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ORIGINAL PAPER

Vulnerable island carnivores: the endangered endemic dwarf procyonids from Cozumel Island

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Abstract Insular carnivores represent some of the most critically threatened species, but also the least known. To evaluate the conservation status of these species, thorough abundance estimates are urgently required. To better understand the population biology and conservation status of the endemic and threatened pygmy raccoon (*Procyon pygmaeus*) and dwarf coati (*Nasua nelsoni*) on Cozumel Island, Mexico, we worked island-wide to identify the presence of these species, and for the pygmy raccoon we studied several

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populations in depth during 2001–2003. On Cozumel, trapping was conducted for >6,600 trap nights in 19 locations of varying habitat types. A total of 96 pygmy raccoons (47 males and 49 females) and a single adult, male dwarf coati (*N. nelsoni*) were captured. Estimated total annual pygmy raccoon population size ± SE was 80 ± 26.1, resulting in an average density of 22 ± 5.1 raccoons/km^2 for the three small sites where the animals persist. Based in part on the findings of this study that indicate these species have a restricted range and small population numbers, the IUCN recently changed the listing of the pygmy raccoon to Critically Endangered from Endangered. In contrast, the status of the dwarf coati (Endangered) has not been changed, although the taxon is in eminent danger of extinction and in need of immediate conservation action.

Keywords Carnivore conservation · Dwarf coati · Mark-recapture · *Nasua nelsoni* · *Procyon pygmaeus* · Pygmy raccoon · Population ecology

Introduction

Tropical and temperate islands typically lack terrestrial mammals, particularly mammalian carnivores, due to the poor over-water dispersal abilities and large body sizes of these taxa, as well as the low carrying capacities of islands (Williamson 1981; Alcover and McMinn 1994). Insular mammalian carnivores are particularly intriguing conservation subjects for several reasons. Species in the order Carnivora tend to exist at low densities, are often heavily harvested or persecuted by humans, are subject to epidemics via pathogen spillover from high-density domestic carnivore populations, and tend to have relatively large home-ranges which increase their likelihood of contact with habitat edges or altered landscape pressures (Gittleman et al. 2001). On islands, collectively these factors may place insular carnivore populations at particular risk relative to other mammalian guilds. Furthermore, because of the potential for strong top-down effects, the alteration of a carnivore community has the potential to result in strong and sometimes dramatic indirect effects—a scenario that has been documented repeatedly on island ecosystems (Roemer et al. 2009). Thus the status of island carnivores represents a significant conservation concern.

Cozumel Island, Mexico, is unusual in supporting several insular, endemic carnivores, of which the best described, are the pygmy raccoon (*Procyon pygmaeus*; Merriam 1901) and the dwarf coati (*Nasua nelsoni*; Thomas 1901). As is the trend for island fauna, both species are smaller, or dwarfed, compared to their mainland ancestors (Goldman 1950; Jones and Lawlor 1965). The pygmy raccoon's IUCN listing status has recently been changed from Endangered (EN) to Critically Endangered (CR) by the World Conservation Union (CR2a(i)b) (Cuarón et al. 2008). In contrast, the dwarf coati, whose status as a distinct species remains unclear (McFadden et al. 2008) has previously been listed as Endangered (EN C2a) despite recent work indicating these species should be considered Critically Endangered (CR A2c + C2a(i)b) according to the IUCN system (Cuarón et al. 2004; McFadden 2004). Given that conservation management of these species is urgently needed, information on the distribution, abundance, and population structure of these taxa across Cozumel is a priority to support the development of educated management strategies. Here we report the results of our work to address these topics.

Dwarf coatis and pygmy raccoons have existed on Cozumel Island for at least 3,500 years (Hamblin 1984) and phylogenetic analyses suggest divergence times from the mainland taxa that predate human colonization of the island (McFadden et al. 2008). A recent assessment of the status of these two species, however, suggests that populations of both have declined precipitously (Cuarón et al. 2004). The exact causes of their decline are unknown but both species are thought to be adversely affected by predators (dogs, *Canis familiaris*, and boas, *Boa constrictor*), habitat degradation, hunting, and possibly by resource competition and disease spill-over from free-ranging domestic carnivores (Navarro and Suárez 1989; Martínez-Morales and Cuarón 1999; Cuarón et al. 2004; McFadden 2004; García-Vasco 2005; McFadden et al. 2005; Bautista 2006; Mena 2007; Romero-Nájera et al. 2007). Natural threats such as hurricanes may also negatively impact these and other species given their already reduced population sizes (Navarro and Suárez 1989; Perdomo 2006; Copa-Álvaro 2007).

Little information exists on the abundance of either taxon. A brief survey carried out in 1987–1988 identified a few localized populations of pygmy raccoons and dwarf coatis in the mangrove forest of Chankanaab, the northwest tip of the island, and the adjacent Isla de la Pasión (Navarro and Suárez 1989). Martínez-Morales and Cuarón (1999) assessed the dwarf coati population in 1994–1995 based on line transect surveys, observing only two dwarf coatis in over 386 km of transects. Using these data, a preliminary estimate of the population density of dwarf coatis was 0.43 individuals/km^2 (Cuarón et al. 2004). Aside from these studies, however, no broad-based examination of either taxon has occurred. Therefore, we assessed the locations of pygmy raccoon and dwarf coati populations on the island and estimated the current population size and structure.

Materials and methods

Study sites, capture and handling

Cozumel, Mexico (20°16′18″ to 20°35′33″N; and 86°43′23″ to 87°01′31″W), is a c. 478 km^2 oceanic island located 17.5 km east of the Yucatan peninsula (Fig. 1). The island encompasses a variety of terrestrial habitats including semi-evergreen tropical forests, subdeciduous tropical forest, mangrove stands, sandy palm areas and other coastal vegetation (Téllez and Cabrera 1987; Cuarón 2009). Mean annual temperature is 25.5°C, and mean annual rainfall is 1,505 mm (Martínez-Morales 1996; Cuarón 2009), with a pronounced seasonality that influences the availability of foods such as fruit and insects (McFadden et al. 2006).

Trapping sites were selected based on pilot studies suggesting the possible presence of native carnivores, as well as an attempt to sample multiple habitats and regions of the island. An additional consideration was accessibility, as many areas on Cozumel are isolated and too wet (i.e., mangrove areas prone to flooding) to survey using a trapping-based approach. Ultimately we selected 19 sites throughout the island to sample with the majority of these sites sampled for at least 2 weeks (mean = 13 days, range = 4–22 days) per site over 3 years (2001–2003; Fig. 1). We attempted to trap throughout the year to examine if significant variation existed in capture probabilities between wet and dry seasons. The first sampling period was conducted from July through September 2001 (wet season), the second spanned from April (late dry season) to August 2002 (mid wet season), then every 2 weeks from September through December 2002 (late wet, early dry season), and the third season was February to March 2003 (dry season).

Three locations (sites 1–3; Fig. 1) in the northwestern mangrove-dominated habitats were further studied based on the identification of pygmy raccoon populations at these sites. Although these three sites are in relatively close proximity to each other (<4 km), we

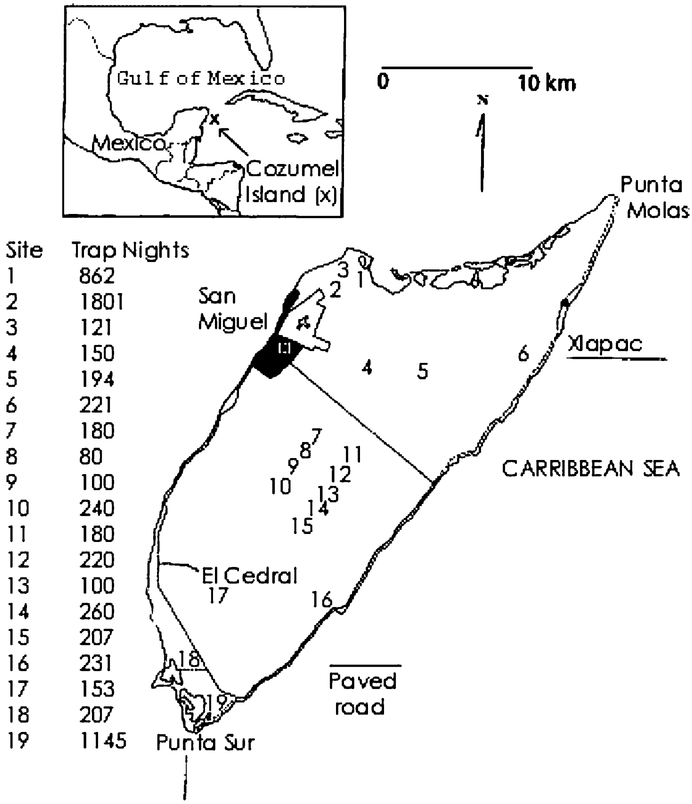

Fig. 1 Map of Cozumel Island, Mexico, and the locations of the 19 trapping sites and total sampling effort (number of trap nights) at each location from 2001 to 2003. Symbol *X* represents Cozumel Island

consider them to be independent populations because we did not detect movement of marked animals between sites.

During each sampling session, live traps (Tomahawk #207 box traps, Tomahawk Live Trap Co., Tomahawk, WI, USA or Havahart #1089, Havahart Live Trap Co., Lititz, PA, USA) were placed at 25–50 m intervals in each site. The placement and numbers of traps used differed between sites and depended on the habitat. Thus, we calculated trapping area differently depending on the configuration and shape of the trap site and placement of traps (i.e., polygon vs. linear). For sites 1 and 2 the trapping configuration was polygon shaped, so trapping area (T) was calculated as the area prescribed by a minimum convex polygon of the traps. Site 3 was configured as a strip transect, and traps were placed 0.02 km off both sides of a 0.40 km linear transect, and T was calculated as the total area the traps made up within this strip transect (0.04×0.40 km $= 0.016$ km^2).

Using GPS data, the mapping program TNTmips version 6.9 (MicroImages 2004), and a digitized satellite image of Cozumel Island (Landsat, Google Earth Professional v. 4.2 2007) the effective trapping area (A) was calculated by adding a buffer or boundary strip of width (W) to the area defined by the outer traps (T), so that the effective sampling area also includes areas covered by the outer traps beyond the outer polygon limits (Karanth and Nichols 1998). Based on Kenward (1985), we used a buffer width (W) of 1/2 the mean home range of pygmy raccoons (0.65 ± 0.26 km^2, based on 85% harmonic mean estimates, $n = 8$; García-Vasco et al., unpublished data).

Site 1 was primarily mangrove habitat, close to Isla de la Pasión. Site 2 was surrounding and within a golf course (i.e. not directly on golfing greens, but adjacent to), with trapping areas consisting of both semi-evergreen tropical forest and mangrove forests. Site 3, was located approximately 1.0 km north–northwest of site 2 (3.5 km from site 1) and consisted of mangrove forest close to the coast. For the three sites, $T = 0.02$–1.28 km^2, and $A = 0.69$–3.08 km^2 (Table 1).

Traps were baited with canned cat food, sardines, or a honey-banana mixture and checked at least once daily. We also explored additional bait types, including commercially available scented carnivore bait, various fruits, fish, and crabs. Trapped animals were immobilized with ketamine hydrochloride (10–12 mg/kg) and xylazine (2 mg/kg) prior to handling and ear tagging (Hasco Tag Co., Dayton, KY). Age was approximated as juvenile (0–12 months), subadult (13–21 months), or adult (>21 months) from tooth wear, body size, reproductive status, and recapture history (Grau et al. 1970; Sanderson and Nalbandov 1973). For males, canine size and the descent of the testes were used to differentiate subadult and adults. Females were considered to have bred based on nipple enlargement. Uncertainty about breeding status occurred in some cases, however, and these individuals were classified as non-breeding. All captured animals were released at the trap site after recovery from immobilization (within 2 h of checking the trap).

Population analysis

Capture frequencies were examined for variation by year, age, and sex, using chi-square tests. Using the CAPTURE feature in program MARK (White and Burnham 1999), chi-squares test were also used to assess time-related variation and behavioral response to capture. Specifically, the tests used to assess these factors were: Tests for heterogeneity of trapping probabilities in a population, tests for behavioral response after initial capture, tests for time-specific variation in trapping probabilities, goodness of fit tests of model. Results of these tests were used to select the appropriate model estimators. Due to low sample sizes, data sets for each site were pooled between years for each of these tests.

Using Pollock's (Pollock et al. 1990) robust population model in program MARK, annual capture ($\hat{p}$) and recapture ($\hat{c}$) probabilities, and abundance ($\hat{N}$) were calculated for Sites 1 and 2, for which we had trapped for three and two consecutive years, respectively. We used a Schnabel closed population model to estimate population size for Site 3, which was only sampled for one field season (2003) and which also had a relatively small population size. We used a robust design model, allowing closely-spaced trapping sessions to be viewed as a closed capture survey whereas longer intervals between sessions allows

Table 1 Effectively sampled areas calculated from mark recapture data and their resulting pygmy raccoon density estimates ($\hat{N}$) and standard error (SE)

Site	Sampled area size (km^2) outer trap polygon (T)	Effective sampled area (km^2) (A)	Mean $\hat{N}$	Resulting density estimate (raccoons/km^2)	±SE
1	0.030	0.74	23	31	3.72
2	1.280	3.08	41	13	2.40
3	0.016	0.69	16	23	0.97
Mean	0.45	1.26	27	22	1.13

for the possibility of temporary emigration from the trapping area and are viewed as an open capture survey. Thus, the primary sampling periods where gains (birth and immigration) and losses (deaths and emigration) are examined using a closed population model Cormack-Jolly-Seber (CJS) and the secondary sampling periods, or the day-to-day trapping sessions, are effectively closed to gains and losses (Kendall and Nichols 1995; Kendall et al. 1997). This model is powerful in that the probability that an animal is captured at least once in a trapping session can be estimated from just the data collected during the session using models developed for closed populations, and abundance and recruitment are less biased by heterogeneity in capture probability (Otis et al. 1978). The robust design model assumes: (1) the population is closed across all sampling days (i.e. within a field season); (2) samples are instantaneous and releases are made immediately after the sample; (3) animals do not lose marks between the sampling periods, (4) movement in and out of the area is random; (5) every marked animal in the population has an equal chance of survival and/or capture and (6) marking individuals does not affect their catchability. Assumptions 1–3 were met in our sampling design and marking procedures. Assumptions 4–6 were examined using the chi-square tests in CAPTURE as described above.

Average population size ($\hat{N}$) for each study site was calculated as the mean of the estimated abundance calculated by program CAPTURE over the 3 year study period. We estimated the total population size ± standard error of pygmy raccoons at our three main sites by combining multi-year averages from each site. Crude density estimates for each site were based on the average estimated population size over the entire study divided by the effective trapping area for each site (A).

Results

Variation in capture probability

We trapped at 19 sites for 6,652 trap nights, but captured pygmy raccoons or dwarf coatis at only three sites (Sites 1–3, 2,784 trap nights) in the northwestern tip of the island (Fig. 1). Throughout the study there were 175 captures of 96 (47 males and 49 females) pygmy raccoons (Appendix 1). Only a single, adult male dwarf coati was trapped in 2002 at Site 1. Therefore, the focus of our results refers to population estimates of the pygmy raccoon.

After our initial trapping program at Sites 1 and 3, traps were placed further inland (approximately 0.7 and 0. 3 km, respectively) from the edge of the coast, and near tropical forest mixed mangrove areas. However, at each of these sites, we did not capture any pygmy raccoons, despite regularly capturing individuals in close proximity to the coast.

At Sites 1 and 2 the distribution of the frequency of captures of males and females did not vary over the three-year study ($X^2 = 0.364$, $df = 1$, $P = 0.546$; Appendix 1). We captured more females at Site 1 in both 2002 and 2003 ($X^2 = 45.27$, $df = 1$, $P = 0.001$; $X^2 = 17.05$, $df = 1$, $P = 0.002$, respectively). The ratio of males and females in each of the three age classes (juvenile, subadult, adult) also significantly varied ($X^2 = 8.12$, $df = 2$, $P = 0.017$). Site 3 had nearly twice as many adult males captured as females ($X^2 = 3.84$, $df = 1$, $P = 0.050$), whereas all other age classes tended to have more females than males. The overall ratio of females to males for all individuals at all sites was equal (1:1). Adults made up the majority of captures (59%), followed by juveniles (22%), and subadults (19%). Although the proportion of each age class captured varied between sites ($X^2 = 12.60$, $df = 4$, $P = 0.013$), adults were the largest proportion of captures at all sites.

Program CAPTURE indicated the Zippin estimator (model M_b) as the most appropriate approach for population estimations for Site 1. Significant variation in capture probabilities may be due to behavioral responses to capture (trap happiness or shyness: $X^2 = 6.54$, $df = 1$, $P = 0.01$). The goodness of fit test for model M_b showed a reasonable fit ($X^2 = 45.53$, $df = 30$, $P = 0.03$). For Site 2, program CAPTURE recommended the jackknife estimator (model M_h). The goodness of fit test for model M_h showed a reasonable fit ($X^2 = 18.72$, $df = 1$, $P = 0.04$). No behavioral heterogeneity to capture was seen in Site 3 and we therefore used the null estimator (model M_o).

Average capture probability ($\hat{p}$) for the three pygmy raccoon populations (Sites 1–3) was 0.151. Probability of capture ($\hat{p} = 0.210$) was highest at Site 1 during the dry season of 2003, but this site also had the lowest probability of capture during the late dry and early wet season of 2002. There was no significant variation in capture or recapture probabilities among years or sites ($t = 1.28$, $P = 0.157$). The probability of recapture ($\hat{c}$) was highest at Site 3 (0.082) and lowest at Site 2 (0.004) (Table 2).

Population analysis

Average population estimates (±SE) for the three pygmy raccoon populations was 27.8 ± 5.5 individuals. Abundance estimates ranged from a low of 14 individuals at Site 1 (95% CI = 10–19) to a high of 48 individuals at Site 2 (95% CI = 39–79; Table 2). Site 2 was the largest trapping site ($A = 3.08$ km^2), resulting in the lowest density ($d = 13$). At Site 1, 34 individuals were captured in 2002; this was also one of our most comprehensive trapping efforts where after 1 month of intensive trapping only previously marked individuals were captured thereafter (3 year mean = 23). For Site 1 in 2002, population size was approximately 34 individuals (95% CI = 19–45), whereas in 2003, the estimate was 48 individuals (95% CI = 39–79; mean of 2002–2003 = 41). Closed capture models estimated the number of individuals at Site 3 to be 16 (range 13–20). Using the mean estimated population size calculated for each site over the 3 years (averaging abundance for site 1 for the 3 years, etc.), total population size at the three sites was 80 ± 26.1 individuals (95% CI = 72–103). Based on the average age structure (59% of all captures were adults), this translates to a population of approximately 47

Table 2 Pygmy raccoon population estimates based on Pollock's robust method of marking (*M*) and recapture (*C*)

Year	Site	Trapping occasions	*M*	*C*	$\hat{p}$	$\hat{c}$	$\hat{N}$	±SE	95% CI
2001	1	27	11	12	0.1042	0.0054	36	12.263	22–73
2002	1	31	19	34	0.1003	0.0312	19	0.763	19
	2	58	22	39	0.1451	0.0121	34	5.248	19–45
2003	1	16	8	13	0.2104	0.0208	14	4.677	10–19
	2	22	31	50	0.1566	0.0038	48	9.587	39–79
	3[a]	16	13	25	0.1919	0.0820	16	3.856	13–20

The number of nights, or trapping occasions, the probability of being captured ($\hat{p}$), probability of recapture ($\hat{c}$), estimated number of individuals ($\hat{N} \pm$ SE), and the range of population estimates based on 95% confidence intervals are noted for each year and site

[a] This site was only sampled for a single sampling session and therefore population estimates were based on a Schnabel closed population model

mature individuals. Average density for the three sites is 22 ± 5.1 raccoons/km^2 (range 13–31; Table 1).

Discussion

In assessing the abundance of pygmy raccoons on Cozumel Island, the most striking finding was that we did not capture any animals except in the most northwestern quadrant of the island. Although both species have been occasionally sighted in the northeastern, southern and central parts of Cozumel (Cuarón et al. 2004; personal observations), we only trapped a single coati throughout our three year study, and only captured pygmy raccoons at 3 of 19 sites. Mainland coatis (*N. narica*) and raccoons (*P. lotor*), and pygmy raccoons are fairly easy to capture when present (e.g., Gompper 1997; Valenzuela 1998; Carrillo et al. 2001), as is verified by our success at Sites 1–3. We tried numerous baits and worked in varying habitats, at many different times of the year. We trapped in areas where residents, or we, had previously seen these species on Cozumel (Cuarón et al. 2004), but if additional populations existed, they were too small to be detected through trapping. Thus, we feel confident our results reflect the true rarity of these insular species.

While variation in capture probabilities occurred between field seasons, even when we greatly increased trapping efforts capture probabilities slightly decreased. Small population estimates are therefore not likely an artifact of our trapping effort at these sites. Pygmy raccoons were caught primarily in mangrove habitats, or in semi-evergreen tropical forest adjacent to mangroves. Dietary studies have shown the reliance of pygmy raccoons on food items (i.e., crab) found in this type of habitat (McFadden et al. 2006). However, pygmy raccoons were not captured in mangrove areas on either the southern portion of the island (Fig. 1; Sites 18 and 19), where we spent considerable trapping effort (over 1,000 trap nights), or on the unpopulated northeastern side of the island (Site 6), although sightings of tracks and individuals have occasionally been made in both areas (Cuarón et al. 2004; personal observations). Even in the northwestern area of the island, where the most significant populations of pygmy raccoon exist, the range of the pygmy raccoon habitats was extremely patchy. For example, individuals trapped in mangrove habitat along the mangrove-bordered 2 km road leading to Isla de la Pasión, were only in the last 200 m of this habitat, closest to the ocean. Moreover, at Site 3, traps placed further inland by 300 m did not successfully trap individuals outside of the original trap area, even though this trap site had a high capture rate. It therefore appears that pygmy raccoon populations are locally clustered in areas closest to the shore. This may correspond to the availability of a preferred prey item, crabs (McFadden et al. 2006), and may also be associated with the distribution and abundance of potential predators such as *B. constrictor* and dogs, as the latter are less abundant in mangrove areas (Bautista 2006).

The number of pygmy raccoons captured at the three sites did not vary significantly over the course of our study. Some behavioral heterogeneity to capture occurred, which may in part reflect harassment by dogs, which was especially prominent at Site 3. Free-ranging dogs are abundant and widespread in Cozumel (Bautista 2006), and whereas we detected both pet and free-ranging dogs at all sites, Site 3 was the only locale that a raccoon died due to a dog attack (McFadden 2004; García-Vasco 2005). Also, dwarf coati remains have been identified in dog scats (Bautista 2006) indicating the threat this species plays to both carnivores.

Only a single dwarf coati was captured in over 6,600 trap nights, an alarming indication of the rarity of this species. Although we did observe dwarf coatis on several different occasions (once at Site 1, twice at Site 6, twice at Site 19, and several times at Sites 7–15, near San Gervasio, and between Xlapac and Punta Molas; Fig. 1), this species is clearly very rare on the island. These areas included semi-evergreen tropical forests, mangroves, and other coastal vegetation. Never were more than two individuals sighted together, providing further evidence of their rarity, as coatis generally travel in bands, and these tend to be quite notable when present. Although it is possible that small remnant populations exist elsewhere in the island, we conclude that the Cozumel coati is now extremely rare and in immediate danger of extinction.

Based in part on unpublished data from our population assessment, the IUCN recently changed the listing of the pygmy raccoon from Endangered to Critically Endangered (CR2a(i)b) (Cuarón et al. 2008). Although some propose that the dwarf coati be designated as a unique species (Glatston 1994; McFadden 2004; McFadden et al. 2008; Merriam 1901; Thomas 1901), the most recent Global Mammal Assessment (GMA) treated this taxon as a subspecies following Decker (1991). Because subspecies were not reassessed in the GMA, the IUCN status of the dwarf coati remains unresolved, as the taxon is currently listed as a subspecies of *N. narica*, which in turn is listed as a species of least concern (Samudio et al. 2008). However, based on our population estimates, as well as justification put forth by Cuarón et al. (2004), we propose that their designation be immediately changed to Critically Endangered (CR A2c + C2a(i)b). The requirements of the CR designation that both the pygmy raccoon and dwarf coati fulfill are (1) that population size is <250 mature individuals, and (2) no subpopulation estimated to contain >50 mature individuals (IUCN 2008). After having intensively trapped on Cozumel for over three field seasons, we feel the major populations have clearly been identified, and these populations are undoubtedly small, isolated, and patchily distributed. Both species also show extreme fluctuations in the number of mature individuals due to the effect of periodic major hurricanes. In addition to these criteria, there is evidence that the dwarf coati population has experienced significant reductions in their population size over the last 10 years. This species is extremely rare on Cozumel, while historically they were found throughout the interior of Cozumel (Glatston 1994). Therefore, both species clearly qualify as Critically Endangered and we consider their risk of immediate extinction to be extremely high.

Our work suggests that the habitat requirements of the Cozumel dwarf carnivores remain poorly understood. Population sizes are very small and heterogeneously distributed in mangrove habitat in the case of the pygmy raccoons. A conservation recommendation arising from this study is to minimize future reductions to the extent of mangrove habitat where the largest populations of pygmy raccoons persist in northern Cozumel and from semi-evergreen tropical forests (central Cozumel) and coastal areas in the northeast and eastern side of Cozumel where dwarf coatis have been recorded. Habitat protection measures, including the establishment of protected areas comprising key habitat areas for these Cozumel endemic species, are urgently needed. The spirit of the new (2008) Ecological Ordinances (*Programa de Ordenamiento Ecológico Local*) for Cozumel is that a substantial area of these habitats should be set for protection and conservation (Secretaria de Desarrollo Urbano y Medio Ambiente 2008), so these protected areas should be decreed immediately.

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Appendix 1

See Table 3.

Table 3 Trapping effort and capture success for each sex (M, Males, F, Females) and age class of pygmy raccoon at three main study sites on Cozumel Island, Mexico, from 2001 to 2003

Year	Site	Trap nights	Juveniles		Subadults		Adults		Total captures	Capture per effort
			F	*M*	*F*	*M*	*F*	*M*		
2001	1	354	0	0	2	1	1	8	12	0.034
2002	1	428	4	4	13	1	6	6	34	0.079
	2	1,246	1	0	3	9	17	10	40	0.032
2003	1	80	7	1	1	0	4	3	15	0.187
	2	555	10	4	0	4	13	17	48	0.086
	3[a]	121	4	3	0	0	4	15	26	0.216
Total	1	862	11	5	16	2	11	17	61	0.071
	2	1,801	11	4	3	13	30	27	88	0.049
	3[a]	121	4	3	0	0	4	15	26	0.216
All sites and years		2,784	26	12	19	15	45	59	175	0.063

[a] Site 3 was only trapped at during one field season and therefore the number of trap nights and individuals captured are the total for this site

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