Received: 30 June 2023 | Revised: 24 October 2023 | Accepted: 4 February 2024

DOI: 10.1111/btp.13315

ORIGINAL ARTICLE

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

Niche expansion of capuchin monkeys to forest floor on guild-reduced islands increases interspecific spatio-temporal overlap

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Associate Editor: Jennifer Powers
Handling Editor: Laurence Culot

Abstract

Interspecific interactions play an important role in structuring wildlife communities. On islands, which often have reduced species assemblages, species may expand their niches resulting in unusual patterns of interactions with other members of the ecological community. In this study, we compared spatio-temporal interactions of two food competitors between a site with predators and two predator-free islands in the Coiba archipelago, Panama. Here, capuchin monkeys (*Cebus capucinus imitator*) exhibit high levels of terrestriality, and some groups engage in stone tool use. This potentially leads to competition with sympatric agoutis (*Dasyprocta coibae*), which have overlapping diets. We used camera-trap surveys to estimate temporal overlap between both species, distinguishing between arboreal and terrestrial activity of capuchins. We also compared detection rates and intervals between consecutive detections of both species at sites in which the monkeys use stone tools (tool-use area) and sites in which they do not (non-tool-use area). We found high spatio-temporal overlap between agouti and capuchin on the forest floor of both islands. While capuchins visited the tool-use area four times as often as the non-tool-use area, agoutis avoided the tool-use area, capture rates being 25 times as low. Waiting times were shorter for both species at the tool-use area. These results suggest temporal overlap and spatial segregation. Niche expansions on islands thus cause unique interactions that do not occur on the mainland.

Abstract in Spanish is available with online material.

KEYWORDS

activity patterns, camera trapping, *Cebus*, competition, *Dasyprocta*, ecological segregation, interspecific interactions, Panama

1 | INTRODUCTION

Interspecific competition for food and space is a major selective force on the evolution of mammal behavior (Kotler & Holt, 1989; Lima & Dill, 1990). When sympatric species have highly overlapping diets, a dominant species can completely displace a subordinate one from a foraging patch through behaviors such as mobbing, harassment, or intimidation, or by finding and exploiting resources more efficiently (Crofoot, 2013; Damas-Moreira et al., 2020; Houle et al., 2006; Palomares & Caro, 1999; Wootton, 1994). Consequently, species with similar dietary requirements can only coexist if they segregate along at least one of their niche axes, through behavioral adaptations and coexistence strategies that maximize their fitness and survival, a process called niche differentiation (Grevé et al., 2019; Hardin, 1960). One key strategy for species with overlapping diets to avoid competition is segregation in space and time (Pianka, 1974). For instance, kudus (*Tragelaphus strepsiceros*) and zebras (*Equus quagga*) avoid areas with elephants (*Loxodonta africana*) in the African plains (Ferry et al., 2016). Similarly, cheetahs (*Acinonyx jubatus*) hunt during daytime to minimize encounters with lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) who most often hunt at night (Durant, 1998).

Predation pressure may reduce competitive interactions between species via a process called apparent competition (Holt & Bonsall, 2017). For example, terrestrial predators facilitate some terrestrial frugivore species by driving other, more wary, frugivores into trees—generating niche separation. In the absence of mammalian predators, arboreal frugivores readily come to the ground and exploit resources. This has been documented for several primates, including orangutans (*Pongo pygmaeus*) in Borneo (Ashbury et al., 2015), crab-eating macaques (*Macaca fascicularis*) in the Island of Simeulue (van Schaik & van Noordwijk, 1985) and white-faced capuchins (*Cebus capucinus imitator*) in the Coiba Archipelago (Monteza-Moreno, Crofoot et al., 2020). A common aspect between these primate populations in island systems is that predation pressure is lower, compared to mainland (Cooper et al., 2014).

Guild composition in islands might vary based on the distance to the mainland (MacArthur & Wilson, 1967). Consequently, insular populations may have reduced predation and interspecific competition. In the absence of predators, some island populations have undergone losses of anti-predatory behaviors (Blumstein & Daniel, 2005; Zenth et al., 2021), while interspecific resource competition may be reduced on islands when there are fewer species with similar niches (Adler, 1996; Diamond, 1978). Because competition plays an important role in evolution, it is worth exploring the consequences of reduced guilds in island environments. Predator-free islands, such as many landbridge islands, offer an opportunity to study interspecific interactions, especially between species with overlapping diets. Here, we compare interactions of sympatric white-faced capuchins (*C. capucinus imitator*) and agoutis (*Dasyprocta coibae*) living in two mammalian predator-free landbridge islands in Coiba National Park (CNP), Panama. The local white-faced capuchin monkeys exhibit high levels of terrestriality compared to mainland populations (Monteza-Moreno, Crofoot et al., 2020), and include the only groups of white-faced capuchins documented to use stone-tools (Barrett et al., 2018; Monteza-Moreno, Dogandžić et al., 2020). Such levels of terrestriality among capuchins in CNP may lead to interspecific interactions with ground-dwelling agouti (*D. coibae*), a medium-sized (2–4 kg) caviomorph rodent.

On the mainland, although ground-dwelling agoutis and predominantly arboreal capuchins have highly overlapping distributions and diets (Emmons, 2016; Williams-Guillén et al., 2021), direct interspecific interactions are uncommon, except by sporadic displacement (“mobbing”) of agoutis by capuchins (Rose et al., 2003). Indirect interaction occurs, for example, when capuchins harvest fruits many are dropped to the ground that can be consumed by ground-dwelling animals, including agoutis (Havmøller et al., 2021). Potentially, the sound of agoutis chewing on the ground attracts other frugivores, including capuchins, as has been documented for other species (Galef & Giraldeau, 2001; Pollock et al., 2017). Many of the known shared food items between agoutis and capuchins occur in the islands of CNP (Ibáñez, 2011), hence there is potential for increased interspecific competition.

Whether or not agoutis and capuchins coexisting on islands with no predation pressure overlap spatially and temporally remains unknown. Further, the unusual tool use tradition in some groups of this capuchin population creates additional opportunities for interaction, as tool use is a predominantly terrestrial activity. At tool-use sites, capuchins may leave debris from fruits opened with stone tools, such as *Terminalia catappa*, *Bactris major*, and *Astrocaryum standleyanum*, potentially attracting agoutis, who wish to avoid the costs of locating and processing structurally protected fruits. On the other hand, capuchin populations are known to harass, mob, and displace sympatric species, including agoutis (Jack et al., 2020; Rose et al., 2003). If this antagonistic behavior also takes place in the islands, capuchins might displace agoutis from tool-use areas.

Our study aimed to assess the likelihood of direct temporal and spatial overlap between agoutis and capuchins on island systems with reduced predation pressure. We placed camera traps at two CNP islands on the ground at capuchins' stone tool-use areas and at non-tool-use areas, and in the canopy. We surveyed a site with predators to serve as a comparator. We then tested the predictions that: (a) daily activity patterns of agouti and capuchin on the islands overlap more when capuchins are in the trees than when they are on the ground, that is, strata partitioning; (b) temporal overlap between agouti and capuchin is higher at the control site than on the islands, due to strata partitioning; (c) agoutis visit tool-use areas more often than non-tool areas, benefitting from food leftover from capuchins' stone tool-use; (d) capuchin visit latency at the tool-use area will be shorter after an agouti visit, potentially signaling displacement.

2 | METHODS

2.1 | Study sites and study species

We surveyed three sites located in Panama (Figure S1). At Coiba National Park (CNP), an archipelago off the Pacific coast, we surveyed the two largest islands, Coiba (50,134 ha) and Jicarón (2002 ha), where annual mean temperature is around 27°C, and mean annual rainfall is 3500 mm (Cardiel et al., 1997). Both islands have been isolated from the mainland since the last glacial maxima about 14,000 years ago (Titcomb & O'Dea, 2020). CNP has a marked dry season (mid-December to mid-April) and a rainy season (mid-April to mid-December). No mammalian predators are known to occur on either island (Ibañez et al., 1997; Monteza-Moreno, Crofoot et al. 2020). In addition to capuchins and agoutis, Coiba island is also inhabited by the howler monkey (*Alouatta palliata coibensis*), common opossum (*Didelphis marsupialis*), white-tailed deer (*Odocoileus virginianus*), and several small mammals (<1 kg body mass) (Ibañez et al., 1997). On Jicarón island, the mammalian assemblage is composed of just howler monkeys, capuchin monkeys, agouti, and small mammals (<1 kg body mass). Hereafter we refer to Coiba and Jicarón as "the islands sites".

The site for comparison was Barro Colorado Island (BCI), a 1540-ha artificial island in central Panama that was recently formed in 1914 by the damming of the Chagres River to create a water supply for the Panama Canal. BCI has a wide variety of mammalian species typical of central Panama, including predators and competitors of the two study species (Kays et al., 2009; Rodgers et al., 2017). BCI is covered by lowland tropical rainforest, with around 2600 mm of rain per year and annual mean temperature averages 27°C (Windsor, 1990).

The white-faced capuchin, a small platyrrhine (c. 3 kg), lives in troops of 4 to ≥20 individuals that are mutually intolerant and aggressively confront one another when encounters occur in areas of home-range overlap (Crofoot, 2007; Crofoot et al., 2008; Perry et al., 2011; Tórrez-Herrera et al., 2020). White-faced capuchins are omnivores; fruits comprise 50%–70% of the species' diet while also consuming invertebrates, flower nectar, and vertebrate prey (Chapman & Fedigan, 1990; Hogan et al., 2016). Intraspecific aggression is common in this species, with documented cases of lethal encounters between groups (Gros-Louis et al., 2003). On the islands of CNP, the local capuchins exhibit levels of terrestrial activity that are up to 100 times higher than populations at mainland sites, presumably in response to the absence of carnivores (Monteza-Moreno, Crofoot et al., 2020).

Several localized groups, at least one on each island of CNP, engage in stone tool-use and are the only populations of this species known to do so (Barrett et al., 2018; Monteza-Moreno, Dogandžić et al., 2020). In the tool-use area of Jicarón island, capuchins use stone tools to crack structurally protected fruits of sea almonds (*T. catappa*), a highly nutritious food item (Kassim et al., 2017), as well as other food items including hermit crabs (*Coenobita compressus*) and marine snails (*Nerita scabricosta*) (Barrett et al., 2018). Tool-use has been documented at three types of sites, classified by the amount of debris and tools present (Barrett et al., 2018; Goldsborough et al., 2023): elusive sites with little debris accumulation, such as the intertidal zone; sites in streambeds, with low to medium accumulation of debris, removed by seasonal flooding; and high accumulation sites (hereafter "fixed anvils") with large quantities of debris accumulated over time across several anvils and concentrated on the ground of the forest edge.

The agouti, a medium-sized scatter-hoarding rodent (2–4 kg; Smythe, 1978) of the Dasyproctidae family, is present throughout the Neotropics. Based on morphology, the Coiban agouti (*D. coibae*) is considered a separate species from the Central American agouti (*Dasyprocta punctata*) (Roach & Naylor, 2019). However, genetic evidence for this differentiation is needed, particularly because morphological support for species differentiation in agoutis has been mixed (i.e., *Dasyprocta ruatanica*; Ruiz-García et al., 2022). Agoutis feed mostly on fruit seeds and pulp, with minor amounts of fungi and insect consumption (Henry, 1999). Mainland populations of agoutis compete for resources with several ground-dwelling frugivores, including collared peccaries, white-lipped peccaries, and tapirs (Akkawi et al., 2020; Smythe, 1986), none of which occur in the Coiba archipelago. At mainland sites, agoutis can obtain leftover food from arboreal primates as they drop fruit to the ground (Havmøller et al., 2021).

2.2 | Camera trapping

We placed camera traps at 95 unique sampling locations (Jicarón = 71; Coiba = 20; BCI = 4) in three different sampling surveys. We used unbaited IR camera traps (Hyperfire PC900, HC600 and HF2X; Ultrafire XR6, and XP9, Reconyx, Inc, WI, USA). We conducted Survey 1 from February through June 2015, installing a total of 15 camera traps in Coiba island and 11 on Jicarón island. This survey was aimed to investigate terrestrial mammal communities on both islands, with cameras spaced out on average 1-km from each other. Survey 2 was conducted from March to July 2019, with sampling in Coiba, Jicarón, and BCI, including arboreal and ground camera trapping. We installed 22 paired cameras on tree trunks, at about 20 m above the ground (Coiba = 6, Jicarón = 8, BCI = 8), facing towards branches potentially connected with neighboring trees, and without prior knowledge of capuchin movement. At each arboreal sampling location, we deployed a respective ground camera, adding 12 camera traps (Coiba = 4, Jicarón = 4, BCI = 4). This survey aimed to assess terrestriality levels of capuchin monkeys and consisted of opportunistic sampling (mean distance between camera traps: Coiba = 7.3 km, Jicarón = 3.5 km, BCI = 1.7 km).

Finally, we conducted Survey 3 from 2017 to 2022, with a gap in 2020 due to the COVID pandemic. This survey is part of a larger sampling effort focused on tool using behavior at Coiba and Jicarón. We sampled a total of 38 locations within the range of a tool-using group of monkeys in Jicarón (hereafter tool-use area) (Goldsborough et al., 2023). Specifically, we sampled 12 fixed anvils where habitual stone tool use occurs (Figure S2), 11 locations in streambeds where opportunistic tool use may occur, and 15 random locations within the tool using troop's home range. Additionally, we sampled 23 locations further inland (Coiba = 2, Jicarón = 21), in areas where no tool use is known to occur. Ground cameras in all three surveys were installed at 50 cm above ground. See Table 1 and Figures S3–S6 for further details on sampling effort and survey characteristics. We processed all camera trap photos using the Agouti camera-trap-image-processing platform (www.agouti.eu; Casaer et al., 2019). We scored the number of individuals per species per detection event, which we defined as consecutive detections of the same species in a 2-min window.

TABLE 1 Study site characteristics and relevant sampling information.

Study site	Area (ha)	Sampling period	Sampling locations	Sampling effort[c]
Coiba[a]	50,300	February–June 2015 / March–July 2017 / March–July 2019	20	1596 (ground)[d]/623 (canopy)
Jicarón[a]	2000	February–June 2015 / March 2017–August 2019 / July 2021–July 2022	71	8575 (ground)[e]/603 (canopy)
BCI[b]	1540	March–July 2019	4	444 (ground)/844 (canopy)

[a] Island site.

[b] Control site.

[c] Sampling effort in camera-days.

[d] All ground cameras were classified as non-tool-use areas.

[e] 5141 camera-days on the tool-use area and 3434 camera-days on non-tool-use area.

2.3 | Data analysis

2.3.1 | Activity patterns of agoutis compared to capuchins

We analyzed activity patterns of both species from camera trapping data using kernel density estimation (Rowcliffe et al., 2014). We calculated activity-density curves to compare agouti activity with the following categories of capuchin activity: (a) BCI arboreal activity (population is predominantly arboreal); (b) island arboreal activity, and (c) island ground activity (excluding observations from the tool-use area due to oversampling). For each pairwise comparison, we obtained overlap coefficients, ranging from 0 (no overlap) to 1 (perfect overlap), and 84% confidence intervals through 10,000 smoothed bootstrap iterations (Meredith & Ridout, 2021). We used 84% confidence intervals to assess difference in temporal overlap, as they mimic hypothesis testing using an alpha level of 0.05 (MacGregor-Fors & Payton, 2013). These analyses were conducted using the “overlap” package (Ridout & Linkie, 2009) in the R environment v. 4.2.1 (R Development Core Team, 2011).

2.3.2 | Species detection rates at the tool-use and non-tool-use areas

To compare terrestrial activity of agouti and capuchin between tool and non-tool-use areas, we fitted a negative binomial generalized linear mixed effects model using the “glmmADMB” (Skaug et al., 2014) package in R. We coded as non-tool-use area cameras all ground cameras from Surveys 1 and 2 (excluding BCI as no documented tool using capuchins live there), as well as the cameras outside the tool-using troop's home range on Survey 3. We defined as the tool-use area all cameras from Survey 3 that were located within the tool-using troop's range (including fixed anvils, streambeds, and random locations within the troop's range). Our outcome variable was the number of detection events, which we used to estimate monthly detection rates for each species at the tool-use and non-tool-use areas. We also used an interaction term between species and sites, and we treated camera-specific location as a random intercept to account for unmeasured heterogeneity between different camera-trap locations. We used camera-specific deployment duration as an offset to account for unequal sampling effort, as log (deployment_duration_in days/30). This offset helps generate predictions for the number of detections per species per month, where detection rates are interpreted as a proxy of intensity of site use or frequency of visits.

2.3.3 | Interspecific attraction versus avoidance

We used survival analyses to test differences in visit latency of both species at the tool-use and non-tool-use areas, and compared, respectively, each species' “waiting times” (Lau et al., 2021; Swinkels et al., 2023). The waiting time is the time interval between consecutive detections of the alternative species at a camera trap location (Figure 1). Agouti waiting time is calculated as the temporal interval between an agouti and the previous capuchin, and the capuchin waiting time as the interval between an agouti and the next capuchin. If agoutis are attracted to the tool-use area due to potential leftover food from capuchins, we expect agouti waiting times to be shorter in the tool-use area than in the non-tool-use area. If capuchins exhibit territoriality, we expect their waiting times to be shorter in the tool-use area than in the non-tool-use area.

For the subset of data from the tool-use area, we compared agouti waiting times when the previous capuchin did, or did not, engage in tool use. In this case we defined agouti waiting time as the temporal interval between a capuchin and the next agouti (Figure S7) and recorded whether the capuchin detection event involved stone tool use or not. If agoutis consistently use leftover food from capuchins, we expect agouti waiting times to be shorter after a monkey engaged in tool use versus not. Intervals for the very first agouti detection were categorized as censored for the agouti waiting time, as the preceding capuchin detection occurred before camera set-up. Intervals for the very last agouti detection were categorized as censored for the capuchin waiting time, as the subsequent capuchin detection occurred after camera pick-up (Figure S8). At camera deployments where only one of the species was detected, we censored the respective waiting time for each event. We fit Kaplan–Meier survival/event time curves to the data and compared waiting times

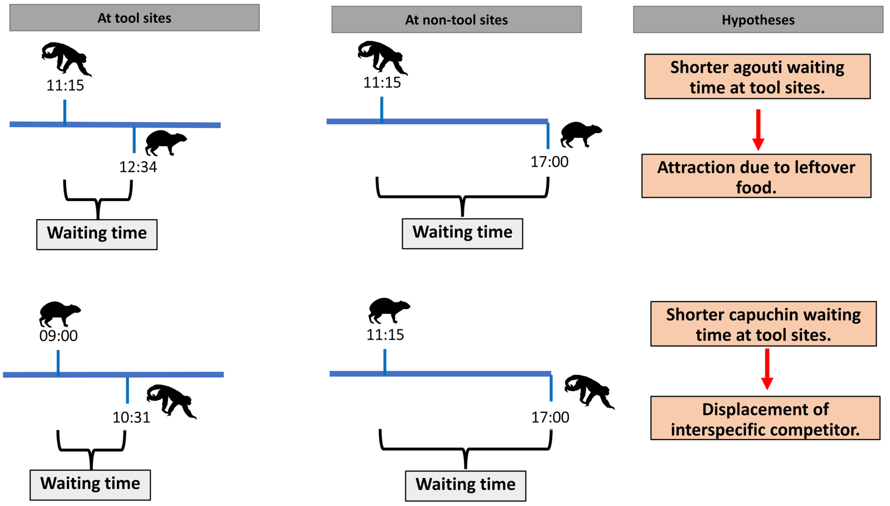


FIGURE 1 Visual representation of hypotheses for the waiting time analysis. Waiting time consists of a time interval between detections of one species after detection of the other.

between tool-use and non-tool-use area through Mann Whitney *U* tests. These analyses were conducted using the R package "survival" (Therneau et al., 2022).

3 | RESULTS

The total effort was 12,685 trap-days. This yielded 12,269 detection events of white-faced capuchins and 5214 of agoutis. Of the capuchin detection events, 127 were arboreal observations (*N*=85 in BCI; 42 in islands) and 12,140 ground observations (*N*=1 in BCI; 12,139 in islands), of which 10,212 were at the tool-use area (*N*=1842 using tools; *N*=8371 with no tool use). Out of the tool-using capuchin detection events, 1822 were recorded at fixed anvils and 20 at random locations and streambeds within the tool-use area. A total of 257 agouti events were obtained on Jicarón, representing the first report of the species in this island (Ibañez et al., 1997; Roach & Naylor, 2019).

3.1 | Temporal overlap

Activity overlap between capuchins and agoutis was high, regardless of whether the capuchins were in the canopy or on the ground, but it was higher on BCI than on the islands (Figure 2, Table 2). Capuchin terrestrial activity was recorded throughout the day on the islands, with a peak before sunset, while activity in the canopy was much higher in the morning. Agouti activity was similar between mainland and island populations—bimodal with a higher morning peak and a lower afternoon peak. On the islands, agouti activity peaked roughly at the same time as canopy-based capuchin activity peaked.

3.2 | Detection rates

Agouti detection rates were 25 times lower at the tool-use area, with an average of four visits per month there (84% CI: 2–7) and 100 visits per month at the non-tool-use area (84% CI: 46–215). In contrast, capuchin detection rates were four times higher at the tool-use area, with 155 visits per month (84% CI: 120–199) and 35 visits per month (84% CI: 27–44) at the non-tool-use area. Thus, the ratios of agouti–capuchin visits at the tool-use and non-tool-use areas were 4:155 versus 20:7, a more than hundred-fold difference. The contrast in detection rates between tool-use areas was 7.23 ± 0.35, suggesting average detection rates between both areas are different (Figure 3).

3.3 | Waiting times

Both species exhibited shorter waiting times in the tool-use area (Figure 4, Table 3, Figure S9). Median waiting time for agouti was 28.0 h at the tool-use area (range: 0.13–1964.4) and 173.3 h at the non-tool-use area (range: 0.04–1988.0). For white-faced capuchins, median waiting times were 22.2 h at the tool-use area (range: 0.03–555.2) and 127.2 h in the non-tool-use area (range: 0.06–1471.6). Within the tool-use area, median agouti waiting times were 932.2 h after a capuchin engaged in stone tool use (range: 12.51–4357.8) and 675.3 h after a capuchin not using tools (range: 0.13–5340.8) (Figure 5). The difference in waiting times between tool-use and non-tool-use areas was statistically significant for both agouti (W=87,202, difference=−5.20, 84% CI=−6.25 to 2212 −4.24, $p<.001$) and capuchin (W=68,079, difference=−3.92, 84% CI=−4.66 to −3.22, $p<.001$). Within the tool-use area we found slightly longer agouti waiting times whenever capuchins engaged in tool use (W=434,701, difference=2.51, 84% CI=0.58–4.67, $p=.07$).

4 | DISCUSSION

Our findings provide empirical evidence of interspecific interactions between a ground-dwelling rodent and a typically arboreal primate that expanded its niche onto the ground in an island system with reduced predation pressure and interspecific competition. We found

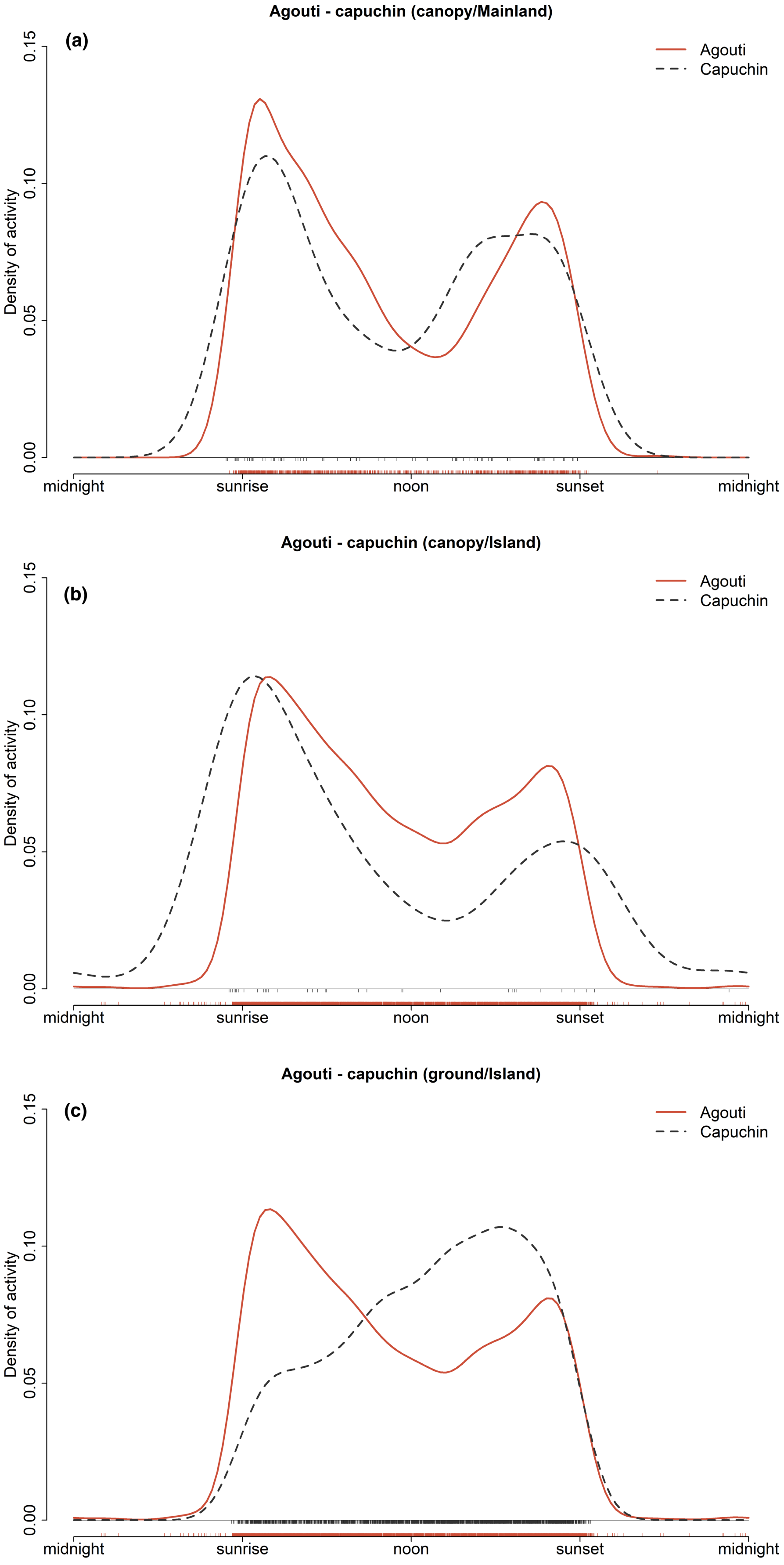


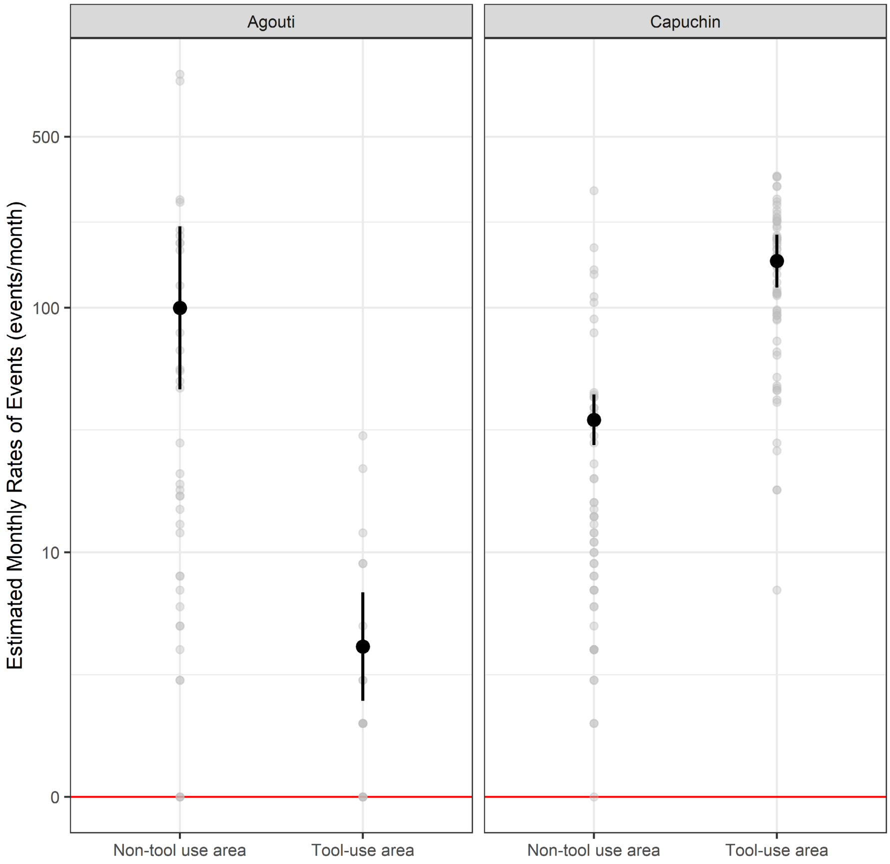
FIGURE 2 Daily activity patterns of capuchin (black) and agoutis (red): (a) Agouti and canopy-based capuchin activity at the control site. (b) Agouti and canopy-based capuchin activity at island sites. (c) Agouti and ground-based capuchin activity (non-tool-use area) at island sites. Observations of raw data are plotted along the x-axis.

TABLE 2 Pairwise comparisons of agouti and capuchin activity patterns, with estimated overlap coefficients and associated 84% confidence intervals.

Pairwise comparison	Overlap coefficient	84% confidence interval
Agouti—capuchin on the ground (Island sites)[a]	0.78	0.64–0.80
Agouti—capuchin in the canopy (Island sites)	0.73	0.64–0.81
Agouti—capuchin in the canopy (BCI)	0.89	0.83–0.94

[a] Excluding capuchin observations from the tool-use area.

FIGURE 3 Estimated monthly detection rates of agoutis and white-faced capuchins at the tool-use and non-tool-use areas of Coiba National Park. Agoutis displayed a 25-fold lower detection rate at the tool-use area, whereas capuchin detection rates were 4 times higher at the tool-use area. Dots represent estimated mean monthly detection rates and lines represent the estimated 84% confidence interval. Raw data is plotted as a jitter in gray. Detection rates are expressed per month (30 days) to facilitate comparisons.



high temporal overlap in activity between agoutis and a highly terrestrial population of capuchins, as well as high temporal overlap in activity between predominantly arboreal capuchins and agoutis on a system with predators. We found differences in capuchin and agouti space-use at tool-use and non-tool-use areas of CNP. Contrary to our prediction, temporal overlap between both species was similar regardless of the vertical strata in which the capuchins were detected. Agouti detection rates were 25-fold lower at the tool-use area, whereas capuchin detection rates were four times higher there. Both species had lower waiting times in the tool-use area.

Activity overlap between agoutis and capuchins was high across the three categories of capuchin activity. As predicted, the highest overlap levels were observed for the BCI population (Figure 2a; Table 2). Capuchins and agoutis have lived sympatrically in mainland Central America for approximately 1.9 Ma (Lynch Alfaro et al., 2012). Their temporal and dietary overlap implies direct competition. However, under normal conditions the species are unlikely to directly interact because they live in separate strata of the forest (spatial segregation along the vertical axis).

At island sites with no predators, where agoutis and capuchins share the ground stratum, temporal overlap between agoutis and capuchins was also high, regardless of whether the capuchins were engaged in canopy-based or ground-based activity. Nevertheless, peak activity was more similar between agoutis and canopy-based capuchin activity, both of which displayed their respective activity peaks in the morning hours. Dietary preferences could potentially explain this pattern of early morning peak activity. Flowering and fruiting plants often produce higher nectar in the morning hours, and both agouti and capuchins are known to eat several flowering and fruiting plant species (Timewell & Mac Nally, 2004; Table S1). In the absence of mammalian predators and most of the frugivores that typically inhabit forest landscapes on the mainland, capuchins and agoutis on the islands likely experience predator release and reduced competition. High rates of ground-based activity by capuchins on these islands results in lower temporal overlap between agoutis and capuchin canopy activity, when compared to the predominantly arboreal BCI population (Figure 2b). At the non-tool-use area, temporal overlap between agoutis and ground capuchin

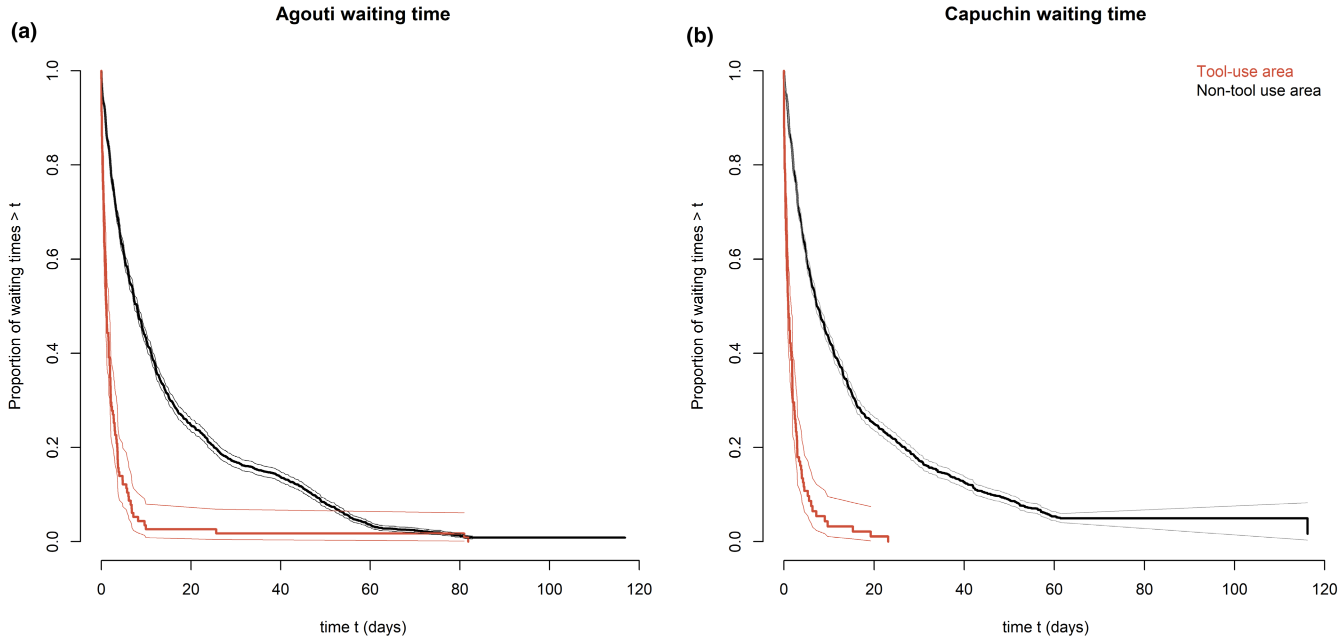


FIGURE 4 Empirical Kaplan–Meier survival curves of waiting times at the too-use and non-tool-use areas of Coiba National Park: (a) agouti waiting time after a passing capuchin, (b) capuchin waiting time after a passing agouti. Color denotes the area (tool-use vs. non-tool-use). Dotted lines represent the 95% confidence interval of the Kaplan–Meier estimator. Curves that are truncated before reaching a proportion of 0.00 denote censored data.

TABLE 3 Summary statistics (1st quartile, median, and 3rd quartile) for survival analyses of intervals between visits of agoutis and capuchins at the tool-use and non-tool-use areas of Coiba National Park. All waiting times are given in hours.

	Waiting time (h)					
	Tool-use area			Non-tool-use area		
	1st	Median	3rd	1st	Median	3rd
Agouti	10.12	28.0	68.30	57.52	173.3	412.29
Capuchin	7.83	22.2	57.41	50.70	127.2	314.50
Agouti (capuchin used tools)	222.84	932.2	1433.13	–	–	–
Agouti (capuchin did not use tools)	217.21	675.3	1365.63	–	–	–

activity was also high (Figure 2c), stemming from high rates of capuchin ground activity observed throughout the day. However, the timing of peak activity differed. Agouti activity peaked in the morning hours, just after sunrise, whereas capuchin ground activity peaked late in the afternoon before sunset. Different activity peaks would reduce encounter opportunities and thus direct interference competition. Nevertheless, our current data are limited to further our understanding about whether this difference in the timing of activity peaks is due to temporal partitioning or another factor. In the tool-use area capuchin activity was highly skewed towards the sunset period with hundreds of observations—even during the night, while agoutis exhibited the same bimodal peak as in the non-tool-use area (Figure S10). Sample sizes for each species at the tool-use area however differed markedly ($N = 10{,}212$ for capuchin, and $N = 115$ for agouti), and thus our inferences about temporal overlap between the species at this area must be interpreted with caution.

We had predicted higher agouti detection rates in the tool-use area due to the potential attraction to leftover food in the anvils and other foraging resources. Notwithstanding, agoutis exhibited far lower detection rates in the tool-use area, both at the anvils and in surrounding forest. A possible explanation for this could be that most of our sampling sites in the tool-use area were in the island's edges, whereas agoutis might be more common in the forest-interior (Duquette et al., 2017). Nevertheless, most sampled sites were within 1.5 km from both island's respective coasts. Studies on BCI have reported a daily path length of 850 m for Central American agoutis and home ranges of less than 2.5-ha (Aliaga-Rossel et al., 2008). Moreover, agoutis are commonly seen on the edge of both Coiba and Jicarón islands (C.M.M. personal observation), suggesting the agouti individuals detected in this study all have home ranges near the islands' edges. Further, sea almonds are abundant near the coastal area of Jicarón, and this is a resource that agoutis could exploit or be attracted to. Thus, the observed pattern of

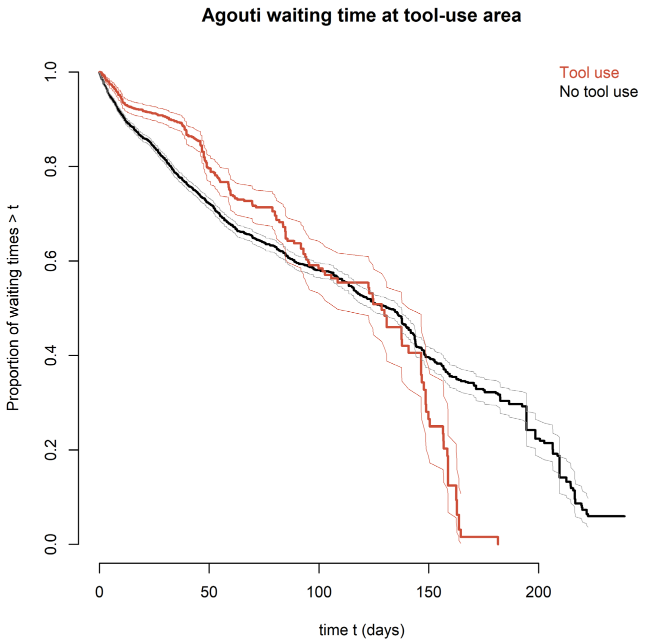


FIGURE 5 Kaplan–Meier survival curves of waiting times for agouti at the tool-use area, given previous capuchin engaged in tool use or not. Color denotes the site type (tool use observed vs. tool use not observed). Dotted lines represent the 95% confidence interval of the Kaplan–Meier estimator. Curves that are truncated before reaching a proportion of 0.00 denote censored data.

lower agouti detection rates in the tool-use area is not necessarily due to edge effects. Rather, it could be due to spatial avoidance to minimize encounters with capuchin troops. Mainland capuchin populations are known for being territorial and displacing other species from feeding sites (Rose et al., 2003). Of the 115 agouti detection events in the tool-use area, only 16 occurred at fixed anvils which is where capuchins exhibited the highest detection rates. This is also consistent with agoutis spatially avoiding capuchins on the ground.

Capuchins had higher detection rates in the tool-use area, likely stemming from our oversampling at fixed anvils, as well as retriggers of the same individual at the same site for extended periods of time. Sampling in the tool-use area was biased towards areas of foraging importance (i.e., anvils) whereas at the non-tool-use area, cameras were not necessarily deployed in areas with foraging resources. We did not measure food availability in the non-tool-use area, and it is likely that some of the cameras did not fall on resource-rich patches. Therefore, differences in capuchin detection rates between areas likely reflect sampling biases rather than ecological processes of abundance or habitat use. It is possible that tool-users and non-tool-user capuchin troops invest similar amounts of their respective activity budgets foraging. Our data is insufficient to address intergroup differences in time allocation at foraging sites, particularly when contrasting tool-use versus non-tool-use areas, which is an interesting line for future research.

Our waiting times results suggest agoutis do not make use of leftover food from capuchins at the tool-use area. Agouti waiting times were very long when capuchins engaged in tool use, with a median value equivalent to almost 40 days. Any leftover food at the anvils is not likely to last long, as other animals such as birds, rats (*Rattus* sp.) and hermit crabs, as well as other capuchins, may take advantage of it within hours. Thus, any consumption of capuchin leftover food by agoutis at fixed anvils is likely to be incidental. Further, some of the food resources that capuchins crack open at the fixed anvils are available to the agoutis regardless of monkeys' tool use. Almond and coconut seeds, for example, are consumed by agouti populations elsewhere (Lee et al., 2006). Incidental consumption of leftover capuchin food could happen at the non-tool-use area as well. Capuchins may break fruits such as coconuts by hitting them into the rocky ground, without using a stone tool to crack it open (Méndez-Carvajal & Valdés-Díaz, 2017).

Differences in agouti abundance could account for some of the variation in agouti detection rates and waiting times between the tool-use and non-tool-use areas. Agoutis are a species with high site fidelity, small home ranges centered around fruiting trees, and high turnover rates in camera trap studies (Aliaga-Rossel et al., 2008; Jansen & Forget, 2001; Kays et al., 2009). Therefore, even if agouti densities were lower in the tool-use area, resident individuals should still be attracted to and visit frequently foraging patches of sea almonds, which are dense in the tool-use area. Hence our long waiting times coupled with the low frequency of monthly visits in the tool-use area are unlikely to be reflecting abundance differences alone. Lack of attraction to resource-rich patches in the tool-use area could signal displacement of agoutis by capuchins.

Capuchin waiting times were shorter in the tool-use area, which is consistent with capuchins chasing other animals away. In island systems, populations have been suggested to be less exposed to interspecific competition than mainland populations (Diamond, 1978; Duhamel et al., 2020). The observed pattern of short capuchin waiting times could thus be explained by the frequency of visits and the interval between them. Shorter waiting times may arise from a higher visiting rate over a long period of time at the tool-use area. Our analysis of activity patterns and monthly detection rates discussed above suggest a high frequency of capuchin visits at the tool-use area throughout the day. Future behavioral research on these islands' capuchins could explore their degree of territoriality, to disentangle if the short capuchin waiting times found in this study are a product of species' territoriality, a matter of likelihood due to a high frequency of visits, or a combination of both.

4.1 | Concluding remarks and future directions

Niche expansions on islands with reduced predation and competition risk have been documented on several of the world's islands. On the islands of Coiba and Jicarón, white-faced capuchins have expanded their spatial niche to occupy the ground for large amounts of time and some groups habitually use stone tools. Our study sheds light on the potential interspecific interactions between ground-dwelling agoutis and capuchins, in scenarios with reduced guilds. We found that agoutis are detected at lower rates at a tool-use area heavily used by capuchins. We have also shown that the temporal distribution of activity of both species overlap greatly, regardless of whether the capuchins are in the canopy or on the ground.

Future research should address the role of species composition on the behavioral tendencies of individuals in an ecological community. A reduced guild of predators and competitors could select against costly anti-predator behavioral strategies (Blumstein & Daniel, 2005; Kavaliers, 1990). On the other hand, reduced resource availability could exacerbate competition among conspecifics (Cooper et al., 2015). Quantifying resource availability would allow us to evaluate how the degree of dietary overlap influences capuchin and agouti potential interactions. While we did not account for seasonal variation, our surveys periods included dry and rainy season, suggesting any potential seasonal variation in resources among study sites is unlikely to explain the observed patterns.

Island environments are hubs of behavioral innovation and adaptations. Novel behaviors in one species are likely to have consequences on the other species in the community. Given the role of species interactions as one of the drivers of a species' occurrence, understanding the factors driving these interactions have conservation implications. In an ever more fragmented world, mainland environments are becoming increasingly isolated, and this isolation may exacerbate species interactions (Parsons et al., 2019). Thus, understanding the key factors shaping these interactions will be crucial for management purposes.

AUTHOR CONTRIBUTIONS

Conceptualization: CMM, LFR, MCC; Data Curation: ZG, CMM, LFR, BJB; Formal Analysis: LFR, CMM; Funding Acquisition: MCC, BJB, CMM, ZG, PAJ, KML; Investigation: CMM, BJB, KML, MCC, ZG, PAJ; Methodology: CMM, LFR, MCC; Project Administration: BJB, CMM, MCC, ZG, PAJ; Resources: CMM, BJB, KML, MCC, PAJ; Supervision: CMM, MCC, BJB, PAJ; Validation: LFR, CMM; Visualization: LFR, CMM; Writing – original draft: LFR, CMM; Writing – review & editing: all authors.

ACKNOWLEDGMENTS

We thank the staff at the Smithsonian Tropical Research Institute for their support and assistance, and Lucia Torrez, Katrin Dieter, Mary Brooke McElreath, Yorick Liefting, Angie Ruiz, Christian Ziegler, Omar Lopez, Valerie McMillan, and the late Kevan Mantell and José Batista for logistic support. We further thank; Eliezer Vega, Chris Dillis, Pedro Luis Castillo, Zarluis Miguel Mijango, Rafael Bultron, Lilisbeth Rodriguez and Evelyn del Rosario for field assistance; Sylvia Garza and Evelyn del Rosario for help with annotation; Mark Grote for the statistical analysis; Alison Ashbury for writing suggestions, and the Panamanian Ministry of Environment MiAmbiente for permits. This research was supported by donors that made possible the Coiba Bioblitz, a Packard Foundation Fellowship (2016-65130), a National Science Foundation grant (NSF BCS 1514174), and an Alexander von Humboldt Professorship endowed by the Federal Ministry of Education and Research awarded to M.C.C.; a SENACYT (BIDP-2017-2018) and DAAD Scholarship awarded to C.M.M.M., an Smithsonian Tropical Research Institute Short-term Fellowship, a Coss Award for International Field Research through the University of California Davis, an L.S.B. Leakey Foundation grant, and Max Planck Institute funds awarded to B.J.B. It was also supported by the University of Konstanz Center for the Advanced Study of Collective Behavior Small Research Grant awarded to B.J.B and Z.G. BJB and ZG also received funding from the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy – EXC 2117 – 422037984. This research was authorized by the Panamanian Ministry of Environment MiAmbiente Panamá, with the following research permits: SE/APH-1-15, SC/A-23-17, SE/A-98-18, SE/A-6-2020. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

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

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.2fqz612xb.

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SUPPORTING INFORMATION

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

How to cite this article: Fox-Rosales, L. A., Monteza-Moreno, C. M., Barret, B. J., Goldsborough, Z., Jansen, P. A., McLean, K., & Crofoot, M. C. (2024). Niche expansion of capuchin monkeys to forest floor on guild-reduced islands increases interspecific spatio-temporal overlap. *Biotropica*, *56*, e13315. https://doi.org/10.1111/btp.13315