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Notes on the coexistence of sympatric northern raccoons and white-nosed coatis in a dry forest of northwest Costa Rica

Notas de coexistencia simpátrica entre mapache y pizote en el bosque seco al noroeste de Costa Rica

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Differential resource use of sympatric species that co-exist is poorly known. Considering sympatric procyonid species inhabiting the dry forest of northwest Costa Rica (Santa Rosa National Park) we hypothesized northern raccoon (*Procyon lotor*) occurrence is relatively high in cover types where white-nosed coati (*Nasua narica*) is absent. We deployed 56 camera traps from June 2016-June 2017 to compare distribution and occurrence in cover types at each location. Additionally, we examined activity patterns derived from these and 45 other cameras in the same area monitored irregularly from 2011-2016. Over the course of a year, both species were detected only in Riparian Forest. Northern raccoons photo rates were higher in Mangrove and Beach Forest cover-types, with no records in Primary and Secondary Forests, whereas white-nosed coati's records were higher in Secondary Forest and absent in Mangrove and Beach Forest or Grassland with Trees cover-types. Raccoons were nocturnal, and coatis were diurnal, throughout 24-hr diel period, and coati photo rates (1.37/100 trap nights [tn]; n = 20,416 tn) were more than twice those of raccoons (0.48). Differences observed for these species in the distribution of photos by cover type, time of day, and photo rates might suggest local allopatry in Santa Rosa National Park, likely the result of interspecific avoidance but perhaps also due to differences in food habits and predation, and competition with other species. Other techniques should be used to investigate these factors, but cameras can provide important insights into elusive species' ecology.

Key words: Activity; camera; cover type use; distribution; *Nasua narica;* photo rates; *Procyon lotor*; sympatry.

El uso de recursos por especies simpátricas que coexisten es poco conocido. Considerando las especies de prociónidos simpátricos en el bosque seco de Costa Rica (Parque Nacional Santa Rosa), planteamos la hipótesis que la presencia del mapache (*Procyon lotor*) es relativamente alta en tipos de cobertura donde el pizote (*Nasua narica*) está ausente. Colocamos 56 cámaras trampa entre junio de 2016 y junio de 2017 para comparar la ocurrencia y actividad del pizote y el mapache en diferentes tipos de cobertura, incluyendo éstas y otras 45 cámaras monitoreadas de manera irregular entre 2011 y 2016. En un año, ninguna cámara registró ambas especies, con la excepción del bosque ribereño. Las tasas fotográficas de mapache fueron mayores en el manglar y bosque de playa, no obteniendo registros en bosque primario y secundario. Los registros de pizote fueron mayores en bosque secundario y ausentes en el manglar y bosque de playa o pastizales arbolados. El mapache mostró mayor actividad nocturna mientras el pizote diurna, observando tasas fotográficas de pizotes (1.37/100 noches de trampa [tn]; n = 20.416 tn) que fueron más del doble que los mapaches (0.48). Las diferencias en los registros fotográficos para cada especie por tipo de cobertura y horario sugieren un patrón de alopatría local. Esta segregación interespecífica entre pizote y mapache puede atribuirse a diferencias en alimentación, además de competencia. Finalmente, este estudio mostró que las cámaras pueden proporcionar información valiosa sobre la ecología de las especies crípticas como este estudio.

Palabras clave: Actividad; cámara; distribución; *Nasua narica*; *Procyon lotor*; simpatría; tasas fotográficas; uso del tipo de cobertura.

Temporal avoidance and differential resource use are among the variety of ways in which sympatric species can co-exist and thus minimize competition (Arlettaz 1999; Kronfeld-Schor and Dayan 2003). The potential for competition is increased for species within a particular guild, and especially for species that are closely related taxonomically (MacArthur and Levins 1967). Studies of sympatric carnivores in the same taxonomic family and guild can provide revealing insights into ecological co-existence (*e.g.*, Powell and Zielinski 1983; Johnson *et al.* 1996; Santos *et al.* 2019).

Northern raccoons (*Procyon lotor*) and white-nosed coatis (*Nasua narica*) are the only terrestrial Procyonids that also can climb trees in the dry forests of northwestern Costa Rica (Carrillo *et al.* 2000). Both species are omnivorous and reportedly feed on fruits, nuts, invertebrates, turtles, turtle and bird eggs, and frogs; northern raccoons also feed on crustaceans and fish, while coatis also feed on small mammals, and eggs of lizards (Eckrich and Owens 1995; Reid 1997; de la Rosa and Nocke 2000; Wainwright 2007). The species are similar in size (4-5 kg; Wainwright 2007), as well, and the possibility of interspecific competition seems reasonable.

Here we begin to elucidate factors that allow for co-existence between these 2 sympatric procyonid species in a dry forest of northwest Costa Rica. We derived aspects of their space use, activity patterns, and relative abundance from camera trap data collected during long-term studies of jaguars (*Panthera onca*; Montalvo *et al.* 2020). We aimed to assess patterns of relative activity and cover-type use in an area where both species co-existed and thus identify if interspecific avoidance might be a means of co-existence. For sympatric species that are taxonomically related, of similar size, and with overlapping omnivorous diets, we expected that activity pattern overlap would be low but hypothesized that raccoons would have relatively higher occurrence in the lowlands near the beach whereas coatis would be more common in the upland forests.

Study area. We collected procyonid photos in the Santa Rosa National Park located in Northwest Costa Rica (10° 53´ N, 85°46′W). This 387 km^2 area is dominated by one of the few seasonally dry forests remaining in Central America (Jimenez *et al.* 2016). It has undergone a large-scale restoration effort that was initiated in the 1980's and involved protected area status, the recovery of abandoned pastures by active fire suppression, protection from many human activities, and the recovery of large vertebrate populations (Janzen and Hallwachs 2016). The sector contains evergreen forests dominated by live oak (*Quercus oleoides*), many other species that co-occur in the adjacent mixed deciduous forest where oaks are rare, and more typical species from tropical dry forest (Powers *et al.* 2009). Several areas of Santa Rosa are covered with a mosaic of pasture and secondary growth in various stages of regeneration and have different land use histories, past land use intensities, and different occurrences of discrete anthropogenic events such as fire (Kalacska *et al.* 2004). Mangrove forests occur in the lowlands near the coast at stream and river outlets.

Mean annual rainfall in Santa Rosa (~1,600 mm) is highly seasonal; the wet season (months with an average > 100 mm of rain; average maximum temperatures ~ 29-31 °C) is May to November, and the dry season (with almost no rain and maximum temperatures > 35 °C) is December to April (Janzen 1993; Waylen *et al.* 1996). During the dry season, many forest patches lose their leaves though a few evergreen-forest patches retain them. Most of the rivers and streams in the study area run dry and the remaining waterholes become important providers of free water for wildlife (Campos and Fedigan 2009).

Photograph collection. To compare procyonid cover type use and occurrence, part of our survey effort included one period (June 15, 2016 to June 13, 2017) when we had a constant camera trap effort using 56 automatic trail cameras (Bushnell®, Trophy Cam models 119436, 119446, 119456) in a grid array over an area of 87 km^2. Half of the cameras (1 camera per site) were at a trail location that jaguars (*Panthera onca*) were likely to use, and the other half at an off-trail location an average of 0.59 km ± 0.25 SD away from the nearest trail camera (Figure 1). For assessment of procyonid activity patterns, we used a larger camera trapping data set (all within the grid array) from 2011-2017 (including the survey noted above) to increase sample size. Cameras were deployed at a total of 101 different sites, including waterholes, on pathways (*e.g.*, roads, human trails, and animal paths) and at random sites within the forest, for 34-365 days during each year. Camera placement often differed from 1 year to the next and the duration of continuous camera deployment at individual sites each year was affected by camera malfunctions, limited battery life in combination with logistics of camera checks, vandalism, and initial study design for deployment.

For all surveys, each camera was attached to a tree at a height of approximately 40 cm and set to be active for 24 hr/day. Cameras were set either in video mode (30-sec video, minimum 1 sec between successive videos) or photograph mode (3 consecutive photos with a minimum delay of 1 sec between consecutive triggers). Once deployed, cameras were checked on every month or so to replace batteries and change SD memory cards, if necessary. This research followed ASM guidelines (Sikes *et al.* 2016).

Photographs or videos were considered independent photo events of a species if they were: 1) taken at least 30 min apart (*e.g.*, a series of 3 photos of the same animal[s] taken in consecutive seconds = 1 photo event); 2) consecutive photos of the same species could be identified as different individuals (spots, scars, sex) and not part of the same group (*e.g.*, > 15 min apart, going in opposite directions = 2 photo events); or 3) photos of the same species separated by photos of a different species (*e.g.*, species A, followed 2 min later by a species B, followed 5 min later by species A = A species with 2 photo events and another species B with 1 photo event).

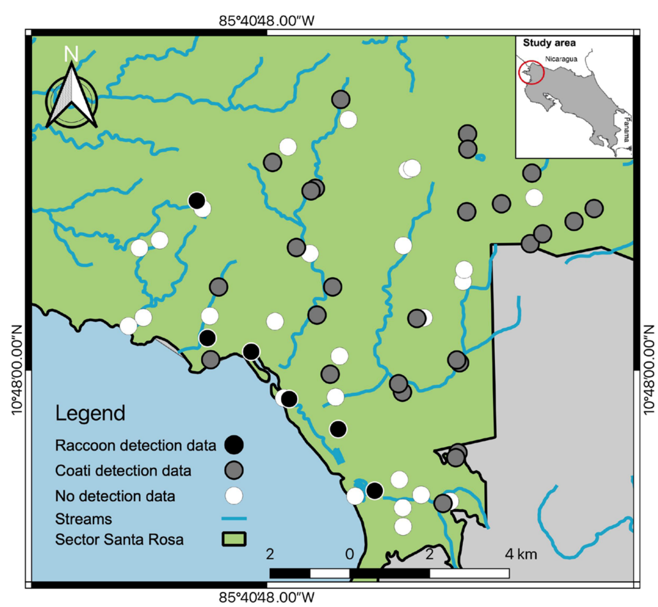

Figure 1. Detections of Northern raccoons (*Procyon lotor*) and white-nosed coatis (*Nasua narica*) during June 15, 2016, to June 13, 2017 at camera trap locations in Santa Rosa National Park, northwest Costa Rica.

Data analyses. We pooled cover types at capture sites into 5 categories: Primary Forest; Secondary Forest, including early and later stage forests, some mixed with lesser amounts of primary forest; Mangrove and Beach Forest; Riparian Forest, sometimes with some secondary forest; and Grassland with Trees, sometimes with some secondary forest. Chi-square tests (Snedecor and Cochran 1972) were used to compare the frequency distribution of photos of each species taken at trap sites in different cover types, as well as photo rates (number of independent photos/100 trap nights) for each species among cover types. We also used Chi-square tests to compare species-specific differences in the photo rates between species.

For comparison of relative activity patterns, we used the times that the first photo of an independent photo event was taken. To quantify relative activity patterns (Ridout and Linkie 2009) we used the R software package activity 1.3 (Rowcliffe 2019), and a Wald test to contrast temporal distribution aggregation differences for circular data smoothed with 10,000 bootstrap resamples to calculate confidence intervals (Rovero and Zimmermann 2016).

Coatis were photographed at almost half of the camera stations (27 of 56) throughout the study area, but raccoons were photographed at only 7, mostly near the coast (Figure 1). During June 2016-June 2017 photo rates of coatis (1.37; 280 independent photos/20,416 trap nights) in our study area were 2.9x's those of raccoons (0.48; 98 independent photos/20,416 trap nights; $x^2 = 88.45$, d. f. = 1, $P < 0.001$).

At any given trap, only 1 of the species was ever photographed; that is, at no single camera were both species photographed over the course of the year. A comparison of the number of trap sites in different cover types where a species was photographed (Table 1) indicated that each species was captured at traps in 3 of 5 cover types, but both species were only photographed in the Riparian Forest cover-type and thus the overall distribution of captures differed by species ($x^2 = 42.04$, d. f. = 8, $P = < 0.001$). Comparing photo rates of each species among cover types (Table 2), the rate for raccoons was higher in Mangrove and Beach Forest (3.43 independent photos/100 trap nights[raccoons] *vs* 0 independent photos/100 trap nights[coatis]; $x^2 = 572.2$, d. f. = 4, $P < 0.001$), and for coatis was highest in Secondary Forest (0 independent photos/100 trap nights[raccons] *vs* 2.73 independent photos/100 trap nights[coatis]; $x^2 = 151.5$, d. f. = 4, $P < 0.001$). Raccoons also were photographed in the Grassland with Trees cover-type, and coatis in Primary and Secondary Forests.

Table 1. Distribution of northern raccoons (*Procyon lotor*) and white-nosed coatis (*Nasua narica*) captures at camera trap sites in different cover types in Santa Rosa National Park, northwest Costa Rica during June 15, 2016 to June 13, 2017. $x^2 = 42.04$, 8 d. f., *P*-value < 0.001.

Covertype	Number of cameras sites at which procyonid species were captured			
	Only northern raccoon	Only white-nosed coati	Neither	Total
Secondary Forest	0	11	6	17
Mangrove and Beach Forest	5	0	1	6
Grassland with Trees	1	0	6	7
Primary Forest	0	13	7	20
Riparian Forest	1	3	2	6
Total	7	27	22	56

Table 2. Photo rates (No. independent photo events/100 trap nights; *n* = 20,416 trap nights in total) of northern raccoons (*Procyon lotor*) and white-nosed coatis (*Nasua narica*) in different cover types in Santa Rosa National Park, northwest Costa Rica during June 15, 2016 to June 13, 2017. [a] $x^2 = 572.2$, 4 d. f., $P < 0.001$. [b] $x^2 = 151.5$, 4 d. f., $P < 0.001$.

Cover type	Northern raccoon [a]	White-nosed coati [b]
Secondary Forest	0.0	2.73
Mangrove and Beach Forest	3.43	0.0
Grassland with Trees	0.09	0.0
Primary Forest	0.0	1.26
Riparian Forest	0.14	1.16

Relative activity patterns derived from photographs indicated that although raccoons were clearly nocturnal and coatis were diurnal (only 30 % overlap), both species we recorded as having some activity throughout the 24 hr diel period (Wald (x^2) statistic = 0.942, d. f. = 1, $P = 0.331$), showing a pattern of temporal segregation with no statistical evidence (Figure 2).

Of the 6 species in the family Procyonidae resident in Costa Rica, the olingo (*Bassaricyon gabbii*), the cacomistle (*Bassariscus sumichrasti*), and the kinkajou (*Potos flavus*) are considered terrestrial as well as arboreal, nocturnal, and solitary (de la Rosa and Nocke 2000; Wainwright 2007). Both, the crab-eating raccoon (*Procyon cancrivorus*) and the northern raccoon, though mostly nocturnal and solitary, are terrestrial as well as arboreal. The white-nosed coati is both terrestrial and arboreal like the raccoons, but is diurnal and, unlike any of the other Procyonids, is social (females and young, but not adult males; de la Rosa and Nocke 2000; Wainwright 2007).

In general, northern raccoons in Central America are said to be uncommon in mature evergreen forest (Reid 1997) but are otherwise widespread "in a variety of habitats, including primary and secondary forests (generally at low elevations), swamplands, mangrove forests, beaches, abandoned and cultivated farms, and urban habitats" (de la Rosa and Nocke 2000). White-nosed coatis are also widespread, and can be found in dense tropical rain forests, deciduous and evergreen forest, secondary growth, and more temperate scrub lands (Reid 1997; de la Rosa and Nocke 2000). Results from our study, where the species are sympatric, concur with these general patterns; we found that raccoons were more common near the coast and coatis more in upland forests. In coastal sites of Western Costa Rica, crabs are a particularly common prey of raccoons (Carrillo *et al.* 2001; Timm *et al.* 2009; Yaney-Keller *et al.* 2022), and raccoons preferred mangrove forests where coatis preferred palm stands (Yaney-Keller *et al.* 2022). Inland from coastal areas, Cove *et al.* (2014) found that forest cover had a negative influence on detection probabilities for coatis and their distribution

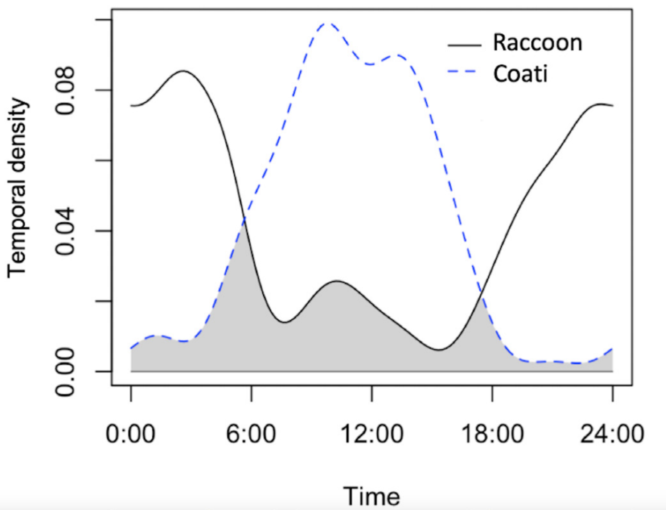

Figure 2. Northern raccoons (*Procyon lotor*) and white-nosed coatis (*Nasua narica*) activity overlap (gray shaded area = 30 % overlap, but not statistically different; Wald (x^2) statistic = 0.942, d. f. = 1, P = 0.331) as estimated from camera-trapping records collected during 2011-2017 in Santa Rosa National Park, northwest Costa Rica.

was likely influenced by agricultural food resources (*i.e.*, pineapple), and that their raccoon model contained minimal support for habitat covariates influencing detection but suggested that potential avoidance of agricultural food resources (perhaps an artifact of limited raccoon detections or avoidance of areas of high use by tayras and coatis; Cove *et al.* 2014). In an inland site in Sonora, México, coatis showed selection for oak forest and oak-pine forest while raccoons showed selection for the natural grassland (Sáenz Amador 2015). From a compilation of camera trapping studies throughout Central America in which both species were "captured" (Table 3), our ratio of raccoon captures to coati captures (0.35) was a median value within a wide range (< 0.1-7.39). Importantly, the 2 locations where photo rates of raccoons were higher than for coatis were in coastal areas (elevation = 0-10 m).

Activity patterns of co-occurring raccoons and coatis in other areas are similar to those we found. In Southern Costa Rica, Costa Rica coatis were 91 % diurnal, but raccoons were 96 % nocturnal (Botts *et al.* 2020), and in Sonora, México, coatis were mostly crepuscular while raccoons were active mostly at night (Sáenz Amador 2015).

The few studies of coexisting brown-nosed coatis (*Nasua nasua*) and crab-eating raccoons (*Procyon cancrivorus*) in South America parallels that of their northern counterparts. In one study, there was high diet overlap between species but raccoons, and not coatis, consumed fish and crustaceans (Aguiar *et al.* 2011). In Brazil for both species, there was 45 % overlap in active periods, with raccoons more nocturnal and coatis more diurnal (Bianchi *et*

Table 3. Photos rates (number of events/100 trap nights), and ratios of photo rates, of co-occurring northern raccoons (*Procyon lotor*) and white-nosed coatis (*Nasua narica*) in Central America. *Includes both *Procyon lotor* and *P. cancrivorus*.

Location	Latitude (°N)	Elevation (m)	No. of trap nights	Photo rate raccoon (r)	Photo rate coati (c)	Ratio r/c	Reference
Sierra Zapote Reserve, northwestern Costa Rica	10.2	260-350	2,135	0.05	14.60	< 0.01	Marín Pacheco *et al.* 2022
Lapa Verde Wildlife Refuge, northcentral Costa Rica	10.5	50-100	1,584	0.13	3.79	0.03	Mattey Trigueros *et al.* 2022
Piedras Blancas National Park, southern Costa Rica	8.7	0-350	1,440	0.35	5.76	0.06	Beal *et al.* 2020
Los Tuxtlas Biosphere Reserve, southern Veracruz, México	18.3	100-700	936	0.75	13.57	0.06	Flores-Martinez *et al.* 2022
Ecoparque Panama protected area, central Panamá	9.1	50-100	2,400	0.17	2.13	0.08	Springer *et al.* 2012
Yaxchilan, Chiapas, México	16.9	< 320	3,973	0.50	5.29	0.09	Arroyo-Gerala *et al.* 2024
Sierra Madre del Sur (SMS) ecoregion, Guerrero, México	17.8	350-1500	24,974	0.16	1.66	0.10	Ruiz-Gutiérrez *et al.* 2020, 2023
Montes Azules, Chiapas, México	16.2	~200	3,841	0.78	3.91	0.20	Arroyo-Gerala *et al.* 2024
San Juan–La Selva Biological Corridor, northern Costa Rica	10.5	30-60	6,356	0.33	1.13	0.29	Pardo Vargas *et al.* 2016
Northeastern Sonora, México	30.9	~900-1,500	14,700	4.66	13.70	0.34	Sáenz Amador 2015
Santa Rosa National Park, northwest Costa Rica	10.9	3-350	20,416	0.48	1.37	0.35	This study
Private reserves w/forest and coffee plantations, southwest Guatemala	14.5	1700-1900	630	1.90	4.90	0.39	Escobar-Anleu *et al.* 2023
Marqués de Comillas, Chiapas, México	16.1	140-200	2,824	1.06	2.48	0.43	Arroyo-Gerala *et al.* 2024
Osa-Golfito region, southwest Costa Rica	8.7	0-450	12,276	4.16*	8.06	0.52	Vargas Soto *et al.* 2022
Barra del Colorado Wildlife Refuge, northeastern Costa Rica	10.6	10-40	1,611	0.37	0.68	0.54	Arroyo-Arce *et al.* 2016
Barbilla-Destierro Biological Corridor, central Costa Rica	10.0	300-800	16,904	0.94	1.63	0.58	Salom-Pérez *et al.* 2021
Cinchona, central Costa Rica	10.3	800-1450	1,556	0.39	0.51	0.76	Villegas-Arguedas 2022
Osa-Golfito region, southwest Costa Rica	8.7	25-1,500	753	10.2	10.9	0.94	Yaap *et al.* 2015
La Encrucijada Biosphere Reserve, Chiapas, México	14.7	0-10	5,400	4.35	3.91	1.11	Hernández Hernández *et al.* 2018
Cabuyal and Zapotillal estuaries, northwest Costa Rica	10.7	0-20	1,498	11.82	1.60	7.39	Yaney-Keller *et al.* 2022

al. 2016), and in a third area, activity was reported as diurnal for coatis and nocturnal for crab-eating raccoons (Dutra et al. 2023). Finally, pygmy raccoons (*Procyon pygmaeus*) and dwarf coatis (*Nasua* [*narica*] *nelsoni*), both endemic to Cozumel Island, México, were both cathemeral with 78 % overlap in activity (Lara-Godínez *et al.* 2023), both species, however, have very limited distribution on the island, with the raccoons in a few coastal sites and coatis so rare as to preclude habitat designations (McFadden *et al.* 2010).

Differences we observed in the distribution of photos by cover type, camara location, and time of day for the procyonid species were notable and might suggest local allopatry, likely the result of interspecific avoidance. We recognize that there were limitations to our data analyses because of low numbers of photos, and inequal survey sampling across cover types. Previous modeling (Montalvo *et al.* 2023) indicated that photo rates of raccoons were higher at cameras located on trails than off trails, but likely did not vary between seasons. For coatis, photos rates were higher at cameras located off trails *vs* on trails and, like raccoons, likely did not vary between seasons. Sample sizes for our study were too small to assess location- or season-specific differences in raccoon and coati distribution related to cover-types, species-specific food habits and predation, or competitive interactions with other species, but such analyses certainly would be of interest in future, more extensive studies. Other techniques should be used to investigate these factors, but cameras can provide important insights into elusive species' ecology.

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