Mammalian Biology
https://doi.org/10.1007/s42991-024-00440-4

ORIGINAL ARTICLE

Aspects of coexistence of two sympatric skunks in a dry forest of northwest Costa Rica

Todd K. Fuller[1] · **Victor H. Montalvo**[2] · **Carolina Sáenz-Bolaños**[2] · **Eduardo Carrillo**[2]

Received: 6 November 2023 / Accepted: 4 July 2024

Abstract

We examined some factors that might allow for the coexistence of two sympatric skunk species, southern spotted skunks (*Spilogale angustifrons*) and striped hog-nosed skunks (*Conepatus semistriatus*), in a dry forest of northwest Costa Rica (Santa Rosa Sector of Guanacaste National Park) by comparing distribution of captures and occurrence in cover-types derived from 56 camera traps monitored from June 2016-June 2017, as well as relative activity patterns derived from these and 45 other cameras in the same area monitored irregularly from 2011 to 2016. Photo rates of spotted skunks in our study area were twice those of striped skunks. At no camera were both species photographed over the course of a year, but both species were commonly recorded in the same cover types. Photo rates of spotted skunks, however, were higher than expected in Secondary Forest and lower in Riparian Forest, whereas for striped skunks the rate was higher than expected in Mangrove and Beach Forest. Both species were clearly nocturnal, and the plots suggesting that spotted skunks were more active than striped skunks before midnight, and striped skunks were more active after midnight, were not significantly different. Differences we observed in the distribution of photos by cover types and camara location for the two skunk species were notable and suggest local allopatry, likely the result of interspecific avoidance. Species-specific food habits, predation, and competition with other species may also be an important factor affecting these observations, and other techniques should be used to investigate these factors. Still, cameras can provide important insights into cryptic species' ecology.

Keywords Activity · Camera · *Conepatus semistriatus* · Cover type use · Distribution · Photo rates · *Spilogale angustifrons* · Sympatry

Introduction

A long-standing research focus in community ecology and biogeography is the coexistence among ecologically similar species within communities (MacArthur and Levins 1967; Hubbell 2005), a topic that has important implications for conservation (Dempster 1975). In animals, sympatric coexistence may be a result of niche partitioning and differentiation (Schoener 1974), and niche breadths (e.g., resource use, habitat type use) of coexisting species are expected to influence the mechanisms for niche differentiation (Büchi and Vuilleumier 2014). Among the variety of ways in which sympatric species can co-exist, and thus minimize competition, are temporal avoidance and differential resource use (Arlettaz 1999; Kronfeld-Schor and Dayan 2003). Within a particular guild, the potential for competition is increased, especially for species that are closely related taxonomically (MacArthur and Levins 1967). Thus, studies of carnivores in the same taxonomic family (i.e., "confamilial"), for example, can provide revealing insights into ecological co-existence (e.g., Powell and Zielinski 1983; Johnson et al. 1996; Santos et al. 2019), and on the potential for strong competitive interactions (Simberloff and Dayan 1991).

Two or more of the 12 species of skunks (Family Mephitidae) of the Americas (Hernández-Sánchez et al. 2022; McDonough et al. 2022) occur sympatrically throughout much of their range. Where more than one species has been studied, there appear to be some differences in activity peaks

Handling editor: Amando Bautista.

✉ Todd K. Fuller
tkfuller@eco.umass.edu

[1] Department of Environmental Conservation, University of Massachusetts, Amherst, MA 01003, USA

[2] Instituto Internacional en Conservación y Manejo de Vida Silvestre, Universidad Nacional, Apdo, 1350-3000 Heredia, Costa Rica

and patterns (Neiswenter et al. 2010; Farías-González and Hernández-Mendoza 2021), likely caused by interference competition (Hernández-Sánchez & Santos-Moreno 2022). In one recent study of sympatric skunks, a temporal avoidance strategy to decrease the potential for direct encounters with the dominant species, but activity patterns were also influenced by the activity of prey and native and exotic predators, as well as relative humidity, precipitation, cloud cover, and night length (Hernández-Sánchez and Santos-Moreno 2022). In addition, smaller spotted skunks (*Spilogale* spp.) are less generalist in habitat use (Doty and Dowler 2006; Neiswenter and Dowler 2007) and often differ in use from other skunk species (Cervantes et al. 2002).

Range overlap between southern spotted skunks (*Spilogale angustifrons*; 0.5–1 kg) and larger striped hog-nosed skunks (*Conepatus semistriatus*;1.4 to 3.5 kg) is reported to occur from the central and eastern Yucatan in Mexico in the north, and south through Belize, eastern Guatemala, central Honduras, eastern Nicaragua, to northwestern Costa Rica (Cuarón et al. 2016a; Helgen et al. 2016), but little is known of their co-existence. A third species, the hooded skunk (*Mephitis macroura*), is rarely reported as inhabiting northwestern Costa Rica, as well (Janzen 1983; Wainwright 2007, but see Cuarón et al. 2016b), and we obtained no photos of hooded skunks.

In this study we were interested in elucidating some factors that allow for co-existence between two sympatric skunk species in a dry forest of northwest Costa Rica. To that end, aspects of their space use, activity patterns, and photo rates were derived from camera trap data collected during long-term studies of jaguars (Montalvo et al. 2020). Our objective was to assess patterns of cover-type use and relative activity patterns in an area where both species co-exist. From these results, we also sought to identify if interspecific avoidance might be a means of co-existence.

Methods

Study area

We collected skunk photos in the Santa Rosa Sector of Guanacaste National Park located in northwest Costa Rica (10°53N 85°46′W; Boza 1992). The 387-km^2 Santa Rosa Sector is dominated by one of the few seasonally dry forests remaining in Central America (Jimenez et al. 2016), and has undergone a large-scale restoration effort that was initiated in the 1980’s involving protected area status, the recovery of abandoned pastures by active fire suppression, protection from many human activities, and the recovering of large vertebrate populations (Janzen and Hallwachs 2016). The sector contains evergreen forests dominated by live oak (*Quercus oleoides*) but also including a large number of 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). The forests on the hill slopes and in the lowlands are more diverse and with varying degrees of deciduousness. Several areas of Santa Rosa are covered with a mosaic of pasture and secondary growth in various stages of regeneration with areas that have different land use histories, past land use intensities as well as different occurrences of discrete anthropogenic events such as fire (Kalacska et al. 2004). Mangrove forests occur in lowland areas near the coast at stream and river outlets.

Mean annual rainfall in Santa Rosa totals ~ 1,600 mm but 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 2011–2017, total precipitation during the rainy season varied from 617 to 2531 mm (mean = 1524). During the dry season, many forest patches lose their leaves and few evergreen-forest patches retain them. In addition, 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 skunk cover type use and encounter rate, we used data collected continuously from 15 June 2016 to 13 June 2017 using 56 automatic trail cameras (Bushnell®, Trophy Cam models 119,436, 119,446, 119,456) in an area of 87 km^2. Cameras were set in pairs throughout the area. For each pair, one of the cameras was set at a trail location that jaguars (*Panthera onca*) were likely to use; the other camera was set at an off-trail location an average of 0.59 km ± 0.25 SD away from the nearest trail camera (Fig. 1; Montalvo et al. 2023). Skunks have not been identified in jaguar diets (Hayward et al. 2016) and thus we did not consider that the results could have been biased by the presence/absence of jaguars. Also, a previous analysis (Montalvo et al. 2023) indicated no trail or season effects on striped hog-nosed skunk distribution (samples were too small to assess spotted skunks), and thus those factors were not considered in this analysis.

For assessment of skunk relative activity patterns, we used a larger camera trapping data set from 2011 to 2016 (including data from the survey noted above and restricted to cameras within that survey area). 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 one year to the next. The duration of

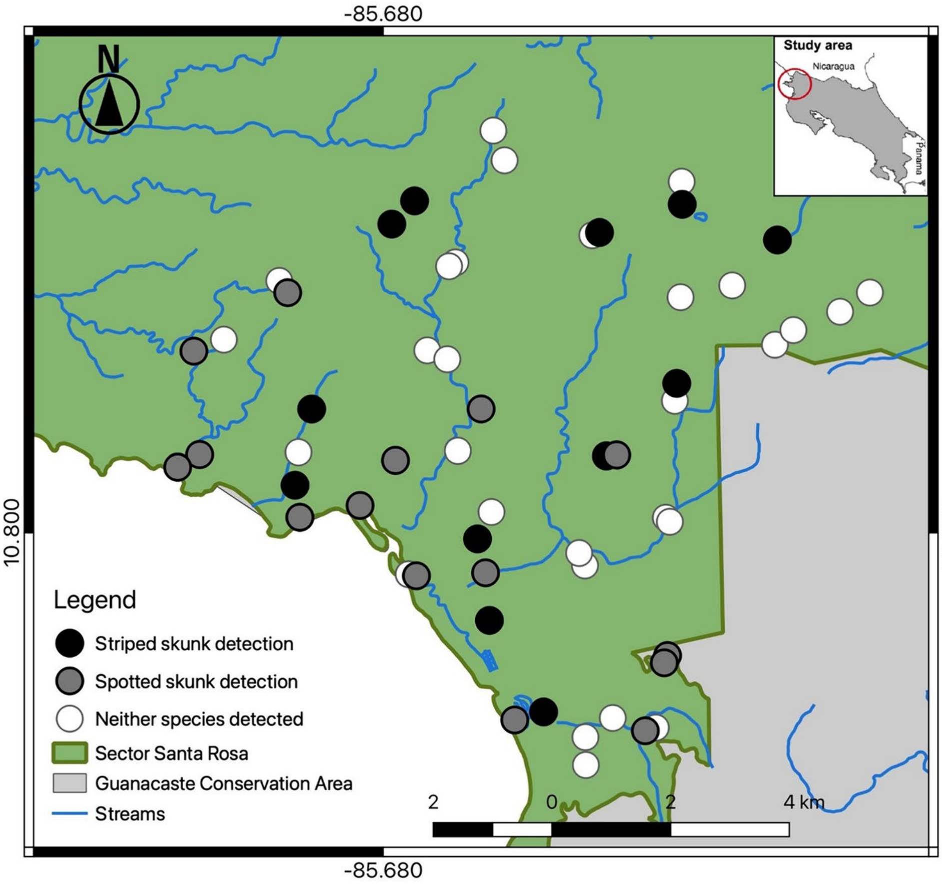

Fig. 1 Detections of two skunk species during 15 June 2016 to 13 June 2017 at camera trap locations in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica. There were no locations where both species were detected over the course of the study

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 h/day. Cameras were set either in video mode (30-s video, minimum 1 s between successive videos) or photograph mode (3 consecutive photos with a minimum delay of 1 s 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 an independent photo events of a species if they were: (1) taken at least 30 min apart (e.g., a series of three 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 = two photo events); or (3) photos of the same species separated by photos of a different species (e.g., species 1, followed 2 min later by a species 2, followed 5 min later by species 1 = one species with two photo events and another species with one photo event).

Data analyses

Cover types at the 56 capture sites were pooled into five categories that included: 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 were used to compare the number of trap sites in different cover types where a species was photographed, as well as photo rates (number of independent photos/100 trap nights) for each species among cover types. Photo rates did not differ for either species between seasons (P = 0.416–0.580), or by site (trail vs. off-trail; P = 0.138–0.263) so data were pooled across the year and sites. We also used Chi-square tests (Social Science Statistics—https://www.socscistatistics.com/tests/chisquare2/default2.aspx) to compare species specific-differences in the photo rates between species and among studies.

Table 1 Number of trap sites (i.e., camera sets) in different cover types where a species was photographed in Santa Rosa National Park, northwestern Costa Rica during 15 June 2016 to 13 June 2017

Covertype	Only southern spotted skunk	Only striped hog-nosed skunk	Neither	Total
Secondary forest	5	2	10	17
Mangrove and beach forest	3	2	1	6
Grassland with trees	2	2	3	7
Primary forest	5	4	11	20
Riparian forest	0	2	4	6
	–	–	–	–
Total	15	12	29	56

There were no significant differences detected in the species-specific distribution of skunks among cover types; see results text for details on statistics

For relative activity comparisons, the time that the first photo of an independent photo event was taken was used in analyses. To quantify relative activity patterns, we used Ridout and Linkie's (2009) approach with the R (https://www.r-project.org) software package activity 1.3.3 (Rowcliffe 2023), using 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).

Results

Though during June 2016-June 2017 photo rates of spotted skunks (0.66; 135 independent photos/20,416 trap nights) in our study area were twice those of striped skunks (0.32; 65 independent photos/20,416 trap nights; $\chi^2 = 24.62$, df = 1, $P < 0.001$), skunks of both species were photographed at camera stations throughout the study area (Fig. 1). However, at any given trap, only one of the species was ever photographed; that is, at no single camera were both species photographed over the course of the year.

We first compared the number of trap sites in different cover types where a species was photographed (Table 1). Each species was captured at traps in four or five cover types (no spotted skunks were photographed in Riparian Forest), and the number of sites in cover types where each skunk species were photographed was not significantly different ($\chi^2 = 6.61$, df = 8, $P = 0.579$). We then compared photo rates of each species among cover types (Table 2), and found that for spotted skunks, the rate was significantly higher than expected in Secondary Forest (partial $\chi^2 = 4.70$, df = 1, $P = 0.030$), and significantly lower in Riparian Forest (partial $\chi^2 = 11.63$, df = 1, $P < 0.001$; overall $\chi^2 = 22.02$, df = 4, $P < 0.001$). For striped skunks, the rate was significantly higher than expected in Mangrove and Beach Forest (partial $\chi^2 = 21.73$, df = 1, $P < 0.001$; overall $\chi^2 = 26.30$, df = 4, $P < 0.001$).

Table 2 Photo rates (independent photos/100 trap nights; total = 20,416 trap nights) of skunk species in different cover types in Santa Rosa National Park, northwestern Costa Rica during 15 June 2016 to 13 June 2017

Cover type	Total trapnights	Southern spotted skunk	Striped hog-nosed skunk
Secondary forest	5888	0.89(+)[a]	0.22
Mangrove and beach forest	2712	1.00	0.86(+)
Grassland with trees	2241	0.77	0.18
Primary forest	7558	0.52	0.30
Riparian forest	2071	0(-)	0.25

[a] Significantly higher (+) or lower (–) than expected as indicated by partial Chi-square value; see results text for details on statistics

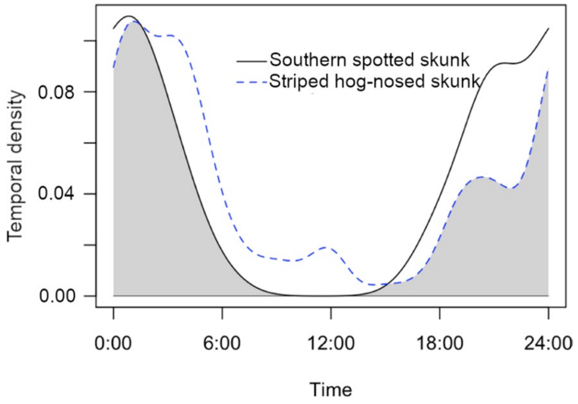

Fig. 2 Southern spotted skunk and striped hog-nose skunk activity overlap (gray shaded area = 77% overlap; Wald χ^2 statistic = 0.10, df = 1, $P = 0.917$) as estimated from camera-trapping records collected during 2011–2017 in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica

Relative activity patterns derived from photographs suggested that both species were clearly nocturnal (Fig. 2). We did not find statistical evidence that spotted skunks were more active than striped skunks before midnight, and striped skunks were more active after midnight. However, the only daytime photos we acquired were those of striped skunks.

Discussion

In our study, striped hog-nosed skunks photo rates were highest in mangrove and beach forest, though they were recorded in all other forest types. The striped hog-nosed skunk is fairly common in most parts of Costa Rica and reported to be found mostly in relatively open habitats such as pastures, secondary growth, and dry forest, but also in primary forest, where it feeds on small insects and vertebrates, and fruit (de la Rosa and Nocke 2000; Wainwright 2007). In general, striped hog-nosed skunks occur along the edges and in gaps of evergreen forests (and rare in areas with pronounced dry seasons; Reid 1997) and seem to be adaptable to some level of human disturbance such as agroforestry, forest edge, grasslands, plantations, etc., with a reported diet concentrated primarily on insects, but also small vertebrates such as lizards and birds, and some fruit (Reid 1997; Cuarón et al. 2016a).

Spotted skunks in our area seemed to be most common secondary forests, and were found in all other forest types except riparian forests. This skunk is restricted to the northwest and Central Valley of Costa Rica (but see Pacheco et al. 2006) and reported to be found in open areas with some cover, brush, and relatively dry forest (Wainwright 2007) and human habitations and farms (de la Rosa and Nocke 2000). Like the striped hog-nosed skunk it also is insectivorous, but also eats fruits and eggs. It also is considered more carnivorous than other skunks, preying or scavenging on rodents, lizards, snakes, and birds (Reid 1997; de la Rosa and Nocke 2000; Wainwright 2007; Helgen et al. 2016). Unlike other skunk species, southern spotted skunks can climb trees to escape predators, forage, or sleep/shelter.

Similar to our findings, where other species of spotted and hog-nosed skunks co-occur, there have been some habitat-specific differences in distribution reported, such as in the relative proportion of observations in grassland (less for spotted skunks) vs. scrubland for each species (Cervantes et al. 2002). Also, like our results, hog-nosed skunks were reported to be more active earlier during the night and spotted skunks more active later in the night (Farias-Gonzalez and Hernandez-Mendoza 2021). However, these two studies (Cervantes et al. 2002; Farías-González and Hernández-Mendoza 2021) also reported that the relative encounter rate and photo rates, respectively, of spotted skunks was lower than for hog-nosed skunks, in contrast to our findings. However, in the only other camera study we could find in which both species were photographed (in Costa Rica, just south of our study; Yaney-Keller et al. 2022), it appeared that, despite relatively small sample size (1498 trapnights), photo rates (number of independent photos/100 trap nights) of southern spotted skunks (2.20) were also significantly higher than for striped skunks (0.33).

Differences we observed in the distribution, activity, and photo rates of two skunk species were notable and seemed to point to local allopatry, or at least spatially interspecific avoidance. But the previously identified differences in species size and species-specific food habits, and perhaps the activity of prey and native and exotic predators, relative humidity, precipitation, cloud cover, and night length (Hernández-Sánchez and Santos-Moreno 2022), also could be factors that allow for co-occurrence in our area and other areas where the species are sympatric.

As a research technique, camera trapping certainly allows for site-specific identification of active (but not inactive) skunks. From these data, we can make preliminary inferences on the species' occurrence, cover type use, and relative activity patterns, but cannot consider the influence of other factors. Clearly, site-specific studies on skunk foraging, food habits, predators, and other environmental factors, as have been conducted elsewhere (e.g., Jachowski and Edelman 2021; Dukes et al. 2022) will better clarify the means by which the species successfully co-occur.

Acknowledgements We thank all of the volunteers and students who collaborated in the field work, and Roger Blanco and the personnel of Guanacaste Conservation Area for their support in the field. We also thank the editors and reviewers for helpful edits, comments, and suggestions.

Author contributions All authors contributed to the study conception and design, data collection, and preparation. The analyses were performed by TKF and VHM. TKF wrote the first draft of the manuscript and all authors commented on previous versions of the manuscript and read and approved the final manuscript.

Funding The National University of Costa Rica (0390–16), the Rufford Foundation, the Gifford-Wyle family, the University of Massachusetts Amherst, and the National Ministry of Science and Technology of Costa Rica (FI-142B-14) provided financial support.

Data availability Data are available from the corresponding author upon request.

Declarations

Conflict of interest The authors state no conflict of interest.

References

Arlettaz R (1999) Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. J Anim Ecol 68:460–471. https://doi.org/10.1046/j.1365-2656.1999.00293.x

Büchi L, Vuilleumier S (2014) Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. Am Nat 183:612–624. https://doi.org/10.1086/675756

Campos FA, Fedigan LM (2009) Behavioral adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Am J Phys Anthro 138:101–111. https://doi.org/10.1002/ajpa.20908

Cervantes FA, Loredo J, Vargas J (2002) Abundance of sympatric skunks (Mustelidae: Carnivora) in Oaxaca, Mexico. J Trop Ecol 18:463–469. https://doi.org/10.1017/S0266467402002328

Cuarón AD, Helgen K, Reid F (2016a) *Conepatus semistriatus*. The IUCN Red List of Threatened Species 2016:e.T41633A45210987 https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41633A45210987.en

Cuarón AD, González-Maya JF, Helgen K, Reid F, Schipper J, Dragoo JW (2016b) *Mephitis macroura*. The IUCN Red List of Threatened Species 2016:e.T41634A45211135 https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41634A45211135.en

de la Rosa CL, Nocke CC (2000) A guide to the carnivores of Central America. University of Texas Press, Austin, Texas

Dempster JP (1975) Animal population ecology. Academic Press, New York, New York

Doty JB, Dowler RC (2006) Denning ecology in sympatric populations of skunks (*Spilogale gracilis* and *Mephitis mephitis*) in west-central Texas. J Mammal 87:131–138. https://doi.org/10.1644/04-MAMM-A-172R2.1

Dukes CG, Jachowski DS, Harris SN, Dodd LE, Edelman AJ, LaRose SH, Lonsinger RC, Sasse DB, Allen ML (2022) A review of camera trapping methodology for eastern spotted skunks. J Fish Wildl Manage 13:295–305. https://doi.org/10.3996/JFWM-21-073

Farías-González V, Hernández-Mendoza KH (2021) Coexistence of three mephitids in Tehuacán-Cuicatlán Biosphere Reserve, México. Therya 12:527–536. https://doi.org/10.12933/therya-21-1118

Hayward MW, Kamler JF, Montgomery RA, Newlove A, Rostro-García S, Sales LP, Van Valkenburgh B (2016) Prey preferences of the jaguar *Panthera onca* reflect the post-Pleistocene demise of large prey. Front Ecol Evol 3:148. https://doi.org/10.3389/fevo.2015.00148

Helgen K, Reid F, Timm R (2016) *Spilogale angustifrons*. The IUCN Red list of threatened species 2016:e.T136636A45221538. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T136636A45221538.en

Hernández-Sánchez A, Santos-Moreno A (2022) Drivers of activity patterns of two sympatric skunks (Carnivora: Mephitidae). J Mammal 103:1030–1044. https://doi.org/10.1093/jmammal/gyac038

Hernández-Sánchez A, Santos-Moreno A, Pérez-Irineo G (2022) The Mephitidae in the Americas: a review of the current state of knowledge and future research priorities. Mamm Biol 102:307–320. https://doi.org/10.1007/s42991-022-00249-z

Hubbell SP (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. Funct Ecol 19:166–172. https://doi.org/10.1111/j.0269-8463.2005.00965.x

Jachowski DS, Edelman AJ (2021) Advancing small carnivore research and conservation: the Eastern spotted skunk cooperative study group model. Southeast Nat 20(Special Issue 11):1–12

Janzen DH (1983) Costa Rican natural history. University of Chicago Press, Chicago, Illinois

Janzen DH (1993) Caterpillar seasonality in a Costa Rican dry forest. In: Stamps NE, Casey TM (eds) Caterpillars: ecological and evolutionary constraints on foraging. Chapman and Hall, New York, pp 448–477

Janzen DH, Hallwachs W (2016) Biodiversity conservation history and future in Costa Rica: the case of Área de Conservación Guanacaste (ACG). In: Kappelle M (ed) Costa Rican ecosystems. University of Chicago Press, Chicago, Illinois, pp 290–341

Jimenez Q, Carrillo E, Kappelle M (2016) The northern Pacific lowland seasonal dry forests of Guanacaste and the Nicoya Peninsula. In: Kappelle M (ed) Costa Rican ecosystems. University of Chicago Press, Chicago, Illinois, pp 247–289

Johnson WE, Fuller TK, Franklin W (1996) Sympatry in canids: a review and assessment. In: Gittleman J (ed) Carnivore behavior, ecology, and evolution, vol 2. Cornell Univ. Press, Ithaca, New York, pp 189–218

Kalacska M, Sanchez-Azofeifaa GA, Calvo-Alvarado JC, Quesada M, Rivard B, Janzen DH (2004) Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. For Ecol Manag 200:227–247. https://doi.org/10.1016/j.foreco.2004.07.001

Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. An Rev Ecol Evol Syst 34:153–181. https://doi.org/10.1146/annurev.ecolsys.34.011802.132435

MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. Am Nat 101:377–385. https://doi.org/10.1086/282505

McDonough MM, Ferguson AW, Dowler RC, Gompper ME, Maldonado JE (2022) Phylogenomic systematics of the spotted skunks (Carnivora, Mephitidae, Spilogale): additional species diversity and Pleistocene climate change as a major driver of diversification. Mol Phylogenet Evol 167:107266. https://doi.org/10.1016/j.ympev.2021.107266

Montalvo VH, Fuller TK, Saénz-Bolaños C, Cruz-Díaz JC, Hagnauer I, Herrera H, Carrillo E (2020) Influence of sea turtle nesting on hunting behavior and movements of jaguars in the dry forest of northwest Costa Rica. Biotropica 52:1076–1083. https://doi.org/10.1111/btp.12803

Montalvo VH, Saenz-Bolanos C, Cruz-Diaz JC, Kamilar JM, Carrillo E, Fuller TK (2023) Effects of camera trap placement on photo rates of jaguars, their prey, and competitors in northwestern Costa Rica. Wildl Soc Bull 47:e1428. https://doi.org/10.1002/wsb.1428

Neiswenter SA, Dowler RC (2007) Habitat use of western spotted skunks and striped skunks in Texas. J Wildl Manage 71:583–586. https://doi.org/10.2193/2005-623

Neiswenter SA, Dowler RC, Young JH (2010) Activity patterns of two sympatric species of skunks (*Mephitis mephitis* and *Spilogale gracilis*) in Texas. Southwest Nat 55:16–21. https://doi.org/10.1894/PS-51.1

Pacheco J, Ceballos G, Daily GC, Ehrlich PR, Suzán G, Rodríguez-Herrera B, Marcé E (2006) Diversidad, historia natural y conservación de los mamíferos de San Vito de Coto Brus Costa Rica. Rev Biol Trop 54:219–240. https://doi.org/10.15517/rbt.v54i1.13998

Powell RA, Zielinski WJ (1983) Competition and coexistence in mustelid communities. Acta Zool Fenn 174:223–227

Powers JS, Becknell JM, Irving J, Perez-Aviles D (2009) Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. For Ecol Manag 258:959–970. https://doi.org/10.1016/j.foreco.2008.10.036

Reid FA (1997) A field guide to the mammals of Central American and southeast Mexico. Oxford University Press, New York and Oxford

Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J Agric Biol Envir Stat 14:322–337. https://doi.org/10.1198/jabes.2009.08038

Rovero F, Zimmermann F (2016) Camera trapping for wildlife research. Pelagic Press, UK

Rowcliffe JM. 2023. activity: Animal activity statistics. R package version 1.3.3. Available from https://cran.r-project.org/package=activity (Accessed Oct 2023).

Santos F, Carbone C, Wearn OR, Rowcliffe JM, Espinosa S, Lima MGM, Ahumada JA, Gonçalves ALS, Trevelin LC, Alvarez-Loayza P, Spironello WR (2019) Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. PLoS ONE 14:e0213671. https://doi.org/10.1371/journal.pone.0213671

Schoener TW (1974) Resource partitioning in ecological communities. Science 185(4145):27–39. https://doi.org/10.1126/science.185.4145.27

Sikes RS, the Animal Care and Use Committee of the America Society of Mammologists (2016) 2016 guidelines of the American Society of Mammologists for the use of wild mammals in research and education. J Mammal 97:663–688. https://doi.org/10.1093/jmammal/gyw078

Simberloff D, Dayan T (1991) The guild concept and the structure of ecological communities. Annu Rev Ecol Syst 22:115–143. https://doi.org/10.1146/annurev.es.22.110191.000555

Wainwright M (2007) The mammals of Costa Rica. Cornell University Press, Ithaca, New York

Waylen PR, Caviedes CN, Quesada ME (1996) Interannual variability of monthly precipitation in Costa Rica. J Clim 9:2606–2613. https://doi.org/10.1175/1520-0442(1996)009%3c2606:IVOMPI%3e2.0.CO;2

Yaney-Keller A, Santidrián-Tomillo P, Jordan MA, Lopez-Navas JF, Paladino FV (2022) Patterns of vertebrate biodiversity in a tropical dry and mangrove forest matrix. Rev Biol Trop 70:668–687