

ISSN 1027-2992

CAT news

N° 77 | Spring 2023





CATnews is the newsletter of the Cat Specialist Group, a component of the Species Survival Commission SSC of the International Union for Conservation of Nature (IUCN). It is published twice a year, and is available to members and the Friends of the Cat Group.

For joining the Friends of the Cat Group please contact
Christine Breitenmoser at ch.breitenmoser@kora.ch

Original contributions and short notes about wild cats are welcome
Send contributions and observations to
ch.breitenmoser@kora.ch.

Guidelines for authors are available at www.catsg.org/catnews

CATnews is produced with financial assistance from the Friends of the Cat Group.

Design: barbara surber, werk'sdesign gmbh
 Layout: Eline Brouwer, Tabea Lanz and Christine Breitenmoser
 Print: Stämpfli AG, Bern, Switzerland
ISSN 1027-2992 © IUCN/SSC Cat Specialist Group

Editors: Christine & Urs Breitenmoser
 Co-chairs IUCN/SSC
 Cat Specialist Group
 c/o KORA, Villettengässli 3, 3074 Muri
 Switzerland
 Tel ++41(31) 951 90 20
 Fax ++41(31) 951 90 40
 <u.breitenmoser@kora.ch>
 <ch.breitenmoser@kora.ch>

Associate Editors: Brian Bertram
 Maximilian Allen
 Juan Reppucci
 Giridhar Malla
 Sugoto Roy

Cover Photo: Jaguarundi
 Photo: Juan Reppucci

The designation of the geographical entities in this publication, and the representation of the material, do not imply the expression of any opinion whatsoever on the part of the IUCN concerning the legal status of any country, territory, or area, or its authorities, or concerning the delimitation of its frontiers or boundaries.

SAMANTHA BARON¹, JENNIFER L. MCCARTHY^{2*}, KYLE P. MCCARTHY¹, KING SOLOMON EHINOLA², SAMANTHA MCGONIGLE¹, JORGE PEREA³, MILTON YACELGA⁴ AND KIMBERLY CRAIGHEAD⁴

Jaguarundi occupancy and interaction with sympatric felids in Panama

Though jaguarundi *Herpailurus yagouaroundi* are considered a species of “Least Concern,” the data dictating this status is limited owing to few targeted studies of the felid. In Panama, expanding the knowledge of jaguarundi ecology is essential to inform conservation decisions as the country continues to experience habitat conversion. With a decrease in habitat availability, it is important to elucidate interactions and resource partitioning between jaguarundi and sympatric felids. In this study, we used presence-only data from camera traps deployed in the Mamoní Valley of Panama and in the Guna Yala Comarca, in a maximum entropy framework as an index of occurrence probability for jaguarundi. We included habitat variables as covariates to evaluate their relative importance to jaguarundi occupancy. Using spatial and temporal data, we then assessed the co-occurrence of jaguarundi with four sympatric felid species: margay *Leopardus wiedii*, ocelot *Leopardus pardalis*, puma *Puma concolor*, and jaguar *Panthera onca*. Models indicated that jaguarundi were more likely to occur in secondary forests at lower slopes, and avoided open pasture land. Only the distribution of the ocelot affected modelled jaguarundi occurrence, and this relationship was positive. Jaguarundis had a likelihood of coexisting with all felid species in 57% of the jaguarundi’s predicted occurrence range at the 0.5 threshold, and this was likely facilitated by temporal and ecological niche partitioning among the sympatric species. The data from this research suggest that though jaguarundis occur sympatrically with other felid species, their habitat use is unique from larger, charismatic species and targeted conservation efforts may be necessary to ensure the conservation of jaguarundis in Panama.

40

Owing to a paucity of species observations and few targeted research studies, little information about the behaviour, habitat use, distribution and overall ecology of the jaguarundi is known. As a result, the International Union for Conservation of Nature’s (IUCN) Red Listing of “Least Concern” for the species is relatively uninformed, with IUCN Red List assessors noting that it may be “Near Threatened,” but insufficient data exists to fully evaluate the status (Giordano 2015, Caso et al. 2015). Existing research has been primarily focused in Mexico or Brazil, with little focus on other South American or Central American countries. Expanding our knowledge base on the species is necessary to facilitate data driven conservation planning.

Panama comprises the narrowest section of the Mesoamerican Biological Corridor (MBC) and is thus inherently important for the population connectivity of any terrestrial species, such as the jaguarundi, whose distribution spans the region. However, anthropogenic changes to land cover for agriculture and cattle ranching in Panama has caused significant habitat loss and forest degradation,

and threatens the continuity of the MBC (Slusser et al. 2015). Indeed, Panama lost 7% (~2,000 km²) of its forest cover between 1992 and 2000 (Reymondin et al. 2013). This trend has continued, with a further loss of 7.7% forest cover between 2001 and 2020 identified by the “Primary Forest Loss” model (Panama Deforestation Rates and Statistics 2021). Given the continued deforestation and habitat fragmentation in Panama, as well as the country’s importance in maintaining connectivity throughout the range of many Neotropical species such as the jaguarundi, it is crucial that researchers better understand the habitat requirements and patterns of affected species. It is also important to understand the spatial and temporal dynamics of the jaguarundi in relation to other sympatric felid species including the margay, ocelot, puma, and jaguar. Elucidating these interspecific relationships is especially pertinent in the face of habitat loss in Panama. Anderson et al. (2008) indicate that generalist species may outcompete sensitive species in incidences of habitat loss, as they may be able to adjust more easily to human dominated landscapes.

Defining the ecological niche of the jaguarundi in Panama will aid in highlighting the impact that continued deforestation in the region may have on the species.

The temporal habits, preferred habitat, and interspecific interactions of jaguarundis have been previously assessed in both Brazil and Mexico. In Brazil, jaguarundis are observed to temporally separate from sympatric felid species, with jaguarundis being largely diurnal, margays catemeral, and ocelots nocturnal (Nagy-Reis et al. 2018). Scat analysis revealed moderately overlapping diets between jaguarundis and margays, with the least overlap between jaguarundis and ocelots. Overall, the coupled factors of differences in temporal activity patterns and in diet were thought to have decreased the number of negative competitive interactions between felid species, allowing them to live in sympatry (Nagy-Reis et al. 2018).

In Mexico, a radio collaring study revealed that jaguarundis and ocelots were found to have overlapping home ranges, but little overlap in their core areas (Caso 2013). Further, ocelots occurred most commonly in areas of tropical sub-deciduous forest, while jaguarundis occupied tropical sub-deciduous forests and pasture-grasslands evenly. Similar to what was seen in Brazil, Caso (2013) found that jaguarundis in their study area in Mexico were primarily diurnal while ocelots were primarily nocturnal. Also in Mexico, via a meta-analysis, Espinosa et al. (2017) identified a 76% overall niche similarity between jaguarundis and margays, but different favourable habitats in which suitability primarily depended on temperature and precipitation.

One theory proposed to explain the apparent distributional overlap of sympatric felids in Panama has been niche partitioning through prey selection. Studies throughout Central and South America have conducted scat analyses to determine the prey items that jaguarundi, jaguar, puma, ocelot, and margay consume with the highest frequencies of occurrence, revealing possible prey resource partitioning between the species. Apart from Bianchi et al. (2011), which found that jaguarundis primarily consume birds, studies have determined that mammals occur with the highest frequency in jaguarundi scat samples (Tófoli et al. 2009, Giordano 2015). Jaguarundis appear to target small mammals, specifically sigmodontine rodents (Tófoli et al. 2009, Giordano 2015). Diet studies of ocelots and margays suggest that they also primarily consume small mammals, with rodents comprising the largest portion

(Villa Meza et al. 2002, Wang 2002, Bianchi & Mendes 2007). Didelphimorphia species also occurred in high frequencies in the diet of margays (Wang 2002, Bianchi et al. 2011). Ocelots, margays and jaguarundis have all also been recorded consuming birds, reptiles, fish and invertebrates, though to a lesser degree than mammals (Villa Meza et al 2002, Wang 2002, Bianchi & Mendes 2007, Bianchi et al. 2011). When assessing the diet of the larger jaguar and puma, prey size appears to be a differentiating factor from the smaller felids. Analyses of jaguar scat have determined that mammals also comprise the majority of jaguar's diet, though they are targeting medium to large-sized mammals weighing from three to ten kilograms (Garla et al. 2001, Weckel et al. 2006, Sollman et al. 2013). Scat analyses have also revealed that birds and reptiles contribute to the jaguar's diet, but to a much lesser extent than mammals (Garla et al. 2001, Sollmann et al. 2013). Pumas also primarily target mammals, though the size range of their prey is slightly more expansive than that of the jaguar, with prey ranging in size from small rodents to large artiodactyls. They also consume lizards and birds (Núñez et al. 2000, Rau & Jiménez 2002, Rueda et al. 2013).

Prior research has not only allowed for the comparison of felid diets, but also of their morphology. In the book, *Felids and Hyenas of the World* (2020), Castelló found that the jaguar is the largest felid of the five species by weight, body length, and skull dimensions. Pumas, ocelots, jaguarundis, and margays follow in rank of decreasing size. Species ranking by height to shoulder deviates from the other morphological trends, with pumas, jaguars, ocelots, margays, and then jaguarundis ordered from tallest to shortest (Castelló 2020). Based on size similarity as well as prey selection, it is expected that there may be more intense interspecific competition for prey between the jaguarundi and the smaller ocelot and margay, rather than with the larger jaguar and puma. However, though competition over prey may be minimal between the jaguarundi and the puma and jaguar, the larger felids may also impact the small felids through intraguild predation (IP) or intraspecific killing (IK; de Oliveira & Pereira 2014).

The goal of the current research was to assess jaguarundi occupancy, temporal activity, and sympatry with other felids in an established conservation corridor in Panama. The data from this research elucidates the habitat variables that are associated with jaguarundi oc-

cupancy and the effect of sympatric felids on their predicted occupancy in Panama. It also provides additional information on the regional distribution of the jaguarundi, and overlap with the distribution of margay, ocelot, puma, and jaguar. Finally, this research examines the temporal overlap in activity patterns, and perceived overlap in diet and morphology in relation to jaguarundi occupancy and sympatric felid presence.

Study area

Panamanian forests are comprised of premontane, gallery, tropical moist, and mangrove forests. Tropical moist forests are dominated by emerging deciduous trees such as *Ceiba pentandra* and *Cavanillesia platanifolia* (Golley et al. 1969). Panama experiences marked wet and dry seasons. The wet season occurs from May to November while the dry season occurs from December to April (Condit et al. 2001). The amount of precipitation that falls during the wet season depends on the coast and elevation. The Pacific Coast receives 1,700 mm of annual rainfall and the Atlantic coast receives 3,000 mm of annual rainfall. Higher elevations are subject to more precipitation as well (Ibáñez et al. 2002).

Within Panama, this study was specifically located in the Mamoni Valley and the adjacent Guna Yala Comarca. The Mamoni Valley is situated in the Tumbes-Chocó-Magdalena eco-region at the narrowest section of the Panamanian Isthmus. It borders Parque Nacional Chagres, the Guna Yala Comarca, and Reserva Natural Cocobolo. Located within the Mamoni Valley is the Mamoni Valley Preserve, a non-profit organisation working to preserve large

tracts of land within the valley. The Guna Yala Comarca is an indigenous province which extends from the border of the Mamoni Valley Preserve to the Caribbean Sea. It is bordered on the West by the Province of Colon and the East by Colombia. It remains one of the least developed regions along the Mesoamerican Biological Corridor, and comprises a majority of the remaining intact habitat in the region. The old growth rainforest and watersheds of the Mamoni Valley consist of a mixed matrix of various land cover types including late successional forest, mature secondary forest, middle secondary forest, young secondary forest, pasture, and fallow (Klooster et al. 2021).

Methods

From 25 May 2017 to 11 October 2017, and then from 9 July 2019 to 2 February 2020, we deployed Bushnell Trophy Cam HD™ camera traps across 142 km² (Derived from a polygon of camera locations) of the Mamoni Valley and the Guna Yala Comarca in Panama (Fig. 1). The cameras were placed across a wide variety of habitats in order to represent the varying habitats within the study site, including: intact secondary forests, forest fragments, edge habitats, agricultural landscapes, areas in close proximity to villages, and agroforestry sites. The cameras were spaced at increments of one to two kilometers within established grid cells and were set along game trails or at locations with other signs of wildlife presence. The cameras were active for 24 hours a day and were set to collect data in both photo and in hybrid modes (three photos followed by a 10-second video). Metadata for photographs

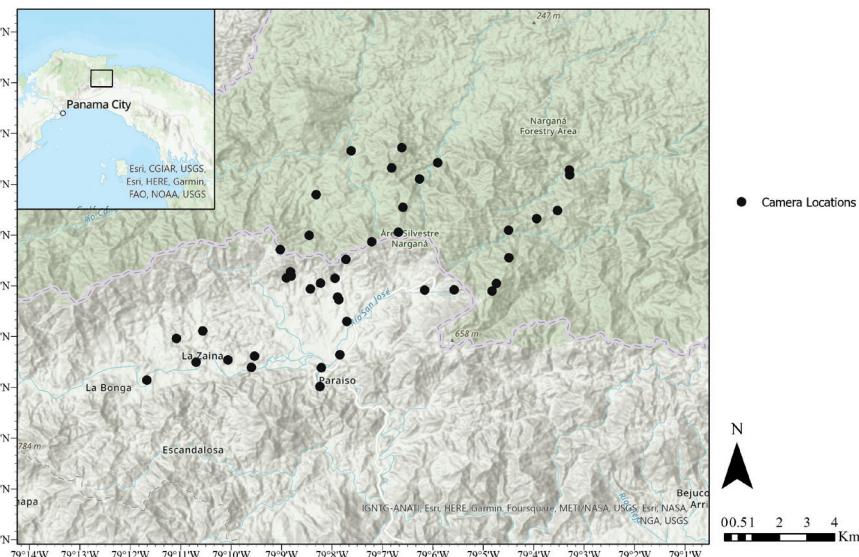


Fig. 1. Study area and camera locations used in predicting jaguarundi and sympatric species occurrence in the Mamoni Valley of Panama, 2017–2020.

Table 1. Range of covariate values at sampling locations and across study area as used in predicting jaguarundi and sympatric species occurrence in the Mamoni Valley and Guna Yala Comarca of Panama, 2017–2020.

Covariate	Camera Min	Camera Max	Study Area Min	Study Area Max
Distance to River (m)	0	722	0	2,257
Slope	0	32	0	83
Ruggedness Index	2	25	0	64
Elevation	100	530	24	909
Pasture 0.01 km ²	0	69	0	100
Pasture 10 km ²	0	40	0	78
Mixed Secondary and Plantation 0.01 km ²	0	100	0	100
Mixed Secondary and Plantation 10 km ²	0	60	0	85
Mixed Mature 0.01 km ²	0	100	0	100
Mixed Mature 10 km ²	0	100	0	100

were extracted and recorded. Species were then identified from photo or video, with verification of all photographs made by a second observer. Any photographs where species identification was uncertain were excluded. These data were then used for all subsequent analyses.

To determine what habitat variables influence the occurrence of jaguarundi and the other sympatric felid species, we implemented maximum entropy modeling via R and Java using program Maxent (Phillips et al. n.d., Java 2014, R Core Team 2021). Typically, a presence/absence occupancy modelling framework is preferential to presence only models such as Maxent. Occupancy models account for non-detections, imperfect detection probabilities, and provide more directly interpretable results (i.e., probability of occurrence rather than an index of that probability). Unfortunately for rare and elusive species such as the jaguarundi and its sympatric felids, camera capture-recapture data is often too sparse to inform occupancy models. Prior to selecting Maxent we did attempt to model jaguarundi occurrence using both frequentist and Bayesian techniques, but the extreme number of zeros (capture rate = 0.004 captures/trap night) in the capture history, even when collapsed, and limited recaptures led to a lack of convergence

and unreasonable variance. Maxent, while less informative than occupancy models, is an alternative that relies only on presence data and can provide valuable information which can help to inform future, targeted studies.

In Maxent we used felid occurrence records from the camera data and a suite of potential habitat covariates in an ad-hoc polygon surrounding the camera locations. The initial habitat covariates used included both land-cover and climate data. However, we ultimately discarded the climate variables, as the study area was so small that slight variations in these predictors were likely the result of differences in landcover and topography rather than true climatic variations. In our final model we included ten habitat covariates: percent mixed mature forest, pasture, or mixed secondary forest/plantation within 10 km², percent mixed mature forest, pasture, or mixed secondary forest/plantation within 0.01 km², distance to nearest river, terrain ruggedness index, slope, and elevation. Percent landcover types were calculated using a rectangular moving window. We chose these scales to represent both the immediate perceived area (0.01 km²) as well as an area approximating the landscape potentially used across a broader time scale (10 km²). Camera locations (Fig. 1) did not entirely sample the range of 6

of the selected covariates (Table 1) used in Maxent modeling. This may introduce bias as Maxent randomly sampled “background” points from throughout the study area, however, much of the unsampled area would be considered suboptimal habitat for jaguarundi and appropriate for use to inform habitat associations. Further, any bias introduced will be similar for each species.

All landcover covariates were derived from the 2012 Forest Cover and Land Use dataset provided by the Ministry of the Environment of Panama, elevation and its derivatives of slope and ruggedness were based on NASA Shuttle Radar Topography Mission data, and hydrography data was obtained from the Smithsonian GIS Data Portal. All spatial data was converted to a raster format with a 5 m cell size for use in Maxent.

For each felid species, we first implemented a full Maxent model (i.e., with all covariates). We enabled all standard features in Maxent except for hinge, product, and threshold features, and used 10,000 background points. The output was kept at its default logistic format. We then removed covariates that provided zero percent contribution to the full model, and implemented a reduced model, with the same features enabled previously, to increase the area under the respective

Table 2. Contribution and importance of habitat covariates in a maximum entropy model of jaguarundi occurrence.

Variable	Percent contribution	Permutation importance
Slope	61.7	82.4
Pasture 10 km ²	13.2	17.6
Pasture 0.01 km ²	10.9	0.0
Mixed Secondary Forest/Plantation 0.01 km ²	8.2	0.0
River Distance (m)	5.0	0.0
Mixed Secondary Forest/Plantation 10 km ²	1.0	0.0

receiver operator curve. We then used the output index of occurrence probability raster datasets from these reduced models for subsequent analyses.

To ascertain how jaguarundi occurrence overlapped with the habitat use of sympatric felids, we first used a 0.5 threshold to convert index of occurrence probability for each species into a binary 0 or 1 value. For each cross comparison between jaguarundi and individual sympatric species we then used the Raster Calculator Geoprocessing tool to classify cells as 0,0 = neither species predicted to occur; 1,0 = jaguarundi predicted to occur but sympatric species is not; 0,1 = sympatric species predicted to occur but jaguarundi is not; and 1,1 = jaguarundi and respective sympatric species both predicted to occur.

We then calculated the temporal overlap between the jaguarundi and margay, ocelot, puma, and jaguar's activity patterns. We considered a new photograph of the same species at the same camera as a novel capture event when the images were taken twenty or more minutes apart from each other. We then converted the times at which the camera trap took photographs of the felids to decimal time in Excel. Using the "overlap" package in R, we calculated the percentage of temporal activity overlap between jaguarundi and a given sympatric felid species (Ridout & Linkie 2009). For all comparisons we used the Dhat1 coefficient

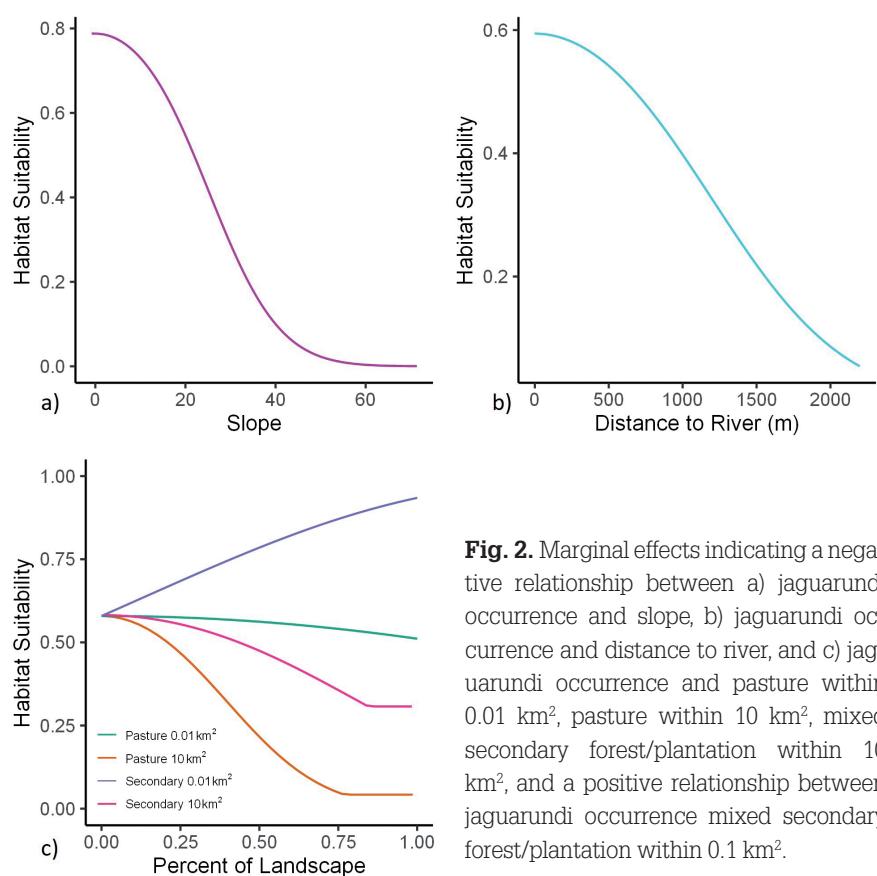


Fig. 2. Marginal effects indicating a negative relationship between a) jaguarundi occurrence and slope, b) jaguarundi occurrence and distance to river, and c) jaguarundi occurrence and pasture within 0.01 km², pasture within 10 km², mixed secondary forest/plantation within 10 km², and a positive relationship between jaguarundi occurrence mixed secondary forest/plantation within 0.1 km².

of overlap recommended for small sample sizes.

Results

In 2017, 24 camera traps were deployed for a total of 3,073 trap nights. In 2019, 20 cameras

were deployed for a total of 1,796 trap nights. Jaguarundi were captured at 12 camera trap stations, with 19 unique capture events. Jaguars were caught at 14 camera trap sites with 29 unique capture events. Pumas were captured at 17 camera trap stations with a to-

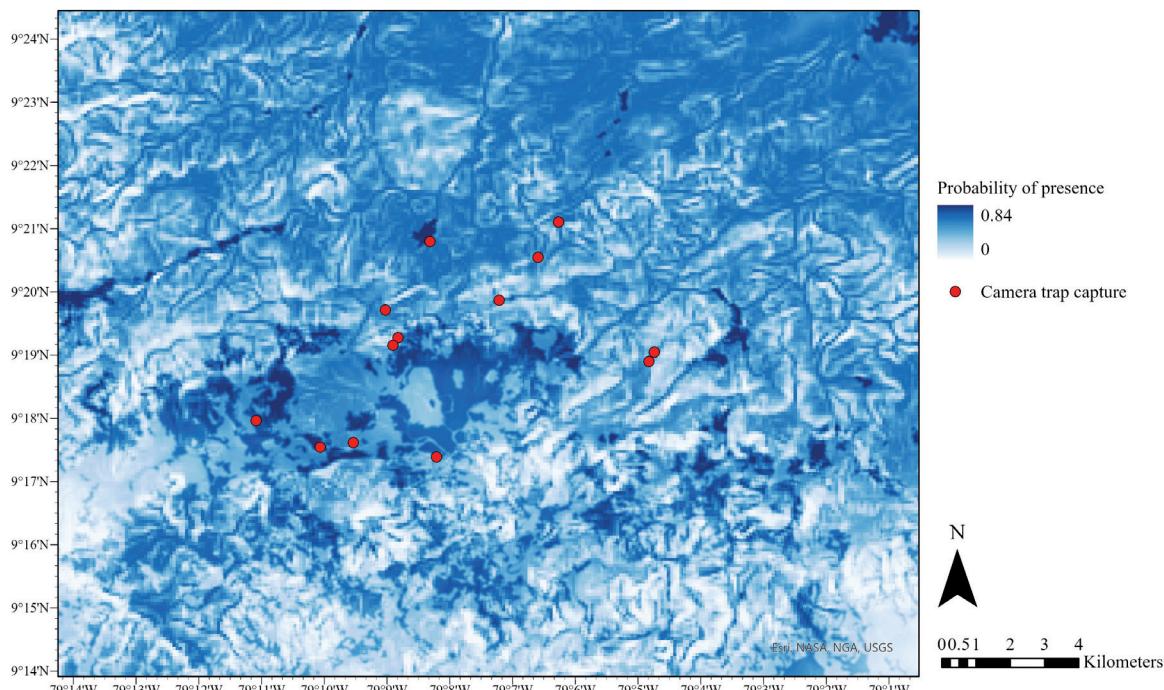


Fig. 3. Predicted jaguarundi presence in the study area in and surrounding the Mañí Valley and Guna Yala Comarca of Panama.

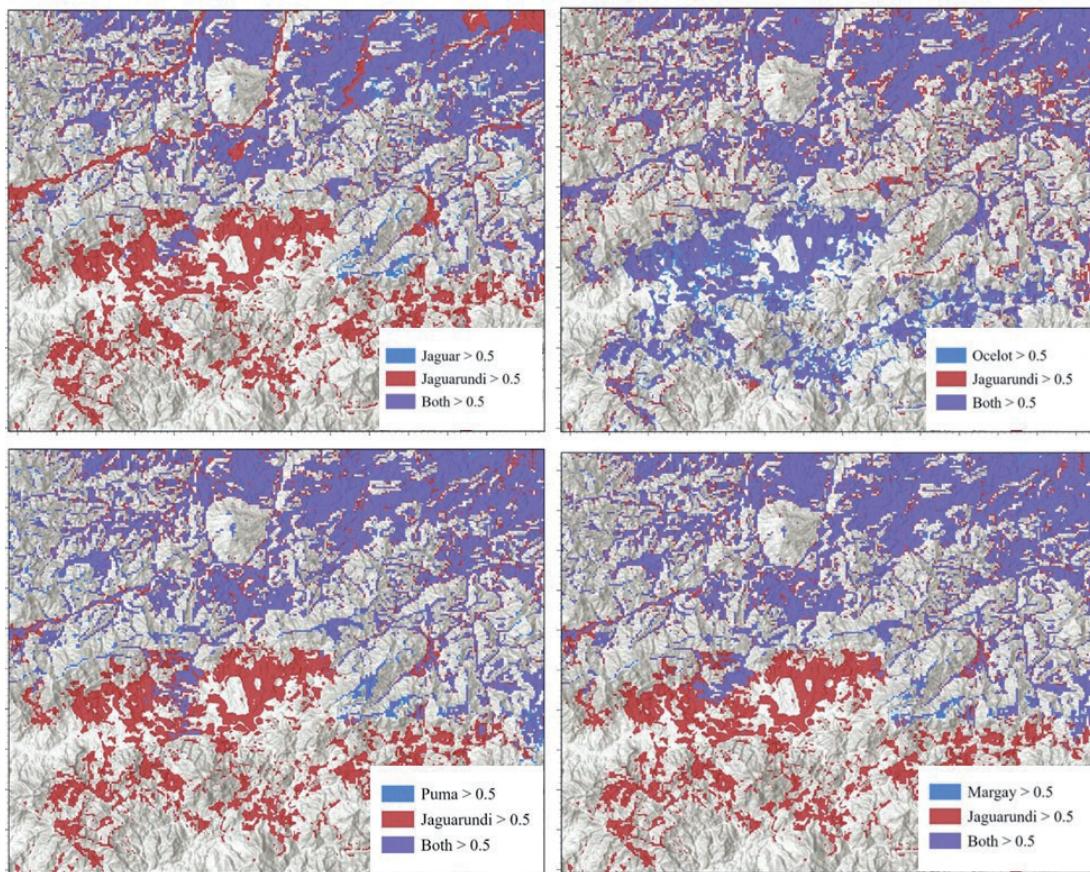


Fig. 4. Comparison of jaguarundi and sympatric felid species habitat suitability in Mamóní Valley and Guna Yala Comarca of Panama. Suitability mapped at a 0.5 threshold based on maximum entropy modelling from data collected in 2017 and 2020 via camera trap survey.

tal of 52 unique capture events. Ocelots were captured at 26 camera trap locations with a total of 125 unique capture events. Finally, margays were captured at 14 camera trap stations and had a total of 38 unique capture events.

The jaguarundi Maxent model yielded an area under the receiver operator curve of 0.775, meaning the model is potentially useful (Phillips & Dudik 2008). Of the habitat covariates, Maxent modelling identified slope, pasture within 10 km², pasture within

0.01 km², mixed secondary forest/plantation within 0.01 km², river distance (m), and mixed secondary forest/plantation within 10 km² as contributors to jaguarundi occurrence (Table 2). Out of these covariates, jaguarundi occurrence had a negative relationship with slope, pasture within 10 km², pasture within 0.01 km², mixed secondary forest/plantation within 10 km², and river distance. Jaguarundi occurrence had a positive relationship with mixed secondary forest/plantation within 0.1 km² (Fig. 2).

Modelled jaguarundi index of occurrence probability ranged from 0 to 0.86 in the study area, with 35% of the study area at >0.50 probability of occurrence (Fig. 3 & 5). At this 0.50 probability of occurrence threshold, jaguarundis and jaguars were predicted to co-occur in 57% of the jaguarundi's predicted occurrence range (Fig. 4 and 5), jaguarundis and pumas were predicted to co-occur in 63% of the jaguarundi's predicted range (Fig. 4 and 5), jaguarundis and ocelots were predicted to co-occur in 80% of the jaguarundi's predicted range (Fig. 4 & 5), and jaguarundis and margays were predicted to co-occur in 66% of the jaguarundi's predicted range (Fig. 4 and 5).

Analysis of temporal data suggests that jaguarundis were diurnal, jaguars and pumas were cathemeral, and ocelots and margays were nocturnal. The amount of temporal activity overlap between jaguarundis and the other four sympatric felid species varied. Jaguarundis had a 63.43% overlap with jaguars, 56.79% overlap with pumas, 37.15% overlap with ocelots, and 36.75% overlap with margays (Fig. 6).

Discussion

The results of this research suggest that jaguarundis occupy regions with greater mixed secondary forest/plantation at the local scale

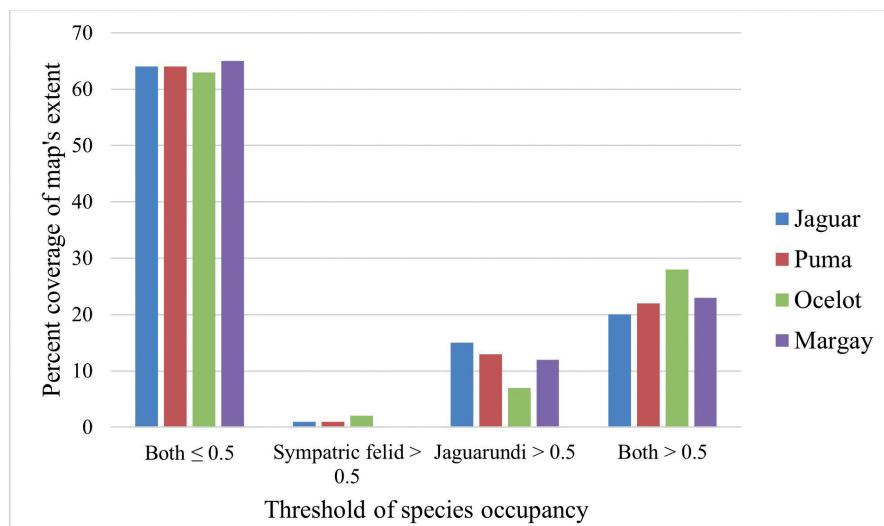


Fig. 5. Comparison of the 0.5 threshold occupancies of margays, ocelots, pumas, and jaguars in relation to jaguarundis in the Mamóní Valley and Guna Yala Comarca of Panama.

(0.01 km²) closer to rivers and with less slope, and avoid areas with more pastureland at both the local and regional scale and more mixed secondary forest/plantation at the regional scale (10 km²). While the avoidance of mixed secondary forest/plantation at the regional scale may be somewhat contradictory, this is likely driven by the inclusion of several large agroforestry plantations in the MVP. These results are important because they indicate that jaguarundis may not be as tolerant of disturbed habitats (plantations, farms, and pastureland) as has been historically presumed. Similar to our research, some studies have demonstrated that jaguarundis prefer tropical sub-deciduous forests and gallery forests, and have a negative relationship with pasture (Caso 2013, Boron et al. 2018, Giordano 2019). However, other research has indicated that jaguarundis are abundant in areas with grassland and agriculture, which was not supported by our research (Giordano 2015, Coronado Quibrera et al. 2019). In addition, though elevation did not indicate jaguarundi occurrence in our models, it was an important predictor of jaguarundi occurrence in a former study in Mexico (Coronado Quibrera et al. 2019). It is also important to note that there may be bias due to inadequate sampling of some covariates in our study area (e.g. areas of high ruggedness or slope, or far from rivers; Table 1).

There was a great degree of similarity between the covariates associated with jaguarundi occurrence and ocelot occurrence, and a lack of similarities between the covariates associated with jaguarundi occurrence and the occurrence of the other sympatric felid species. Jaguarundis and ocelots both occupied areas with more coverage of mixed secondary/plantation forests at the local scale closer to rivers and with less slope, and avoided greater amounts of pasture at the local and regional scale and mixed secondary forest/plantation at the regional scale. However, ocelots but not jaguarundis avoided areas with high elevations and greater amounts of mixed mature forest at the regional scale. While both the jaguarundi and jaguar had a negative association with pasture and mixed secondary forest/plantation at the regional scale with high slope, only the jaguar had a strong affinity for mature forest at the local scale (Craighead et al. 2022). Additionally, the jaguarundi and puma both had predicted occurrence in regions closer to rivers and with less slope, but were less likely to occur land with more pasture at the

local and regional scale and mixed secondary forest/plantation at the regional scale. Unlike jaguarundis, pumas were positively associated with elevation and were likely to occur in regions with more mixed mature forest at the local and regional scales. Jaguarundis and margays similarly had greater predicted occurrence in areas closer to rivers and with less slope, and had negative relationships with land cover of pasture at the local and regional scale and mixed secondary forest/plantation at the regional scale. Of the two species, only margays were more likely to occur in areas with higher elevations and more mixed mature forest at the regional scale.

Given the estimated spatial overlap of 57–80% between jaguarundi and sympatric felid species, plus the camera trap photographs of multiple species at individual camera stations in the Mamoni Valley, there are likely other means of niche separation (Fig. 5). The jaguar had the least amount of overlap with jaguarundi, likely because of the jaguar's dependence on mixed mature forest within 0.01 km² and the jaguarundi's lack thereof. Still, they could potentially coexist in 57% of the jaguarundi's predicted occurrence area at the 0.5 threshold. Since jaguarundis had the highest temporal overlap (61.16%) with jaguars, their sympatry is likely possible because of their differing sizes and diets. Jaguars are 10 to 20 times the weight of

jaguarundis, and their skull dimensions are up to three times that of the jaguarundi's skull dimensions (Castelló 2020). This size difference creates dietary distinctions between the species, as bite force has a positive relationship with mass and jaw length and felids that consume larger prey items have greater bite forces (Christiansen & Wroe 2007, Hartstone-Rose et al. 2012). The literature indicates dietary distinctions between jaguarundis and jaguars exist. Jaguarundis primarily eat small sigmodontine rodents and jaguars only consume prey items that weigh more than one kilogram (Garla et al. 2001, Giordano 2015). Out of those prey items, most were within the weight class of three to ten kilograms (Garla et al. 2006). Literature from differing regions reveal conflicting data of what mammalian species occur most frequently in the jaguar's scat samples. The giant anteater *Myrmecophaga tridactyla* occurred most frequently in jaguar scat from Emas National Park (Sollmann et al. 2013), white-lipped peccary *Tayassu pecari* and armadillo *Dasypus* spp. had the highest percent occurrence in jaguar scat from the Linhares Forest Preserve (Garla et al. 2001), and jaguars preferred to eat collared peccary *Tayassu tajacu* in Guam Bank (Weckel et al. 2006). Despite the variances these studies exhibit, they all indicate that jaguars do not appear to feed on small mammals to the extent that jaguarundis do.

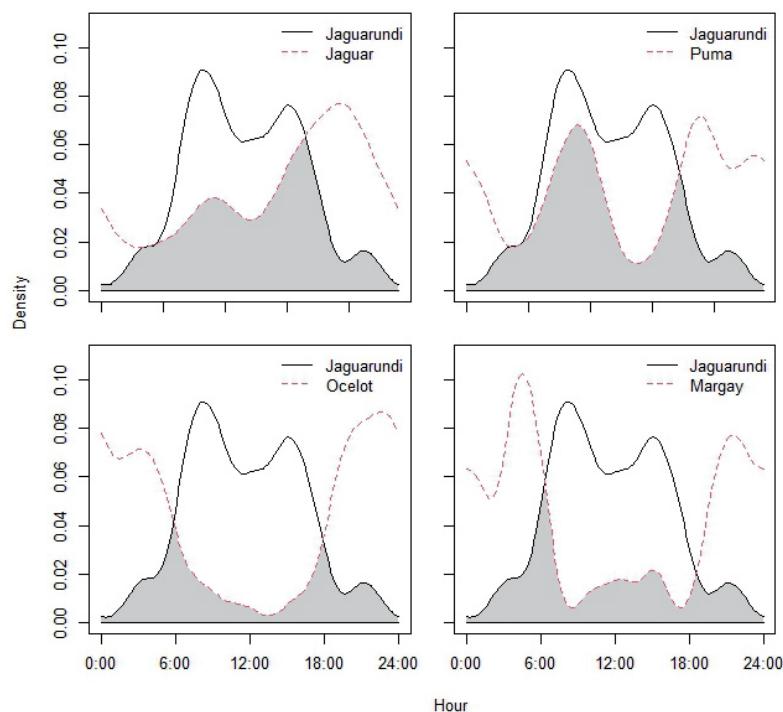


Fig. 6. Temporal overlap of jaguarundis with margays, ocelots, pumas, and jaguars in the Mamoni Valley and Guna Yala Comarca of Panama.

Jaguarundis also have a relatively high temporal overlap with pumas (56.92%), especially when compared to their temporal overlap with margays and ocelots. Therefore, jaguarundi and puma coexistence is also likely due to their differences in size and thus diet. Pumas are six to sixteen times the weight of jaguarundis, and their skulls are double the size of jaguarundi skulls (Castelló 2020). Though jaguarundis and pumas may target prey items from many of the same orders, the species consume different prey items with high frequencies. While jaguarundis primarily target small mammals, pumas tend to take the largest prey available (Rau & Jiménez 2002). Pumas mainly consumed collared peccary in San Luis Potosí, Mexico (Rueda et al. 2013) and white-tailed deer *Odocoileus virginianus* in Jalisco, Mexico (Núñez et al. 2000).

The possible diet partitioning between jaguarundis and ocelots is less obvious than seen between jaguarundis and both jaguars and pumas. Even though ocelots can be up to double the weight of jaguarundis and are also larger in length, height, and skull dimensions (Castelló 2020), some research has determined that the two felids both consume rodents with the highest frequency (Villa Meza et al. 2002, Wang 2002, Abreu et al. 2007, Giordano 2015). Variations exist among the types of small rodents consumed, with jaguarundis primarily eating *Sigmodon*, *Oryzomys*, and *Zygodontomys* rodents (Giordano 2015) and ocelots mainly eating *Calomys* species (Bianchi & Mendes 2007), *Akodon* species (Wang 2002), or murids weighing less than 100 grams (Abreu et al. 2007). Even more distinct, Villa Meza et al. (2002) discovered that the prey item with the highest frequency of occurrence in ocelot scat samples was not even a mammal but rather the spiny-tailed iguana *Ctenosaura pectinata*. However, the general size of prey consumed is similar and there is likely some overlap in target prey. In the case of the jaguarundi and ocelot, species coexistence may be accounted for by temporal distinctions. Jaguarundis only had a 28.53% temporal overlap with ocelots, as jaguarundis were diurnal and ocelots were nocturnal. This was confirmed by prior research that has also attributed temporal partitioning to the sympatry of jaguarundis and ocelots (Boron et al. 2018, Santos et al. 2019).

Jaguarundi co-occurrence with the margay can be explained by the dietary, temporal, and behavioural differences of their ecologies. Though Wang (2002) determined that margays

and jaguarundis primarily consume small rodents, other published research indicates that margays mostly eat arboreal mammals, or at least in higher frequencies than jaguarundis (Oliveira Calleia et al. 2009, Bianchi et al. 2011, Giordano 2015). Out of these arboreal mammals, Didelphimorphia has the highest frequency of occurrence in margay scat samples (Bianchi et al. 2011). The distinctions between the diets of jaguarundis and margays are likely not the result of morphological differences, as jaguarundis are most similar to margays in size (Castelló 2020). Instead, diet segregation might be accredited to the fact that jaguarundis are terrestrial and margays are assumed to be largely arboreal (Bianchi et al. 2011, Giordano 2015). In addition to having different diets, jaguarundis were diurnal and margays were nocturnal, only having a temporal overlap of 36.75%. Similarly, Santos et al. (2019) suggested that jaguarundis and margays may coexist largely through temporal divisions.

To further elucidate the ecology and sympatry of the jaguarundi an expanded targeted camera trapping effort is warranted. With broader spatial coverage, additional occurrence data could be used to better train the Maxent model. Also, our inferences regarding dietary niche partitioning relied on a literature review of papers from Mexico, Brazil, Venezuela, Belize, and Chile. There are likely to be regional discrepancies in felid diets, so scat analyses with samples taken from the Mamoni Valley and the Guna Yala Comarca would offer a more concrete explanation to the coexistence of jaguarundis, jaguars, pumas, ocelots, and margays of this specific region. However, this study is the first to focus specifically on jaguarundi occurrence, as well as interspecies relationships between jaguarundis and sympatric felids in Panama. All five species were less likely to occur in regions with more pasture at the regional scale, and every species but the jaguar had negative associations with pasture at the local scale. This is concerning as more of Panama's forests are converted to ranchland. Also, though jaguarundis can coexist with jaguars and pumas, their range overlap with these two big cats were the least of the sympatric felids. This is concerning as jaguars and pumas are frequently used as umbrella species for the conservation of co-occurring mammals, but the mixed mature forest that indicated jaguar and puma presence had no effect on jaguarundi occupancy (Dickman et al. 2015, Thornton et al. 2016). If further habitat loss threatens the conserva-

tion status of jaguarundis, they will require more species-specific conservation efforts, especially those aimed at maintaining mixed secondary forest and plantation rather than mixed mature forests. This research provides important foundational information on the species in Panama, which will contribute to targeted conservation efforts for jaguarundis in the future.

Acknowledgements

This research was supported by the Panthera Small Cat Fund, Alongside Wildlife Foundation and the Arthur Vining Davis Grant. We also wish to thank the Mamoni Valley Preserve, Geoversity and the Kaminando Habitat Connectivity Initiative for their logistical support. We thank the Guna Yala Congress and Miambiente who provided the permits to perform the research. Finally, we are also grateful to our field assistants and the local people of the Mamoni Valley.

References

- Abreu K. C., Moro-Rios R. F., Silva-Pereira J. E., Miranda J. M. D., Jablonski E. F. & Passos F. C. 2008. Feeding habits of ocelot (*Leopardus pardalis*) in southern Brazil. *Mammalian Biology* 73, 407–411.
- Anderson E., Cherrington E. A., Flores A., Perez J. B., Carrillo R. & Sempris E. 2008. Potential impacts of climate change on biodiversity in Central America, Mexico, and the Dominican Republic. CATHALAC / USAID, Panama City, Panama. 105 pp.
- ArcGIS Pro. 2020. Esri Inc. <https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview> (accessed April 27, 2022).
- Bianchi R. C. & Mendes S. L. 2007. Ocelot (*Leopardus pardalis*) predation on primates in Caratinga Biological Station, Southeast Brazil. *American Journal of Primatology* 69, 1173–1178.
- Bianchi R. C., Rosa A. F., Gatti A. & Mendes S. L. 2011. Diet of margay, *Leopardus wiedii*, and jaguarundi, *Puma yagouaroundi*, (Carnivora: Felidae) in Atlantic Rainforest, Brazil. *Zoologia* (Curitiba) 28, 127–132.
- Boron V., Xofis P., Link A., Payan E. & Tzanopoulos J. 2018. Conserving predators across agricultural landscapes in Colombia: Habitat use and space partitioning by jaguars, pumas, ocelots and jaguarundis. *Oryx* 54, 554–563.
- Caso A., de Oliveira T. & Carvajal S. V. 2015. *Herpailurus yagouaroundi*. The IUCN Red List of Threatened Species 2015: e.T9948A50653167. <https://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T9948A50653167.en>. Accessed on 27 April 2022.
- Caso A. 2013. Spatial differences and local avoidance of ocelot (*Leopardus pardalis*) and jaguarundi

(*Puma yagouaroundi*) in northeast Mexico. Dissertation. ProQuest, Ann Arbor, MI, 109 pp.

Castelló J. R. 2020. Felids and hyenas of the world. Princeton University Press, Princeton, New Jersey. 280 pp.

Christiansen P. & Wroe S. 2007. Bite forces and evolutionary adaptations to feeding ecology in carnivores. *Ecology* 88, 347–358.

Condit R., Robinson W. D., Ibáñez R., Aguilar S., Sanjur A., Martínez R., ... & Heckadon, S. 2001. The status of the Panama Canal watershed and its biodiversity at the beginning of the 21st Century: Long-term ecological studies reveal a diverse flora and fauna near the Panama Canal, harbored within a corridor of forest stretching from the Caribbean to the Pacific, but deforestation, land degradation, erosion, and overhunting remain threats. *BioScience* 51, 389–398.

Coronado Quibrera W. P., Olmos Oropeza G., Beníder L. C., Rosas Rosas O. C., Palacio Núñez J., Tarango Arámbula L. A. & Herrera Haro J. G. 2019. Adaptability of the threatened jaguarundi (*Herpailurus yagouaroundi*, Schreber, 1777) to human-altered environments in San Luis Potosí, Mexico. *Acta Zoológica Mexicana* 35, 1–15.

Craighead K., Yacelga M., Wan H. Y., Vogt R. & Cushman S. A. 2022. Scale-dependent seasonal habitat selection by jaguars (*Panthera onca*) and pumas (*Puma concolor*) in Panama. *Landscape Ecology* 37, 129–146.

Dickman A. J., Hinks A. E., Macdonald E. A., Burnham D. & Macdonald D. W. 2015. Priorities for global felid conservation. *Conservation Biology* 29, 854–864.

Espinosa C. C., Trigo T. C., Tirelli F. P., da Silva L. G., Eizirik E., Queirolo D., Mazim F. D., Peters F. B., Favarini M. O. & de Freitas T. R. 2017. Geographic distribution modeling of the Margay (*Leopardus wiedii*) and jaguarundi (*Puma yagouaroundi*): A comparative assessment. *Journal of Mammalogy* 99, 252–262.

Garla R. C., Setz E. Z. & Gobbi N. 2001. Jaguar (*Panthera onca*) food habits in Atlantic Rain Forest of Southeastern Brazil. *Biotropica* 33, 691–696.

Giordano A. J. 2015. Ecology and status of the jaguarundi (*Puma yagouaroundi*): A synthesis of existing knowledge. *Mammal Review* 46, 30–43.

Golley F. B., McGinnis J. T., Clements R. G., Child G. I. & Duever M. J. 1969. The structure of tropical forests in Panama and Colombia. *BioScience* 19, 693–696.

Hartstone-Rose A., Perry J. M. & Morrow C. J. 2012. Bite force estimation and the fiber architecture of Felid Masticatory muscles. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* 295, 1336–1351.

Ibáñez R., Condit R., Angehr G., Aguilar S., García T., Martínez R., ... & Heckadon S. 2002. An Ecosystem Report on the Panama Canal: Monitoring the Status of the Forest Communities and the Watershed. *Environmental Monitoring and Assessment* 80, 65–95.

Java. 2014. Oracle. <https://www.java.com/en/> (accessed May 11, 2022).

Klooster D., Strout N. & Smith D. 2021. GIS in the jungle: Experiential environmental education (EEE) in Panama. *Journal of Environmental Studies and Sciences* 12, 164–176.

Mamoni Valley Preserve. (n.d.). <http://www.mamonivalleypreserve.org/> (accessed April 27, 2022).

de Oliveira T. G. & Pereira J. A. 2014. Intraguild Predation and Interspecific Killing as Structuring Forces of Carnivoran Communities in South America. *Journal of Mammal Evolution* 21, 427–436.

Nagy-Reis M. B., Iwakami V. H. S., Estevo C. A. & Setz E. Z. F. 2019. Temporal and dietary segregation in a Neotropical small-felid assemblage and its relation to prey activity. *Mammalian Biology* 95, 1–8.

Núñez R., Miller B. & Lindsey F. 2000. Food habits of jaguars and pumas in Jalisco, Mexico. *Journal of Zoology* 252, 373–379.

Oliveira Calleia F., Rohe F. & Gordo M. 2009. Hunting strategy of the Margay (*Leopardus wiedii*) to attract the wild pied tamarin (*Saguinus bicolor*). *Neotropical Primates* 16, 32–34.

Panama Deforestation Rates and Statistics. 2021. University of Maryland and World Resources Institute. <http://www.globalforestwatch.org/> (Accessed 27 April 2022).

Phillips S. J., Dudik M. & Schapire R. E. (n.d.). Maxent software for modeling species niches and distributions. Available from http://biodiversityinformatics.amnh.org/open_source/maxent (Accessed 27 April 2022).

Phillips S. J. & Dudik M. 2008. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography* 31, 161–175.

R Core Team. 2021. R: A language and environment for statistical computing.

Rau J. R. & Jiménez J. E. 2002. Diet of puma (*Puma concolor*, Carnivora: Felidae) in coastal and Andean ranges of southern Chile. *Studies on Neotropical Fauna and Environment* 37, 201–205.

Reymondin L., Argote K., Jarvis A., Navarrete C., Coca A., Grossman D., Villalba A. & Suding P. 2013. Road Impact Assessment Using Remote Sensing Methodology for Monitoring Land-Use Change in Latin America: Results of Five Case Studies. *Tech. Inter-American Development Bank*, Washington, D.C.

Ridout M. S. & Linkie M. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* 14, 322–337.

Rueda P., Mendoza G. D., Martínez D. & Rosas-Rosas O. C. 2013. Determination of the jaguar (*Panthera onca*) and puma (*Puma concolor*) diet in a tropical forest in San Luis Potosí, Mexico. *Journal of Applied Animal Research* 41, 484–489.

Santos F., Carbone C., Wearn O. R., Rowcliffe J. M., Espinosa S., Lima M. G. M., ... & Peres C. A. 2019. Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. *PLoS ONE* 14 (3): e0213671.

Slusser J. L., Calle A. & Garen E. 2015. Sustainable ranching and restoring forests in agricultural landscapes, Panama. *European Tropical Forest Research Network (ETFRN)*. News 57, 31–38.

Sollmann R., Betsch J., Furtado M. M., Hofer H., Jácomo A. T., Palomares F., Roques S., Torres N. M., Vynne C. & Silveira L. 2013. Note on the Diet of the jaguar in Central Brazil. *European Journal of Wildlife Research* 59, 445–448.

Thornton D., Zeller K., Rondinini C., Boitani L., Crooks K., Burdett C., Rabinowitz A. & Quigley H. 2016. Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). *Ecological Applications* 26, 1112–1124.

Tófoli C. F., Rohe F. & Setz E. Z. F. 2009. Jaguarundi (*Puma yagouaroundi*) (Geoffroy, 1803) (Carnivora, Felidae) food habits in a mosaic of Atlantic rainforest and eucalypt plantations of southeastern Brazil. *Brazilian Journal of Biology* 69, 871–877.

Villa Meza A., Martinez-Meyer E. & López González C.A. 2002. Ocelot (*Leopardus pardalis*) food habits in a tropical deciduous forest of Jalisco, Mexico. *The American Midland Naturalist* 148, 146–154.

Wang E. 2002. Diets of ocelots (*Leopardus pardalis*), Margays (*L. wiedii*), and oncillas (*L. tigrinus*) in the Atlantic rainforest in southeast Brazil. *Studies on Neotropical Fauna and Environment* 37, 207–212.

Weckel M., Giuliano W. & Silver S. 2006. Jaguar (*Panthera onca*) feeding ecology: Distribution of predator and prey through time and space. *Journal of Zoology* 270, 25–30.

¹ University of Delaware, Department of Entomology and Wildlife Ecology, Townsend Hall, Newark, Delaware 19716, USA

² Lincoln University, Biology Department, Nelson Science Center, 1570 Baltimore Pike, Lincoln University, Pennsylvania 19352, USA
*jmccarthy@lincoln.edu

³ Mamoni Valley Preserve/Geoversity, Mamoni Centro, Panama

⁴ Kaminando Habitat Connectivity Initiative, Oakland, California 94612