Neotropical Naturalist

No. 1 2020

Camera Trapping Scavenging Vertebrates of the Chiriquì Province of Western Panama

Shem D. Unger, Caleb R. Hickman, and Kevin L. Murray

NEOTROPICAL NATURALIST

♦ The *Neotropical Naturalist* (ISSN 2327-5472) is a peer-reviewed journal that publishes articles on all aspects of the natural history sciences of terrestrial, freshwater, and marine organisms and the environments of the neotropics from Mexico through the southern tip of South America. Manuscripts based on field studies outside of this region that provide information on species within this region may be considered at the Editor's discretion.

♦ Manuscript subject matter - The *Neotropical Naturalist* welcomes manuscripts based on fieldwork, observations, and associated lab work that focus on terrestrial, freshwater, and marine fauna, flora, and habitats. Subject areas include, but are not limited to, field ecology, biology, conservation applications, behavior, biogeography, taxonomy, evolution, anatomy, and physiology.

♦ It offers article-by-article online publication for prompt distribution to a global audience.

♦ It offers authors the option of publishing large files such as data tables, and audio and video clips as online supplemental files.

♦ Special issues - The *Neotropical Naturalist*-welcomes proposals for special issues that are based on conference proceedings or on a series of invitational articles. Special issue editors can rely on the publisher's years of experiences in efficiently handling most details relating to the publication of special issues.

♦ Indexing - As is the case with Eagle Hill's other journals, the *Neotropical Naturalist* is expected to be fully indexed in Elsevier, Thomson Reuters, Proquest, EBSCO, Google Scholar, and other databases.

♦ The journal's staff is pleased to discuss ideas for manuscripts and to assist during all stages of manuscript preparation. The journal has a page charge to help defray a portion of the costs of publishing manuscripts. Instructions for Authors are available (http://www.eaglehill.us/neon).

♦ It is co-published with the *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, *Urban Naturalist*, and *Eastern Paleontologist*.

♦ It is available online in full-text version on the journal's website (http://www.eaglehill.us/neon). Arrangements for inclusion in other databases are pending.

Cover Photograph: Image of a *Cathartes aura* (Turkey Vulture) captured by camera traps in Chiriqui, Panama. Photograph © Shem Unger.

The ***Neotropical Naturalist*** (ISSN # 2327-5472) is published by the Eagle Hill Institute, PO Box 9, 59 Eagle Hill Road, Steuben, ME 04680-0009. Phone 207-546-2821 Ext. 4, FAX 207-546-3042. E-mail: office@eaglehill.us. Webpage: http://www.eaglehill.us/neon. Published on an article by article basis. **Special issue proposals are welcome**. The *Neotropical Naturalist* is an open access journal. **Authors**: Submission guidelines are available at http://www.eaglehill.us/neon. **Co-published journals:** The *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, *Urban Naturalist, and Eastern Paleontologist*, each with a separate Board of Editors. The Eagle Hill Institute is a tax exempt 501(c)(3) nonprofit corporation of the State of Maine (Federal ID # 010379899).

Camera Trapping Scavenging Vertebrates of the Chiriquì Province of Western Panama

Shem D. Unger[1*], Caleb R. Hickman[2], and Kevin L. Murray[3]

Abstract - We evaluated the efficacy of short-term baited camera trapping surveys to assess the presence of scavenging vertebrate wildlife in the high elevation mountainous and low elevation coastal areas of the Chiriquì province, western Panama, in January 2018. We detected a total of 12 species on camera traps, including 10 mammals and two birds. The most commonly encountered species across both sites was *Didelphis marsupialis* (Common Opossum). *Bassariscus sumichrasti* (Cacomistle) was the second-most dominant species in high elevation sites, while *Matachirus nudicaudatus* (Brown Four-eyed Opossum) was the second-most common vertebrate at low elevation sites. Other mammals detected during the study included *Dasyprocta punctata*, (Agouti), *Marmosa isthmica* (Isthmian Mouse Opossum), *Scotinomys xerapelinus* (Chiriquì Brown Mouse), *Cuniculus paca* (Lowland Paca), *Nasua narica* (White-nosed Coati), *Dasypus novemcinctus* (Nine-banded Armadillo), and *Canis latrans* (Coyote). Only two bird species were observed, *Rupornis magnirostris* (Roadside Hawk) and *Cathartes aura* (Turkey Vulture). Species activity patterns were predominantly nocturnal (70.9%) with similar Shannon diversity indexes observed of 1.943 and 1.823, for high and low elevation sites, respectively, across 965.6 camera hours, or 40.2 trap days. This report provides baseline data on potential vertebrate scavengers of the Chiriquì province, an area experiencing increasing development and potential loss of habitat connectivity for many Neotropical species.

Introduction

Tropical forests are threatened with increasing fragmentation and deforestation (Brinck et al. 2017, Potapov et al. 2013). Moreover, across Neotropical ecosystems in Central America, native forest vegetation is being increasingly converted for agricultural use (Baltensperger and Brown 2015, Laurance et al. 2014). Mammals inhabiting these environments may play important ecological roles, yet are often restricted to protected habitats (Ripple et al. 2015). Among these ecological roles, scavenging, the use of carrion or dead organisms by vertebrates and invertebrates, has been recently recognized as an important ecological process and important potential food source for many mammals and birds (Beasley et al 2015, Devault et al. 2003). In areas lacking protected reserves or conservation properties, as once contiguous forests become remnant forests, these areas may provide the only vestige of viable habitat remaining in many tropical communities and should be included in surveying for mammals. This is the case in Panama, where increased fragmentation and anthropogenic pressure is threatening species (Meyer et al. 2015, Moreno 1993). Therefore, assessing methods for baseline surveys in understudied areas, e.g., private lands, remains an important goal given the potential for loss of biodiversity in remaining Neotropical habitats.

Camera trap surveys have become an increasingly affordable and effective tool to survey for biodiversity, of primarily mammal populations (Rovero et al. 2014, Rowcliffe and Carbone 2008, Wearn and Glover-Kapger 2019). In some cases they provide similar, if not more precise, measures of relative abundance than more traditional live trapping surveys (Wearn and Glover-Kapfer 2019). Moreover, non-invasive camera trapping in tropical environments allows for ease of species identification, insight into activity patterns, and collection of environmental data measured by cameras, e.g. time,

[1]Biology Department, Wingate University, Bridges Science Building, Wingate, NC 28174, USA. [2]Eastern Band of the Cherokee Indians, 1840 Painttown Road., PO Box 1747, Cherokee, NC 28719, USA. [3]Western Ecosystems Technology, 408 W 6th Street, Bloomington, IN 47404, USA. *Corresponding author - s.unger@wingate.edu.

Manuscript Editor: Kevina Vulinec

temperature (Sunarto et al. 2013). Many camera surveys in tropical habitats rely on long deployment times to monitor population or obtain recapture data (Ahumada et al. 2013, Trolliet et al. 2014). Baiting cameras in tropical areas has been suggested as a method for increasing trap success rate (Kays et al. 2011, Wellington et al. 2014) and may allow for shorter survey and species assessments. However, the use of bait in tropical mammal studies may indirectly alter normal activity patterns and requires further study (Duarte et al. 2018). Herein, we assess the use of short-term baited camera trapping to conduct rapid assessments of vertebrate communities in remnant forested sites in western Panama near agricultural and developed areas on private lands. We also report on comparisons between vertebrate relative abundance sampled in high versus low elevation areas and potential mammalian and avian scavengers. We hypothesized relative abundance would differ between these areas, reflecting local home range distributions across species.

Methods and Materials

Study area. This study was conducted at two locations within Chiriquì province, western Panama (Fig. 1). Site 1 consisted of high elevation primary mountain forest patches (8°49'52"N, 82°36'44"W, elevation = 1630–1840 m) surrounded by agriculture and development near the town of Bambito, while Site 2 consisted of a combination of low elevation coastal cleared land with secondary forest patches predominated by cattle grazing pastures, teak plantations, and development (8°13'2"N, 82°11'2"W, elevation = 14–62 m) near the town of Boca Chica. Both locations are experiencing increasing urban and agricultural development, and remaining forests likely provide important habitat corridors for mammals. The forest type in these areas consists of tropical evergreen/woodland forest (Lyra 2017) in the moist broadleaf forest biome (Reid 2009).

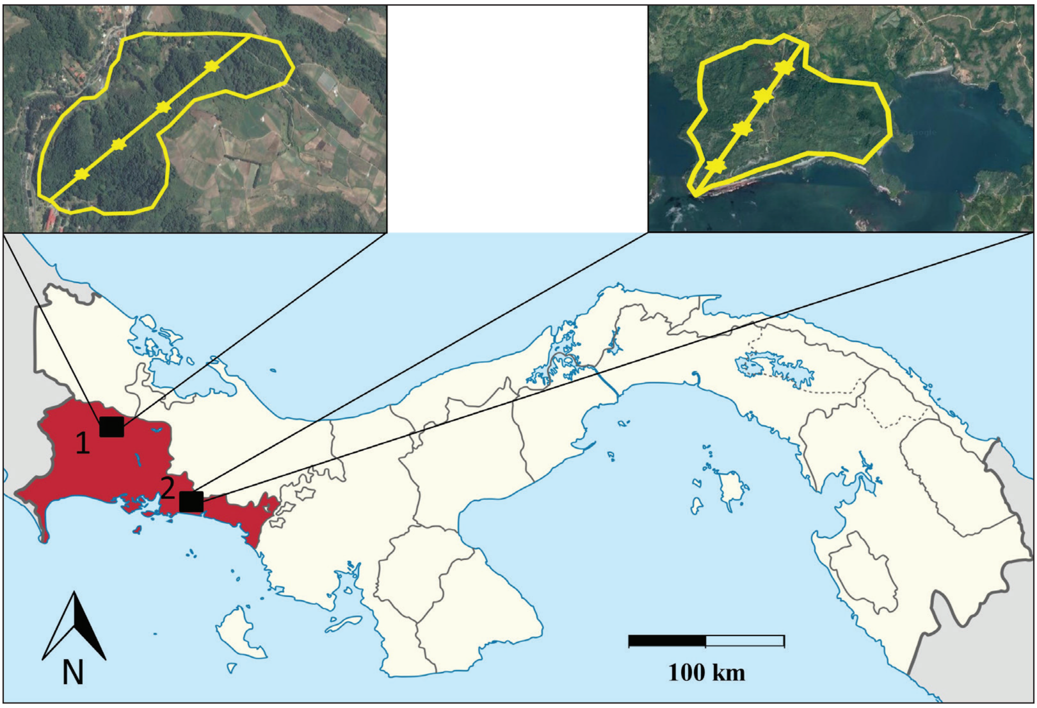

Figure 1. Locations of camera trapping, site 1 (high elevation site), and site 2 (low elevation site) in Chiriquì Province, Panama. Image courtesy of Open Street Map and Google Maps.

Field surveys. We deployed camera traps across 3 km transects covering 55.7 ha of Site 1, and 80.6 ha of Site 2, with vegetation cover area estimated from Google Earth maps (Fig. 1) to maximize area covered for both low and high elevation sites. Each deployment consisted of 4 camera traps per site run simultaneously for 6 days at each location, with Site 1 transect run between 4 and 9 January 2018 and Site 2 transect run between 10 and 15 January 2018 during the "dry" season. Within each transect, we placed cameras ~1000 meters apart to minimize potential resampling of individuals within transects. We used Bushnell Aggressor Trail cameras secured to trees at a height of ~20 cm with keyed locks. Individual cameras were deployed to allow for maximum view, at minimal slope in areas with minimal vegetation obstructing camera view under full forest canopy. Camera settings were as follows: 24 hr recording, infrared and motion capture on, and three pictures per trigger event. We placed locally obtained fish lures (canned sardines) ~2 m directly in front of cameras as bait to increase the likelihood of detection (Thorn et al. 2009) and as a proxy for scavenging, in lieu of carrion (Schwartz et al. 2018). Each camera station was re-baited every 3 days. Temperatures during the deployment period ranged from 21.6–32.2°C to 19.4–32.8°C for high elevation and low elevation, respectively (www.accuweather.com).

Camera trap analysis. We calculated the total number of vertebrates observed, the number of capture events (series of encounter photos >30 minutes apart to limit repeat events from the same individual of the same species) of each following Meek et al. (2014) and Obrien et al. (2003) as a measure of relative abundance. Total trap hours were determined by multiplying the total number of deployment hours by the total number of cameras, and this value was divided by 24 to determine total trap days. As our data was not normally distributed, we used a non-parametric Man-Whitney U test to compare standardized capture event frequency across species (number of capture events/1000 camera days) between sites as a standard measure of frequency to account for variation in camera trap deployment and to make our results more comparable to other published studies of longer deployment efforts (Tobler et al. 2008). We calculated a Shannon diversity index and species richness across sites, and described activity periods for camera captures. Identification of species was conducted by analyzing morphological traits in capture images utilizing Eisenberg (1989), Emmons and Feer (1997), Reid (2009), and Ridgeley and Gwynne (1976), and often using multiple images to aid species identification. We also calculated the mean and range of temperatures (from camera images) associated with capture events for all species. We used R version 3.6.2 for all statistical tests (R Core Team 2019).

Results

In total we collected 4265 images across all trail cameras and locations from 965.6 hours or 40.2 trap days. Trap effort was similar across Site 1 and Site 2, with slightly greater effort at the highland site (550.8 hrs) versus the coastal site (414.8) due to logistical field constraints. We found 12 total species (richness = 12) captured on trail camera images across sites (seven at Site 1 and eight at Site 2; Fig. 2) represented by 141 unique capture events (79 for Site 1, 62 for Site 2), 70.9% of which were nocturnal. The most dominant scavengers encountered across sites were *Didelphis marsupialis* L. (Common Opossum), comprising 50.3% of capture events at both sites combined (33 and 38 capture events for Sites 1 and Site 2, respectively), and *Bassariscus sumichrasti* L. (Cacomistle) which was detected only at the high elevation site where it comprised 17.0% of total capture events (24 capture events at Site 1). Activity patterns were highest during nocturnal hours, early evening and night (1900–0500 h), or with some minimal activity during early daylight hours (0600–1200 h) (Fig. 3). The mean number of species captured by cameras differed between low (6.58 ± 3.4 SE) and high (5.17 ± 3.25) elevation sites, but this difference was not significant, (U = 67, P = 0.3974). Average temperature during capture events was 17.4 ± 0.45 °C and ranged from

8.9–31.7 °C. We noted inter-site differences in the presence of scavengers, with several species only encountered at a single site (Table 1). Across both sites, the Shannon diversity index was 2.3, with values of 1.9 and 1.8 for highland and lowland sites, respectively.

Discussion

Camera surveys provided an effective rapid assessment tool to collect baseline data on tropical vertebrate communities of Panama Neotropical forests. Previous studies have found similar abundances of mammals (Common Opossum, Agouti, and Nine-banded Armadillo) in other provinces of central Panama (Meyer et al. 2015). Agouti densities have been found to be positively correlated with percentage of primary forest (Duquette et al. 2017), and may explain Agouti and Cacomistle presence at the higher elevation site. Many species observed in this study including Lowland Paca, White-nosed Coati, Common Opossum, and Agouti, showed little preference for camera trap location of either random or trail placement in previous studies (Kays et al. 2011). The cacomistle capture events observed in the present study may indicate this scavenger is more frequently encountered at higher elevations, as we did not detect it in any coastal lowland site (Goldman 1920). Our observation of a Coyote at our lowland site provides further evidence of their presence in western Panama, thought to represent more recently expanded geographic range for the species, partially utilizing newly deforested areas (Hidalgo-Mihart et al. 2004, Hody 2016).

The activity patterns we observed were largely consistent with other studies. Cacomistles as generalist feeders have been found to be most active at 1800 h to 0300 h, and have home ranges of 19.8 ha found in secondary forests (Garcia et al. 2002). Most interestingly, we documented several observations of a pair of Cacomistles in the highland site, indicating the benefit of camera traps to

Figure 2. Representative images across all sites from capture events showing dominant vertebrates, the Lowland paca (upper left), Common opossum (upper right), and Cacomistle (lower left) and Turkey vulture (lower right).

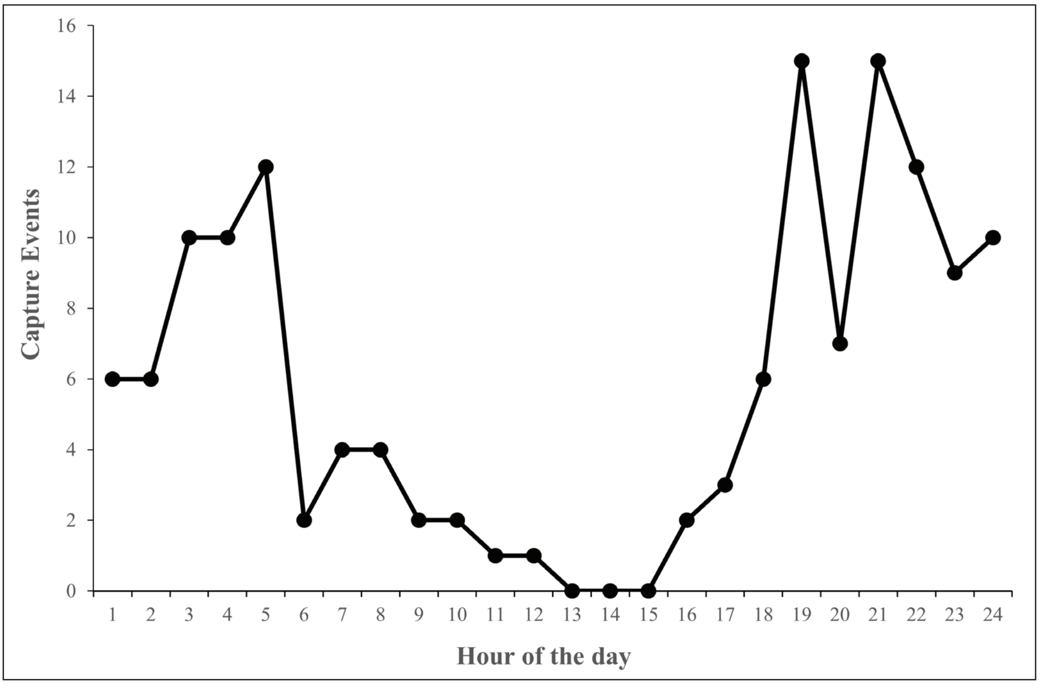

Figure 3. Activity patterns of capture events across military time periods across all trap locations and sample events in Chiriquì Province, Panama.

Table 1. Number of capture events for each species encountered in mountain high elevation (Site 1), and coastal low elevation (Site 2), total encounters and percent of total encounters.

Common name	Species	Order	Highland mountains site 1	Coastal lowlands site 2	Total	%
Common Opossum	*Didelphis marsupialis*	Didelphimorphia	33	38	71	50.4
Cacomistle	*Bassariscus sumichrasti*	Carnivora	24	0	24	17.0
Agouti	*Dasyprocta punctata*	Rodentia	16	1	17	12.1
Brown Four-eyed Opossum	*Matachirus nudicau-datus*	Didelphimorphia	0	10	10	7.1
Isthmian Mouse Opossum	*Marmosa isthmica*	Didelphimorphia	2	4	6	4.3
Chiriqui Brown Mouse	*Scotinomys xerapelinus*	Rodentia	0	6	6	4.3
Lowland Paca	*Cuniculus paca*	Rodentia	2	0	2	1.4
White-nosed Coati	*Nasua narica*	Carnivora	1	0	1	0.7
Nine-banded Armadillo	*Dasypus novemcinctus*	Cingulata	1	0	1	0.7
Coyote	*Canis latrans*	Carnivora	0	1	1	0.7
Turkey Vulture	*Cathartes aura*	Accipitriformes	0	1	1	0.7
Roadside Hawk	*Rupornis magnirostris*	Accipitriformes	0	1	1	0.7

study social behavior and interactions involving either siblings, juvenile and adults, or breeding pairs in this lesser studied tropical mammal, which is either rare to uncommonly encountered, or characterized by a patchy distribution (Goldman 1920, Reid 2009). Moreover, we observed the Common Opossum to have nocturnal crepuscular activity patterns similar for those observed for *Didelphis* in other tropical forests (Oliveira-Santos et al. 2008) as they are known to be frugivores and omnivores (Robinson and Redford 1986). Future research should emphasize differences between seasons as previous studies have found some effect of rainy versus dry season for removal of carcasses in tropical ecosystems (Villegas-Patraca et al. 2012). However baiting cameras may bias or confound observations of normal (non-baited) animal activity patterns, so future work should compare methods of baited versus unbaited activity patterns of Neotropical mammals.

We detected many potential scavengers on camera traps not normally associated as scavenging mammals, including several instances of Lowland Paca and Agouti, both primarily frugivores, during diurnal periods (Reid 2009). Within Neotropical areas, the role of scavengers has received less attention relative to studies of scavenging in other geographic areas, with facultative scavenging by predators being largely ignored in food web ecology studies (Moleon et al. 2014, Wilson and Wolkovich 2011). Additional camera trap studies should be conducted in tropical areas on different bait types and validate if sardines are an adequate proxy for carrion, as species encounters may differ between fresh fish and decaying carrion.

This short-term study provides further evidence of how camera trapping can elucidate species presence and baseline species frequencies in a variety of Neotropical habitats to inform mammal conservation with little financial or temporal investment. These findings in terms of species presence are comparable to other more prolonged studies of camera trapping Neotropical mammals, for which camera deployment strategies vary (Table 2). While we documented the Common Opossum as a tropical scavenging mammal across both high and low elevation sites, we noted differences in relative frequencies in other mammals, with the Cacomistle and Agouti detected more frequently at higher elevations. Our findings indicate the frequency of functional mammalian scavengers may be a result of either present species range distributions, variations in species ability to persist in secondary forests, differences in species detection, or other factors.

Table 2. Comparisons of this study to other camera trapping studies of mammals in Neotropical regions, including location of study, species observed, study length, relative abundance (reported when available), camera traps used and primary habitat (disturbed or undisturbed).

Citation	Location	Species Observed	Study Length	Relative Abundance	Cameras Traps Used	Habitat
Current study	*Western Panama*	*12*	*<1 month*	*139*	*4*	*disturbed*
Meyer et al. 2015	Eastern and Central Panama	12–31	9 years	—	16–30	undisturbed
Springer et al. 2012	Central Panama	16	5 months	306	20	undisturbed
Rowcliffe et al. 2011	Central Panama	19	12 months	1555	20	undisturbed
Tobler et al. 2008	Southeastern Peru	27	2 years	814	24–40	undisturbed/ disturbed
Harmsen et al. 2010	Central Belize	10	2.5 years	—	110	undisturbed/ disturbed
Ahumada et al. 2013	Western Costa Rica	26	5 years	—	56–60	undisturbed

Our results highlight the need for further study or rapid biological assessment approaches in secondary forested habitats when surveying tropical mammals outside of protected areas, including private lands. When taken together, trail cameras appear to be ideal for collecting baseline data on Neotropical vertebrate scavenger communities under threat of increasing deforestation and development.

Acknowledgements

We thank La Fundaciòn Kucikas for support, access to study site, and the Smithsonian Tropical Research Institute for animal care and use approval and permitting (STRI 2018-0222-2021). All research was conducted on private land. We also thank Wingate University Biology Department for supplies and travel funding (2018 WINGS grant)

Literature Cited

Ahumada, J.A., J. Hurtado, and D. Lizcano. 2013. Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: A tool for conservation. PLoS ONE 8:e73707.

Baltensperger, A.P., C.L. Brown. 2015. Mammalian biodiversity conservation at two biological stations in Nicaragua and Costa Rica. Pp. 351–389, *In* F. Huettmann (Ed.). Central American Biodiversity: Conservation, Ecology, and a Sustainable Future. Springer Press, New York, NY. USA 805 pp.

Beasley, J.C., Z.H. Olson, and T.L. Devault. 2015. Ecological role of vertebrate scavengers. Pp. 107–127, *In* E.M. Benbow, J. Tomberlin, and A. Tarone (Eds). Carrion Ecology, Evolution, and Their Applications. CRC press, Boca Raton, FL. USA 622 pp.

Brinck, K., R. Fischer, J. Groeneveld, S. Lehmann, M.D. De Paula, S. Putz, J.O. Sexton, D. Song, and A. Huth (2017). High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. Nature Communications 8:14855.

DeVault, T., O.E. Rhodes, and J.A. Shivik (2003). Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234.

Duarte, H., D. Norris, and F. Michalski (2018). Assessment of attractants for Neotropical mammals. Tropical Conservation Science. 11:1–11.

Duquette, J.F., L. Urena, J. Ortega, I. Cisneros, R. Moreno, and E.E. Flores (2017). Coiban agouti (*Dasyprocta coibae*) density and temporal activity on Coiba Island, Veraguas, Panama. Mammal Study 42:153–160.

Emmons, L.H., and F. Feer. 1997. Neotropical Rainforest Mammals: A Field Guide. University of Chicago Press, Chicago, IL. 396 pp.

Eisenburg, J.F. 1989. Mammals of the Neotropics, Volume 1, The Northern Neotropics: Panama, Columbia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago, IL. 550 pp.

Garcia, N.E., C.S. Vaughen, and M.B. McCoy (2002). Cacomistle Ecology in Costa Rica. Vida Silvestre Neotropical 11:52–59.

Goldman, E.A. 1920. Mammals of Panama (With Thirty-nine Plates). Smithsonian Institution Press, Washington, D.C. 364 pp.

Harmsen, B.J., R.J. Foster, S. Silver, L. Ostro, and C.P. Doncaster (2010). Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. Biotropica 42:126–133.

Hidalgo-Mihart, M.G., L. Cantu-Salazar, A. Gonzalez-Romero, and C.A. Lopez-Gonzalez (2004). Historical and present distribution of coyote (*Canis latrans*) in Mexico and Central America. Journal of Biogeography 31:2025–2038.

Hody, J.W. 2016. Canid Collision Range Expansion by Coyotes (*Canis latrans*) and Crab-eating Foxes (*Cerdocyon thous*) in Panama and Interpretation of Camera Trap Data. Masters Thesis. North Carolina State University, Raleigh, NC. 80 pp.

Kays, R., S. Tilak, B. Kranstauber, P.A. Jansen, C. Carbone, M. Rowcliffe, T. Fountain, J. Eggert, and Z. He (2011). Camera traps as sensor networks for monitoring animal communities. International Journal of Research and Reviews in Wireless Sensor Networks 1:19–29.

Laurance, W.F., J. Sayer, and K.G. Cassman (2014). Agricultural expansion and its impacts on tropical nature. Trends in Ecology and Evolution 29:107–116.

Lyra, A., P. Imbach, D. Rodriquez, S.C. Chou, S. Georgiou, and L. Garofolo (2017). Projections of climate change impacts on central America tropical rainforests. Climate Change 141:93–105.

Meek, P.D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'Brien, A. O'Connell, J. Sanderson, D.E. Swann, M. Tobler, and S. Townsend (2014). Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation 23:2321–2343.

Meyer, N.F.V., H.J. Esser, R. Moreno, F. van Langevelde, Y. Liefting, D.R. Oller, C.B.F. Vogels, A.D. Carver, C.K. Nielsen, and P.A. Jansen (2015). An assessment of the terrestrial mammal communities in forests of Central Panama, using camera-trap surveys. Journal for Nature Conservation 26:28–35.

Moleon, M., J.A. Sachez-Zapata, N. Selva, J.A. Donazar, and N. Owen-Smith (2014). Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 89:1042–1054.

Moreno, S.H (1993). Impact of development on the Panama Canal environment. Journal of Interamerican Studies and World Affairs 35:129–149.

O'Brien, T.G., M.F. Kinniard, and H.T. Wibisono (2003). Crouching tigers, hidden prey: Summatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6:131–139.

Oliveira-Santos, L.G.R., M.A. Tortato, and M.E. Graipel (2008). Activity pattern of Atlantic Forest small arboreal mammals as revealed by camera traps. Journal of Tropical Ecology 24:563–567.

Potapov, P.M.C., L. Hansen, Laestadius, S. Turubanova, A. Yaroshenko, C. Thies, W. Smith, I. Zhuravleva, A. Komarova, S. Minnemeyer, and E. Esipova (2013). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances 3:e1600821.

Reid, F.A. 2009. A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, New York, NY. 346 pp.

Ridgely, R.R., and J.A. Gwynne. 1976. A Guide to the Birds of Panama. Princeton University Press, Princeton, NJ. 404 pp.

Ripple, W.J., T.M. Newsome, C. Wolf, R. Dirzo, K.T. Everatt, M. Galletti, M.W. Hayward, G.I.H. Kerley, T. Levi, P.A. Lindsey, D.W. Macdonald, Y. Malhi, L.E. Painter, C.J. Sandom, J. Terborgh, and B. Van Valkenburgh (2015). Collapse of the world's largest herbivores. Science Advances 1:e1400103.

Robinson, J.G., K.H. Redvord (1986). Body size, diet, and population density of Neotropical forest mammals. American Naturalist 128:665–680.

Rovero, F., F. Zimmermann, D. Berzi, and P. Meek (2014). Which camera trap type and how many do I need? A review of camera features and study designs for a range of wildlife research applications. Hystrix, the Italian Journal of Mammalogy 24:148–156.

Rowcliffe, J.M., C. Carbone (2008). Surveys using camera traps: are we looking to a brighter future? Animal Conservation 11:185–186.

Rowcliffe, J.M., C. Carbone, P.A. Jansen, R. Kays, and B. Kranstauber (2011). Quantifying the sensitivity of camera traps: An adapted distance sampling approach. Methods in Ecology and Evolution 2:464–476.

Schwartz, A.L.W., H.F. Williams, E. Chadwick, R.J. Thomas, and S.E. Perkins (2018). Roadkill scavenging behavior in an urban environment. Journal of Urban Ecology 4:1–7.

Springer, M.T., A.D. Carver, C.K. Nielson, N.J. Correa, J. R. Ashmore, J.R. Ashmore, and J.G. Lee (2012). Relative abundance of mammalian species in a central Panamanian Rainforest. Revista Latinoamericana de Conservacion 2:19–26.

Sunarto, S., R. Sollmann, A. Mohamed, and M.J. Kelly (2013). Camera trapping for the study and conservation of tropical carnivores. The Raffles Bulletin of Zoology 28:21–42.

Thorn, M., D.M. Scott, M. Green, P.W. Bateman, and E. Z. Cameron (2009). Estimating brown hyaena occupancy using baited camera traps. South African Journal of Wildlife Research 39:1–10.

Tobler, M.W., S.E. Carrillo-Percastegui, R.L. Pitman, R. Mares, and G. Powell (2008). An evaluation of camera traps for inventorying large and medium-sized terrestrial rainforest animals. Animal Conservation 11:169–178.

Trolliet, F., M. Huynen, C. Vermeulen, and A. Hambuckers (2014). Use of camera traps for wildlife surveys: A review. Biotechnologie, Agronomie, Societe et Environment 18:446–454.

Villegas-Patraca, R., S. Macias-Sanchez, I. MacGregor-Fors, and C. Munoz-Robles (2012). Scavenger removal: Bird and bat carcass persistence in a tropical wind farm. Acta Oecologica 43:121–125.

Wearn, O.R., P. Glover-Kapfer (2019). Snap happy: camera traps are an effective sampling tool when compared with alternative methods. Royal Society of Open Science 6:181748.

Wellington, K., C. Bottom, C. Merrill, and J.A. Litvaitis (2014). Identifying performance differences among trail cameras used to monitor forest mammals. The Wildlife Society Bulletin 38:634–638.

Wilson, E.E., E.M. Wolkovich (2011). Scavenging: how carnivores and carrion structure communities. Trends in Ecology and Evolution 25:129–135.