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Research Article

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Does predation risk constrain behavior in prey species? A test with five species of Neotropical forest mammals

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Abstract

Predation is a major force structuring ecological communities, and it is well known that predation risk can exert strong effects on behavior and ecology of prey species. One of the potential effects of predation risk is the constraint on the activity patterns and activity budgets of prey. Island populations that evolve under reduced predation risk provide valuable opportunities to assess the effects of such risk on prey behavior. We tested whether diel activity patterns and anti-predator behavior differed between mammal populations living on 2 land-bridge islands of the Coiban Archipelago off the Pacific coast of Panama—where predators are nearly absent—and the adjacent mainland where a diverse community of predators persists. Using ground-based and arboreal camera trapping, we compared temporal activity kernel density curves, foraging and ranging behavior, and visit duration between 2 island and 4 mainland populations of 5 tropical forest mammal species. We also tested whether temporal overlap between prey competitor species differed between island and mainland populations. Overall, we found that activity levels during risky times were higher on islands than on the mainland for two species of agouti and the White-faced Capuchin monkey. Island prey populations showed far less anti-predator behavior and more foraging behavior than their mainland counterparts. They did not, however, show higher levels of nocturnal activity during darker nights nor longer visits, both considered as indicative of predation release. We also found lower spatiotemporal overlap between the white-faced capuchins and the mantled howler monkeys on islands than their counterparts on the mainland. This result suggests that when predation pressure is relaxed, there is a decrease in direct competitive interactions between these species, which may also be associated with changes in the use of forest strata. These findings provide partial support for the hypothesis that predation risk constrains activity patterns and influences spatiotemporal niche differentiation among competing mammalian prey species.

Key words: *Alouatta palliata*, activity budget, animal behavior, camera traps, *Cebus capucinus imitator*, *Dasyprocta coibae*, *Dasyprocta punctata*, *Didelphis marsupialis*, moon phase, *Odocoileus virginianus*

¿Limita el riesgo de depredación el comportamiento en especies de presa? Una prueba con cinco especies de mamíferos de bosque Neotropical.

Resumen

La depredación juega un papel esencial en la estructuración de comunidades ecológicas, y el riesgo de depredación puede ocasionar fuertes efectos sobre el comportamiento y ecología de las especies presa. Uno de los efectos potenciales del riesgo de depredación son los cambios en los patrones de actividad de la presa, así como de la distribución de tiempo destinado a los diferentes patrones de comportamiento. Las poblaciones de presas en islas que evolucionaron bajo un riesgo de depredación reducido son ideales para evaluar los efectos de dicho riesgo en el comportamiento de las poblaciones. Evaluamos si los patrones de actividad diaria y el comportamiento anti depredador difieren entre las poblaciones de mamíferos de cinco especies que habitan dos islas del archipiélago de Coiba, frente a la costa del Pacífico de Panamá - donde prácticamente no existen depredadores -, y las poblaciones de tierra firme donde aún persiste una comunidad diversa de predadores. Realizamos muestreos con cámaras trampa en suelo y en dosel, y comparamos las curvas de densidad de actividad de kernel,

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comportamiento de forrajeo y de desplazamiento, así como la duración de eventos de detección, con el fin de comparar dos poblaciones insulares y cuatro poblaciones continentales de cinco especies de bosque. También evaluamos si el riesgo de depredación afecta la sobreposición temporal entre especies con sobreposición de dieta. En general, existe evidencia de un aumento de actividad en horarios de mayor riesgo para dos especies: agutí y mono capuchino. Además, registramos una menor frecuencia de comportamiento anti depredador, y una mayor frecuencia de forrajeo en islas comparando con tierra firme. Sin embargo, no detectamos un aumento de actividad nocturna en noches con baja luminosidad ni un aumento en la duración de los eventos de detección en las poblaciones insulares versus las de tierra firma. También detectamos una menor sobreposición espacio-temporal entre monos aulladores y capuchinos insulares respecto de sus contrapartes de tierra firme. Esto sugiere que, a menor riesgo de depredación, habría una reducción en la competencia directa entre los dos primates, que puede estar asociado con cambios en el uso de los estratos del bosque. Estos resultados respaldan parcialmente la hipótesis de que los predadores afectan la actividad y diferenciación espacio-temporal de nicho entre especies de mamíferos presa.

Palabras clave: Alouatta palliata, cámaras trampa, Cebus capucinus imitator, comportamiento animal, Dasyprocta coibae, Dasyprocta punctata, Didelphis marsupialis, fase lunar, Odocoileus virginianus

Diel activity patterns describe the timing and duration of animal activity over a 24 h cycle. Diel activity patterns vary greatly between species (Refinetti 2008; Tucker et al. 2014; Russell et al. 2015), depending on intrinsic (e.g., body size; Vallejo-Vargas et al. 2022) and extrinsic (e.g., seasonality; Schweiger and Frey 2021) factors. The time of peak activity varies considerably across species, with different species adapted for diurnal, nocturnal, or crepuscular lifestyles (Cox et al. 2021), while others are active during both day and night (Cox and Gaston 2024). These differences lead to temporal niche differentiation, allowing coexistence of species with similar habitat and dietary requirements. The time of day at which an individual is active will determine the degree to which its behavior is influenced by a variety of biotic (e.g., interactions with other species) and abiotic (e.g., temperature) factors (Hut et al. 2012).

Animals engage in a suite of behaviors in their quest to survive and reproduce. The time allocation to such behaviors is known as the activity budget, with species allocating differing amounts of time to sleeping, resting, traveling, foraging, mating, territorial defense, and avoiding predators. Foraging plays a major role in shaping activity budgets because it provides the energy needed to perform all other behaviors and ultimately enhance reproductive success. The time spent foraging varies widely among species, depending on feeding modes and diets. Nevertheless, it ranks as the behavior with the highest time allocation in a wide variety of species (e.g., Arunachal Macaque, Kumar et al. 2007; chamois, Pęksa and Ciach 2018; and red squirrels, Wauters and Dhondt 1986). Although foraging results in energy gain, it also has the potential to be costly to an individual. For instance, an individual might be less likely to detect a predator while foraging (Lima and Dill 1990; Brown and Kotler 2004), resulting in trade-offs between rewards and risks (LaManna and Martin 2016)—animals are expected to adjust the proportion of time allocated to and timing of each behavior to maximize rewards while minimizing risks. Thus, the activity budget profile is a major determinant of individual fitness (Barker 2009).

Predation risk in particular has been identified as a major driver of time allocation of individuals throughout the day (Brown 1999). Because predation requires that predator and prey species encounter each other at the same place and time, prey species can reduce predation risk by concentrating their activity at times when predators are less active (Suselbeek et al. 2014; Makin et al. 2017; Kohl et al. 2018; Wu et al. 2018). For example, vicuñas (*Vicugna vicugna*) reduce predation risk by foraging while pumas (*Puma concolor*) are resting (Smith et al. 2019). Similarly, Cape Buffalo (*Syncerus caffer*), Giraffe (*Giraffa camelopardalis*), and Kudu (*Tragelaphus strepsiceros*) have been documented to avoid waterholes at night, when lions (*Panthera leo*) are more likely to hunt (Valeix et al. 2009). Nevertheless, there are cases in which predation risk is unrelated to diel activity of prey, which has been documented for snowshoe hares (*Lepus americanus*) whose probability of being predated by Lynx (*Lynx canadensis*) did not differ between periods of activity or inactivity (Shiratsuru et al. 2023). As such, the degree to which predation risk constraints diel activity patterns seems to vary across taxonomic and geographic scales.

Animals can change their behavior to mitigate risk. For example, prey species often dedicate a portion of their time to vigilance, which can enhance predator detection and reduce the probability of an attack (Elgar 1989). Increased vigilance, as an antipredator strategy, has been documented in several species including South American Coati (*Nasua nasua*; Di Blanco and Hirsch 2006), Elk (*Cervus elaphus*; Liley and Creel 2008), and White-tailed Deer (*Odocoileus virginianus;* Lashley et al. 2014). However, these studies provide insights about vigilance behavior, particularly on focal individuals in groups. If these patterns scale up to the population level, we would expect anti-predator behavior to differ between populations experiencing different levels of predation risk.

Predation risk may also influence interspecific interactions among prey species via their impact on the timing of, and investment in, different behaviors. In laboratory experiments with fish, the presence of a predator altered the competitive regime between prey species, reversing the dominance hierarchy, for example, Roach (*Rutilus rutilus*) and Perch (*Perca fluviatilis*; Persson 1991). Competing prey species with shared predators face trade-offs between balancing competitive interactions and reducing predation risk. Species may segregate into habitat patches of different safety and resource availability based on their foraging strategies (Kotler and Holt 1989). However, if species have both dietary overlap and shared predators, competition for spatial refuges may increase (Slade et al. 2022). Conversely, in areas with lower predation risk, competition might be resource-driven and spatial overlap may arise, for example, at foraging patches. In extreme cases, the absence of predators may lead to the exclusion of less-suited competing prey species (Norrdahl and Korpimäki 1995).

Our understanding of the impact of predation risk on prey behavior is largely based on empirical studies from settings with gradients of predation risk and from controlled experiments in laboratory settings. Gradient-based studies indicate that some prey species avoid predators spatially (e.g., wild dogs; Dröge et al. 2017), while other species avoid predators temporally (e.g., Elk; Kohl et al. 2018). Moreover, laboratory experiments have assessed the effects of the complete removal of a predator from a predator-prey system, leading to increases in movement (Heads 1985) and increases in total biomass (Worsfold et al. 2009). Further insight into the effects of predation on prey behavior could also be obtained by comparing populations of the same species under different levels of predation risk. Predator-free islands offer an ideal study system to make such comparisons. Studies from temperate environments have documented reduced anti-predator behavior on mammalian populations living in predator-free environments. For example, eastern chipmunks (*Tamias striatus*) on Beaver Island, Michigan, are 40% less vigilant than their mainland counterparts (McWaters and Pangle 2021). Tammar wallabies on Kawau Island, New Zealand, form smaller group sizes when compared to the same species at islands with at least 1 predator species (Blumstein et al. 2004).

Here, we aim to understand how predation risk affects the activity patterns and budgets of mammalian prey species by comparing populations with contrasting predation pressure. For 5 species, we compared low-risk populations on 2 islands of the Coiba Archipelago, off the Pacific coast of Panama, with high-risk populations on the mainland. Mammalian predators are reportedly absent (Ibañez et al. 1997; Monteza-Moreno et al. 2020) at the islands, and there is limited exposure to humans there, while mainland populations are exposed to an array of mammalian predators and humans. We used terrestrial and arboreal camera trapping to compare diel activity patterns and 4 behaviors for each population. We formulated 6 predictions to test 3 hypotheses: (H1) predation risk constrains diel activity patterns of prey species; (H2) predation risk constrains activity budgets of prey species; and (H3) predation risk constrains temporal niche differentiation between prey species with shared diets (Table 1).

Methods

Study sites and species.

We sampled a total of 6 study sites on the Isthmus of Panama (Supplementary Data SD1), including 2 oceanic islands with low predation risk (Coiba, 50,134 ha), and (Jicarón, 2,002 ha); and 4 mainland sites with high predation risk (Bahía Honda, 175 ha), Barro Colorado Island (hereafter BCI, 1,540 ha), Metropolitano Natural Park (hereafter Metropolitano, 265 ha), and Soberania National Park (hereafter Soberania, 22,000 ha). Coiba and Jicarón are located off the Pacific coast, have been isolated from the mainland for 12,000 to 18,000 yr (Titcomb and O'Dea 2020), and are also the largest islands in Coiba National Park. Rainfall totals 3,500 mm per year, falling mostly in the wet season (mid-April to mid-December). Historically, these islands were inhabited by people, as early as 250 CE to the mid-sixteenth century; the original inhabitants were wiped out by European conquistadors (Isaza-Aizpurúa 2022). From 1919 to 2004, there was a penal colony on Coiba with inmates distributed among 30 prison camps across the island. Although the prison only officially closed in 2004, the inmate population already had declined from around 850 prisoners in the 1990s to 130 before closure (ANAM 2009). Since the closing of the penal colony, there have been no permanent human populations living on either island, although tourists, researchers, and officials are allowed for short-term visits, particularly in the northeastern portion of Coiba. Both islands lack terrestrial mammalian predators (Monteza-Moreno et al., 2020), though there are American crocodiles (*Crocodylus acutus*) and a number of snakes, including boa constrictors (*Boa constrictor*) and fer-de-lance (*Bothrops asper*).

Among the 4 mainland sites, Bahía Honda is located on the southwestern Pacific coast of Panamá; while BCI, Metropolitano, and Soberania are located in Central Panama. Bahía Honda holds both primary and secondary broadleaf forest, and temperature and rainfall patterns are similar to those of Coiba due to geographical proximity. The remaining 3 sites are covered by lowland tropical rainforest. Soberanía and BCI have mean annual temperature of 27 °C and annual rainfall exceeding 2,500 mm/year (Windsor 1990), whereas Metropolitano is drier, with a mean annual rainfall of 1,501 to 1,800 mm (Rodríguez and Medianero 2022). These mainland sites are home to a more diverse mammalian community. For instance, BCI is home to Jaguarundi (*Herpailurus yagouaroundi*), Ocelot (*Leopardus pardalis*), and Tayra (*Eira barbara*); while at the remaining 3 mainland sites, Coyote (*Canis latrans*) and Puma (*Puma concolor*) also occur (Meyer et al. 2015).

Our study species are agouti (*Dasyprocta coibae* O. Thomas, 1902 on islands and *D. punctata* on mainland), Common Opossum (*Didelphis marsupialis*), Mantled Howler Monkey (*Alouatta palliata*), White-faced Capuchin (*Cebus capucinus imitator*), and White-tailed Deer (*Odocoileus virginianus*; Ibañez et al. 1997). Common Opossum and White-tailed Deer are absent from Jicarón, while the other 3 species live in all 5 sites. We treated the Coiban Agouti (*D. coibae*) and the Central American Agouti (*D. punctata*) as 1 species (Santos et al. 2021) due to their ecological similarities. Hereafter, we refer to the species as agouti, opossum, deer, capuchin, and howler, respectively. Detailed species descriptions can be found in the Supplementary Data SD2.

Camera trapping.

We sampled measured species activity at all study sites using unbaited IR camera traps (HC600 and PC900 Hyperfire, Reconyx, Inc., Wisconsin, USA) with a total of 81 deployments (Table 2). From February through June 2015, we installed a total of 15 camera traps on Coiba Island and 11 on Jicarón Island. From June through August 2015, we installed 4 camera traps on Bahía Honda. Then, in 2019, we conducted paired (canopy-ground) camera trapping in Coiba, Jicarón, and BCI by installing camera traps in the canopy (roughly 20 m above ground), at the intersection of branches, and on the ground at the base of the same trees. From September 2020 through February 2021, we installed a total of 8 camera traps in Soberanía and 9 in Metropolitano. At all 6 sites, terrestrial cameras were installed at 40 to 50 cm above the ground and off-trail without prior knowledge of animal usage of the site. Distance between camera trap stations and interstation distance varied from site to site (Table 2).

We programmed all cameras to take either 5 ($n=2$) or 10 pictures per trigger ($n=79$), with no delay between triggers. To distinguish camera malfunctioning from wildlife absence, we programmed each camera to automatically take a photo at midnight and noon. We processed all camera-trap photos using the online platform Agouti (Casaer et al. 2019). We defined detection events as the sequence of all pictures of the same species obtained from consecutive triggers within a 2 min period. For each detection event, we annotated the species, number of individuals, and 4 focal behavior types, including traveling, vigilance, foraging, and miscellaneous (Supplementary Data SD3). We classified individuals as "traveling" if they moved past the camera, as "vigilant" if they scanned the environment moving the head laterally, and as "foraging" if they had food visible in their mouth or were with the head down with open mouth. For sequences in which individuals displayed more than 1 behavior, we annotated them in combination. Previous works have also assessed mammalian

Table 1. Overview of hypotheses, predictions, and test species for each prediction.

Hypothesis	Prediction (island versus mainland populations)	Species tested
H1. Diel activity patterns. Predation risk constrains prey activity patterns.	**P1.1.** Higher activity at risky times. **P1.2.** Higher nighttime activity during darker nights.	**P1.1.** agouti, capuchin, deer, howler. **P1.2.** deer, opossum.
H2. Activity budget. Predation risk constrains prey behaviors.	**P2.1.** Higher frequency of foraging and lower frequency of vigilance and traveling. **P2.2.** Longer duration events while foraging and traveling.	**P2.1.** agouti, deer, opossum. **P2.2.** agouti, deer, opossum.
H3. Interspecific interaction. Predation risk constrains temporal niche differentiation between prey species.	**P3.1.** Lower temporal overlap. **P3.2.** Longer waiting times between consecutive detections.	**P3.1.** capuchin, howler. **P3.2.** capuchin, howler.

Table 2. Study site characteristics and specifications of camera-trapping surveys including sampling period, number of sampling locations, mean distance between sampling locations, and total sampling effort.

Study site	Site area (ha)	Sampling period	Sampling locations	Interstation distance (m)[a]	Sampling effort (days)
Island sites					
Coiba	50,300	February to June 2015	15	1,701	1,220 (ground)
		March to July 2019	4	7,269	440 (ground)/623 (canopy)
Jicarón	2,002	February to June 2015	11	1,215	1,132 (ground)
		March to July 2019	4	3,526	376 (ground)/603 (canopy)
Mainland sites					
BCI	1,540	March to July 2019	4	1,719	444 (ground)/844 (canopy)
Bahía Honda	175	June to August 2015	4	1,216	187 (ground)
Soberanía	22,000	September to December 2020	8	230	757 (ground)
Metropolitano	265	September 2020 to February 2021	9	352	1,219 (ground)

[a] Interstation distance for vertical surveys is based on ground cameras only.

behavior from camera-trap pictures in a variety of taxa, including ungulates (Burton et al. 2022) and mesopredators (Meek et al. 2016).

Data analysis.

Diel activity patterns

We compared diel activity levels at risky times (P1.1) between island and mainland populations of agouti, deer, capuchin, and howler. We defined risky times as dawn, dusk, and night (Prugh and Golden 2014) because most mammalian predators at the mainland sites are more active during crepuscular and nocturnal hours (Rowcliffe et al. 2014; Suselbeek et al. 2014; Santos et al. 2019). We fitted a non-parametric kernel-density function to the timestamp of each event (Rowcliffe et al. 2014). We estimated 95% confidence intervals from 1,000 bootstrap iterations from the data to produce graphical displays. We conducted the analyses using the package "activity" (Rowcliffe 2022).

We also compared activity levels during darker nights (P1.2; e.g., New Moon) between island and mainland populations of 2 species (deer and opossum). We assumed that anti-predator responses would be higher on darker nights, as nighttime hunting success for some felid species has been correlated with lower luminosity levels (Harmsen et al. 2011; Palmer et al. 2017). We extracted night-time (period between sunset and sunrise) observations of both species. We obtained the moon phase for each observation using the date on the camera timestamp and the "getMoonIlumination" function on the "suncalc" package (Thieurmel and Elmarhraoui 2022). Finally, we fitted kernel activity curves, as described above, for each species contrasting island and mainland populations, where instead of a 24 h cycle we displayed moon-phase cycles, similar to Botts et al. (2020). We classified lunar phases as: $0 =$ New Moon; $\frac{\pi}{2}$ = First Quarter; π = Full Moon; $\frac{3\pi}{2}$ = Last Quarter; 2π = New Moon.

Activity budgets

We contrasted foraging, traveling, and vigilance levels between island and mainland populations (P2.1) for 3 species: agouti, opossum, and deer. We estimated intraspecific differences using a Bayesian categorical multinomial model with the counts of behavior type (foraging, traveling, vigilance, foraging+vigilance, and miscellaneous) as the outcome variable with Sites (Island vs Mainland) as the predictor variable. To account for unmodeled heterogeneity between camera-trap stations, we included station ID as a random effect. We ran models separately for each species using 4 chains of 2,000 iterations each, discarding the first half as burn-in. We fitted models with the "brms" package v2.13.3 (Burkner 2017) in R version 4.2.1 (R Development Core Team R 2011).

We assessed differences in the visit duration of events between island and mainland populations of agouti, opossum, and deer (P2.2). We distinguished 2 modes of displacement: either an animal only travels in front of the camera or it invests time in foraging; while engagement in other behavior types was labeled as non-traveling and non-foraging, respectively. We defined visit duration as the time difference between the last and first pictures with the appearance of a species within a given detection event. We used visit duration to study predation risk based on the assumption that in lower predation risk areas animals will linger for longer in front of the cameras (Burton et al. 2022). We consider this assumption to be reasonable because we installed the cameras in places with a natural field of view (medium to open understory vegetation), which implies that an animal is exposed. We compared visit duration between sites (island vs mainland) by applying a Kaplan–Meier survival curve to the visit duration in package "survival" (Therneau et al. 2022). We defined the event of interest as the end of the visit duration and compared differences between island and mainland populations by looking at the 95% confidence bands.

Temporal niche differentiation

Finally, we contrasted temporal overlap of 2 prey species (howler and capuchin) under different levels of predation risk, between island and mainland populations, using 2 metrics: diel activity patterns (P3.1) and intervals between consecutive events (P3.2; e.g., waiting time). We contrasted these 2 species due to their dietary and spatiotemporal overlap (Tomblin and Cranford 1994). We first assessed temporal overlap between both species by estimating the overlap coefficients for island and mainland populations, ranging from 0 (no overlap) to 1 (complete overlap). We used the Δ_1 estimator, as the smallest sample was <75 (Ridout and Linkie 2009). We estimated 95% confidence intervals from 10,000 smooth bootstrap samples. Then, we compared intervals between consecutive events of both species at island and mainland sites by applying a Kaplan–Meier survival curve to the timestamp data using the package "survival" v. 3.7.0 (Therneau et al. 2022). We are interested in differences in waiting time because shorter intervals signal higher spatio-temporal overlap and increased competition risk. We assessed differences using a Mann–Whitney U test, with a significance level of $P < 0.05$.

Results

The total camera-trap effort was 7,845 trap-nights—5,775 from the ground surveys and 2,070 from canopy surveys (Table 2). Ground surveys yielded 7,595 detection events of agouti (Islands = 3,965; Mainland = 3,630), 1,389 of deer (Islands = 1,224; Mainland = 165), 331 of opossum (Islands = 74; Mainland = 257), and 264 of capuchin (Islands = 263; Mainland = 1). Canopy surveys yielded 127 events of capuchin (Islands = 42; Mainland = 85), and 201 of howler (Islands = 84; Mainland = 117). We obtained a total of 53 detections from 5 predator species across our mainland sites: Coyote ($n=3$ at Soberanía), Jaguarundi ($n=1$ at Soberanía), Ocelot ($n=7$ at BCI, 4 at Soberanía, 1 at Metropolitano, and 1 at BH), Puma ($n=1$ at BH).

Diel activity patterns.

Agouti and capuchin had higher activity at night and dusk, respectively, on islands than on the mainland (Fig. 1A and C), as predicted (P1.1); but deer and howler did not (Fig. 1B and D). Activity of deer and opossum during dark nights was similar between island and mainland populations, in disagreement with our prediction (P1.2; Fig. 2).

Island populations of agouti exhibited consistent activity spread out through the night ($n=208$ from sunset to sunrise), including detections ($n=27$; 0.7% of all agouti detection events on islands) between 8:00 PM and 5:00 AM (Fig. 1A). Conversely, for mainland agouti, we recorded just 3 nocturnal events (0.008% of all agouti detection events on mainland). Island nocturnal events included individuals foraging and caring for offspring (Supplementary Data SD4), whereas all 3 nocturnal events on mainland involved individuals traveling.

Capuchins also exhibited higher activity at risky times on islands, specifically at dusk in the canopy, including 1 detection event close to midnight (Fig. 1B). Ground activity on islands occurs throughout the day, peaking in the morning. In contrast, we recorded only a single terrestrial capuchin event on the mainland.

On dark nights, nocturnal activity of deer and opossum populations did not differ between islands and mainland. However, deer were less active in the transition from Full Moon to Third Quarter on islands than on the mainland (Fig. 2A). For opossum, island populations exhibit greater activity levels at First Quarter and lower activity levels at Third Quarter than their mainland counterparts (Fig. 2B).

Activity budgets.

Agouti and opossum showed lower vigilance levels on islands, as predicted (P2.1; Fig. 3). On islands, agouti engaged nearly twice as much in foraging and in miscellaneous behaviors than on the mainland; nearly 2.5 times less vigilant on islands; and exhibited 1.5 times lower engagement in traveling (Fig. 3A). Deer were 7 times less likely to be vigilant while foraging on islands, while their engagement in the other behaviors were similar (Fig. 3B). For opossum, we detected no vigilance events on islands, while on the mainland they spent a small proportion of their time being vigilant (Fig. 3C), and no differences in the other behaviors.

Contrary to our prediction, we did not find differences in time spent in front of the cameras for any of the 3 ground-dwelling species, with consistent overlapping confidence intervals of hazard rates for populations of all 3 species (Fig. 4).

Temporal niche differentiation.

We found support for the predicted (P3.1) decrease in temporal overlap (Fig. 5) and the increase (P3.2) in waiting times for island populations of capuchin and howler (Fig. 6). The coefficient of temporal overlap between arboreal capuchins and howlers was 0.58 (CI = 0.43 to 0.72; Fig. 5A) on islands, whereas on the mainland it was 0.74 (CI = 0.64 to 0.83; Fig. 5B). On both islands and mainland, capuchins started activity earlier than howlers. However, while on the mainland both species exhibited high overlap in the afternoon, on islands

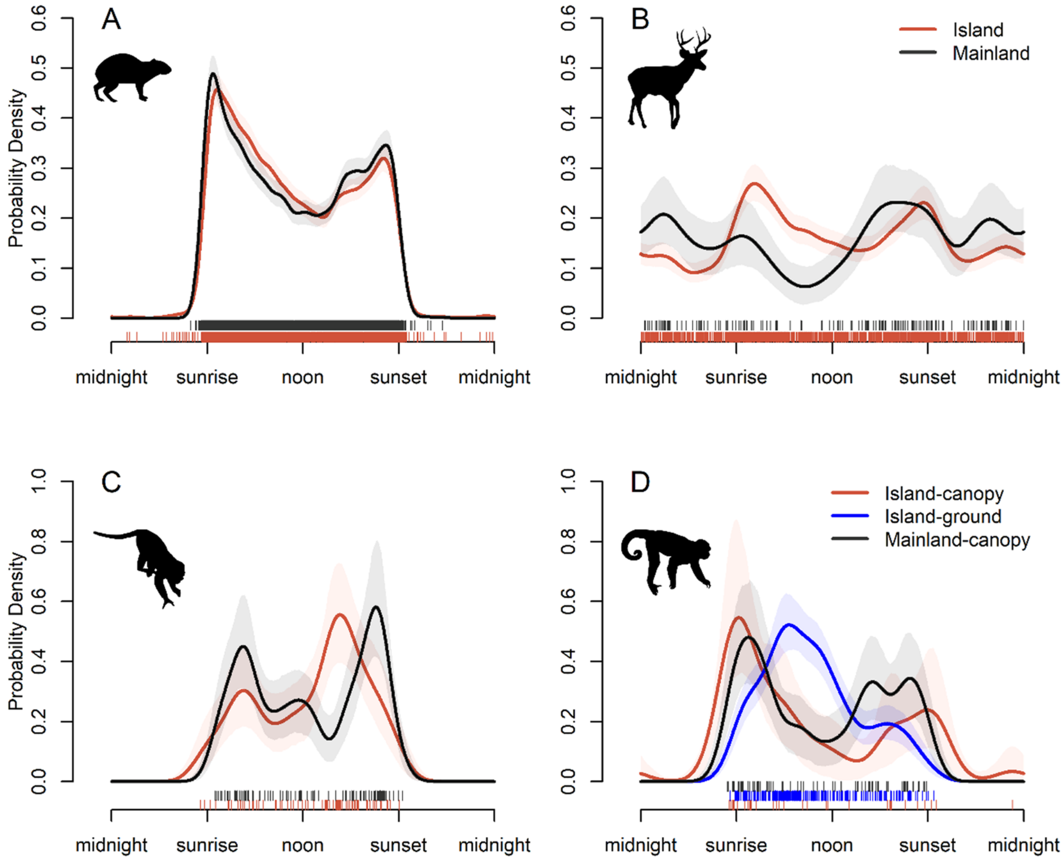

Fig. 1. Kernel density curves of activity patterns contrasts between island (red) and mainland (black) populations of: (A) agouti; (B) deer; (C) howler; and (D) capuchin. Sample sizes are: agouti islands ($n=3{,}965$); agouti mainland ($n=3{,}630$); opossum islands ($n=74$); opossum mainland ($n=257$); deer islands ($n=1{,}224$); deer mainland ($n=165$); howler monkey islands ($n=84$); howler monkey mainland ($n=117$); capuchin island in the canopy ($n=42$); capuchin monkey island on the ground ($n=263$); and capuchin monkey mainland in the canopy ($n=85$).

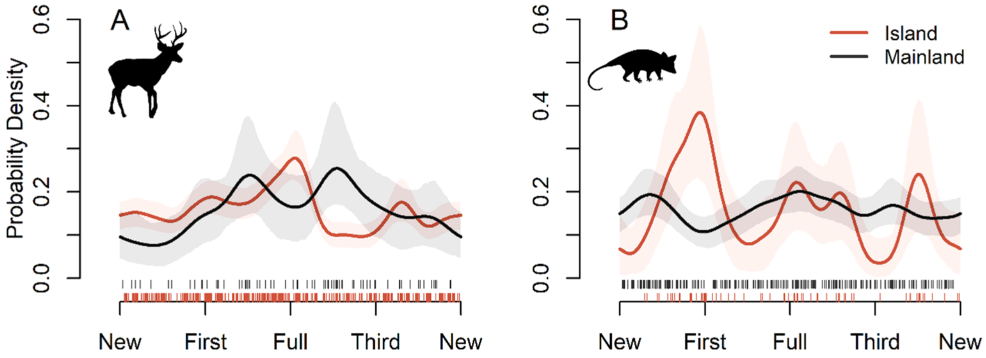

Fig. 2. Kernel density curves of night-time activity patterns in relation to moonphase between island (red) and mainland (black) populations of: (A) deer; and (B) opossum. Sample sizes are: deer island (*n* = 494); deer mainland (*n* = 88); opossum island (*n* = 72); opossum mainland (*n* = 256).

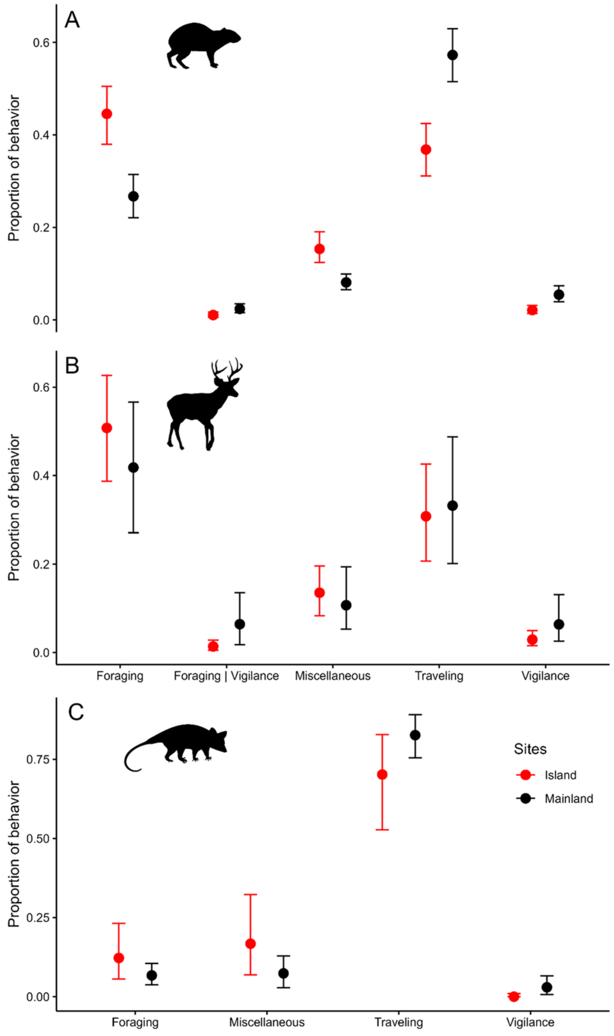

Fig. 3. Estimated proportion of activity budget of ground-dwelling mammals at island and mainland sites. Dots represent model estimates and bars represent 95% credible intervals.

howler activity peaked in the afternoon while arboreal capuchin activity declined.

Finally, the intervals between consecutive events (waiting time) of both species were longer on islands than on the mainland (Fig. 6). The interval between a capuchin event and a subsequent howler event was 7.44 d (0.01 to 35.49 d) on islands and 3.69 d (0.007 to 24.93 d) on the mainland, with a statistical difference of 3.4 d (95% CI = 1.61 to 5.23 d, *P* < 0.01). Conversely, the interval between a howler event and a subsequent capuchin event was 14.63 d (0.1 to 58.16 d) on islands and 4.79 (0.01 to 28.76 d) in the mainland, with a statistical difference of 8.4 d (95% CI = 4.2 to 10.9 d, *P* < 0.01).

Discussion

Overall, our results provide partial support for the hypothesis that predation risk constrains activity patterns, activity budgets, and temporal niche differentiation in prey species. On islands with low predation risk, we found higher diel activity at risky times only for agouti and capuchin, not in the other 2 species. We found that vigilance of agouti and opossum was lower on islands than on the mainland. We also found lower temporal overlap between interspecific competitors on islands. Overall, although all species showed some difference between populations, not a single one showed the full spectrum of predicted responses. Our findings suggest that differences between island and mainland populations under distinct predator risk (absent vs present) are specific to species.

Diel activity patterns.

We found evidence of increased activity at risky times (dawn, dusk, and/or night) on islands for 2 species: agouti and capuchin. Agouti, specifically, exhibited activity throughout the night at the 2 island sites (Coiba and Jicarón), including adult individuals accompanied by infants (Supplementary Data SD4). Such activity patterns have not been recorded on the mainland in past studies (Lambert et al. 2009; Emsens et al. 2014; Rowcliffe et al. 2014; Botts et al. 2020). Recently, Gálvez et al. (2024) reported extensive and consistent nocturnal activity for agouti on Cébaco Island off the Pacific coast of Panama but sparse detections at night on Coiba. In contrast, our recorded nocturnal activity at Coiba (*n* = 194) was more spread throughout the night, including 19 detections from 8:00 PM to 5:00 AM. Additionally, nocturnal activity of agouti has previously been documented at BCI (Lambert et al. 2009), but this mostly involved individuals switching resting places or caching food to prepare for times of scarcity; however, we are not aware of any reports of nocturnal agouti with infants at mainland sites. We note that an alternative explanation for the observed patterns is that the island agouti are released from competition from the Lowland Paca (*Cuniculus paca*), a nocturnal rodent twice the size of agouti. On the mainland, temporal niche differentiation minimizes encounters between these 2 rodents (Blake et al. 2011).

Capuchin populations at island sites exhibited higher activity during the dusk hours than mainland populations. Several of the documented mammalian predators of capuchin are either crepuscular or nocturnal (e.g., Jaguar, Puma, Ocelot; Santos et al. 2019). Hence, our results for capuchins are consistent with the hypothesis that predation risk constrains diel activity at dusk. We cannot, however, rule out other factors that could potentially contribute to

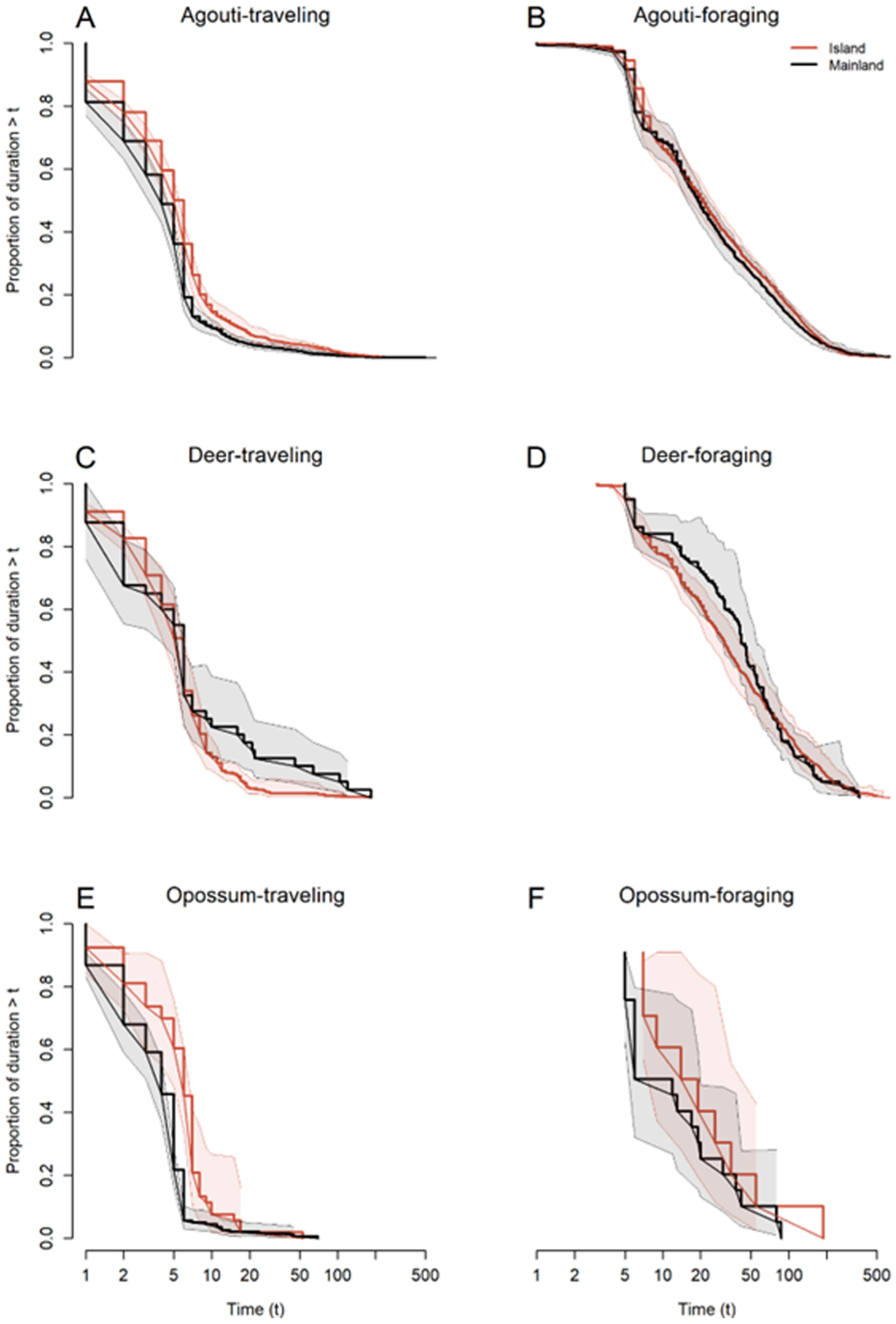

Fig. 4. Kaplan–Meier survival curves of visit duration for ground-dwelling mammals on islands and mainland: (A) agouti traveling; (B) agouti foraging; (C) deer traveling; (D) deer foraging; (E) opossum traveling; and (F) opossum foraging.

increased activity at dusk for this species. For example, differences in population density and/or resource availability could also affect when a species is active. A higher population density on the islands of Jicaron and Coiba could lead to between-group temporal avoidance (Campera et al. 2019) and a lower resource base could force capuchins to extend their foraging time. A next research step would be to record the behavior of these animals at dusk on islands in order to assess if they are actively foraging at those hours.

Two species, deer and howler, did not exhibit higher activity during risky times (dawn, dusk, and night) at the islands compared to the mainland. However, our results do show higher diurnal activity for deer on islands, with a distinct activity peak in the morning period (7:00 AM to 12:00 PM). Across their widespread range, White-tailed Deer seem to exhibit consistent flexibility in their diel activity patterns, ranging from more nocturnal populations (e.g., North Carolina mountains; Higdon et al. 2019). Whether these population contrasts are due to predation risk or human influence remains unclear. Human activity at some of our mainland sites could have contributed to the higher nocturnal activity of deer on the mainland. Higher nocturnality as a result of human disturbance has been documented for several mammals across different habitats (Gaynor et al. 2018). Future research could assess the effect of humans on deer activity patterns by contrasting sites with different levels of human activity.

We found no support for the higher activity during darker nights on islands compared to mainland for deer or opossum. However, for both species, overall patterns of nocturnal activity in relation to moon phases seem different and this warrants attention. Opossum, in particular, exhibited a higher activity level in the First Quarter on the

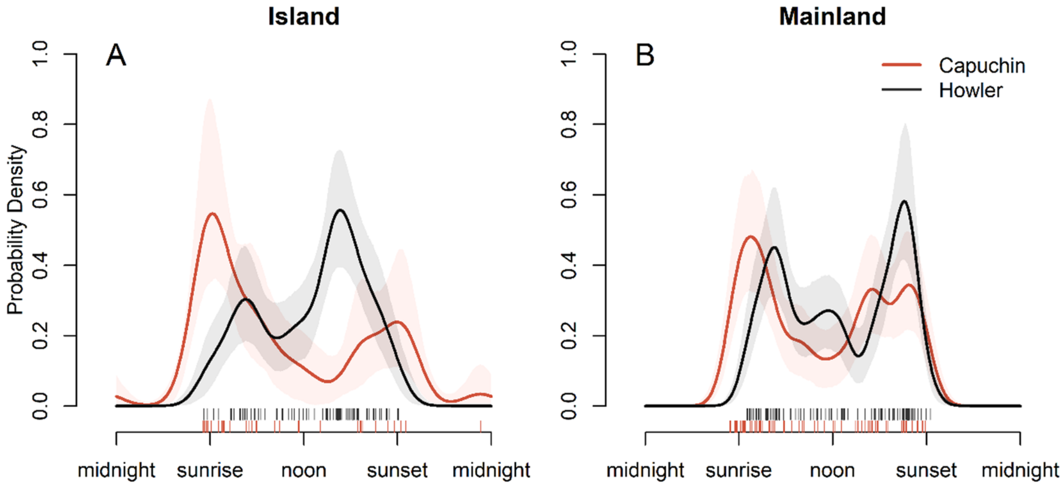

Fig. 5. Kernel density curves of activity patterns contrasts between white-faced capuchins (red) and mantled howler monkeys (black) populations in: (A) Coiba and Jicarón islands; (B) Barro Colorado. All data used to build these curves come from cameras in the canopy. Sample sizes are: capuchin island (n=42); capuchin mainland (n=85); howler island (n=84); howler mainland (n=117).

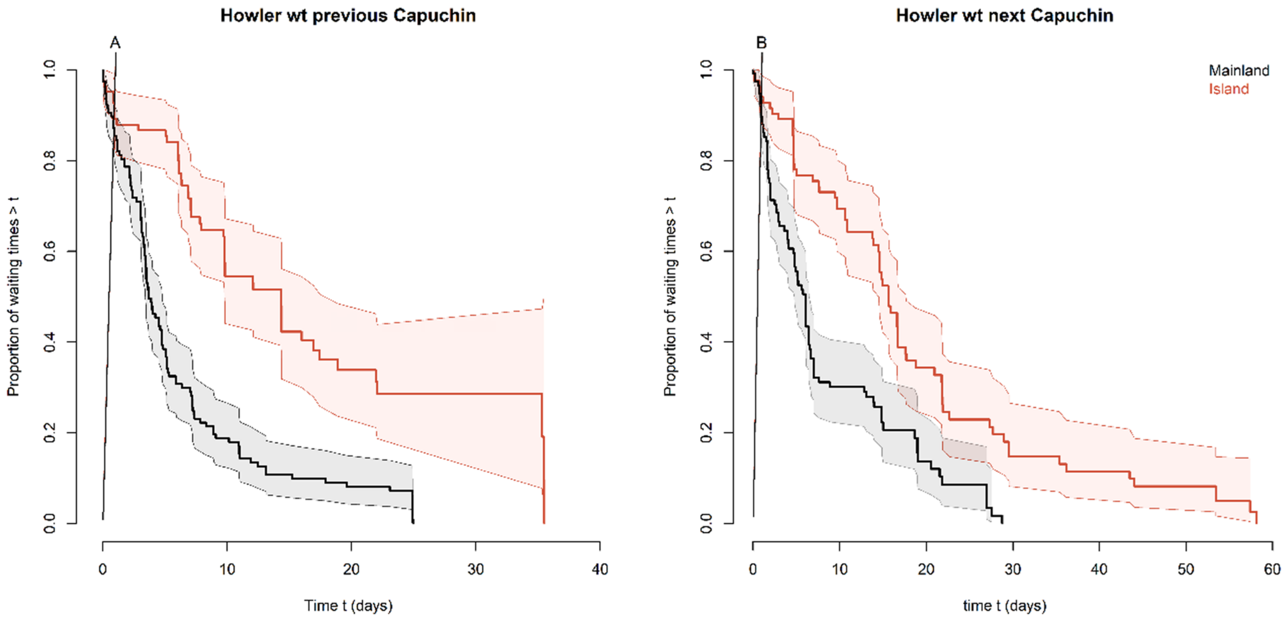

Fig. 6. Estimated waiting times from a survival model of detection intervals between howler and capuchin based on arboreal camera trapping at island and mainland sites. Shaded regions indicate 95% confidence intervals. (A) Howler waiting time. (B) Capuchin waiting time.

islands. It is possible that opossums are more active during peaks of arthropod activity on the islands, which have occurred during the First Quarter moon phase (CMM personal observation). Finally, our data are limited for exploring further aspects of such patterns due to sample size.

Activity budget.

Differences in the activity budget of ground-dwelling mammals were consistent with release from predation. Island populations were consistently far less vigilant than mainland populations, as predicted (P2.1), specifically for agouti (2.5 times less vigilant) and opossum (no vigilance recorded at islands). These results are similar to those for other taxa exposed to reduced predation risk, that is, eastern chipmunks (*Tamias striatus*; McWaters and Pangle 2021). Deer did not exhibit differences in vigilance behavior alone; nevertheless, island deer seemed to be 7 times less vigilant while foraging than mainland deer. Foraging frequency was higher on islands for agouti but not for the other 2 species. Whether this difference is due to varying levels of predation risk is not clear. Island systems tend to have poorer and more variable resources than mainland sites (Graham et al. 2017), and this could lead to organisms having to allocate a greater proportion of their time to food acquisition.

Contrary to our prediction, we did not find major differences in duration of detection events for ground-dwelling mammals. However, based on median duration estimates, we observed signals towards increased visit duration for agouti and opossum, but not for deer on islands. The lack of observed response in our study system could reflect issues with methodology rather than an ecological response. Despite the large sample size used to analyze visit duration data (n=9,294 observations), these were highly skewed toward 1 s observations (Supplementary Data SD5). Further, cameras only record how long the animal remains within the field of view of the sensor. A foraging individual could actually linger for a long time in the vicinity of the camera but outside the sensor field of view. Still, empirical median visit durations were longer for island populations of all species, regardless of whether the animal was foraging or traveling.

Temporal niche differentiation.

We found lower temporal overlap between capuchin and howler populations on islands compared to on the mainland. Capuchins on the islands of Jicaron and Coiba are known for exhibiting terrestrial activity throughout the day, though their activity was higher between noon and sunset times (Monteza-Moreno et al. 2020). This ground activity has ecological consequences (e.g., dietary overlap) to sympatric species in this island system (Fox-Rosales et al. 2024). On islands, howler activity in the afternoon peaked when capuchins were more likely to be on the ground, and temporal overlap between capuchins and howlers in the trees was lower on islands than at the mainland. It may be possible that island howlers partially shift their activity to actively avoid capuchins to reduce food competition as they overlap in about 30% of their diet (Chapman 1987) and/or to avoid antagonistic encounters (Rose et al. 2003). The latter could also explain why the start and end times of island howler activity remain similar as on the mainland, but start later and end earlier than capuchin activity.

We found shorter intervals between detections of howler and capuchin at mainland sites, which was true regardless of the species detected first (i.e., howler after capuchin and vice-versa). The drivers of this pattern could be differences in population density between sites, differences in dietary preferences between island and mainland populations, increased terrestrial activity of capuchins on islands, or a combination of any of the aforementioned factors. While our data cannot determine causal mechanisms, shorter intervals between consecutive detections of both species signal increased spatiotemporal overlap at our mainland sites and hence increased potential for interference competition.

In conclusion, predation is a major structuring force in ecological communities, and it is likely to exert strong pressure on behavior and diel activity patterns of prey species. In this study, we provide partial support for the hypotheses that predation risk constrains prey activity patterns and activity budgets, and full support for the hypothesis that predation risk influences temporal niche differentiation among prey species. However, predictions were supported for some species but not for others, suggesting that drivers of activity patterns and budgets are specific to species. We cannot rule out other factors contributing to the observed differences in our study; for example, human influence, which in other systems has been suggested to have stronger effects on prey than do apex predators (Zanette et al. 2023).

Future research could focus on other species, taking advantage of other natural laboratories (islands) to assess behavioral and spatial interactions between populations. Also, it would be interesting to compare behavior between islands with and without predators. Finally, comparing sites with different levels of human disturbance but similar levels of predation risk could further elucidate the role of humans in prey antipredator behavior. With ongoing anthropogenic change, understanding the behavioral mechanisms that allow predator and prey to coexist will become ever more important.

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Author contributions

Lester Alexander Alexander Fox Rosales (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing—original draft, Writing—review & editing), Claudio Manuel Monteza-Moreno (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing—original draft, Writing—review & editing), Patrick A Jansen (Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing—review & editing), Kevin McLean (Funding acquisition, Investigation, Resources, Writing—review & editing), and Pedro Luis Castillo-Caballero (Data curation, Investigation, Writing—review & editing), Margaret Crofoot (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing—review & editing)

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary data SD1. Map of the Republic of Panama showing the location of our study sites.

Supplementary data SD2. Study species traits and study site locations from where we obtained data. Dietary classifications are based on Lintulaakso et al. (2023).

Supplementary data SD3. Detailed description for each behavior type used for estimating behavioral repertoire of Agouti, Common Opossum, and White-tailed Deer, at island and mainland sites.

Supplementary data SD4. Agouti behavior at night in Coiba and Jicarón islands: (a) female grooming offspring (01:28:29 AM; Coiba); (b) adult traveling (12:06:34 AM; Coiba); (c) Adult foraging (04:06:09 AM; Coiba); and (d) Adult foraging (04:21:23 AM; Jicarón).

Supplementary data SD5. Histograms of visit duration of ground-dwelling mammals in island and mainland sites.

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Conflict of interest

None declared.

Data availability

Data and code will be deposited in a public repository upon manuscript acceptance https://edmond.mpg.de/dataset.xhtml?persistentId=doi:10.17617/3.PV2ZDZ.

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