in the unique visit component (time between agouti visits) when collared monkeys are present compared to absent (Figure 2). The posterior mean for μ_0 , the log-inter-visit interval when monkeys were absent, is 7.5 (log s) with posterior $SD = 0.2$, and the posterior mean for μ_1 , the log-inter-visit interval when monkeys were present, is 7.1 (log s) with posterior $SD = 0.2$. These posterior means correspond to 30.1 min when collared monkeys were absent and 20.2 min when collared monkeys were present. Finally, the mixing proportion p has posterior mean = 0.53 with posterior $SD = 0.007$, suggesting that slightly more than half of all inter-visit intervals represent within patch movement.

3.3 | Do terrestrial frugivores eavesdrop on arboreal primates?

During playback experiments, six terrestrial frugivores were recorded in camera-traps: collared peccary, white-nosed coati, Central American agouti, red brocket deer (*Mazama americana*), red-tailed squirrel, and lowland paca (*Cuniculus paca*). We used a paired-design where all post-treatments were compared to pre-treatment (one hour prior to the start of each playback) by using a mixed-effects Poisson model, fitted with the R language library lme4 (Bates et al., 2014). Average rates of visits by terrestrial frugivores to our experimental arenas increased, relative to baseline rates, during trials that simulated the presence of arboreal primates (Figure 3, Experiments 1–4). These increases were almost twice the baseline rate, though their confidence intervals, containing the relative rate 1:1, do not rule out the possibility that treatment and baseline rates were the same. Average rates during control trials decreased nominally relative to baseline, though again equality with baseline rates cannot be ruled out. All confidence interval widths were corrected for six comparisons (each treatment compared with baseline) thereby controlling the experiment-wide error rate. Successively narrower intervals

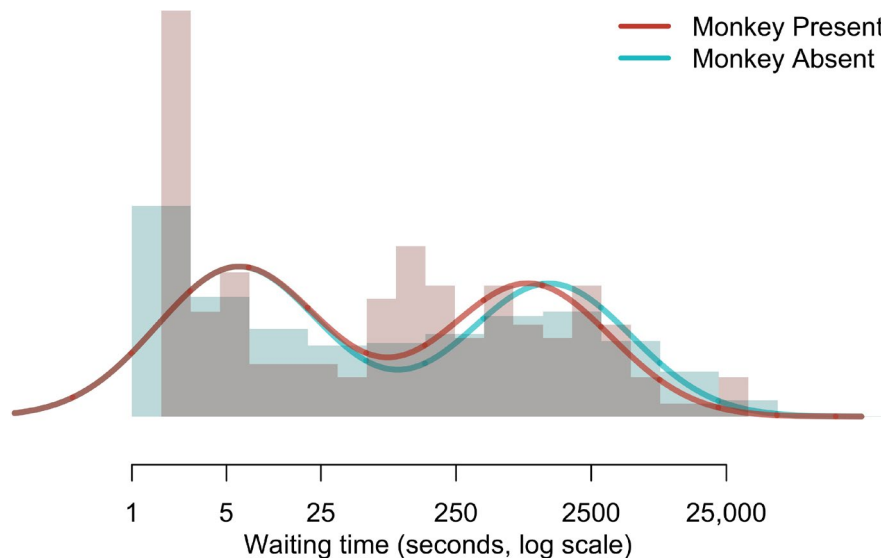


FIGURE 2 Gaussian mixture model showing a slight shift towards shorter inter-visit intervals in time between agouti visits when collared monkeys are present compared to absent. Estimated densities from the Gaussian mixture model for inter-visit intervals, along with observed intervals. Observed inter-visit intervals on the natural log-scale are shown as probability histograms (red represents collared monkeys present, blue collared monkeys absent). Probability histograms show relative frequencies of observations within bins and are therefore scaled compatibly with the estimated densities. The left-hand mode of the Gaussian mixture corresponds to within patch movement of agoutis (recaptures of the same individual moving around the food patch) and the right-hand modes corresponds to unique inter-visit intervals (i.e., new visits). The Gaussian mixture densities are based on posterior mean parameter values from four chains, each having 1,000 warmup iterations and 1,000 sampling iterations. Diagnostic checks implemented in the *rstan* library (Stan Development Team, 2018) indicated that mixing was adequate

for each playback condition correspond to experiment-wide error rates of 5%, 10% and 15%.

We carried out a further, post hoc analysis to investigate whether or not a larger experiment, consisting of more playback trials, could potentially distinguish treatment from baseline conditions. Poisson model-based comparisons with baseline rates were made after pooling observations across the four treatments, and across the two control conditions. After pooling, treatment and control can both be distinguished from baseline at the experiment-wide 85% level (Figure S2).

3.4 | Are coatis attracted to monkeys?

Based on the randomizations, our GPS-collared coatis had an approximately 17 times higher probability of being within 20 m of a monkey both in and outside of a *Dipteryx*, than expected by random chance (p -value < 0.01; Figure 4). This suggests that coatis and monkeys spent more time in close proximity (20 m) than expected by chance in both foraging and non-foraging contexts, even when controlling for mutual attraction to the same foraging resources.

Out of the 114 identified encounters between coati-monkey dyads, 89.5% are within 20 m of a *Dipteryx*. Of the 114 encounters, 69 (58.8%) were initiated by coatis, 39 (34.2%) were initiated by monkeys (see Videos S1 and S2), and 8 (7%) were unknown (e.g., mutual approaches). Coatis were significantly more likely to initiate close interactions (<20 m apart) than monkeys (Wilcoxon rank sum test:

$W = 809, p$ -value = 0.009). Both solitary coati males and group-living females initiated contact with monkeys ($N = 114$; 51.3% = female, 48.7% male). Coatis spent significantly longer at *Dipteryx* when monkeys were present (mean duration of 17.6 min with monkeys, 9.7 min without monkeys; Figure 5; two-sample Kolmogorov-Smirnov test: $D = 0.295, p$ -value < 0.001). Coatis were significantly more likely to change direction and move towards a monkey feeding in a *Dipteryx* (turning angles of 45–180°) than *vice versa* (Wilcoxon rank sum test: $W = 831.5, p$ -value = 0.001).

4 | DISCUSSION

Incorporating multiple lines of evidence, our study demonstrates strong spatial interactions between arboreal and terrestrial frugivores. This study suggests that monkeys play an important role in the foraging ecology of the terrestrial frugivore community by making fruit available to them earlier and in larger quantities than it would have been otherwise. First, the majority (90%) of fruits collected in fruit traps below *Dipteryx* trees showed signs of being dropped to the ground by arboreal frugivores. Second, our camera-trap monitoring found that agoutis returned to fruiting trees more quickly when GPS-collared monkeys were present. Although not statistically significant after correction for multiple tests, the results of our playback experiments are consistent with the hypothesis that terrestrial frugivores use acoustic eavesdropping to locate monkeys. Finally, our GPS tracking data showed that coatis and monkeys

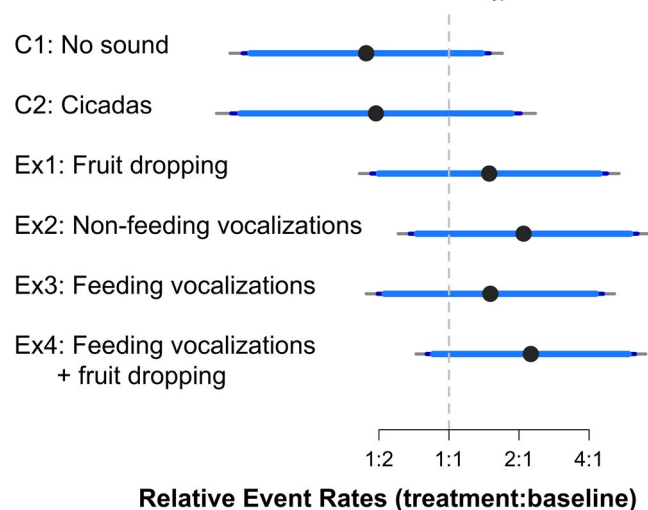


FIGURE 3 Playback experiments showing a trend toward increased response to acoustic stimuli. Rates of unique visits to fruiting trees by terrestrial frugivores under playback conditions relative to baseline rates, with experiment-wide 85%, 90% and 95% confidence intervals from the Poisson mixed model (see Methods). Estimated event rates for each experimental or control condition, relative to baseline (pre-treatment) event rates, are shown by center dots. The horizontal axis has a natural-log scaling, though labels refer to the observational units of measurement—relative numbers of events per unit time. For example, the estimated rate of visits for Ex2 was approximately two times the baseline rate. Ninety five percent, 90% and 85% experiment-wide confidence levels are shown in grey, blue and light blue shading, respectively. Confidence intervals for each playback condition are adjusted for six total comparisons using the Bonferroni correction. Intervals for all conditions at all confidence levels contain the value 1:1, indicating that treatment rates are not statistically distinguishable from baseline rates in these experiments

associated more often and spent more time together than expected by chance, even when controlling for mutual attraction to resources. Coatis were more likely to initiate close contact with monkeys and more often changed direction of their movement path towards monkeys in fruiting trees. Coatis also spent significantly longer periods of time at fruiting trees when collared primates were present. Together, our four lines of evidence—fruit fall, camera-trapping, playback experiments, and GPS tracking—all demonstrate the important role that arboreal primates play as facilitators of foraging for terrestrial mammals in a Neotropical forest in Panama.

Throughout the study period, most of the fruit collected from phenology traps was partially eaten (90%–92%). The majority of fruit on the ground, and thus available to terrestrial frugivores, was there because it had been discarded by an arboreal frugivore. This is a similar result to the observations of (Gompper, 1996) who found zero *Dipteryx* fruits dropping before the presence of large arboreal frugivores, 3.5 fruits per min when large arboreal frugivores were present and only 0.04 fruits dropped per min after large arboreal frugivores left. Our fruit trap data showed that arboreal frugivores regularly drop fruit before they would naturally fall to the ground,

and that much of the edible parts of the fruit are still intact, thus creating sources of food for terrestrial species (Howe, 1980). Based on our camera-trap data, agoutis appeared to visit fruiting trees more quickly/often when collared monkeys were present. This suggests that agoutis might be eavesdropping on feeding arboreal primates to exploit the newly fallen fruits before competitors do. Agoutis are the most commonly detected terrestrial frugivore by camera traps (Rowcliffe et al., 2014) and have relatively small home-ranges (mean 2.56 ha), centered around fruit trees (Aliaga-Rossel et al., 2008). Due to their high abundance and small home ranges agoutis are likely the first species to respond to newly available food resources dropped by monkeys. However, agoutis often have overlapping home ranges (Aliaga-Rossel et al., 2008) and we cannot be certain whether these individuals are new individuals or the same that returned.

We observed a nonsignificant trend that terrestrial frugivores responded to vocalizations and other sounds associated with foraging primates. This trend was also observed with vocalizations made in non-foraging contexts. At least two aspects of our experimental design could explain the limited response: an inadequate number of playback trials, and/or speaker placement (Ellinger & Hödl, 2003). The post hoc results from pooled observations (Figure S2) suggest that the experiment was under-powered, and that increasing the number of trials by at least a factor of four could better distinguish treatment from baseline conditions. Considering the second design aspect, speakers were placed at approximately 1.5 m height, which could limit how far the sound travels compared to monkeys feeding in the crown of a tree at 25–40 m. A more realistic experimental setup and larger sample size would be needed to convincingly test for acoustic eavesdropping. All playback experiments were placed at non-fruiting trees to avoid a potential bias of attraction to resources. However, animals might also use olfaction (Hirsch, 2010) and memory of resource locations (Janmaat et al., 2006; Polansky et al., 2015). This may have resulted in conditional discrimination as suggested by Koda (2012) where animals only respond in the presence of multiple stimuli. Koda (2012) found significantly more visits by Japanese sika deer (*Cervus nippon yakushimae*) at fruit trees when play back experiments with macaque (*Macaca fuscata yakui*) calls were played compared to controls. In our study, terrestrial frugivores may have been less likely to approach experimental playback sites because other relevant stimuli were absent, or because they knew that no fruit was available at the site.

Analysis and visualization of frugivore movement paths supported the hypothesis that coatis are attracted to monkeys. Coatis were significantly more likely to change their direction of travel, re-orienting towards monkeys and initiate close interactions (i.e., approaches to within 20 m) than vice versa. Consistent with results from our playback experiments, coatis seemed to be attracted to monkeys even away from foraging trees. This could be explained by coatis generally associating the presence of monkeys with food or by coatis and monkeys associating at food sources that were not identified in our analysis.

We only investigated the effect of capuchins and spider monkeys on terrestrial species. Mantled howler monkeys are the most

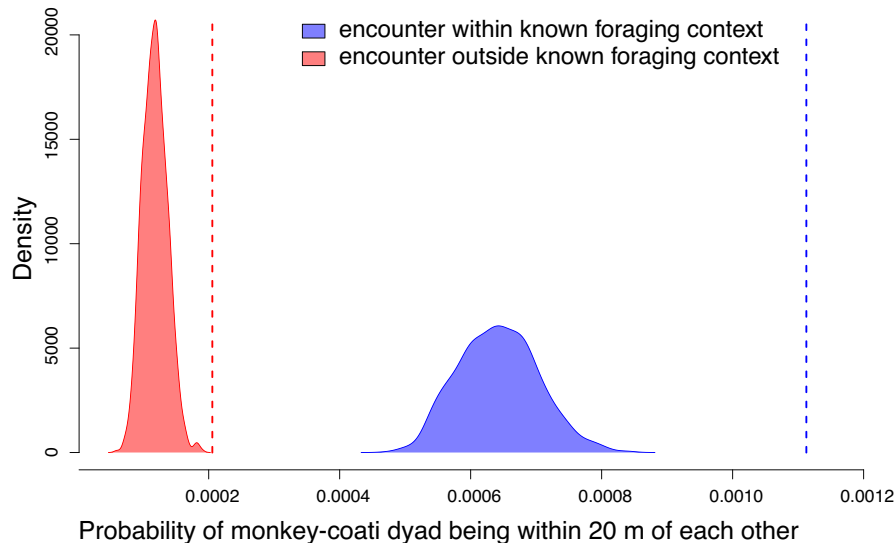
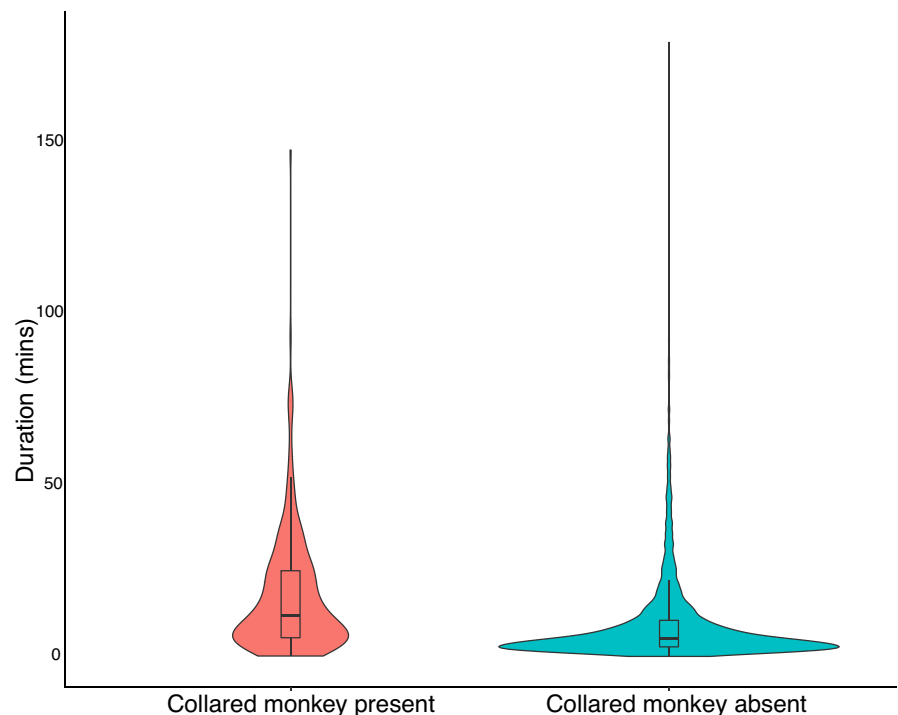


FIGURE 4 Density plot showing that coatis and monkeys spend significantly more time in close proximity (20 m) than expected by chance, both in a foraging and non-foraging context. Comparison between empirical probability of association of coatis and monkeys and those generated from 1,000 movement path randomizations. Distributions represent values produced by randomizations and the dashed lines indicate the empirical values. Red shows the probability of a coati and monkey being within 20 m of each other in a non-foraging context. Blue shows the probability of a coati and a monkey being within 20 m of each other in a foraging context (within 20 m of a fruiting *Dipteryx*). P-values under both conditions are significant ($p < 0.01$) with the distribution of random values falling entirely below the empirical value, thus suggesting that coatis and monkeys spend more time together than expected by random chance

FIGURE 5 Violin plot showing that coatis stay significantly longer at *Dipteryx* when collared monkeys are present compared to absent. Duration in minutes (y-axis) coatis spend at *Dipteryx* in the presence (red) and absence (blue) of collared arboreal primates. Boxplot included showing the mean duration of coati visits to *Dipteryx* in monkey presence 17.9 min (red) and monkey absence 9.7 min (blue)



abundant primate on BCI and may also play an important role as food facilitators, although time spent feeding on *Dipteryx* fruit only accounts for a small percentage (0.91%) of their annual feeding time (Milton et al., 2019). Fruit-eating birds may also provide similar benefits as primates (Douglas et al., 2013). Although the bird species present on BCI have not been recorded to drop fruit at the same

rate as primates (Howe, 1980), parrots have been reported to drop large quantities of fruit at other sites, and may play a similar ecological role to the one we posit here for primates (Sebastián-González et al., 2019).

These associations between arboreal and terrestrial frugivores are complex systems often involving multiple species (McConkey

et al., 2018; Prasad & Sukumar, 2010). Bats are generally considered to be the primary dispersers of *Dipteryx* fruits but multiple species act as seed predators, primary and secondary dispersers (Ruiz et al., 2010) adding to the complexity of the system. Associations might be seasonal occurrences when food resources are scarce. This pattern has been found in other study systems such as collared peccaries associating with wedge-capped capuchin monkeys (*Cebus olivaceus*) (Robinson & Eisenberg, 1985), rock kestrels (*Falco rupicolus*) associating with chacma baboons (*Papio ursinus*) (King & Cowlishaw, 2009) and chital (*Axis axis*), barking deer (*Muntiacus muntjak*) and mouse deer (*Moschiola meminna*) aggregating under fruit trees in India when Hanuman langurs (*Semnopithecus entellus*) are present (Prasad & Sukumar, 2010). In a study from Japan, Agetsuma et al. (2011) found that Japanese macaques provided between 1.7%–10.9% of the seasonal diet for Japanese sika deer by dropping leaves and fruit or bending branches. Monkeys may play a similar role with seasonal fluctuations of food in our study area. *Dipteryx* is the first species to produce fruit after a period of food scarcity for many frugivores (Bonaccorso et al., 1980). Primates may thus provide access to high-energy content foods that would otherwise be unavailable to terrestrial frugivores as suggested by Agetsuma et al. (2011). Coatis are scansorial, and can climb for fruit, but arboreal feeding only accounts for a small proportion (5%–7%) of their total activity budget, which mainly occurs when they are entering or exiting arboreal sleep sites (Kaufmann, 1962). In some cases, a proportion of a coati group will climb a tree to feed, resulting in increased fruit fall for the remaining group members (Hirsch, 2009). This behavior is more common when feeding on smaller fruit trees (Hirsch, personal observation), thus it is unlikely that coatis use this strategy while feeding on tall *Dipteryx* trees. Since both solitary males and group-living females responded equally to arboreal primates, this suggests that group-living coatis are not regularly climbing *Dipteryx* trees for the benefit of terrestrial group members (Hirsch, 2009). Coatis likely gain food at a low cost by associating with primates, and eavesdropping on the cues of feeding primates may provide additional information about the spatiotemporal availability of food resources in the habitat. Other species such as agoutis, peccaries, and deer are unable to climb, and thus have to wait until fruits naturally drop or rely on other species to drop fruit.

Primates are often among the first species to be extirpated in forests where humans hunt (Redford & Robinson, 1987) and are still regularly hunted across the tropics (Peres & Dolman, 2000). Our results suggest that the loss of primates may affect frugivorous mammals in counterintuitive ways. Mature *Dipteryx* fruits tend to remain in trees until they are past ripe unless picked off and dropped by aerial or arboreal species (Bonaccorso et al., 1980). Arboreal frugivores such as primates may therefore increase resource availability at a critical time for terrestrial frugivores unable to climb trees to access fruit. This dynamic may be particularly important following periods of resource scarcity, when fruit availability in the trees has already increased, but there remains little for terrestrial species to eat. The absence of primates from tropical forest communities may extend periods of resource scarcity for terrestrial frugivores,

potentially with negative consequences on the whole ecosystem. Poaching of frugivorous animals may indirectly alter plant regeneration in tropical forests by changing both seed dispersal and seed predation (Wright et al., 2000). Interspecific associations may be more common and widespread than previously known, thus understanding their ecological importance may be critical for predicting how changes to the animal community affect forest dynamics and ecosystem integrity.

5 | CONTRIBUTIONS

MCC, DC, RK, BTH and LWH formulated the idea and designed the protocols. RWH, LTH, MCC, BTH, RK and LWH collected data. LWH, JCL, SEA, RWK, MNG and DC analyzed data and prepared figures. LWH led the writing of the manuscript and all authors contributed to the text.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

Data used in all analyses for this project are available from the Open Science Framework repository: <https://doi.org/10.17605/OSF.IO/2ADG5>. Animal tracking data are hosted on Movebank (Processed data: Movebank ID 1120749252; Unprocessed data: Movebank ID 468460067). Code for all analyses are hosted on github: <https://git.io/JEWjf>

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