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Increased terrestriality in a Neotropical primate living on islands with reduced predation risk

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ABSTRACT

An arboreal lifestyle is thought to be central to primate origins, and most extant primate species still live in the trees. Nonetheless, terrestrial locomotion is a widespread adaptation that has arisen repeatedly within the primate lineage. The absence of terrestriality among the New World monkeys (Platyrrhini) is thus notable and raises questions about the ecological pressures that constrain the expansion of platyrrhines into terrestrial niches. Here, we report the results of a natural experiment, comparing patterns of terrestrial behavior in white-faced capuchin monkeys (*Cebus capucinus imitator*) living on two islands off the Pacific coast of Panama that lack mammalian predators (island sites) with the behavior of capuchins at three sites in central Panama with more intact predator communities (mainland sites). Surveys with camera traps revealed increased terrestriality in island vs. mainland sites. Capuchin detection rates were higher, the range of party sizes observed was larger, and individuals engaged in a wider range of terrestrial behaviors on the islands lacking mammalian predators. Furthermore, females carrying infants were frequently photographed on the ground at the island sites, but never at the mainland sites. These findings support the long-standing hypothesis that predators constrain the exploitation of terrestrial niches by primates. These results are also consistent with the hypothesis that arboreal locomotion imposes costs that primates will avoid by walking on the ground when predation risk is low.

1. Introduction

Arboreality is the primitive condition for primates (Bloch and Boyer, 2002; Szalay, 2007; Kirk et al., 2008; Boyer et al., 2017). Primates are defined by a suite of traits, including adaptations for grasping and leaping, improved vision, and dental features associated with herbivory (reviewed in Silcox et al., 2015), all of which are hypothesized to have evolved in response to the challenges posed by life in the trees (Cartmill, 1974; Szalay and Dagosto, 1980; Sussman, 1991; Orkin and Pontzer, 2011). However, over the course of their evolutionary history, primates have repeatedly expanded out of the trees and into terrestrial niches. It is not known how many times terrestrial adaptations have been independently acquired (Fleagle and Lieberman, 2015), but species that spend a significant portion of each day traveling and feeding on the ground are found across the primate clade, and ground dwelling is a particularly pervasive (and apparently successful) strategy among the Old World monkeys, apes, and humans (McCrossin et al., 1998). In contrast, adaptations for life on the ground are notably absent among the New World monkeys; despite being a large and otherwise highly diverse radiation, no platyrrhine species has adopted a predominantly terrestrial lifestyle (Fleagle, 2013).

What are the ecological pressures that promote, and those that constrain, primates' use of terrestrial niches? This question is generally important for understanding patterns of primate adaptation, but it is of particular interest because of the central role that a transition to ground dwelling played in hominin evolutionary history (Potts, 1998; Richmond et al., 2001; Kingdon, 2003; Patel

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et al., 2009). In both extant and fossil primates, adaptations for terrestrial locomotion are associated with more open, arid habitats, leading to the suggestion that terrestriality in primates emerged primarily as a result of climate-induced loss of canopy cover (Brain, 1981; Potts, 1998). However, primates that spend a significant proportion of their time on the ground also tend to be larger and to live in larger groups than arboreal primates, and generally rely more heavily on the exploitation of terrestrial food sources.

Disagreement exists over which of these changes are causes of the shift in substrate use and which are consequences. For example, based on the morphology and paleoenvironmental context of two early crown catarrhine genera showing clear evidence of terrestrial adaptations—*Victoriapithecus* (Von Koenigswald, 1969; Blue et al., 2006) and *Kenyapithecus* (Le Gros Clark and Leakey, 1951; McCrossin and Benefit, 1997)—McCrossin et al. (1998) argued that the colonization of dry savanna habitats was not responsible for the shift of either cercopithecine monkeys or apes to ground living. Instead, they argued that evidence from the fossil record is consistent with terrestriality originating in woodland habitats, driven primarily by a dietary shift to sclerocarp foraging. Similarly, because large body size and large party size are thought to provide important antipredator benefits (Hamilton, 1971; Pulliam, 1973; Turner and Pitcher, 1986; Cowlishaw, 1994; Caro, 2005; Crofoot, 2012), it is generally argued that these traits evolved in response to the increase in predation pressure that accompanied a shift to ground dwelling. However, it is also possible that changes in body size and sociality evolved in response to other ecological pressures, and were subsequently co-opted for terrestriality (Patel et al., 2009).

A long-standing and pervasive perception in this discussion is that terrestrial primates are more vulnerable to predators than arboreal primates (Dunbar, 1988; Purvis et al., 2003; van Schaik and Deaner, 2003; Shattuck and Williams, 2010). However, empirical support for this assertion is weak and equivocal (Cheney and Wrangham, 1987; Isbell, 1994; Hart, 2000). In fact, the methods traditionally used to study wild primates make it impossible to collect the data needed to address this question directly: human observers likely dissuade many potential predators, but have a particularly large impact on terrestrial predators such as felids that are cryptic and shy (Isbell and Young, 1993).

One way to avoid such biases is to take advantage of new tracking technologies to remove human observers from the equation. In fact, simultaneous Global Positioning System (GPS) tracking of leopards and two primate prey species—olive baboons (*Papio anubis*) and vervet monkeys (*Chlorocebus pygerythrus*)—recently revealed differences in the timing and location, but not the magnitude of predation pressure. Vervets, which are lighter and live in smaller groups, were hunted on the ground, during the day, whereas baboons, which are heavier and live in larger social groups, were most vulnerable to leopard predation at night, in their sleeping trees (Isbell et al., 2018). These results paint a much more nuanced picture of the relationship between felid predators and their primate prey and suggest that connections between predation risk and body size, party size, and other traits providing antipredator benefits are unlikely to be straightforward.

An alternative way to investigate how predators shape primate behavior is through natural experiments, by comparing systems with and without predators. van Schaik and van Noordwijk (1985), for example, used this approach to link a release from felid predation to changes in the social structure in the crab-eating macaque (*Macaca fascicularis*) in Southeast Asia. Macaques on the island of Simeulue, where no cats are found, lived in smaller groups and had smaller home ranges than their counterparts living on Sumatra, where a variety of felids are found.

We took advantage of a similar natural experiment in the New World to test the hypothesis that terrestrial predators constrain primates' exploitation of terrestrial niches. We used camera traps to compare terrestrial behavior in white-faced capuchin monkeys (*Cebus capucinus imitator*) between two islands off the Pacific coast of Panama that lack mammalian predators (hereafter, island sites) and three sites in central Panama with more intact predator communities (hereafter, mainland sites). We compared the frequency and duration of terrestrial activity, as well as the number of capuchins observed on the ground (hereafter, party size) during each event. Specifically, we predict that capuchins at the island sites that have been released from terrestrial predation will (1) visit the ground more often and (2) spend more time on the ground per visit. Furthermore, we predict that more vulnerable age/sex classes will descend to the ground more often, and thus, (3) party size will be larger. Finally, we predict that capuchins will (4) engage in more terrestrial activity during risky dusk and dawn hours (when crepuscular predators such as felids are most active) and thus that their activity will be more uniformly distributed throughout the day.

2. Methods

2.1. Study sites

The five study sites are located in the Republic of Panama (Fig. 1). The Pacific islands of Coiba (50,314 ha) and Jicaron (2002 ha), hereafter referred to as island sites, have previously been reported to lack mammalian predators. They are the biggest islands in Coiba National Park, an archipelago located off the southwest coast of Panama. The annual mean temperature is 25.9 °C, and the archipelago receives up to 3500 mm yr^{-1} of rainfall, which falls with marked seasonality. Less than 60 mm of rain falls during the 4 months of dry season that runs from mid-December to mid-April. The islands are covered by tropical rainforest (Cardiel et al., 1997; Glynn et al., 1983). Coiba National Park is considered a biodiversity hotspot due to its high levels of endemism. Among others, the park has isolated populations of howler monkeys, agouti, and white-tailed deer (Méndez-Carvajal, 2012).

The three study sites in central Panama have more intact predator communities, although like Coiba and Jicaron, they lack the largest avian predator, the harpy eagle (*Harpia harpyja*). Barro Colorado Island (BCI; 1540 ha), Gigante Peninsula (GP; 1570 ha), and Soberanía National Park (SNP; 22,000 ha) are all located in the Panama Canal Area and were part of the same nearly contiguous block of forest until 1913 when the Chagres River was dammed to create Gatun Lake. These sites, hereafter referred to as mainland sites, are in close proximity (<10 km from one another), but movement of animals among them is inhibited by a water barrier. With an average temperature of 27 °C, these sites receive, on average, 2631 mm of rainfall each year and are characterized by lowland tropical moist forests (Holdridge, 1967; Windsor, 1990; Leigh, 1999). Seasonality is marked with a dry season that lasts from December through April. These sites form an important component of the biological corridor that stretches across central Panama, connecting North and South America (Condit et al., 2001; Meyer et al., 2015).

2.2. Study species

The white-faced capuchin monkey, *Cebus capucinus imitator*, is a highly encephalized New World primate that lives in multimale-multifemale social groups characterized by female philopatry and male dispersal (Mitchell, 1989; Perry, 1997). This species is notable for the complexity of its social behavior, culturally transmitted

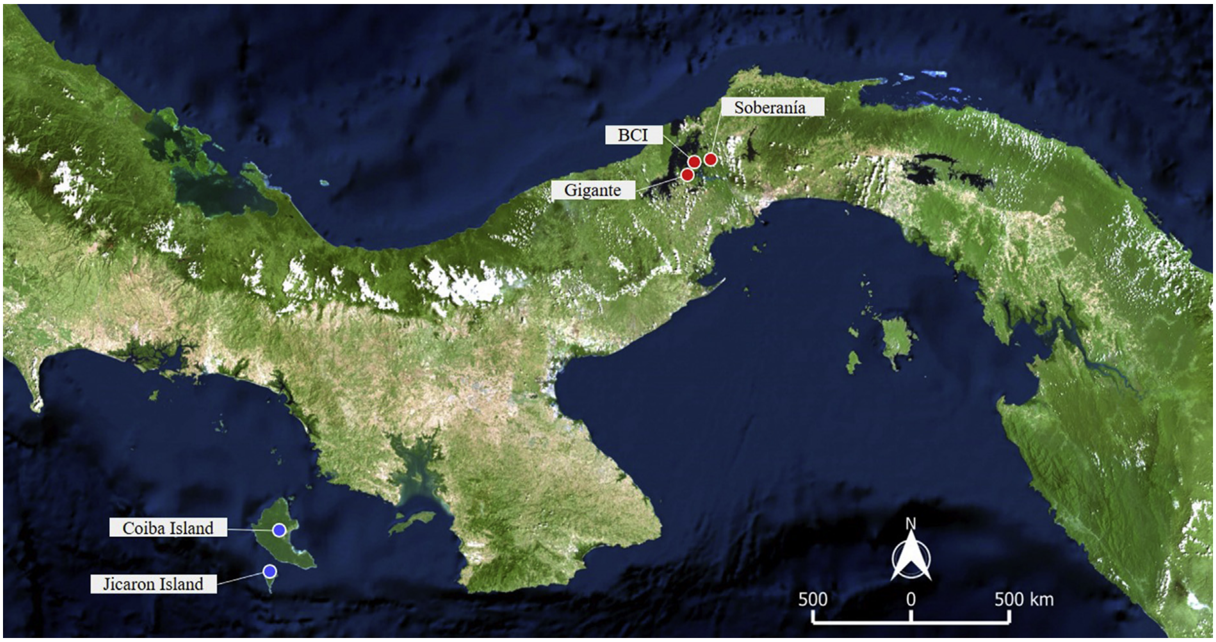

Figure 1. Map of the Republic of Panama, showing the location mainland sites with predators (red) and the two islands without predators (blue). Map was produced in R (R Core Team, 2017). Abbreviations: BCI = Barro Colorado Island. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

traditions, and social learning (Perry et al., 2003; Barrett et al., 2017). Capuchins are medium sized (2.5–3.6 kg), primarily arboreal, diurnal, and vulnerable to a variety of potential predators throughout their distribution range (Rose et al., 2003), including jaguars (*Panthera onca*), pumas (*Puma concolor*), jaguarundis (*Herpailurus yagouaroundi*), tayras (*Eira barbara*), coyotes (*Canis latrans*), ocelots (*Leopardus pardalis*), and margays (*Leopardus weidii*). However, New World primates, including capuchins, have only coexisted with a predator guild dominated by felids since approximately 3–7 Ma. Before the Great American Biotic Interchange, their terrestrial predators would have included mesocarnivores and hypercarnivores, including marsupial relatives (Sparassodonta), terror birds (Phorusrhacidae), and giant snakes (Madtsoiidae; Prevosti and Forasiepi, 2018).

The frequency of predation events by predators on capuchins is unknown. Although direct observations of predation do occur, they are rare. For example, Tórrez et al. (2012) reported a lethal attack by a jaguar on a capuchin on BCI. However, capuchins have been confirmed to be part of the diet of jaguars, pumas, and ocelots via analysis of fecal contents (Chinchilla, 1997; Moreno and Giacalone, 2006). The absence of all these mammalian predators in Coiba National Park creates an opportunity to investigate if capuchins use the terrestrial niche more extensively when predation risk is reduced.

2.3. *Camera trap surveys*

From 2010 to 2016, we conducted surveys at each study site using unbaited camera traps. Surveys were approved by the Ministry of Environment of Panama (MiAmbiente) under the scientific permits SE/APH-1-15 for Coiba National Park and SE/A-3-12 and the corresponding renewals and addenda for SNP. Surveys at BCI and GP were approved by the Smithsonian Tropical Research Institute, which serves as the administrator for Barro Colorado Nature Monument. Surveys took place at different times of the year. BCI was monitored over an entire annual cycle. All other sites were surveyed in the dry season and, in the case of Coiba and Jicaron, in the early months of the wet season due to limitations of site accessibility (Table 1). A systematic grid system was used at all sites, maintaining a consistent distance between camera sites. Unbaited camera traps (Reconyx PC900 Hyperfire, Reconyx, Inc., WI, USA) were mounted on tree trunks at knee height, facing a randomly selected direction, and set to take 10 images on each trigger with no delay between triggers, yielding continuous photosequences of multiples of ten photos. To distinguish the absence of wildlife at a given camera site from camera malfunction, we programmed each camera to automatically take a single image every 12 h for the duration of its deployment. The maximum detection distance for each camera deployment was measured using the walk test mode of the cameras; we used a tape to measure the largest distance at which the camera walk test light could be activated by hand waving. The number of stations (locations at which a camera was deployed) per site ranged from 10 to 30 (Table 1). The servicing or replacement of camera equipment at a given station defines the start of a new deployment. Each station on Jicaron (11 stations) and Coiba (15 stations) had a single long deployment. In contrast, stations on BCI, GP, and SNP had multiple consecutive deployments, with 210, 60, and 174 deployments, respectively. These numbers varied due to differences among sites in the frequency of camera failure and/or theft. In these mainland sites, a typical deployment length was 30 days per station, and successive deployments were separated by no more than 10 min of servicing time. Sampling effort is the sum of all deployment durations, ranging from 1132 to 12,422 camera days per site (Table 1). The camera traps in the surveys of BCI, GP, and SNP were run as part of the Tropical Ecology Assessment and Monitoring Network (TEAM Network, 2011; Jansen et al., 2014). All TEAM data are publicly available at http://wildlifeinsights.org/team-network.

We processed and annotated the photosequences from the archipelago islands and BCI with a custom-made image processing and archiving system called Agouti (Kays et al., 2011). To mitigate issues of temporal autocorrelation in the data, this software groups the photos that result from a camera trigger into a single event. If there are continuous triggers that generate a sequence of more than

Table 1
Characteristics of the five study sites, with specifications of camera-trapping surveys conducted in these sites.

Name	Size (ha)	Sampling period	No. of stations	No. of deployments per station	Interstation distance (km)	Total effort (days)
Jicaron	2000	February–June 2015	11	1	1	1132
Coiba	50,300	February–June 2015	15	1	1	1220
BCI	1540	October 2015–October 2016	30	6–8	0.7	12,422
GP	1570	December–January 2010–2015	10	6	1.4	1949
SNP	22,000	January–March 2010–2015	29	6	1.4	5720

Abbreviations: BCI = Barro Colorado Island; GP = Gigante Peninsula; SNP = Soberanía National Park.

10 photos, the software combines the photos from all of these triggers into a single sequence. The software will only assign a photo to the next event if the time between subsequent photos is >2 min. Data from GP and SNP were processed and annotated with the program DeskTEAM (Baru et al., 2012). We then used spreadsheet operations to format the resulting sequences consistently with the Agouti software output (Monteza-Moreno et al., 2020). Animal identifications were based on Reid (2009). For both capuchins and predators, we calculated detection rates, a measure of relative abundance, as the number of detections per 30 trap days per unit detection distance ($\text{mo}^{-1}\ \text{m}^{-1}$). For each visit of capuchins to the ground, we recorded the time, the party size, and the duration.

2.4. Data analysis

The data were from an observational study rather than from a controlled experiment and were collected at a comparatively small number of spatially clustered sites. Therefore, we adopted an analytical approach that emphasized graphical display of the observations and model-based estimation. We propose that site-level effects are of intrinsic interest and are worthwhile targets of inference because they capture the local environment of capuchins and their predators. Site effects, adjusted for camera-specific variation and sampling effort when appropriate, were thus the focus of our models. These effects can be interpreted subsequently in light of the presence or absence of terrestrial predators across our five study sites. We also took a more formal approach, averaging effects across sites within the two conditions (presence or absence of terrestrial predators) and testing for differences at this higher level of organization.

The data set had a hierarchical structure, consisting of camera trap deployments (the smallest sampling units) nested within unique sampling stations, which were in turn nested within each study site (Table 1). We therefore used hierarchical (mixed) models to study site-level properties while accounting for lower-level nested effects. Random intercepts for stations (cameras) were incorporated to capture camera-to-camera heterogeneity, to accommodate the possibility that repeated deployments within stations in the continental sites are not independent, and to allow unique camera-specific baselines to contribute to model predictions. We fit models for detection rates, party size, and duration of terrestrial events in this hierarchical context (Monteza-Moreno et al., 2020).

The model for terrestrial detection rates was based on the number of observations of capuchins on the ground (e.g., events) per deployment. Events that were separated by more than 2 min were considered independent by Agouti software. The median interevent time in our data was 47 min. Six terrestrial events in the sample were separated by less than 3 min, and 28 events were separated by less than 5 min. Events that are temporally clustered would produce event counts that are overdispersed with respect to the Poisson distribution. We therefore modeled detection rates using the negative binomial distribution (Lindén and Mäntyniemi, 2011).

We fitted a negative binomial mixed model using a likelihood method implemented in the R package glmmADMB (generalized linear mixed model AD Model Builder; Skaug et al., 2014), to compare detection rates across sites while accommodating the hierarchical structure described previously. Camera-specific deployment duration and detection distance were treated as offsets in the model; predictions were generated for the mean number of events per month, per meter detection distance.

We estimated the timing of terrestrial activity for populations living on the two islands and the three mainland sites by extracting the time stamps from the image metadata (Monteza-Moreno et al., 2020). Then, we compared these patterns with those of the activity patterns of ocelots (*L. pardalis*), an important predator of capuchin monkeys at the mainland study sites (Moreno and Giacalone, 2006; Moreno et al., 2006). We used the Ridout and Linkie (2009) method to estimate a coefficient of overlap (Δ, ranging from 0 to 1), comparing the area underlying the density curves between ocelots and the two populations of capuchins, with 95% confidence intervals obtained from a smoothed bootstrap with 10,000 resamples, as implemented in the overlap package in R (Ridout and Linkie, 2009).

The outcome variable party size is the maximum number of individuals captured in any single photo sequence (i.e., for each detection event separately). Unlike the likelihood-based model for terrestrial detection rates, a Bayesian model was necessary for party size, to accommodate the small numbers of observations at GP and SNP. We used a zero-truncated Poisson mixed model, fitted by a Bayesian method implemented in the R package MCMCglmm (Markov Chain Monte Carlo glmm; Hadfield, 2010), to compare party sizes across sites.

Informative Gaussian priors for the site effects regularized the party size estimates (Gelman et al., 2008) for GP and SNP, preventing numerically unstable standard errors that could result from a likelihood method. Camera-specific detection distance was again treated as an offset in the model; predictions were generated for the mean party size per meter detection distance. We used Gaussian priors with mean zero and standard deviation five for site effects (on the log-link scale), and a Gaussian prior with mean one and standard deviation 10^{-4} for ln (detection distance). We used inverse-gamma priors with shape and scale both equal to 10^{-3} for camera site and residual variances. We generated 55,000 MCMC iterations, discarding the initial 5000 for a burn-in and thinning at a rate of 50 iterations, to obtain 1000 posterior parameter samples for inference. We examined trace plots of model parameters to check that mixing was adequate.

Finally, the outcome variable duration was the exact duration in seconds of each photo sequence containing at least one monkey on the ground. Because all visit durations were greater than zero, a natural log transformation was applied to stabilize variances; thus, the variable to be analyzed was ln (duration [in s]). We fitted a Gaussian mixed model to ln (duration) using MCMCglmm

(Hadfield, 2010), with informative priors to accommodate the small numbers of observations at GP and SNP. Three additional covariates were included in the model for ln (duration): party size, behavior (coded as traveling or nontraveling), and the interaction between these. We classified an event as 'traveling' if one or more individuals walked past the camera, without performing any other activity while within view of the camera (foraging, scanning the environment, playing, and so on). Individuals that trigger a camera while traveling are, by definition, moving across the camera's field of view and thus are expected to produce shorter duration events. By including behavior as a covariate in our model, we were able to test for differences in the duration of terrestrial activity while accounting for the fact that the types of activities that capuchins engage in on the ground may vary systematically across sites. Similarly, we controlled for party size because a larger number of individuals is expected to increase our measure of visit duration. Camera-specific detection distance was again treated as an offset. The prior specification and the MCMC settings were the same as for the party size model.

3. Results

Confirming previous reports, our camera trap surveys yielded no evidence of mammalian predators on the islands of Jicaron or Coiba. In contrast, we recorded four species of carnivores at our mainland study sites (BCI, GP, and SNP): tayras, ocelots, jaguarundis, and coyotes. All predators were captured at higher rates in SNP than in BCI and GP. Coyotes, although detected in SNP and Gigante, were not found on BCI. In the sites where predators were detected, ocelots had the highest detection rates, followed by tayras and jaguarundis (Table 2).

3.1. Frequency of terrestrial activity

The empirical average terrestrial detection rate for capuchins ranged 200-fold, from as low as 0.01 $\text{mo}^{-1}\ \text{m}^{-1}$ in SNP—the site with the highest terrestrial predator detection rate—to as high as 1.98 $\text{mo}^{-1}\ \text{m}^{-1}$ on Jicaron Island. A hierarchical model for the number of terrestrial detection events per deployment allowed us to estimate site-specific rates, while accommodating the nesting of cameras within sites. The degree to which capuchins used the ground varied substantially across our study sites and was negatively associated with the presence of key predators. On Jicaron and Coiba, all camera deployments had more than one terrestrial detection event (Supplementary Online Material [SOM] Table S1), whereas at BCI, GP, and SNP, most deployments had zero terrestrial detection events (Fig. 3A).

The extent to which confidence intervals overlapped with each other can be used to make informal inferences about differences across sites: terrestrial detection rates were higher at the island sites than at the three mainland study sites. Summary statistics for the detection rate model are given in Table 3.

Table 2
Detection rates of mammalian predators at the five study sites ($\text{mo}^{-1}\ \text{m}^{-1}$).

Species	Common name	Mainland sites			Island sites	
		BCI	GP	SNP	Jicaron	Coiba
Leopardus pardalis	Ocelots	0.206	0.112	0.320	0	0
Eira barbara	Tayras	0.050	0.065	0.224	0	0
Puma yagouaroundi	Jaguarundis	0.005	0.006	0.048	0	0
Canis latrans	Coyotes	0	0.025	0.007	0	0

Abbreviations: BCI = Barro Colorado Island; GP = Gigante Peninsula; SNP = Soberanía National Park.

We investigated differences in terrestrial detection rates between island and mainland sites more formally by testing a contrast between site effects. Under the null hypothesis that detection rates are the same in island and mainland sites, the average rate among Jicaron and Coiba would equal the average rate among BCI, GP, and SNP, and the difference in averages would equal zero. The site effects shown in Table 3 are estimates of detection rates on the log scale; their averages are $(1.8 + 0.1)/2 = 0.95$ (Jicaron and Coiba) and $(-3.9 - 4.9 - 5.6)/3 = -4.8$ (BCI, GP, and SNP), and the difference in averages—the contrast to be tested—is 5.75. The standard error for the contrast, calculated using a variance/covariance matrix produced by glmmADMB (Skaug et al., 2014), is 0.4, and subsequently, a 95% confidence interval for the contrast is (5.0, 6.6). This interval does not contain the null value zero, so the hypothesis that detection rates are the same in island and mainland sites can be rejected.

3.2. Timing of terrestrial activity

At the mainland sites, capuchins were observed on the ground as early as 7:17 AM and as late as 5:55 PM, but terrestrial activity of capuchins was highly concentrated in the middle of the day ($n = 75$ camera trap observations; Fig. 2A). In contrast, capuchins at the island study sites were active on the ground more evenly throughout the day, including observations as early as 6:00 AM and as late as 6:35 PM ($n = 492$ camera trap observation; Fig. 2B). Ocelot activity was typically much higher during the night than during the day ($n = 284$ camera trap observations; Fig. 2). The estimated overlap index between capuchins and the ocelots was thus higher at the island sites ($\Delta = 0.290 \pm 0.037$) than at the mainland sites ($\Delta = 0.213 \pm 0.042$).

3.3. Terrestrial party size

The empirical average party size was highest on Coiba ($\bar{X} = 2.5$), followed by SNP ($\bar{X} = 1.9$), Jicaron ($\bar{X} = 1.8$), BCI ($\bar{X} = 1.4$), and finally GP ($\bar{X} = 1.0$). However, the range of observed party sizes was higher on the islands of Coiba (1–9) and Jicaron (1–8), where many juveniles and adults carrying infants on the ground were also photographed (Figs. 3B and 4). In contrast, at the mainland sites, the range of observed party sizes was small (BCI: 1–4 individuals; SNP: 1–3 individuals; GP: 1–2 individuals), juveniles were rarely observed on the ground, and infants were never observed on the ground.

The model estimates (Fig. 3B) echo the empirical record of party size, with means slightly higher for Coiba and Jicaron than for GP and BCI. The credibility interval for SNP (having only 5 detection events) is wide compared with the other sites, and so, this site effect should be interpreted with caution. Across all sites, most observations consisted of one or two individuals. Thus, there is little evidence that mean party size varies with the presence or absence of predators.

For terrestrial party size, the contrast between island and mainland sites, analogous to the contrast for terrestrial detection rates, is 1.4(SE = 0.9), calculated from the posterior samples produced by MCMCglmm (Hadfield, 2010). A 95% credibility interval for the contrast is then (−0.4, 3.2). Here, the null value zero is contained in the interval, so the hypothesis that average terrestrial party sizes are the same in island and mainland sites is not rejected.

3.4. Duration of terrestrial events

The observation of several very long terrestrial events meant that visit duration has a right-skewed distribution; thus, median visit duration was more suitable as an empirical metric. SNP had

Table 3
Model summary statistics for differences between five Panamanian populations of white-faced capuchins in the frequency, party size, and duration of terrestrial recordings by camera traps.

	Rate of events[a]	Party size[b]	ln (duration)[c]
Estimates by site			
Jicaron	1.8 (0.9, 2.7)	−1.8 (−2.0, −1.6)	2.6 (2.3, 3.0)
Coiba	0.1 (−0.7, 0.9)	−1.6 (−1.9, −1.3)	1.9 (1.5, 2.4)
BCI	−3.9 (−4.4, −3.4)	−2.5 (−3.0, −1.9)	2.6 (2.1, 3.0)
GP	−4.9 (−6.3, −3.6)	−5.5 (−10.9, −1.4)	1.4 (0.0, 3.0)
SNP	−5.6 (−6.6, −4.6)	−1.3 (−2.5, −0.3)	3.3 (1.9, 4.4)
Covariates			
Offset	Detection distance Deployment duration	Detection distance	Detection distance
Party size	–	–	0.4 (0.3, 0.5)
Traveling	–	–	−1.1 (−1.4, −0.8)
Party size * traveling	–	–	0.2 (0.1, 0.4)
Standard Devitation (camera site)	0.8	0.2	0.4
Sample size	510 deployments	542 terrestrial events	542 terrestrial events

Abbreviations: BCI = Barro Colorado Island; GP = Gigante Peninsula; SNP = Soberanía National Park.
[a] Negative binomial mixed model. Estimates and 95% confidence intervals are on the log-link scale.
[b] Zero-truncated Poisson mixed model. Estimates and 95% credibility intervals are on the log-link scale for the pretruncated variable.
[c] Gaussian mixed model. Estimates and 95% credibility intervals are on the identity-link scale.

the largest median visit duration (51 s), followed by Jicaron (16 s), Coiba (15 s), BCI (11 s), and GP (1 s). However, the longest visit durations were detected on Jicaron (870 s) and Coiba (472 s). Much of the difference in duration was apparently due to the fact that most terrestrial detections at the mainland sites involved traveling capuchins that moved quickly across the field of view of our cameras, yielding shorter duration than other activities. The model estimates suggested that differences in the behavior of terrestrial capuchins were the primary determinant of differences in visit durations between sites. For a given behavior (traveling vs. nontraveling), the visit duration was similar across the sites (Fig. 3C). However, capuchins on the islands of Coiba and Jicaron engaged in nontravel behaviors more often than capuchins on the mainland.

For duration of terrestrial events, the contrast between island and mainland sites, adjusted for party size and behavior, is −0.2, with an SE of 0.4. A 95% credibility interval for the contrast is then (−1.0, 0.6). The null value zero is contained in the interval, so the hypothesis that average durations of terrestrial events are the same in island and mainland sites—party size and behavior held equal—is not rejected.

We examined the magnitude of differences in site-to-site effects for each model, in relation to camera-level standard deviations (Table 3), to assess the importance of camera-to-camera heterogeneity. We found that for the detection rate and party size models, the camera-level variation did not appear to be important. For duration, in contrast, camera-level variation was relatively important.

4. Discussion and conclusions

The results of this study are consistent with the hypothesis that mammalian predators constrain terrestriality in Neotropical primates. Taking advantage of a natural experiment, we found that white-faced capuchin monkeys living on two Pacific islands off the coast of Panama that lack mammalian predators exploit terrestrial niches more extensively than capuchins living in three mainland sites with more intact predator communities. Camera trapping revealed differences in the frequency and timing of terrestrial activity in these capuchin populations, as well as differences in the number and age/sex class composition of individuals observed on the ground.

Despite extensive sampling effort (>1000 camera trap nights), we recorded no terrestrial predators on the islands of Coiba and Jicaron. Generally, 450 camera-trapping nights have been found to be sufficient to photocapture felid species when they are present in a Neotropical forest (Trolle and Kéry, 2003; Silver et al., 2004). These results are thus consistent with previous reports from CNP (Ibáñez et al., 1997) and confirm that mammalian predators are, indeed, absent. In contrast, camera traps at our mainland study sites captured tayras, jaguarundis, and ocelots, with ocelots having the highest detection rates at all sites. We also recorded observations of coyotes in GP and SNP. Coyotes are a relatively new addition to the guild of terrestrial predators in this area, having only recently expanded their range into eastern Panama (Méndez-Carvajal and Moreno, 2014).

Although it is not possible to quantify how much the absence of mammalian predators reduces predation risk for capuchins living at our island vs. mainland sites, the impact is likely substantial. Few studies of wild primates are able to track sources of mortality with any certainty, and predation events are rarely directly observed (but see Tórrez et al., 2012). Although healthy animals that are not of dispersal age who disappear from a study population are generally assumed to have fallen prey to a predator, it is usually impossible to confirm this suspicion. Therefore, it is studies of predators themselves that provide the best insight into the risk various taxa pose. For instance, ocelots are well-documented predators of a wide range of primate species, including capuchins (Bianchi and Mendes, 2007; Abreu et al., 2008; Bianchi et al., 2010), and a dietary analysis at our study site on BCI found capuchins remains in 7% of ocelot scats, representing 5% of the prey items consumed (Moreno et al., 2006). Furthermore, ocelots are found at extremely high population densities in tropical forests (Di Bitetti et al., 2008), magnifying their impact. While comparable data are unfortunately not available for tayras, jaguarundis, or coyotes, it is reasonable to conclude that together, these carnivores impose significant predation pressure on the capuchins at our mainland study sites.

The fact that mammalian predators are not found on Coiba and Jicaron does not mean that terrestrial activity is risk free for capuchins on these islands. While camera traps are poorly suited for detecting the presence of snakes, *Boa* cf. *constrictor* and *Bothrops asper* are known to inhabit the archipelago. It is unlikely that *B. asper* actively hunt capuchins: they are too small to consume a

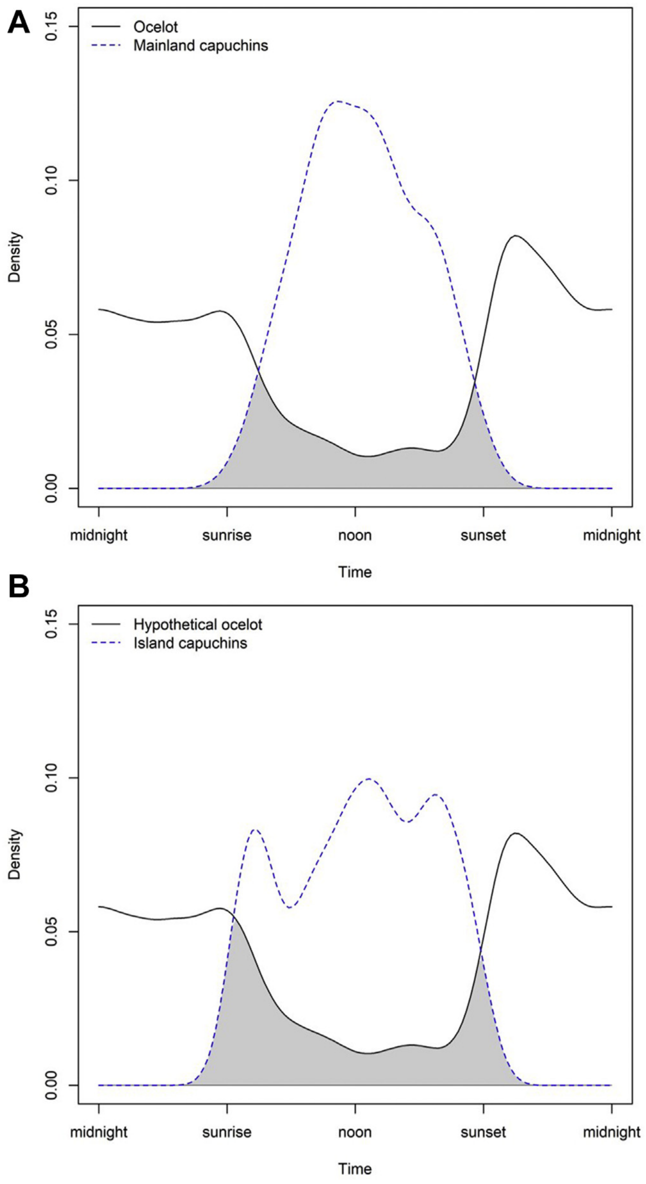

Figure 2. Terrestrial activity patterns for capuchins in mainland sites (A) and island sites (B), compared with the characteristic activity pattern of ocelots, a potential terrestrial predator.

capuchin whole, and their nocturnal sit-and-wait hunting strategy creates few opportunities for encounters (Wasko and Sasa, 2009). Nonetheless, primates have died from encounters with both of these snake species (Chapman, 1986; Corrêa and Coutinho, 1997; Burney, 2002; Ferrari et al., 2004; Cisneros-Heredia et al., 2005; Ferrari and Beltrao-Mendes, 2011; Quintino and Bicca-Marques, 2013), and both prompt strong antipredator responses in capuchins including alarm calling (Digweed and Fedigan, 2005; Fitchel et al., 2005), mobbing (Crofoot, 2012; Meno et al., 2013), and counter attacks (Boinski, 1988; Perry et al., 2003). In fact, Isbell (2006) has argued that a poor ability to visually detect snakes may explain the lack of terrestriality in New World monkeys. Our results seem to challenge this hypothesis as capuchins are highly terrestrial on the islands of Coiba and Jicaron despite the presence of both venomous and constricting snakes.

Differences in capuchin population density, rather than their degree of terrestriality, could account for some of the variation in

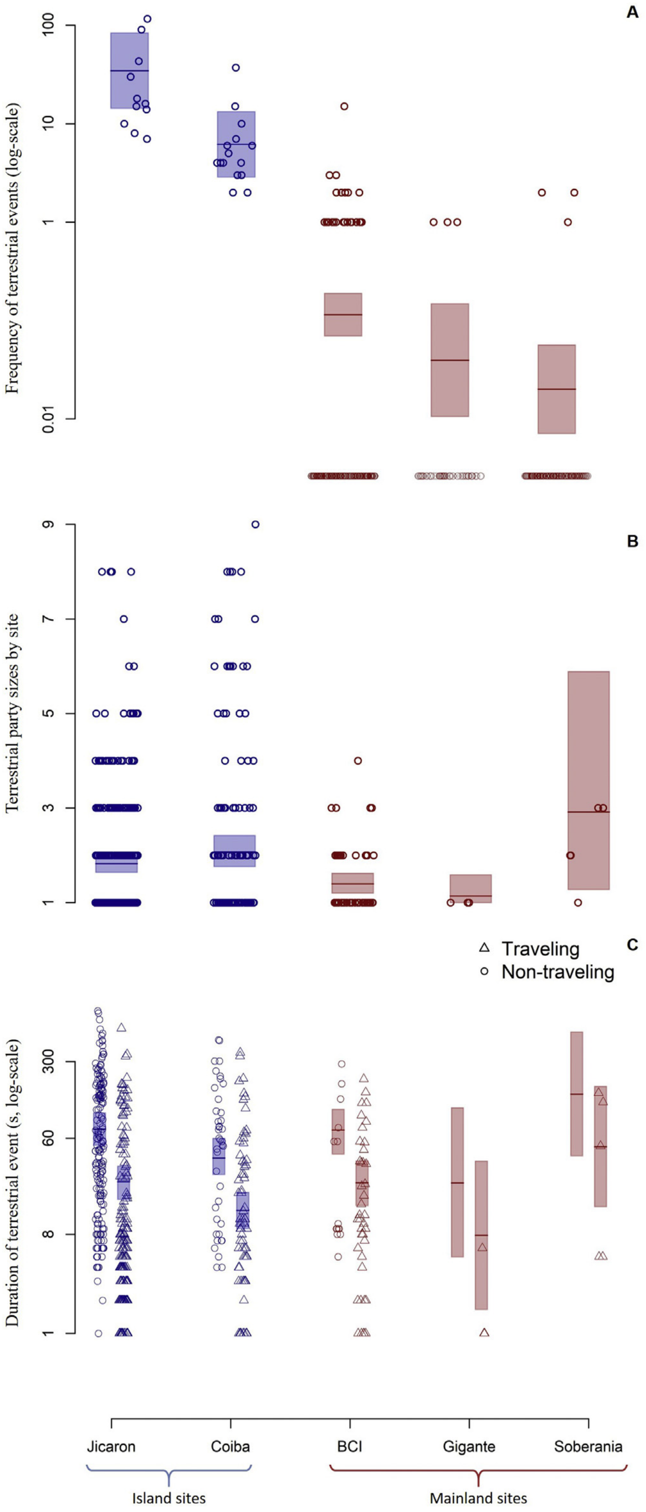

Figure 3. Terrestrial behavior of white-faced capuchin monkeys on two islands lacking mammalian predators and three mainland sites with predators. A) Observed frequency of terrestrial events. Camera deployments that produced zero terrestrial events are shown below the vertical axis; these were included in the data set, and therefore, the model predictions incorporated them. B) Observed party sizes per terrestrial event. C) Observed duration of terrestrial events. Durations for traveling and nontraveling capuchins are projected side by side within sites, and the corresponding observations are marked by triangles and circles, respectively. In graphs A and C, observations and predictions are displayed on the logarithmic scale, and in all graphs, boxes show the predicted mean with 95% confidence interval. Model predictions are for 1.6 months sampling effort and 5.5 m of detection distance—values near the midrange of the data set.

Figure 4. Camera trap photographs from Coiba National Park showing groups of white-faced capuchin monkeys on the ground (A, B), including mothers carrying infants, an individual resting on the ground (C), and two individuals foraging and one stationary (D).

detection rates we observed across sites. Although population density estimates are available for only one of our study sites (~250–300 capuchins are estimated to live in BCI, which translates to 0.16–0.19 individuals/ha; M.C.C., unpublished data), it is our qualitative impression that capuchin population density is somewhat higher on the islands of Coiba and Jicaron than in the three mainland sites. However, it is implausible that a difference in population density alone could account for the differences we observed due to the magnitude of the effect; the terrestrial detection rate of capuchins was as much as 200 times higher at islands vs. mainland sites.

Due to logistical difficulties in accessing our study sites during the wet season, only BCI was surveyed over a complete annual cycle. Because capuchins are known to come to the ground more frequently during certain times of the year—e.g., during the dry season in Costa Rican tropical dry forest (Freese, 1978) and at the end of the wet season in Panamanian lowland tropical moist forest (M.C.C., unpublished data)—it is important to consider if and how such differences in sampling may have impacted the results of our study. Patterns of seasonality in terrestrial behavior do appear to differ across our study sites. On Jicaron and Coiba, the majority of terrestrial detections occurred during dry season months (60% and 59%, respectively). In contrast, if we consider data taken during the matching time frame on BCI, the opposite pattern emerges: only 41% of terrestrial detections on BCI occurred during dry season months, while the majority (59%) took place during wet season months. If these patterns reflect real differences in how capuchins on Coiba, Jicaron, and BCI respond to seasonal variation, this may provide an avenue for examining the environmental factors that draw capuchins to the ground. However, they cannot account for the finding that capuchins on Jicaron and Coiba use the ground much more extensively than capuchins on BCI. For the period from February through June, we observed an order of magnitude more terrestrial activity at our island study sites (367 and 112 events for Jicaron and Coiba, respectively) than at the mainland site of BCI (17 events), despite greatly reduced sampling effort at the island sites (Table 1).

We found distinct differences in the timing of terrestrial activity between the island and the mainland study sites. On the mainland, records of capuchins on the ground were concentrated in the middle of the day. This corresponds to the period of lowest activity of an important terrestrial predator; the ocelot (Rowcliffe et al., 2014; Suselbeek et al., 2014). These results from the mainland are consistent with other studies that have documented a midday peak in terrestrial activity in both gracile (*Cebus*) and robust (*Sapajus*) capuchins (Gilbert and Stouffer, 1995; Porfirio et al., 2017). In contrast, capuchins on Coiba and Jicaron show a much less pronounced midday peak in terrestrial behavior, spending time on the ground both before sunrise and after sunset—periods when they would be especially vulnerable to predation if ocelots were found on the islands.

We predicted that where predation pressure was low, average party size would be larger because more group members from a greater diversity of age/sex classes would engage in terrestrial behavior. Consistent with this prediction, large parties of capuchins (up to 9 individuals) and parties including juveniles and females carrying infants were only observed on the ground on Jicaron and Coiba. However, the median party size was not appreciably different across sites. This is due to the fact that in the camera trap data from the islands, records of single individuals were overrepresented. Although our sampling effort in the mainland study sites was up to 10 times higher than that in the island sites, we only detected lone individuals on the ground a small number of times. If group living provides capuchins with important antipredator benefits via dilution, detection, or selfish herd effects (Krause et al., 2002), lone individuals may be less willing to come to the ground on their own where predation risk is high. Although the fact that we detected comparatively few instances of lone capuchins on the ground in our mainland sites is consistent with this hypothesis, our sample sizes are, by definition, small (because terrestrial activity at these sites is extremely rare), and estimates of mean party size at GP and SNP are especially uncertain.

Although we do not have sufficient data to address the question statistically, the apparent difference in the age/sex class composition of the parties recorded at island vs. mainland sites is interesting and warrants further scrutiny. If predation risk is an important factor deterring exploitation of terrestrial niches, we predict that adult male capuchins, who may be less vulnerable to predators due to their large body size (Masterson and Hartwig, 1998) and large canines (Kay et al., 1988), will use the ground more frequently than other age/sex classes in sites with more predators. Indeed, previous researchers have noted this sex difference, reporting that in capuchins, use of terrestrial substrates is sporadic, mainly done by adults and particularly adult males (Robinson, 1981; Fragaszy, 1986; Moscow and Vaughan, 1987). Similarly, we expected that juvenile capuchins, which may be vulnerable to a wider range of potential predators due to their small size (Bezanson, 2009), would show more terrestrial behavior at sites with fewer predators. The fact that we regularly recorded all age classes on the ground in both Coiba and Jicaron, but only twice observed nonadults in BCI, GP, and SNP, suggests that entire troops have expanded into the terrestrial niche on these islands and is consistent with the idea that predation risk constrains the ranging behavior of capuchins at our continental sites. However, it is also possible that differences in energetic requirements (e.g., resulting from sexual dimorphism in body size or pregnancy and lactation; Rose, 1994) or foraging behavior (e.g., a documented sex bias in tool use; Barrett et al., 2018) could explain why some age/sex classes use the ground more than others, and additional research will be required to distinguish among these alternatives.

Our data on the duration of capuchins' visits to the ground are inherently imperfect due to the nature of our data collection methods. Camera traps only record how long individuals are within the field of view of our cameras, not how long they are actually on the ground. It is therefore not surprising that once the effects of party size and behavior have been statistically controlled, the average duration of capuchins' visits to the ground was similar across study sites. That being said, our results show that on the islands of Coiba and Jicaron, capuchins engage in significant terrestrial travel, but also frequently come to the ground for a range of nontraveling activities. Activities such as foraging, feeding, and interacting socially were rarely observed on the camera traps in sites with mammalian predators. These findings suggest that arboreal travel may impose costs that capuchins avoid by traveling on the ground when it is possible, consistent with past research demonstrating a shift in capuchins' terrestrial activity patterns wherein anthropogenic activities have reduced predator abundance (Gilbert and Stouffer, 1995; Stern et al., 2002; Porfirio et al., 2017).

Also of note is the fact that camera-level variation was a relatively large component of total variation in visit duration. This coincides with our perception, based on direct observations of the behavior of habituated individuals on BCI, that capuchin parties tend to come to the ground to play, rest, and forage in a small number of regularly used sites (M.C.C., pers. obs.). The overlap of some deployments with the commonly used traveling routes within the study subjects' home ranges may also have contributed to this pattern. Further studies in which individuals are observed or tracked over time are needed to test these ideas.

Our findings demonstrate that under the right ecological conditions, capuchins can readily expand into terrestrial niches and suggest that reduced predation risk may be the key to the adoption of a more terrestrial lifestyle. However, additional factors, including reduced connectivity in the forest canopy or the existence of an abundant source of food on the forest floor, may also play an important role. We have not yet explicitly tested these alternative (although not mutually exclusive) hypotheses, but it seems unlikely that the capuchins in our study came to the ground because the structure of the forest prevented them from traveling arboreally. Howler monkeys were never captured by our camera traps in Coiba and Jicaron, suggesting that they are able to move exclusively in the trees. Furthermore, we regularly observe capuchin groups traveling arboreally on both islands, and when we encounter groups of capuchins traveling terrestrially, they often respond to us by fleeing through the trees, demonstrating that arboreal locomotion is possible in these areas.

The potential role of alternative food sources in promoting terrestrial behavior is interesting and warrants further attention. Coiba National Park contains the only population of gracile capuchins (e.g., *Cebus* rather than *Sapajus*) documented to use stone tools (Barrett et al., 2018). Capuchins on the island of Jicaron habitually use hammerstones and anvils to crack open a variety of foods they acquire on the ground, including seeds of *Terminalia catappa*, crabs, and bivalves. It is possible that the availability of abundant terrestrial food resources (or the lack of sufficient food in the trees) helps explain why capuchins on these islands spend so much time on the ground. It is also possible that spending more time on the ground as a consequence of a release from predation pressure may have potentiated the innovation of the tool-use tradition in this population of capuchins, thereby opening up a new terrestrial foraging niche. Terrestriality has been linked to the innovation of tool-use traditions (Visalberghi et al., 2005), but cracking nuts with hammerstones is a loud and conspicuous activity that requires significant attention. Thus, it may only arise where antipredator vigilance can be reduced because predation risk is low (Haslam, 2013).

Over the course of their evolutionary history, primates have repeatedly left the trees to adopt primarily terrestrial lifestyles (Fleagle and Lieberman, 2015), and such a transition is thought to have played a central role in human evolutionary history (Potts, 1998; Richmond et al., 2001; Kingdon, 2003; Patel et al., 2009). Many hypotheses have been proposed to explain the adoption of terrestrial bipedalism in hominins (Potts, 1998), but the fragmentary nature of the fossil record makes it difficult to convincingly assess their relative merits. Furthermore, we do not yet have a well-developed understanding of the ecological conditions that promote terrestriality in primates more generally. Variation in the behavior of living primate populations thus provides an important opportunity to assess the impact of evolutionary pressures that have been hypothesized to promote or constrain terrestriality. Studies such as ours also provide important context for interpreting the patterns of locomotor diversity observed in New World monkeys. While the absence of terrestrial primates in the Neotropics has often been noted (e.g., Fleagle, 2013), our results demonstrate that white-faced capuchin monkeys readily expand into the terrestrial niche under the right ecological conditions. This provides an intriguing opportunity to investigate how a change in substrate use impacts other aspects of biology, behavior, and ecology. We do not yet know how long the population of capuchins on Coiba and Jicaron has been genetically isolated from mainland populations, but the island of Coiba lies 23 km off the coast of Panama and has been geographically isolated from the mainland since at least 12–18 ka (Ibáñez, 2011). Whether these island-living capuchins exhibit changes in the social structure or life history associated with reduced predation pressure, or in skeletal adaptations associated with increases in terrestrial locomotion or stone-tool use, is an interesting topic for further investigation and may inform our understanding of how a transition to ground living can shape a species' evolutionary trajectory.

Conflict of interest

We declare no conflict of interest.

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Supplementary Online Material

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