*Ecology of a versatile canid in the Neotropics: gray foxes (*Urocyon cinereoargenteus*) in Belize, Central America*

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ORIGINAL PAPER

Ecology of a versatile canid in the Neotropics: gray foxes (*Urocyon cinereoargenteus*) in Belize, Central America

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Abstract

Gray foxes are successful habitat generalists within the temperate zone of their geographic range, exploiting a wide variety of habitats, including human-dominated landscapes. However, little is known of their use of tropical habitats or their ability to exploit landscapes with human activity. Here, we report the first study to explore the ecology and behavior of gray foxes within the tropics. Extensive camera-trap data (23,598 trap nights) across two different landscapes in Belize, combined with telemetry data on three collared individuals, showed a preference for more open and drier habitats over tropical moist broadleaf forest which is the dominant habitat type in the region. Although foxes did not use the interior of the broadleaf forests, they were detected at the edges and readily exploited areas that had been converted to support human activities (e.g., tourist centers). Home ranges of collared individuals were relatively large (3–7 km^2) compared to those of temperate gray foxes, suggesting that they occupy a less productive landscape than those studied further north. This study found that although tropical gray foxes readily exploited human-altered landscapes, just as they do in the temperate zone, they are not the habitat generalists as previously thought and seem unable to fully exploit tropical moist broadleaf forest, the regions' most dominant and productive habitat type.

Keywords Gray fox · Home ranges · Diet · Activity patterns · Habitat selection · Neotropics

Introduction

Human-dominated landscapes are increasingly influencing wildlife population dynamics, either as living spaces or corridors connecting populations (Athreya et al. 2013; Chapron et al. 2014). Some species thrive in human-altered landscapes, profiting from high-yield food production, while others are unable to adapt to a changing environment (McKinney and Lockwood 1999), leading to shifts in species community structure (Kark et al. 2006; Ritchie and Johnson 2009). Canids are considered particularly resilient to anthropogenic change. We studied gray foxes (*Urocyon cinereoargenteus*), a highly adaptable species, ranging from southern Canada to northern Colombia, and the only canid with its natural range

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occurring in both North and South America (Hunter 2011). Gray foxes thrive in both the natural as well as the human-dominated landscapes of North America (Harrison 1997; Rountree 2004; Kapfer and Kirk 2012; Nogeire et al. 2013; Deuel et al. 2017a; Lombardi et al. 2017), making them a versatile and adaptable species. Further south, they have been detected in sugarcane and coffee plantations in Mexico and upland pine forest in Belize, but generally little is known about their ecology in broadleaf forest or their adaptability to human activities in the tropics (Davis et al. 2010; Gallina et al. 2016).

In the Northern parts of their range, gray foxes have a wide dietary breadth, including rodents, fruit, plants, arthropods, and birds, adapting their omnivorous diet to local availability (Harrison 1997). Further south, in the tropical parts of their range, we expected this opportunistic feeding behavior to be reflected in a similarly wide dietary niche, using a broad range of habitats (habitat generalist). The small home ranges of temperate gray foxes, of 0.6 to 6 km^2 (median ~ 2 km^2) suggest that they inhabit relatively stable, food-rich environments (Fuller 1978; Haroldson and Fritzell 1984; Harrison 1997; Chamberlain and Leopold 2000; Riley 2006; Deuel et al. 2017b). Given the climatic stability and rich diversity of potential prey in the Neotropics, we expected home ranges of neotropical gray foxes to be comparatively smaller than those recorded in the temperate north. Such variation may already be reflected in the variation in body size across their range, weighing 3–7 kg in the northern temperate zone (Fuller and Cypher 2004) but just 1.8–3.5 kg, in the tropical south (Reid 1997).

Sociality in temperate gray foxes has only been noted within the context of older siblings assisting mated pairs with the rearing of pups; they are generally considered solitary in other activities such as traveling and foraging (Chamberlain and Leopold 2000; Deuel et al. 2017b). Potentially, roads could function as an attractive food source, providing garbage and road kill carcasses for scavenging. Indeed, in the northern part of their range, gray foxes do not seem to avoid road systems, and they are a major cause of fox mortality (Deuel et al. 2017a; Temple et al. 2010; Riley 2006). Concentrated food sources, such as garbage around villages, eco-lodges and road verges are common throughout Belize and could attract multiple foxes. If sociality of foxes were flexible, we might expect aggregation of foxes around such high-yield food sites. Such toleration of conspecifics has not been recorded or well-studied in temperate gray foxes.

In the northern extent of their range, up to 92% of gray fox mortality is attributed to predation by coyotes (*Canis latrans* Farias et al. 2005). As such, they tend to avoid edge and more open habitats with high densities of these larger canids and adopt nocturnal activity patterns to avoid the diurnal coyote (Fedriani et al. 2000; Wang et al. 2015). Coyotes have only recently started expanding their range into Belize. Our study took place when coyotes were still rare in Belize, occasionally detected in the north and west, but [largely] absent from central and southern Belize (unpublished camera-trap and interview data Foster and Harmsen). The two top predators of the Neotropics, jaguars, and pumas are not known to prey on gray foxes in Belize (Foster et al. 2010; Figueroa 2013). With coyotes still lacking, we therefore expected that tropical gray foxes would have a more diurnal activity pattern than temperate foxes, and habitat selection and distribution of the species would not be limited by the presence of sympatric predators.

In this first study of neotropical gray foxes, we studied ranging behavior, habitat use, activity patterns, sociality, and diet of tropical gray foxes in Belize, Central America, and compared results with those from the temperate zone. We expected such a generalist species to thrive across the climatically more stable tropical habitats, within a landscape lacking coyotes. We studied gray foxes within two distinct landscapes: (1) protected tropical broadleaf forest and (2) a mosaic landscape comprising human development (agriculture, settlements), savannah, and tropical broadleaf forest. We used camera-trap data from both landscapes, and VHF telemetry data from the mosaic landscape. This study is the first to provide an overview of the similarities and differences between temperate and tropical gray foxes.

Methods

Study areas

The Central Belize Corridor (CBC, 17°21′N, 88°32′W) is a 750-km^2 mosaic landscape of poorly drained secondary deciduous broadleaf forest, interspersed with lowland savannah and pine forest (*Pinus caribaea*), agriculture (livestock, rice, corn, and citrus plantations), nine settlements and single house dwellings, the national zoo, and an eco-lodge. Human population density is approximately 5 people per km^2. The area is bisected by a two-lane highway with similar pine savannah habitat on either side extending to the tarmac. The highway has no barriers to crossing and is at the same elevation as the surrounding habitat. In October 2010, the area was hit by category-2 hurricane "Richard," which severely damaged the forest structure and the resulting dead wood fueled forest fires during the following dry season (Feb-May 2011, personal observation Harmsen, Foster, Figueroa; Meerman 2011).

The Cockscomb Basin Wildlife Sanctuary (CBWS, 16°47′N, 88°36′W) is a protected area of secondary broadleaf moist tropical forest at an advanced stage of succession. The CBWS lies at the eastern edge of the Maya Mountain Massif, a 5000-km^2 area of contiguous forest (Harmsen et al. 2017). The area was heavily logged until the 1980s and declared a wildlife sanctuary of 425 km^2 in 1990. The former logging roads and more recently tourist footpaths provide a system of established trails. There is a single vehicle dirt road for entry into the sanctuary with a visitor center where tourists can stay overnight, cook, and have picnics.

Camera trapping

We investigated fox behavior using camera-trap photographs of foxes obtained from trail-based camera-trap surveys designed to monitor jaguars in the two study sites (Fig. 1). As gray foxes use trail systems (Davis et al. 2010; Harmsen and Foster unpublished data), the camera locations were suitable for detecting foxes, if present. We investigated activity patterns and broad patterns in habitat use, diet, and sociality.

In the CBC, we monitored 67 camera stations deployed consecutively across three distinct surveys (21, 20, 26 camera stations, respectively). We conducted these three surveys twice, once before hurricane Richard between 1 Dec. 2008 and 18 Mar. 2009 (Cuddeback, film camera, visible light flash, with enforced 3 min delay) and once after hurricane Richard between 21 Dec 2010 and 1 Feb 2012 (Cuddeback Capture IR and Reconynx Rapidfire RM45, both digital camera traps with infra-red flash, set on rapid fire). Survey duration was an average of 120 days (s.d. = 22), with a mean spacing between cameras of 1.7 km (±SD = 0.4 km). In the CBWS, we used data from the 20 permanent camera stations deployed between 2011 and 2014 (Panthercam V3, digital, visible light flash, 8 s delay for flash recharge), with a mean spacing of 2.0 km (± SD = 0.5 km). Survey duration was 90 days in 2011 and 2012 (18 Apr to 16 Jul 2011 and 1 Apr to 29 Jun 2012, respectively). Thereafter, camera traps were active from 15 Mar 2013 until 29 Mar 2014.

Habitat preference We overlaid the camera grids (CBC and CBWS) with habitat layers in four broad categories: broadleaf forest, savannah, agriculture, and settlements, using Meerman's ecosystem classification map (Meerman and Clabaugh 2017). Previous studies have shown that gray foxes have high capture probabilities on trail systems when present (Davis et al. 2010; Harmsen and Foster unpublished data). We therefore assumed that detection rates were a reasonable measure of habitat preference without having to correct for detection probability. For each habitat type, we calculated the number of locations where foxes were detected and frequency of fox detections, corrected for trap effort per location (#detections/number of trap nights). We used chi-square to test if the distribution of fox detections differed from the camera

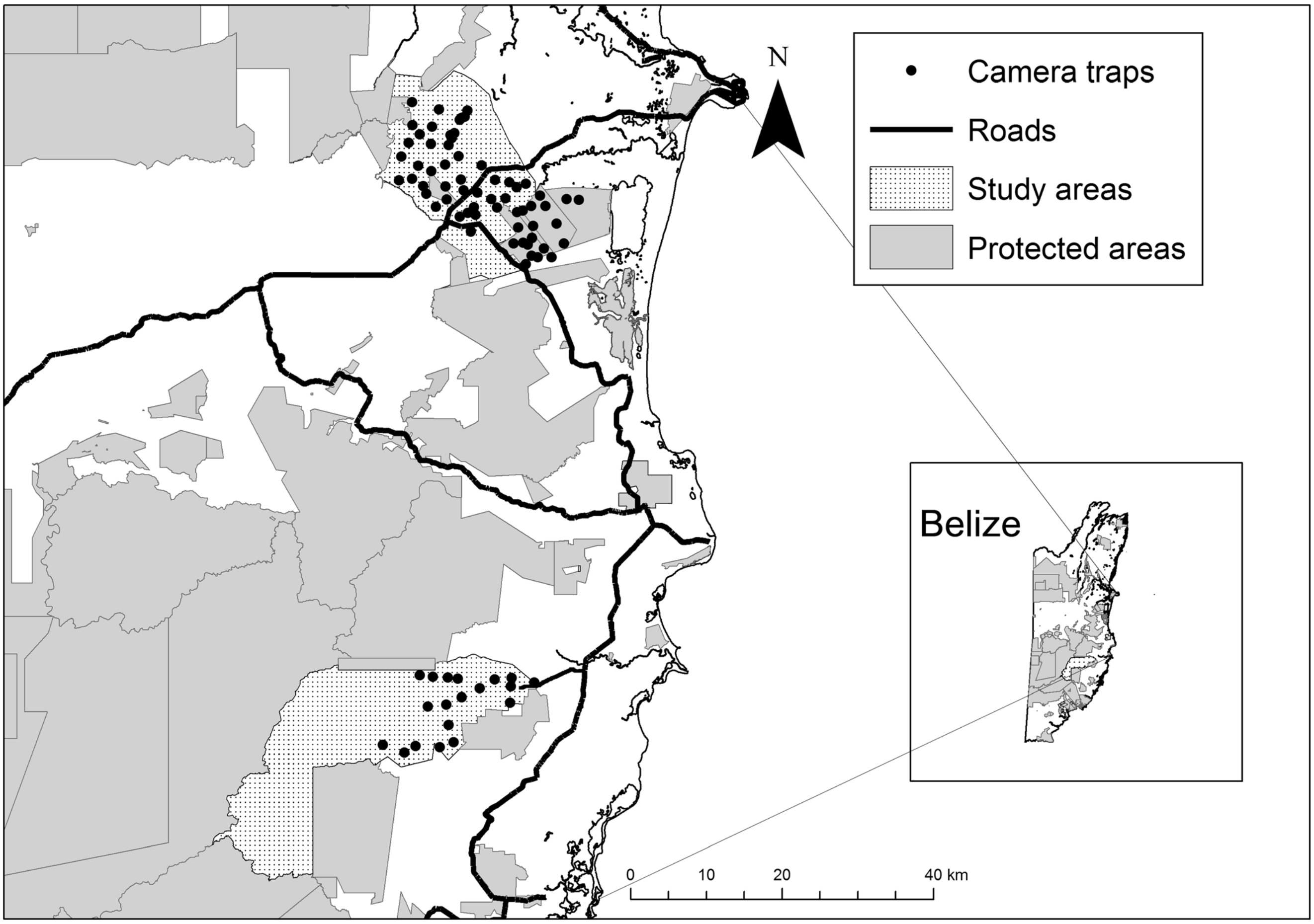


Fig. 1 Study areas (stippled): Central Belize (upper) and the Cockscomb Basin Wildlife Sanctuary (lower), showing camera trap locations (black dots)

distribution across the three habitats (broadleaf forest, savannah, and agriculture).

The cameras within the CBC grid were regularly spaced at relatively equal distance (~ 2 km apart), allowing us to use the distribution of detections as a species utility distribution. We calculated 50 and 95% kernel distributions to represent the species utility distribution across the landscape, using Geospatial Modeling Environment (GME, Beyer 2012) kde function (SCV bandwidth, cell size 10). As we were unable to individually recognize foxes, we only used one detection per camera location within a 24-h period to ensure time independence of events.

Spatial response to hurricane We assessed the utility distribution across the CBC landscape in 2009 and 2011, before and after hurricane Richard, using the 95% kernel distributions based on detection rates per camera location, and tested for a difference in spatial distribution using the utilization distribution overlap index (UDOI, Fieberg and Kochanny 2005). The UDOI was estimated with the R package *adehabitatHR* (Calenge 2006). The UDOI index ranges between 0 (no overlap of home ranges) and 1 (complete uniform overlap of home ranges). The UDOI index can be > 1 if the utilization distribution is non-uniform with a high degree of overlap between individuals.

Activity patterns We investigated the daily activity pattern of foxes, using the time stamps of camera detections of foxes in CBC and CBWS and assuming that the temporal distribution of fox detections on camera represented their 24-h activity pattern. For multiple detections at the same location within the same hour, we used the median time event. We used the R package “overlap” to create a smoothed kernel density distribution of the daily activity pattern, based on the camera-trap time stamps of fox detections for each study site (Ridout and Linkie 2009; Meredith and Ridout 2018). The level of temporal overlap between the sites was estimated using the coefficient of overlap (Dha) between the two populations (Ridout and Linkie 2009; Meredith and Ridout 2018). A Dha value of 0 indicates no overlap, and a value of 1 indicates identical activity patterns. We estimated the precision of the coefficient of overlap by bootstrapping with 999 simulations (Meredith and Ridout 2018).

Diet Both sexes are known to be involved in rearing of cubs, bringing back whole food items to den sites (Chamberlain and Leopold 2000; Deuel et al. 2017b). We therefore noted any photo detections showing foxes carrying food items in their mouths and identified vertebrate prey items as far as the image resolution would allow.

Social behavior We assessed how frequently foxes travel or forage together versus alone, from photos of association: two individuals in a single frame, or successive detections of individuals within 15 min, moving in the same direction. We only used data from rapid-fire camera traps with infra-red flash for this analysis, to ensure that individuals were not missed due to the delay between consecutive triggers or flash recharge.

Live-trapping and telemetry

We live-trapped and collared foxes as part of a larger study of mammals in Central Belize. For details of trapping and handling, see Gutierrez et al. (2017). We anesthetized foxes by hand injection through the bars of the cage traps, using a combination of ketamine (dosage 20 mg/kg; concentration 100 mg/ml) and acepromazine (dosage 0.2 mg/kg; concentration 25 mg/ml). Body conditions was assessed by the lead author only, using a five-point scale, ranging from a score of 1 for bone structure visible along spin and pelvis, to a score of 5 for good fat distribution across body. We assessed ectoparasite loads by visual inspection of the pelt, and parasites were counted and removed for further analyses (ticks, lice, and fleas; Lopes et al. 2016). We fitted three adult foxes (two females and one male) with VHF radio-collars (Telonics MOD080) and released a fourth male without collar due to a canine bite-wound to its neck. We tracked the foxes between June 2011 and May 2012 through triangulation using simultaneous bearings taken by a minimum of three observers at intervals of ≥ 15 min for up to 5 h. We fixed their locations using LOAS 4.0, discarding locations with error ellipses in excess of 100 ha or bearings with a difference < 10°.

Independence of fixes To estimate temporal independence between fixes, we estimated the average time it would take each fox to travel between its two most widely spaced fixes, assuming this was a good estimate of the maximum distance it would travel (maximum detected distance; MDD). We used the GME movement.pathmetrics tool to calculate the step length and time between fixes, and thereby estimated the average speed of travel for each fox (μS), including only fixes ≤ 1 h apart to estimate the distribution of walking speeds between fixes. Using time = MDD/μS, we estimated the average time it would take each fox to travel across its home range. We assumed that fixes were independent if the time interval between them was greater than or equal to MDD/μS in time. Time independence varied between the three foxes (female F1 ≥ 5.4 h, female F2 ≥ 8.8 h, and male M1 ≥ 17.6 h). On the basis of these times, we considered fixes independent at a separation ≥ 17.6 h, and as a conservative measure, we used 24-h periods.

Home range and overlap We estimated home ranges, using GME (GME, Beyer 2012), for estimation of 100% minimum convex polygons (MCP) using the genMCP function and the 50 and 95% kernel ranges using the kde function (SCV bandwidth, cell size 10). For the kernel ranges, we only used independent fixes, randomly chosen from clusters of fixes that were too close in time to be considered independent (24 h, see previous section).

We estimated the overlap between foxes for 100% MCPs using the intersect tool in ArcMap GIS 10.1 and for the 95% kernels using the UDOI index (Fieberg and Kochanny 2005) with *adehabitatHR* R package (Calenge 2006).

Attraction and avoidance of roads We assessed whether the highway acted as a barrier (due to traffic) or an attractant (due to road kill carrion and garbage), by comparing the road-crossing frequency of each fox against the crossing frequency of randomly generated movements based on similar step lengths and number of steps. For each fox, we recorded the frequency of road crossings during each tracking session with > 3 fixes (mean 7.8 fixes; range 4–19), and then simulated 200 randomly generated moves, with the same number of sessions, number of steps, and step lengths, using the GME, movement.simplecrw tool. We set the start location in each simulation as the first location of detection of the fox. We selected turn angle between steps randomly from a distribution between − 180° and 180° and confined the random walks to remain inside the 100% MCP of each individual. We used ArcMap GIS 10.1 to establish how many of the 200 iterations per session included road crossings and the frequency of crossings per session per iteration. For each collared fox, we generated frequency distributions of random highway crossings for 200 simulated foxes, covering the same number of tracking days with similar step lengths as the collared foxes. If the number of detected crossings of the collared foxes fell close to the median of the random distribution, then we could conclude that foxes cross the road randomly, if the observed number fell at the higher or the lower tail of the random distribution, we would conclude that the foxes were either attracted to or avoided the road, respectively. We measured this at two levels: (1) frequency of tracking sessions that included at least one crossing and (2) frequency of crossings, including multiple crossings within a single tracking session. In this manner, we could differentiate between crossing decisions at the macro-level (whether crossing on a given day was random) and the micro-level (whether the frequency of crossings on a given day was random).

Habitat preferences of collared individuals We defined the total study area as the area covered by the 100% MCP of all data points of the three collared foxes combined and calculated the area of each habitat present within it, using Meerman's ecosystem classification map (Meerman and Clabaugh 2017). We described the second- and third-order habitat preferences per fox only, as first-order habitat selection concerns habitat selection at the total species distribution range (Johnson 1980). Second-order habitat selection concerns the choice of home range location within a wider landscape, described as % of habitat X in home range/% of habitat X available in total study area (% Ind. km^2/% total km^2; Johnson 1980). Third-order habitat selection concerns the utility distribution of tracking points within the home range itself, calculated as % tracking points falling in habitat/% habitat in home range (% points/% Ind. km^2; Johnson 1980). We assumed opportunistic use of habitat for ratios close to unity, habitat preference for ratios > 1, and avoidance for ratios < 1. Due to the small sample size of collared foxes, we did not conduct an overall analysis of habitat preference (e.g., compositional analysis of habitat use; Aebischer et al. 1993). All statistical analyses were performed using R (R Core Team 2016).

Results

We obtained 130 independent detections of foxes in the protected broadleaf forest from 11,170 trap nights and 369 independent detections of foxes in the human-influenced mosaic landscape from 12,428 trap nights, equivalent to 1 fox and 3 foxes per 100 trap nights, respectively.

Habitat use Within the homogenous landscape of Cockscomb Basin Wildlife Sanctuary (CBWS), all detections of foxes were confined to the edges of the broadleaf forest. Of the 130 independent detections, 120 (92%) were from a single location on the unpaved entrance road leading to the sanctuary (7 km from the nearest village and 3 km from the Visitors' Center). The remaining 10 detections (0.1 foxes per 100 trap nights) were on the tourist trail system (at 2, 4 and 7 km from the Visitors' Center). We detected no foxes further into the sanctuary, despite having camera traps up to 21 km from the Visitors' Center (Fig. 2). At the Visitors' Center, we frequently observed foxes visiting and foraging around the garbage and picnic areas and single female foxes with cubs. The 10 detections further into the forest were based on a single cluster of captures over 2.5 weeks. Based on the rarity of foxes traveling in this direction, these were potentially dispersing adolescent(s) or an exploratory event.

Within the human-influenced mosaic landscape of Central Belize, the detection rate of foxes increased following the hurricane, from 2 to 5 foxes/100 trap nights. However, we switched from using film camera traps to digital camera traps following the hurricane and this may have increased the detectability of foxes. The foxes were similarly distributed across the landscape before and after the hurricane (UDOI index of overlap = 0.93) and were mostly concentrated at camera-trap locations near the highway and unpaved roads, in savannah, agricultural lands, and the more open degraded habitats closer to human activity (Fig. 3a, b). The distribution of fox detections did not differ detectably from the overall

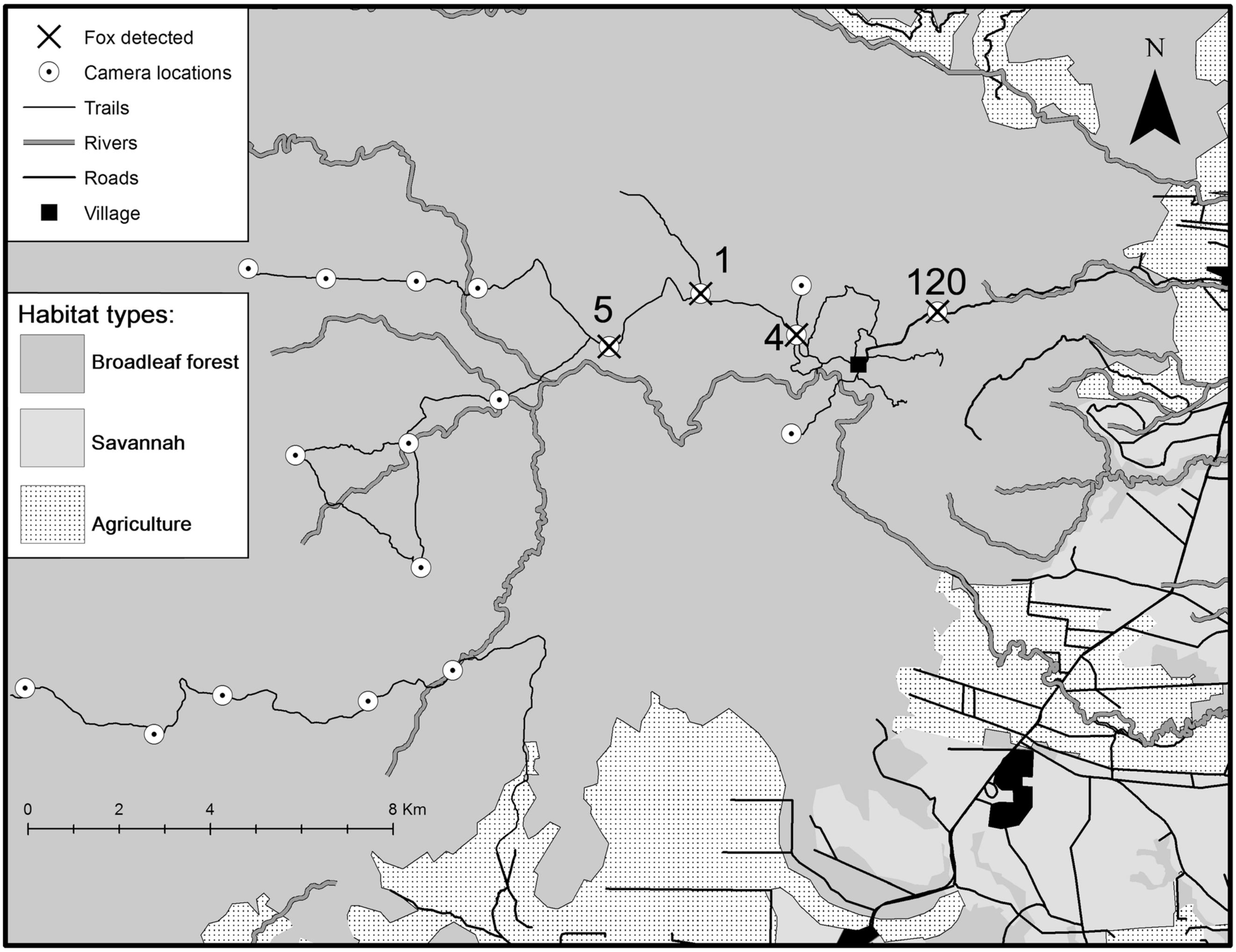


Fig. 2 Distribution of camera traps and gray fox (*Urocyon cinereoargenteus*) presence in the Cockscomb Basin Wildlife Sanctuary for periods 18 Apr to 16 Jul 2011, 1 Apr to 29 Jun 2012, and 15 Mar 2013 to 29 Mar 2014; the number of independent fox detections are shown

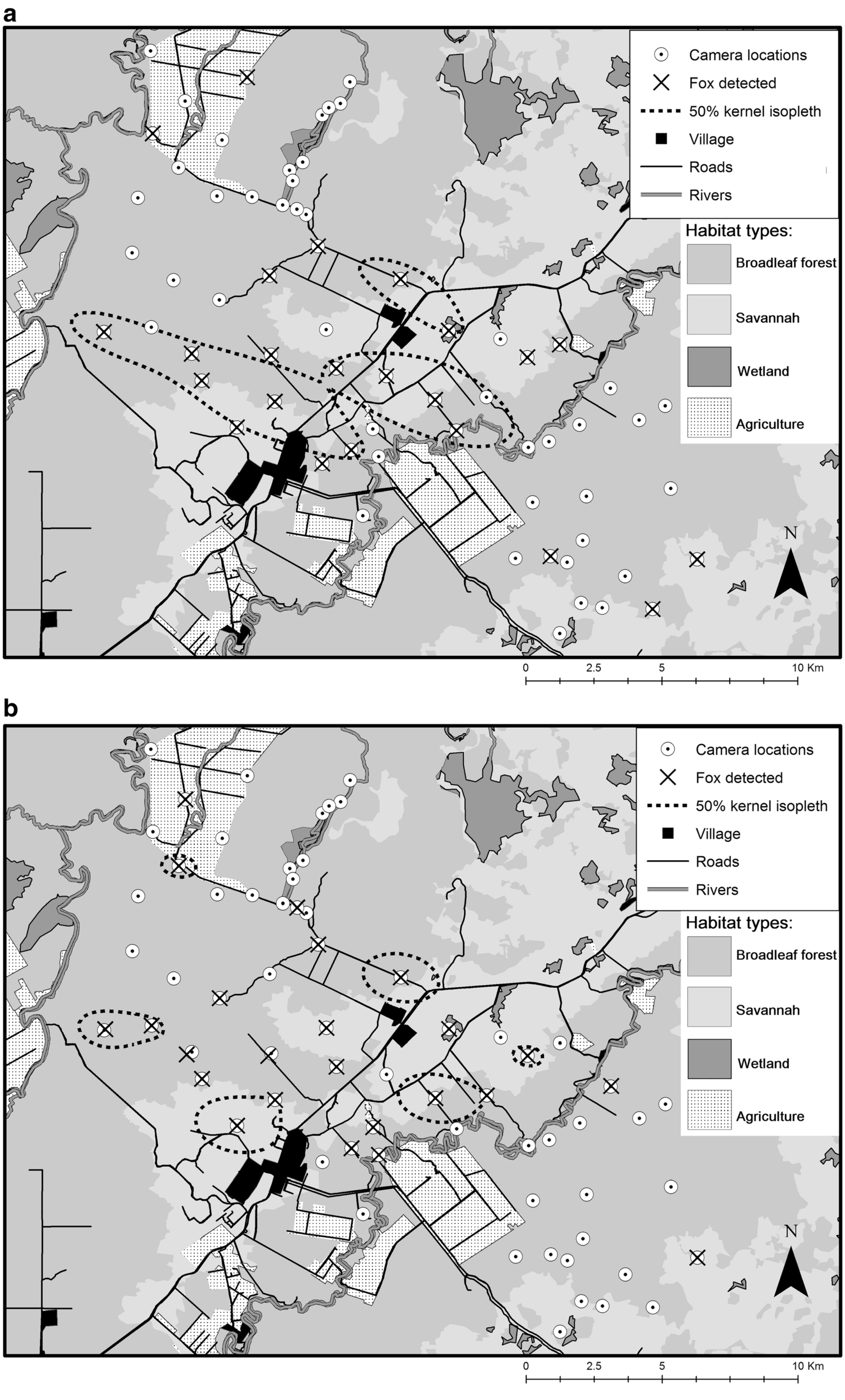
camera distribution across the three habitats (pre- and post-hurricane combined dataset: $\chi^2 = 4.42$, df = 3, $p > 0.1$). Pre-hurricane, we only detected foxes at two broadleaf forest locations > 1 km away from road, agriculture, or savannah (max. 1.5 km). Post-hurricane, this increased to three broadleaf forest locations, up to 2.7 km from road, agriculture, or savannah. Post-hurricane, foxes penetrated further into the broadleaf forest in the north, where post-hurricane fires, originating from the road verges, had been more extreme than elsewhere in the study area, creating more open habitat (Fig. 3a, b). Additionally, the proportion of detections in savannah increased post-hurricane compared to pre-hurricane levels (Table 1).

Activity patterns In both landscapes, foxes were active throughout the day with a peak of activity in the early part of the night between 18:00 and 22:00 and a resting period around 17:00 (Fig. 4). The overlap in activity patterns between the sites was high with a Dha value of 0.84 (CI 0.79–0.89).

Diet Across the two landscapes, we obtained 32 photo events of foxes carrying identifiable food items. Two photos showed foxes carrying two different prey items, creating a total of 34 prey events. The majority of events (27) were from the unpaved road at the entrance of the protected broadleaf forest, and the other seven events were from an unpaved logging road neighboring agricultural fields in Central Belize. Small rodents made up approximately 50% of the prey items; the remainder comprised opossums, lizards, birds, frogs, fruit, and garbage (Table 2).

All incidents of foxes carrying garbage were detected at the entrance of the protected forest; presumably, the foxes were scavenging from the garbage site of the Visitors' Center.

Fig. 3 Distribution of camera traps and gray fox (*Urocyon cinereoargenteus*) presence in Central Belize, **a** before hurricane Richard (between 1 Dec 2008 and 18 Mar 2009) and **b** after hurricane Richard (between 21 Dec 2010 and 1 Feb 2012); for each study area, the 50% kernel distribution of all independent fox detections is shown ▶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Camera locations
Fox detected
50% kernel isopleth
Village
Roads
Rivers
Habitat types:
Broadleaf forest
Savannah
Wetland
Agriculture
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Fox detected
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Village
Roads
Rivers
Habitat types:
Broadleaf forest
Savannah
Wetland
Agriculture
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Table 1 Distribution of camera traps in Central Belize by habitat, during two survey periods, pre-hurricane (6428 trap nights; between 1 Dec 2008 and 18 Mar 2009) and post-hurricane (6000 trap nights; between 21 Dec 2010 and 1 Feb 2012), showing the number (and %) of camera traps per habitat (cameras) and the number (and %) of independent gray fox (*Urocyon cinereoargenteus*) detections per habitat (detections)

Habitat	Total	Pre-hurricane		Post-hurricane	
		Cameras	Detections	Cameras	detections
Agriculture	5 (7)	1 (4)	2 (2)	1 (4)	6 (2)
Savannah	7 (10)	5 (23)	14 (15)	5 (21)	76 (27)
Broadleaf	55 (82)	16 (73)	75 (82)	18 (75)	196 (71)
Total	67	22	91	24	278

Additionally, at this location, one fox was detected carrying two prey items that resembled Norway rats (*Rattus norvegicus*). In contrast, rodents carried by foxes on the logging road neighboring agricultural fields in Central Belize appeared to be hispid cotton rats (*Sigmodon hispidus*, see Fig. 5).

In four events, foxes carried two rodents of the same species, potentially dug from a single nest. In one event, a fox carried two cotton rats and a frog, suggesting that while transporting the prey, the fox opportunistically added to its quarry (Fig. 5).

Social behavior Of the 130 independent detections of foxes in the protected broadleaf forest of CBWS, we detected no individuals traveling together; however, the digital camera traps used here have a white-flash, requiring a delay of 8 s between consecutive photographic triggers while the flash recharges. As such, we may have missed detections of foxes following behind each other.

Of the 277 independent detections of foxes by infra-red flash, fast-trigger digital camera traps in the human-influenced mosaic landscape of Central Belize, only two showed evidence of individuals moving in a pair.

Ranging behavior and habitat preferences in a human-influenced mosaic landscape We collared and tracked three adult foxes, two females and one male (Table 3), over a period of 267 days, yielding respectively 111, 180, and 211 reliable locations. We subsampled these to respectively 19, 32, and 44 time-independent locations. All foxes were in good body condition and had few ecto-parasites.

The estimated range sizes of M1 and F2 reached asymptotes after 89 and 92 days, respectively (Fig. 6). We therefore considered the tracking time for these two individuals sufficient to delineate their total home range use. The cumulative area for F1 did not reach an asymptote after 104 days, suggesting that home range size was underestimated for this individual.

The male range (MCP) was larger than those of the two females and showed minimal to no overlap with either female (Table 4). There was considerable overlap in MCP between the two females along the road but minimal overlap in utility distribution (Fig. 7, Table 4).

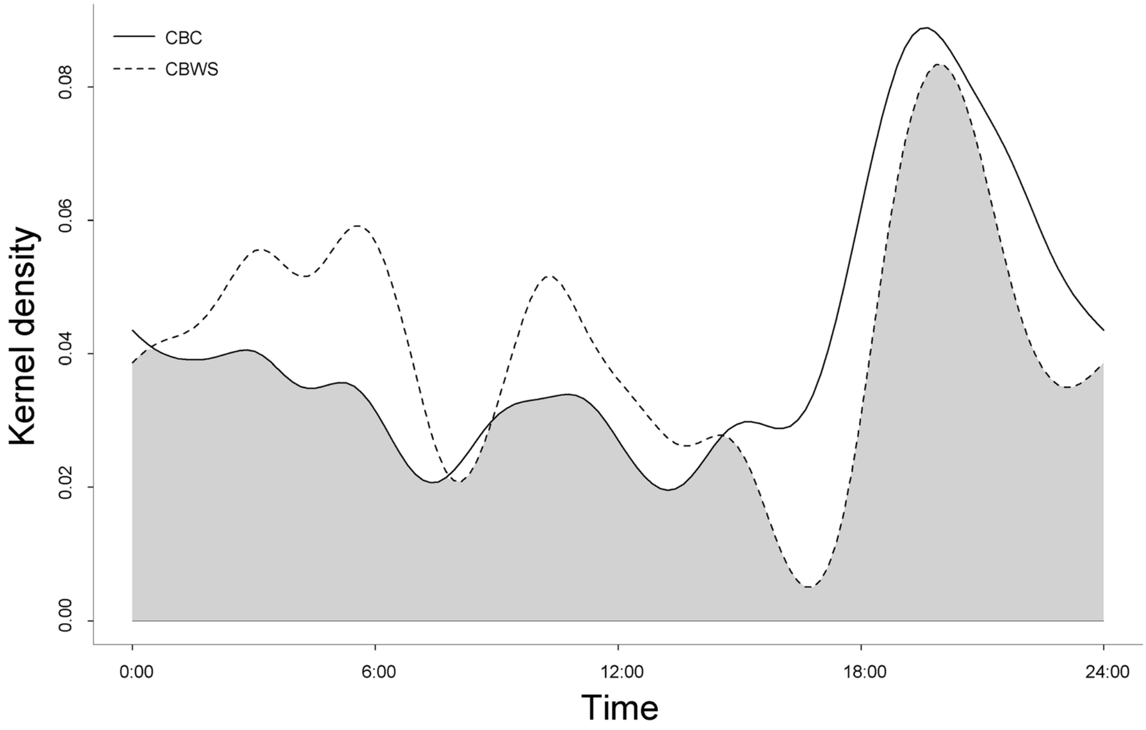

Fig. 4 Activity distribution of gray foxes (*Urocyon cinereoargenteus*) in the Central Belize and the Cockscomb Basin Wildlife Sanctuary, estimating coefficient of activity overlap between the two areas (Meredith and Ridout 2018), based on 628 and 394 independent photo events per area, respectively

Table 2 Diet of gray foxes (*Urocyon cinereoargenteus*) in Belize based on photo detections of foxes with prey items in their mouth, at two study sites: Cockscomb Basin Wildlife Sanctuary (CBWS, protected broadleaf forest) and a human-influenced mosaic landscape in Central Belize; approximate prey sizes are shown where possible; $N = 34$ prey items, foxes were detected carrying > 1 prey items in 4 photos (3 Central Belize, 1 CBWS)

Prey	Number of prey items, N (%)		
	CBWS	Central Belize	Total
Cricetidae (50–80 g)	12 (44.4)	5 (71.4)	17 (50.0)
Didelphinae (~ 300 g)	5 (18.5)	0	5 (14.7)
Garbage	4 (14.8)	0	4 (11.8)
Lacertilia (~ 20 cm)	3 (11.1)	0	3 (8.8)
Fruit	2 (7.4)	1 (14.3)	3 (8.8)
Anura	0	1 (14.3)	1 (2.9)
Aves	1 (3.7)	0	1 (2.9)
Total	27 (100)	7 (100)	34 (100)

Fig. 5 Camera trap photograph of a gray fox (*Urocyon cinereoargenteus*) carrying a frog and two rodents (potentially hispid cotton rats, *Sigmodon hispidus*), in Central Belize (7-Jul-2011)

The core home ranges of both females lay in close proximity without overlapping (Fig. 7). The 95% kernel distribution of the male overlapped with the edge of the zoo (small node), while the core distribution (50% kernel) of one female (F2) overlapped with a garbage site at the Eco-Lodge.

The ranges of both females spanned the highway; in contrast, we only detected the male on one side, despite it living in close proximity to the highway (Fig. 7). Both females crossed the highway on fewer days than expected from random movement (Fig. 8). The total number of crossing events was close to random for F1 and below random for F2 (Fig. 8).

Over half, the available habitat for all three foxes consisted of poorly drained deciduous broadleaf forest (55%), with open savannah making up a large proportion of the remainder (30%, Table 5).

None of the foxes maintained a home range based on the random availability of habitat type in the study area (Table 5). Both female foxes showed strong preference for dense savannah for second-order home range habitat selection ($R^1 \geq 2.33$), avoiding open savannah habitat ($R^1 \leq 0.8$), and either using broadleaf forest roughly to availability (F1 with $R^1 = 0.93$) or avoiding it (F2 with $R^1 = 0.62$). The male showed a reverse pattern, with strong avoidance of dense savannah ($R^1 = 0.25$), limited avoidance of broadleaf forest ($R^1 = 0.78$), and preference for open savannah ($R^1 = 1.80$).

The preferences for closed habitats by females and more open habitat by the male were exemplified by the third-order comparison but to a lesser extent compared to the second-order habitat selection (Table 5). F1 seemed to prefer dense savannah areas within her range ($R^2 = 1.36$), while F2 showed a preference for cover within a small patch of deciduous forest in her range ($R^2 = 1.47$). F1 showed strong avoidance of open savannah ($R^2 = 0.29$), while F2 only showed mild avoidance ($R^2 = 0.83$). In contrast, the male fox preferred open savannah ($R^2 = 1.30$) and dense savannah ($R^2 = 3.00$) and avoided broadleaf forest ($R^2 = 0.49$).

Discussion

Our study demonstrates that tropical gray foxes are as flexible in their exploitation of human-influenced landscapes and resources as those inhabiting the temperate zone. However, our camera-trap data suggest that they are not habitat generalists in this region of the tropics, avoiding the interior of the dominant habitat, tropical moist broadleaf forest, sticking to the forest edge, and preferring the mosaic landscape of well-vegetated savannah, pine forest (Davis et al. 2010), and agricultural lands (Gallina et al. 2016). Potentially, they readily colonize new areas if suitably transformed by human activity, exploiting rodents and food waste associated with human presence, as exemplified by the presence of foxes at the Visitors' Center within the tropical broadleaf forest of a large protected area where they were absent from the interior. Telemetry data indicated the use of broadleaf forest, but this was limited to the edges with no activity in the interior. Their resilience to environmental as well as human perturbations is exemplified by their good body condition and continued use of a human-influenced mosaic landscape following a "category 2" hurricane and their exploitation of anthropogenic food sources.

Tropical gray foxes are smaller compared to those inhabiting the temperate zone (McNab 2010), following Bergmann's rule for diminishing body size at lower latitudes (Bergmann 1874). Our four captured foxes were notably lighter than those recorded in North America or elsewhere in Central America (this study 1–2 kg; compared to 3–7 kg in North America, Fuller and Cypher 2004, 1.8–3 kg elsewhere in Central America, Reid 1997). Variation in body size of mammals has been explained by variation in the availability of resources, with smaller sub-species living in areas with fewer or poorer resources (McNab 2010; Schiaffini 2016).

Table 3 Biometrics of four gray foxes (*Urocyon cinereoargenteus*) live-trapped in Central Belize; three foxes were radio-collared (F1, F2, and F3)

Individual	Weight (kg)	Head-Body (cm)	Tail (cm)	Right forearm (cm)
Male (M1)	2.0	55.0	30.0	10.5
Female (F1)	1.8	47.5	30.5	8.5
Female (F2)	1.9	48.0	31.0	6.0
Male[a]	1.6	43.5	27.0	9.5

[a] Not collared

In the case of gray foxes, this may suggest that the tropics do not provide a more prey-rich and stable environment for this omnivorous carnivore, compared to the temperate northern Americas. Alternatively, physical and behavioral constraints may prevent gray foxes from exploiting the more stable and potentially prey-rich patches. For example, they might be unable to exploit the many water-rich environments of the tropics, confining them to drier areas that tend also to contain human habitations.

The larger home ranges of our three collared foxes, compared to foxes in the temperate zone (4–6 km^2, this study; 0.6–6 km^2, Fuller 1978; Haroldson and Fritzell 1984; Harrison 1997; Chamberlain and Leopold 2000; Riley 2006; Deuel et al. 2017b), also suggests that resources may be poorer or more widely dispersed in our tropical study area. Given the low sample size of fixes and relatively short tracking periods in our study, total range sizes might be larger than those reported in this study. Larger home ranges mean that individuals search further afield to fulfill their nutritional needs, indicating that food resources are sparser and/or food items are of a lower nutritive quality. The savannah, which was used by all three collared foxes, can be considered seasonally variable with periods of extreme drought and flooding compared to the more seasonally stable and potentially more productive broadleaf forest. A home range telemetry study of the herbivorous paca (*Cuniculus paca*) by the authors in the same area measured the largest home range sizes ever detected for the species, ranging widely in order to exploit area patchy and seasonal resources (Gutierrez et al. 2017). Overall, we explain the relatively small body sizes and large home ranges of foxes in our study by extreme seasonal variation in habitat suitability and lower availability of resources overall, compared with the temperate zones. For example, O' Connell (1989) found higher year-round variation of rodent populations in seasonally flooded savannah areas of Venezuela, compared to higher densities and more stable population structures of the neighboring high-ground non-flooded forests.

In the absence of data on gray fox population size, we cannot compare the densities of tropical versus temperate gray foxes. However, the larger ranges of tropical gray foxes compared to those in the temperate zone suggest that the tropical foxes exist at lower density or have more extensive range overlap than temperate foxes. Our three collared foxes provided limited data on range overlap, but none showed any sign of association.

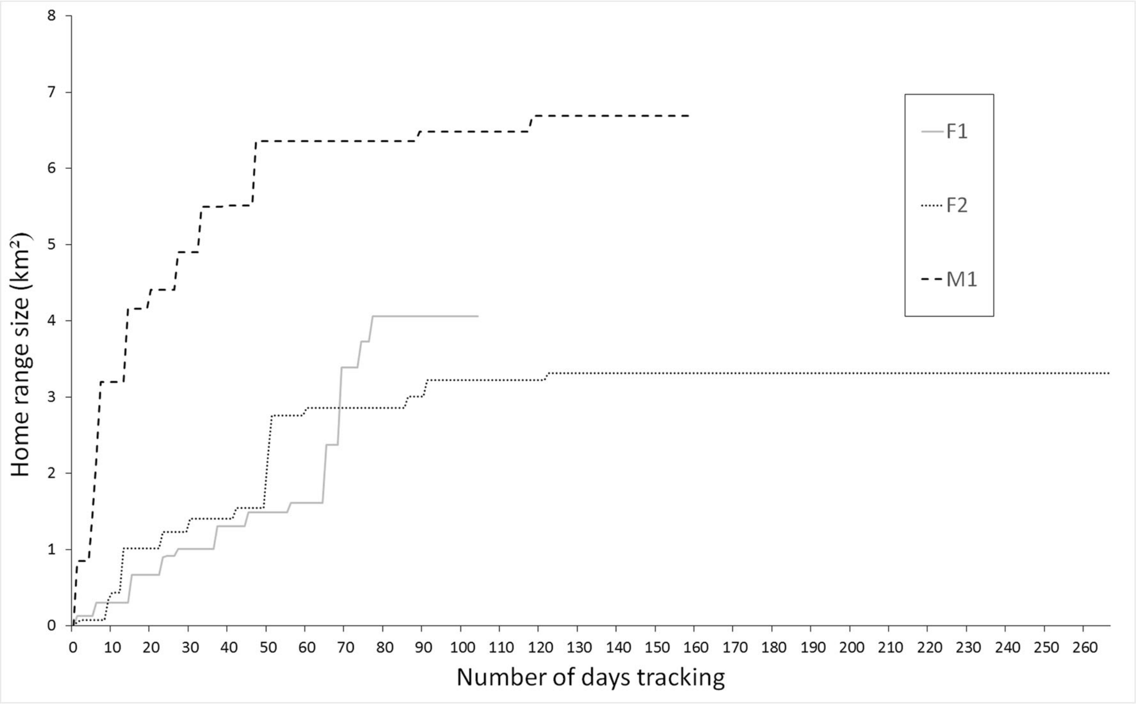

Fig. 6 Cumulative minimum convex polygon areas of three gray foxes (*Urocyon cinereoargenteus*) radio-tracked in Central Belize (based on independent fixes) between June 2011 and May 2012

Table 4 Home range sizes and overlap of three gray foxes (*Urocyon cinereoargenteus*) radio-tracked in Central Belize: 100% minimum convex polygon (MCP), 95 and 50% kernel areas (95 and 50% ke, respectively) with number locations provided in parentheses, % overlap between 100% MCPs, and UDOI overlap distribution for 95% kernel ranges

ID	Range size (km^2)			100% MCP % overlap			UDOI 95% kernel overlap		
	100% MCP	95% ke	50% ke	F1	F2	M1	F1	F2	M1
F1	4.06 (111)	4.06 (19)	0.93	–	52	20	–		
F2	3.31 (180)	3.59 (31)	0.70	39	–	0	0.11	–	
M1	6.69 (211)	3.75 (43)	0.83	11	0	–	0.01	0.0001	–

Sociality in temperate gray foxes has only been noted within the context of older siblings assisting mated pairs with the rearing of pups; they are generally considered solitary in other activities such as traveling and foraging (Chamberlain and Leopold 2000; Deuel et al. 2017b). Even though foxes exploited the open and easily available garbage disposal sites near highways and tourist facilities, we did not detect foxes congregating around these high-yield food sites. It is unlikely that fox density may be so low that there is no potential for aggregations to form at these sites; our camera traps detected collared and un-collared foxes near the garbage sites; however, they were never detected simultaneously or even close together in time.

Apart from exploitation of garbage, our limited data revealed an opportunistic diet of tropical gray foxes, with at least six different natural food items, associated with 34 successful food gathering events. The unique habit of foxes carrying food to pups at den sites, likely increased our sample size compared to other carnivore species detected on camera traps. Camera trap data clearly has a limited scope as a method for describing the diet of a species. It will likely be biased towards larger, visible species and underrepresent small invertebrates and plant species, which are likely highly prolific in tropic environments. Nevertheless, we detected rodents, birds. and plants in the diet of tropical gray foxes, in accordance with the diet of temperate

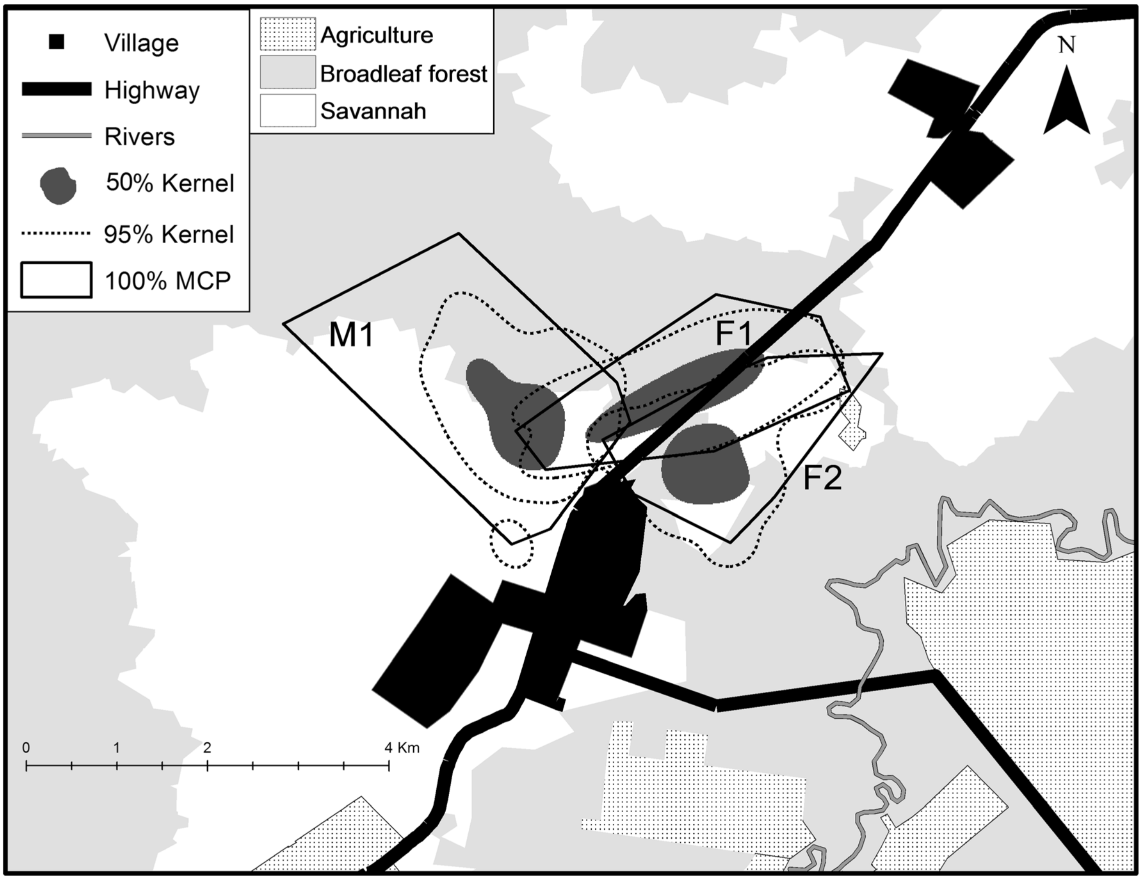

Fig. 7 The minimum convex polygon, 95 and 50% kernel ranges for three gray foxes (*Urocyon cinereoargenteus*), radio-tracked in Central Belize between June 2011 and May 2012; one male (M1) and two females (F1 and F2)

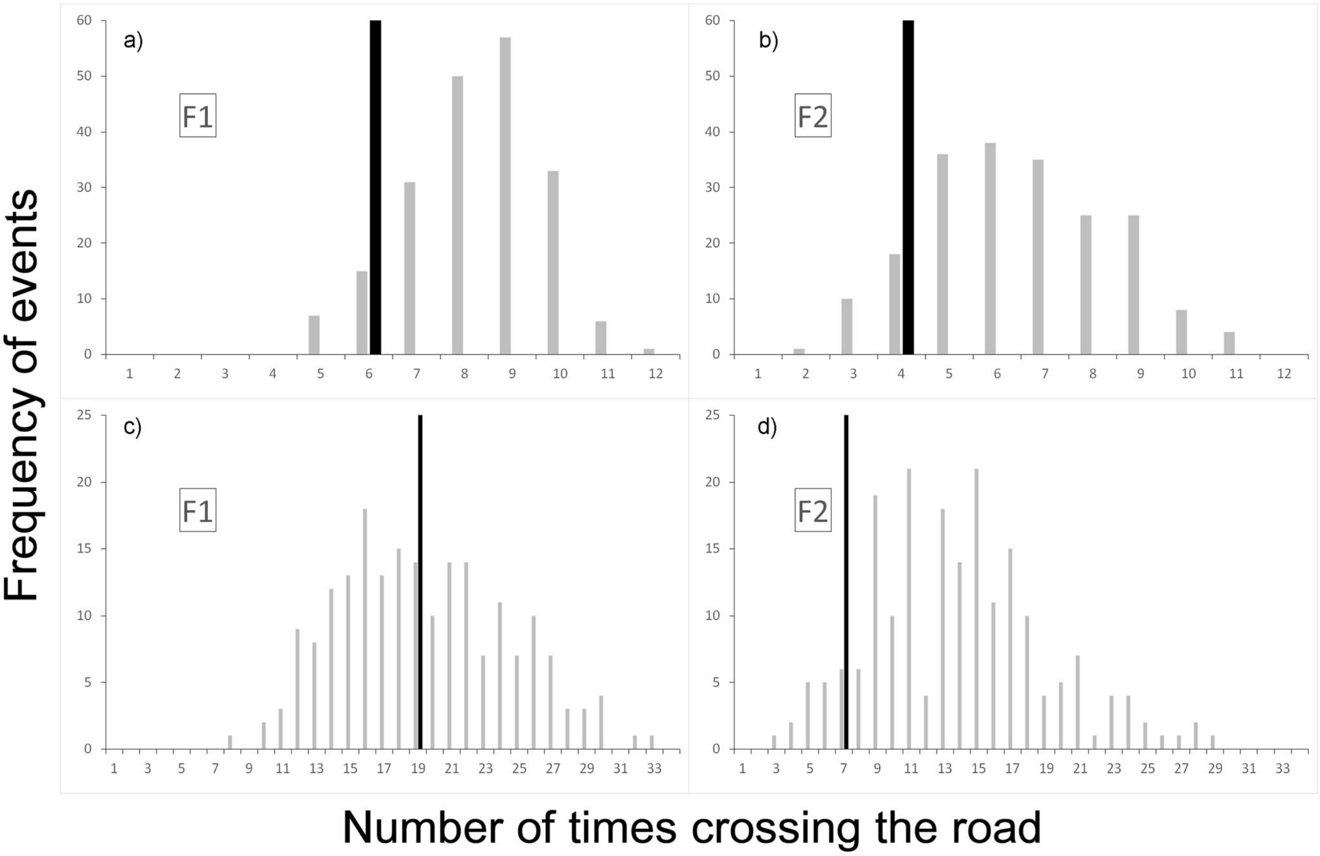

Fig. 8 Frequency of crossing a highway for two female gray foxes (*Urocyon cinereoargenteus*), radio-tracked in Central Belize between June 2011 and May 2012. The black bars in the four panels represent the crossing frequency for the two female foxes; the upper panel (**a**, **b**) shows the distribution of whether or not a fox crossed on a given walk. The lower panel (**c**, **d**) shows total number of crossing events, including crossing multiple times per walk. Right panels (**a**, **c**) show fox F1 and left panels (**b**, **d**) fox F2. The real crossing frequencies of the two foxes were subsequently compared with the distribution of crossing events from 200 random walk pathways (gray bars). The random walks were created, using similar number of steps as for the real foxes, drawing random samples from the distribution of the step lengths per fox, with randomly chosen turning angles between steps. The random walk movement was confined within the 100% MCP of the individual fox

gray foxes (Harrison 1997); we also noted frogs and lizards, a logical expansion of the diet given their higher diversity and abundance in the wetter and warmer tropical environments. Our data indicated that a large part of the diet of foxes might consist of rodents. The transition zone between savannah and broadleaf forest may be suboptimal habitat for rodents, in which

Table 5 Habitat preferences of three gray foxes (*Urocyon cinereoargenteus*) radio-tracked in Central Belize: two females (F1 and F2) and a male (M1), showing the area of habitat available in the study area, and in each individual 100% minimum convex polygon (Ind.km^2), and the number of independent tracking points in each individual 100% minimum convex polygon (points), and R^a = second-order habitat selection (% Ind. km^2/% study area km^2), R^b = third-order habitat selection (% points/% Ind. km^2)

Habitat[a]	Study area[b]	F1		F2		M1	
	km^2 (%)	Ind. km^2 (%)—R^a	Points (%)—R^b	Ind. km^2 (%)—R^a	Points (%)—R^b	Ind. km^2 (%)—R^a	Points (%)—R^b
Broadleaf	9.32 (55)	2.07 (51)–0.93	9 (56)–1.09	1.13 (34)–0.62	15 (50)–1.47	2.87 (43)–0.78	9 (21)–0.49
Savannah (O)	5.06 (30)	0.87 (21)–0.70	1 (6)–0.29	0.79 (24)– 0.80	6 (20)–0.83	3.63 (54)–1.80	30 (70)–1.30
Savannah (D)	1.99 (12)	1.12 (28)–2.33	6 (38)–1.36	1.37 (41)–3.42	9 (30)–0.73	0.19 (3)–0.25	4 (9)–3.00
Village	0.48 (3)	–	–	0.01 (0)–0.00	–	–	–
Aquaculture	0.12 (1)	–	–	0.02 (1)–1.00	–	–	–

[a] Extracted from Meerman and Clabaugh (2017): deciduous poorly drained lowland broadleaf forest (broadleaf), open savannah with sparse trees (savannah (O)), dense savannah with dense trees and undergrowth (Savannah (D)), rural village habitat (village), fish farm with fishponds (aquaculture)

[b] Habitat areas available within the 100% minimum convex polygon based on all locations of all three foxes combined

case the foxes must range widely to satisfy their energetic needs. It is therefore puzzling that foxes seem to be absent from the broadleaf forest interior, the most productive and seasonally stable habitat in the area. Potentially, gray foxes are absent from these areas, to avoid jaguars, pumas, and ocelots for whom broadleaf forest forms the core of their habitat. Although gray foxes were not noted in the diet of jaguars or pumas in either study area (Foster et al. 2010; Figueroa 2013), predation pressure historically might have excluded them from the tropical forests. A more detailed study is required regarding the habitat distribution and dietary variation of gray foxes within the tropical region of the species, and the reasons for their absence from productive interiors of tropical forests.

Within Belize, gray foxes had similar activity patterns across the two landscapes, active throughout the day and night, with a peak between 19:00 and 22:00 in the evening. Temperate gray foxes also increase activity after 19:00 (Harrison 1997; Wang et al. 2015), and these peaks might be associated with a general avoidance of people in a human-dominated landscape. However, gray foxes in temperate regions are less active during the day compared to the tropical gray foxes in our study, potentially avoiding coyotes which are generally diurnal and account for up to 92% of gray fox mortality in areas of coexistence (Farias et al. 2005; Wang et al. 2015). We only detected a coyote once at the end of our study period, after the hurricane, on a camera trap in the mosaic landscape of central Belize. Coyotes are becoming more common across the human-influenced landscapes of Belize, as forest is being cleared for agriculture (Foster and Harmsen, unpubl. data). We may subsequently expect the activity patterns of gray foxes to shift in response to the increasing presence of this predator. In our study areas, predator avoidance may explain why gray foxes avoided villages with an abundance of anthropogenic food, but also many free-ranging domestic dogs, compared to their relatively high activity around tourist resorts (eco-lodge, zoo, sanctuary Visitors' Center) from which dogs were excluded but anthropogenic food sources were equally common and accessible (picnic tables, garbage dumps, tourist kitchen facilities etc.).

In the temperate zone, gray foxes are frequently detected around road systems but are not necessarily attracted to roads (Deuel et al. 2017a; Temple et al. 2010; Riley 2006). Likewise in this study, of the three collared foxes, only the ranges of the two females spanned the highway. Crossing frequencies did not exceed random expectation, showing avoidance of the road compared to random movement. Despite ranging close to the highway, the male never crossed it. This suggests that tropical foxes are not using the highway as a resource but rather a feature that is mostly avoided. During the 1-year tracking period, we opportunistically found two (non-collared) road-kill foxes along the ~ 5 km of highway in our telemetry study area, suggesting that road traffic accidents may contribute significantly to mortality in this fox population.

Our study has shown that in Belize, gray foxes occupy the mosaic landscapes of villages, agriculture, pine savannah, and the edges of broadleaf forests. While many neotropical terrestrial mammals are threatened by forest clearance (Daily et al. 2003), foxes readily use human-influenced edge habitats and may be expected to flourish in areas of small-scale clearing for agricultural development in the absence of predators. However, large-scale habitat degradation is associated with the exploitative range expansion of coyotes, which, combined with uncontrolled stray dog populations around villages, could pose substantial predation risk to gray foxes in these landscapes.

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References

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325

Athreya V, Odden M, Linnell JDC, Krishnaswamy J, Karanth U (2013) Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. PLoS One. https://doi.org/10.1371/journal.pone.0057872

Beyer HL (2012) Geospatial modelling environment (version 0.7.2.1). (software). URL: http://www.spatialecology.com/gme/gmedownload.htm

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197: 516–519

Chamberlain MJ, Leopold BD (2000) Spatial use patterns, seasonal habitat selection, and interactions among adult gray foxes in Mississippi. J Wildl Manag 64:741–751

Chapron G, Kaczensky P, Linnell JDC, von Arx M, Huber D, Andrén H, Vicente López-Bao J, Adamec M, Álvares F, Anders O, Balčiauskas L, Balys V, Bedő P, Bego F, Blanco JC, Breitenmoser U, Brøseth H, Bufka L, Bunikyte R, Ciucci P, Dutsov A, Engleder T, Fuxjäger C, Groff C, Holmala K, Hoxha B, Iliopoulos Y, Ionescu O, Jeremić J, Jerina K, Kluth G, Knauer F, Kojola I, Kos I, Krofel M, Kubala J, Kunovac S, Kusak J, Kutal M, Liberg O, Majić A, Männil P, Manz R, Marboutin E, Marucco F, Melovski D, Mersini K, Mertzanis Y, Mysłajek RW, Nowak S, Odden J, Ozolins J, Palomero G, Paunović M, Persson J, Potočnik H, Quenette PY, Rauer G, Reinhardt I, Rigg R, Ryser A, Salvatori V, Skrbinšek T, Stojanov A, Swenson JE, Szemethy L, Trajçe A, Tsingarska-Sedefcheva E, Váňa M, Veeroja R, Wabakken P, Wölfl M, Wölfl S, Zimmermann F, Zlatanova D, Boitani L (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519

Daily GC, Ceballos G, Pacheco J, Suzán G, Sánchez-Azofeifa A (2003) Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conserv Biol 17:1814–1826

Davis ML, Kelly MJ, Stauffer DF (2010) Carnivore co-existence and habitat use in the mountain pine ridge forest reserve, Belize. Anim Conserv 14:56–65. https://doi.org/10.1111/j.1469-1795.2010.00389.x

Deuel NR, Conner LM, Miller KV, Chamberlain MJ, Cherry MJ, Tannenbaum LV (2017a) Habitat selection and diurnal refugia of gray foxes in southwestern Georgia, USA. PLoS One. https://doi.org/10.1371/journal.pone.0186402

Deuel NR, Conner LM, Miller KV, Chamberlain MJ, Cherry MJ, Tannenbaum LV (2017b) Gray fox home range, spatial overlap, mated pair interactions and extra-territorial forays in southwestern Georgia, USA. Wildl Biol 2017:wlb.00326. https://doi.org/10.2981/wlb.00326

Farias V, Fuller TK, Wayne RK, Sauvajot RM (2005) Survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in southern California. J Zool 266:249–254

Fedriani JM, Fuller TK, Sauvajot RM, York EC (2000) Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270

Fieberg J, Kochanny CO (2005) Quantification of home range overlap: the importance of the utilization distribution. J Wildl Manag 69: 1346–1359

Figueroa OA (2013) The ecology and conservation of jaguars (*Panthera onca*) in Central Belize: conservation status, diet, movement patterns and habitat use. PhD. Thesis, University of Florida. Available: http://ufdc.ufl.edu/UFE0045191/00001

Foster RJ, Harmsen BJ, Valdes B, Pomilla C, Doncaster CP (2010) Food habits of sympatric jaguars and pumas across a gradient of human disturbance. J Zool 280:309–318

Fuller T (1978) Variable home range sizes of female gray foxes. J Mammal 59:446–449

Fuller TK, Cypher BL (2004) Gray fox *Urocyon cinereoargenteus*. In: Sillero-Zubiri C, Hoffman M, Macdonald DW (eds) Canids: foxes, wolves, jackals, and dogs. Status survey and conservation action plan. IUCN Publications, Cambridge, pp 92–97

Gallina S, López-Colunga P, Valdespino C, Farías V (2016) Abundancia relativa de la zorra gris *Urocyon cinereoargenteus* (Carnívora: Canidae) en la zona centro de Veracruz, México. Rev Biol Trop 64:221–233

Gutierrez SM, Harmsen BJ, Doncaster CP, Kay E, Foster RJ (2017) Ranging behavior and habitat selection of pacas (*Cuniculus paca*) in central Belize. J Mammal 98:542–550

Harmsen BJ, Foster RJ, Gutierrez-González CE, Silver SC, Ostro LET, Kelly MJ, Sanchez E, Kay E, Quigley H (2017) Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; implications for camera trap studies of carnivores. PLoS One. https://doi.org/10.1371/journal.pone.0179505

Haroldson KJ, Fritzell EK (1984) Home ranges, activity, and habitat use by gray foxes in an oak-hickory forest. J Wildl Manag 48:222–227

Harrison RL (1997) A comparison of gray fox ecology between residential and undeveloped rural landscapes. J Wildl Manag 61:112–122

Hunter L (2011) Carnivores of the world. Princeton University Press, New Jersey

Johnson D (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Kapfer JM, Kirk RW (2012) Observations of gray foxes (*Ucocyon cinereoargenteus*) in a suburban landscape in the Piedmont of North Carolina. Southeast Nat 11:507–516

Kark S, Iwaniuk A, Schalimtzek A, Banker E (2006) Living in the city: can anyone become an 'urban exploiter'? J Biography. https://doi.org/10.1111/j.1365-2699.2006.01638.x

Lombardi JV, Comer CE, Scognamillo DG, Conway WC (2017) Coyote, fox, and bobcat response to anthropogenic and natural landscape features in a small urban area. Urban Ecosystems 20:1239–1248

Lopes MG, May J Jr, Foster RJ, Harmsen BJ, Sanchez E, Martins TF, Quigley H, Marcili A, Labruna MB (2016) Ticks and rickettsiae from wildlife in Belize, Central America. Parasit Vectors 9. https://doi.org/10.1186/s13071-016-1348-1

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

McNab BK (2010) Geographical and temporal correlations of mammalian size reconsidered: a resource rule. Oecologia 164:13–23

Meerman J (2011) Provisional report on the Belize 2011 wildfires: aftermath of hurricane Richard. p 11. http://biological-diversity.info/Downloads/2011_Wildfire_Report.pdf

Meerman J, Clabaugh J (2017) Biodiversity and environmental resource data system of Belize. Online http://www.biodiversity.bz

Meredith M, Ridout M (2018) Overlap: estimates of coefficient of overlapping for animal activity patterns. R package version 0.3.0. https://cran.r-project.org/web/packages/overlap/vignettes/overlap.pdf

Nogeire TM, Davis FW, Duggan JM, Crooks KR, Boydston EE (2013) Carnivore use of avocado orchards across an agricultural wildland gradient. PLoS One 8:1–6

O' Connell MA (1989) Population dynamics of neotropical small mammals in seasonal habitats. J Mammal 70:532–548

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3–900051–07-0, URL http://www.R-project.org/

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

Ridout M, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J Agric Biol Environ Stat 14:322–337

Riley SPD (2006) Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. J Wildl Manag 70:1425–1435

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Rountree GH (2004) Comparative study of the home range and habitat usage of red foxes and gray foxes in an urban setting: a preliminary report. In: WW Shaw, LK Harris, and L Vandruff (eds) Proceedings 4th International Urban Wildlife Symposium. University of Arizona, USA, pp 238–244

Schiaffini MI (2016) A test of the Resource's and Bergmann's rules in a widely distributed small carnivore from southern South America, *Conepatus chinga* (Molina, 1782) (Carnivora: Mephitidae). Mamm Biol 81:73–81

Temple DL, Chamberlain MJ, Conner LM (2010) Spatial ecology, survival and cause specific mortality of gray foxes (*Urocyon cinereoargentueus*) in longleaf pine ecosystem. Am Midl Nat 163: 413–422

Wang Y, Allen ML, Wilmers CC (2015) Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biol Conserv 190:23–33