

Cozumel Island fox (*Urocyon* sp.) dwarfism and possible divergence history based on subfossil bones

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Abstract

Archeological evidence indicates that a dwarf fox (*Urocyon* sp.) has inhabited Cozumel Island, Mexico at least since the arrival of Mayan peoples, but no taxonomic descriptions or morphological assessments of the animal exist. A recent field study indicates that this fox is on the verge of extinction and therefore it is critical to describe the population. Because no skins or complete skulls of the Cozumel fox exist in museum collections, we examined subfossils collected during archeological excavations of the human-waste middens of Mayans who inhabited the island *c.* 1500–500 years before present. Measurements of 37 bones from a minimum of 12 adult individuals suggest that this animal is diminutive (the body size was *c.* 60–80% of mainland specimens), similar to other Carnivora from Cozumel that are recognized as distinct species. Estimated rates of character differentiation for mainland and island foxes under a range of possible divergence periods (1000–130 000 years) suggest that the Cozumel fox population has been isolated for a minimum of 5000–13 000 years, and perhaps far longer. Colonization of the island by *Urocyon* therefore likely predates the colonization of Cozumel by humans.

Introduction

Animals inhabiting islands are typically faced with a series of unique circumstances that may result in dramatically altered morphology. Mammals found on islands typically contrast in body size, skeletal and dental characteristics with their mainland counterparts, with larger species on islands becoming dwarfed in size (Foster, 1964; Heaney, 1978; Anderson & Handley, 2002). These physical differences, combined with geographic isolation, have led to the designation of many island populations as distinct taxa. For example, the island foxes *Urocyon littoralis* of the California Channel Islands were likely introduced by a combination of rafting and translocation by indigenous peoples 10 000–16 000 years before present (ybp). Despite their relatively short history of isolation, these populations are recognized as morphologically and phylogenetically unique, and therefore deserving of species-level recognition (Gilbert *et al.*, 1990; Goldstein *et al.*, 1999).

On Cozumel Island, Mexico, three mammalian Carnivora have existed for at least several thousand years (Hamblin, 1984; Cuarón *et al.*, 2004). Two are designated as species (the pygmy raccoon *Procyon pygmaeus* and the dwarf coati *Nasua nelsoni*), distinct from mainland congeners based on their reduced stature and colonization his-

ories (*c.* 50 000 ybp; McFadden, 2004) that appear to greatly precede the settlement of the island by Mayan peoples about 2300 years ago. The third species, a population of fox (*Urocyon* sp.), has never been formally described nor designated as taxonomically unique. Observations of this Cozumel fox are periodically recorded (most recently in 2001), but such events are rare (Cuarón *et al.*, 2004). Although survey efforts focusing on Cozumel foxes *per se* have not been carried out, the little evidence available suggests that the fox population size is extremely small and bordering on extinction. Cuarón *et al.* (2004) argue that the Cozumel fox should be considered as critically endangered based on IUCN standards (IUCN, 2001).

The suggestion that the Cozumel fox receive conservation attention assumes that the population is unique: genetically, phenotypically or both. The population has, however, never been formally described, and even the suggestion that the animal is diminutive is derived from second-hand accounts and brief glimpses of foxes (Merriam, 1901; Jones & Lawlor, 1965; Cuarón *et al.*, 2004). Ideally, we would collect living Cozumel foxes and formally describe the animal based on these individuals. However, the apparent current rarity of foxes on Cozumel and the ethical concerns and logistic difficulties associated with collecting individuals from a population that may be on the brink of extinction justify an

alternative strategy. Here we take a paleontological approach to describing this presumably extant taxon based on morphological assessments of cranial and post-cranial subfossil bones of *Urocyon* collected on Cozumel.

In the early 1970s, archeological excavations of human-waste middens took place on Cozumel to better understand the use of animals by the Cozumel Maya (Hamblin, 1984). *Urocyon* bones are fairly common in the archeological materials; Hamblin (p. 149) refers to 530 bones representing a minimum of 48 individuals. The age of bones can be identified based on stratigraphically associated Mayan artifacts; c. 67–78% of the bones derive from the Late Post-classic (c. 1250–1500 AD) and historic periods (post-1500 AD), and 1–4% from the pre-Postclassic periods (c. 100 BC–1250 AD), with the remaining bones from undated proveniences (Hamblin, 1984). We obtained access to many of these bones and used them to describe the Cozumel fox. Our approach was to (1) confirm that the bones were *Urocyon* by comparing them with modern *Urocyon* specimens of known origin and taxonomic affinity, (2) assess the size of Cozumel specimens relative to modern specimens collected from the mainland Yucatan peninsula and (3) determine the rate of morphological change for the taxon under a range of time-of-divergence scenarios.

Materials and methods

Cozumel (20°16′–20°26′N and 86°44′–87°02′W) is a 486 km² island made up of a variety of terrestrial habitats including dry deciduous forests, mangrove stands, sandy palm areas and multistratal tropical evergreen forests. The subfossil specimens collected from Cozumel were originally housed at the University of Arizona before transfer to the senior author for analyses; they are currently housed at the University of Missouri-Columbia. All the remains of putative fox were identified to genus based on a series of canid or *Urocyon*-specific characteristics, allowing the remains to be distinguished from all other Cozumel mid-sized mammals identified in the subfossil collections (*P. pygmaeus*, *N. nelsoni* and *Didelphis marsupialis cozumelae*). For the cranium and dentary, these features included a prominent notch on the posterior bottom of the lower jaw, paired temporal ridges on the upper surface of the cranium that form a lyre or U-shape, prominent carnassials and fox-like dentition. Post-cranial remains clearly represent Canidae (Hildebrand, 1954), and their small size and lack of *Canis*-specific characters preclude their originating in any other canid found in Mesoamerica.

We measured skeletal elements with sufficient anatomical landmarks to unambiguously identify dimensions for comparison with $n = 28$ modern (collected post-1900) specimens of *Urocyon cinereoargenteus* (including specimens from southern Mexico and Central America) housed at the University of Kansas Museum of Natural History and at the University of Missouri Zoological Collection. Five dimensions were measured on the cranium: two on the dentary and one each on the atlas, axis, femur and humerus (see von den Driesch, 1976). For cranial and limb bones, all specimens

represent adult individuals based on evidence of full eruption of the lower M3, fusion of cranial sutures and epiphyseal ossification. All measurements were made to the nearest 0.1 mm with a dial caliper (accuracy ± 0.0015). All measures were made by a single observer (A. E. P.) to avoid inter-observer variation. Cozumel and mainland *Urocyon* were contrasted using box plots and non-parametric Mann–Whitney tests to assess statistical differences between populations.

Dividing the average character size of Cozumel specimens by that of the average of mainland *U. cinereoargenteus* allows an estimate of the average size reduction. The rates of reduction across dimensions were calculated with the formula

$$d = 10^6((\log_e x_2 - \log_e x_1)/t)$$

where d is the proportional rate of change per million years in Darwins, x_1 and x_2 are the population means at the end and beginning of the temporal sequence and t is the time interval expressed in years (Haldane, 1949; Marshall & Corruccini, 1978; Anderson & Handley, 2002). This value was calculated for each dimension across a range of possible divergence times (1000–130 000 years; see Discussion) representing all times of fox arrival on Cozumel. Because we have only two temporal points (modern fox, Cozumel fox), we assumed a constant rate of change in body size over time. Although this assumption would be violated if selection were strongest immediately following island colonization, recent work on island sloths (Anderson & Handley, 2002) indicates a linear relationship between divergence time and body size change, with the former explaining c. 96% of the variance in the latter. Nonetheless, other prehistoric remains of different ages are necessary to test our assumptions.

Results

From the subfossil specimens collected on Cozumel, a total of 37 fox bones recovered from post-classic aged sediments (c. 1000–500 ybp) were selected (Table 1) for study. These

Table 1 Number of *Urocyon* bones examined, number of localities from which the specimens were collected within the San Gervasio Zone of Cozumel, and minimum number of individuals from which these bones could have arisen, assuming conservatively that left and right bones (mandible, femur, humerus) from the same localities originated from the same individual (although this may not be the case)

Skeletal element	Sample size	Minimum number of individuals	Number of localities
Cranium	1	1	1
Mandible	9	7	4
Atlas	7	7	3
Axis	3	3	1
Femur	9 ^a	6	4
Humerus	8 ^a	6	2

^aTwo lacked measurable dimensions.

Table 2 Dimensions measured (in mm; mean \pm sd) on *Urocyon* specimens from Cozumel Island and the mainland (Tables 3 and 4)

Dimension	Cozumel	Mainland	% diff; <i>P</i>
Dentary: length of molar row from anterior alveolus of M1 to posterior alveolus of M3	16.00 \pm 0.61 (15.00–16.70; 9)	20.54 \pm 2.13 (17.0–24.1; 25)	78%; <i>P</i> < 0.001
Dentary: thickness of jaw body under M1 at median wall between anterior and posterior alveoli	4.06 \pm 0.18 (3.8–4.4; 9)	5.09 \pm 0.063 (4.05–5.9; 26)	79%; <i>P</i> < 0.001
Atlas: length of arcus dorsalis (thickest bridge)	6.26 \pm 0.57 (5.6–7.2; 7)	10.55 \pm 1.63 (9.2–14.1; 10)	59%; <i>P</i> < 0.001
Axis: greatest height laying dorsal spine flat	17.10 \pm 0.6 (16.5–17.7; 3)	23.92 \pm 1.23 (21.8–26.1; 11)	71%; <i>P</i> < 0.001
Femur: width at neck of greater trochanter	6.01 \pm 0.48 (5.4–6.9; 7)	8.37 \pm 0.65 (7.4–9.45; 11)	72%; <i>P</i> < 0.001
Humerus: greatest breadth of the distal end (with plane at distal end)	12.17 \pm 0.18 (11.0–12.4; 6)	18.38 \pm 1.14 (16.55–20.3; 11)	66%; <i>P</i> = 0.001
Braincase: greatest neurocranium breadth	24 (1)	24.07 \pm 2.56 (20.6–29.8; <i>n</i> = 22)	<i>P</i> = 1
Braincase: greatest breadth of foramen magnum	11.2 (1)	12.97 \pm 1.28 (10.7–16.8; <i>n</i> = 26)	<i>P</i> = 0.123
Braincase: greatest breadth of occipital condyles	18.3 (1)	22.64 \pm 2.01 (19.2–25.9; <i>n</i> = 26)	<i>P</i> = 0.095
Braincase: breadth at the postorbital constriction	22.7 (1)	26.74 \pm 2.21 (22–31.3; <i>n</i> = 25)	<i>P</i> = 0.125
Braincase: height of the foramen magnum	8.4 (1)	10.05 \pm 0.87 (8.2–11.7; <i>n</i> = 25)	<i>P</i> = 0.124

Values in parentheses are the range and number of bones examined (*n*). Size of the Cozumel specimens is given as percentage of the mean of mainland specimens (% diff), with significance (*P*) assessed by Mann–Whitney tests.

specimens represent a minimum of 12 individuals (and likely more; Gilinsky & Bennington, 1994) and include cranial and post-cranial elements. All specimens represent adults of unknown sex. We measured six skeletal elements: five dimensions of the cranium (from a single Cozumel *Urocyon* specimen), two dimensions of the dentary (*n* = 9) and one dimension each of the atlas (*n* = 7), axis (*n* = 3), femur (*n* = 7) and humerus (*n* = 6). Corresponding dimensions were measured on *n* = 26 *U. cinereoargenteus* skulls and *n* = 11 *U. cinereoargenteus* post-cranial elements.

Of the 11 measured dimensions, only those associated with the cranium did not differ significantly between the island and the mainland (Table 2). The six dimensions of dentary and post-cranial bones indicate that Cozumel *Urocyon* are significantly smaller than mainland *Urocyon* (Fig. 1). Post-cranial dimensions of Cozumel and mainland *Urocyon* specimens do not overlap in size (Fig. 2); Cozumel *Urocyon* are significantly smaller than mainland *U. cinereoargenteus* (*P* \leq 0.001; Table 2; Fig. 2).

Cozumel dentaries are also significantly smaller (*P* < 0.001; Table 2) than those of mainland *U. cinereoargenteus*. Measures of molar row lengths for the two populations do not overlap in size. In contrast to molar row length and post-cranial element size, however, dentary thickness for the Cozumel and mainland specimens overlaps slightly (Fig. 2). Similarly, four of five dimensions from the single Cozumel *Urocyon* cranium overlap with the size of mainland *U. cinereoargenteus* (Table 2), although three of these dimensions fall at or near the minimum size for the mainland distribution.

Means of the Cozumel post-cranial dimensions are 59–72% of mainland *U. cinereoargenteus* dimensions; the Cozumel dentaries are also small but closer in size to mainland specimens than post-cranial bones (78–79%; Table 2). Molar row length and dentary thickness of Cozumel animals are 85.3 and 86.9% of the smallest mainland adult *U. cinereoargenteus* from southern Mexico and Central America (*n* = 12; mean molar row length = 18.75 mm \pm 0.92; mean dentary thickness = 4.67 mm \pm 0.32). Post-cranial materials from mainland southern Mexico and Central America were, unfortunately, limited to a single specimen from Costa Rica (KU 26955). Measures of the atlas (9.3 mm), axis (23.4 mm), femur (7.95 mm) and humerus (16.55 mm) from this individual are less than the mean values of mainland *U. cinereoargenteus* as a whole. Post-cranial dimensions of Cozumel specimens are 67.3% (atlas), 73.1% (axis), 75.6% (femur) and 73.5% (humerus) those of the Costa Rican specimen.

Proportional rates of evolutionary change were calculated by comparing the Cozumel specimens with those from southern Mexico and Central America. The rates were higher for post-cranial dimensions – a function of their greater reduction in size (Fig. 3). Divergence times of 1000 (e.g. change in a brief period following introduction to the island around the time when the subfossil individuals lived), 50 000 (around the period when the dwarfed Cozumel *Nasua* and *Procyon* populations may have become established; McFadden, 2004) and 120 000 ybp (around the maximum possible age of the population; see below) yield rates (min, max) of 139.98–395.83, 2.80–7.91 and 1.17–3.29d, respectively.

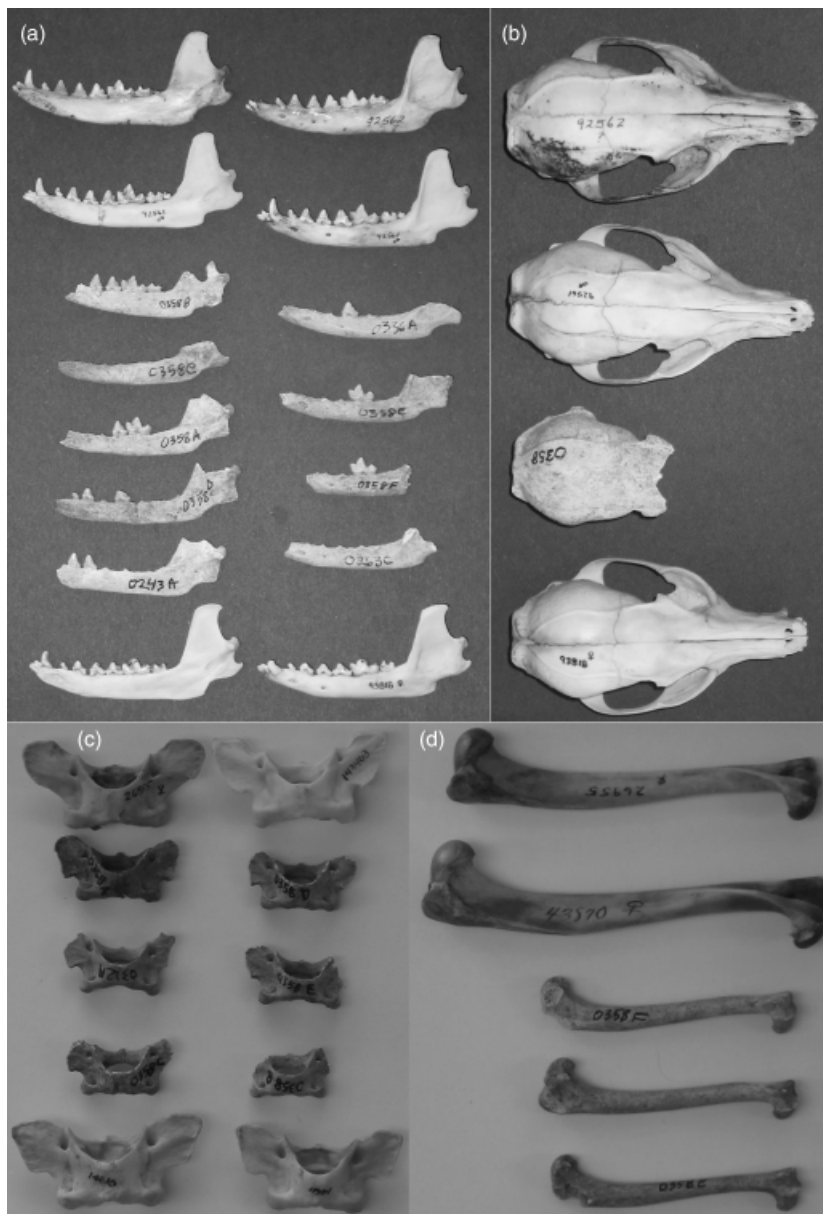


Figure 1 Comparison of Cozumel *Urocyon* specimens with representative specimens of mainland *Urocyon cinereoargenteus*. (a) Lateral views of dentaries. Top to bottom: split paired halves from unknown sex (KU 92562 Campeche, MX); split paired halves from adult male (KU 92561 Campeche); nine adult dentary halves or fragments from Cozumel (MU 0358A; 0358B; 0358C; 0358D; 0358E; 0358F; 0243A; 0263C; 0336A); split paired halves from adult female (KU 93818 Campeche). (b) Dorsal view of the cranium of three *U. cinereoargenteus* from Campeche, Mexico and one Cozumel specimen (third from top). From top to bottom: unknown sex KU 92562; male KU 92561; unknown sex MU 0358; female KU 93818. (c) Ventral view of atlas (top left: female KU 26955 from Cartago, Costa Rica; top right: female KU 143463 from California, USA; middle six specimens: MU 0358A; 0358B; 0358C; 0358D; 0358E; 0312A from Cozumel; bottom left: male KU 14610 from Georgia, USA; bottom right female KU14611 from Georgia). (d) View of humerus of (top to bottom) two mainland specimens (female KU 26955 from Cartago; female KU 43870 from Kansas, USA) and three Cozumel specimens (MU 0358A, 0358E, 0358F).

Discussion

Bones of *Urocyon* collected on Cozumel are significantly smaller than those of mainland *U. cinereoargenteus*. The size reduction of limb bones and vertebral elements was greater than that of dentaries, and with the exception of one dimension of the dentary, as well as the dimensions of the single partial cranium, sizes of all dimensions of Cozumel individuals do not overlap those of the mainland including individuals from southern Mexico and Central America. For the single cranium, three of the five dimensions of braincase size fall at or near the minimum size for the mainland distribution. The differing extent of diminution for the characters may represent a case of mosaic evolution,

with post-cranial measures decreasing in size more rapidly than cranial measures. The extent of diminution of the Cozumel *Urocyon* is similar to that of the Cozumel dwarf coati and pygmy raccoon (Cuarón *et al.*, 2004).

Measuring the rate of evolutionary change of Cozumel *Urocyon* requires assessing possible divergence dates for the island and mainland populations. Cozumel Island developed in the late Mesozoic and Cenozoic from the Yucatan Peninsula via block faulting, and the position of the island relative to the mainland has apparently not shifted over the past 200 000 years (Ward, 1997). However, the island was submerged because of increased sea levels *c.* 121 000 ± 6000 ybp (Spaw, 1978), and the timing of this submergence represents the maximum divergence time of island and

mainland *Urocyon*. Thereafter, the island increased in size with declines in sea level until 15 000–20 000 ybp. Holocene rises in sea level did not reduce the size of the island as greatly as equivalent declines in sea level increased island area, as carbonate deposition occurred along the narrow shelf surrounding the island (Spaw, 1978; Ward, 1997). Earliest evidence of sustained human use of Cozumel c. 2300 ybp (Freidel & Sabloff, 1984) represents a minimum divergence date under the assumption that humans facilitated colonization of Cozumel by *Urocyon*.

Rates of evolution for post-Pleistocene (1000–10 000 ybp) mammals range from 0.11 to 32.0*d* with a mean of 3.7*d* (Gingerich, 1983). For populations inhabiting known-age

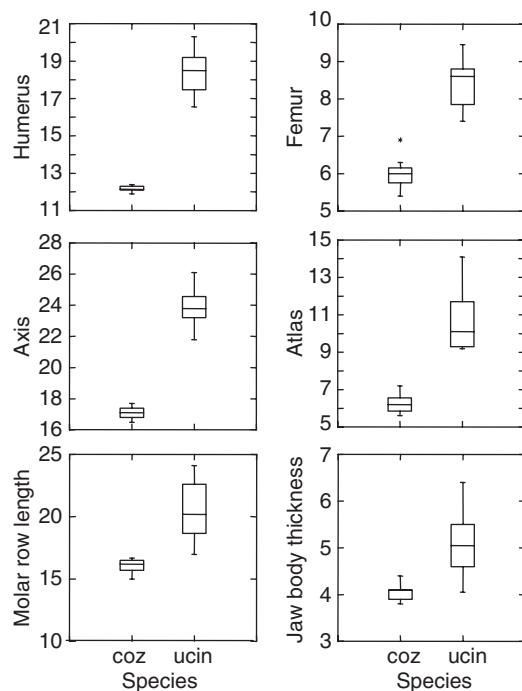


Figure 2 Box plots of two dentary dimensions (in mm) and four post-cranial dimensions of *Urocyon* specimens from Cozumel Island (coz) and mainland localities (ucin). Horizontal lines indicate medians and first and third quartile values. Sample sizes given in Table 2.

islands, analyses of dwarfism in Panamanian *Bradypus* sloth populations (isolated 8.9 kybp) and gigantism in Japanese *Apodemus* rodent populations (isolated 21 kybp) indicate rates of change of 16.18–17.02 and 2.47–5.72*d*, respectively (Anderson & Handley, 2002; Millien & Damuth, 2004). Using a 32*d* rate of change as a maximum plausible value for the Cozumel *Urocyon* population allows us to extrapolate a time of 5000–13 000 ybp as the earliest possible age for the calculated body size to evolve, depending on the trait examined, with the more recent date including a single dimension with a value of <32*d*, and the earlier date allowing all six examined dimensions to fall below 32*d*. Values of 3.7*d* and 16.2*d* would imply minimum divergence dates of >37 000 and >9000 years, respectively. All of these values predate the earliest known use of Cozumel by Mayans (Freidel & Sabloff, 1984). A divergence time of 2300 ybp implies rates of change in Cozumel *Urocyon* of 60.86–172.10*d*. These rates appear implausible, and thus we suggest that the colonization of Cozumel by *Urocyon* predates human colonization of the island.

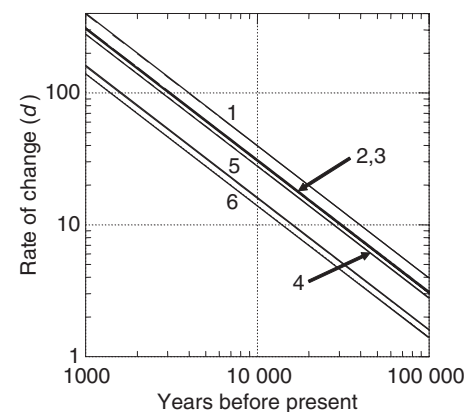


Figure 3 Rates of proportional evolutionary change (quantified in Darwins) that would be necessary for each of six features of Cozumel *Urocyon* to have differentiated from mainland-sized individuals over a range of possible time spans (from 1000 to 100 000 ybp). (1) Atlas; (2–3) humerus and axis (lines overlap); (4) femur; (5) length of molar row; (6) thickness of dentary.

Table 3 Specimens of *Urocyon cinereoargenteus* examined

Urocyon cinereoargenteus: KU 1637; 1638; 93818; 93817; 92559; 92560; 92561; 92562; 26955; 115600; 115601; 71938; 104345; 104346; 47987; 143463; 14610; 14355; 14611; 27337; 43870; 155349; 79714; MU 191; 2704; 1973; 2698; 950;

Museum acronyms: KU, University of Kansas Museum of Natural History; MU, University of Missouri Zoological Collection.

Table 4 Cozumel specimens examined, subdivided by bone

Mandible: MU 0358A, 0358B, 0358C, 0358D, 0358E, 0358F, 0243A, 0263C, 0336A; Braincase: MU 0358; Atlas: MU 0358A, 0358B, 0358C, 0358D, 0358E, 0312A, 0263A; Axis: MU 0358A, 0358B, 0358C; Femur: MU 0352A, 0358B, 0358C, 0358D, 0358E, 0358F, 0358G, 0240A^a, 0247A^a; Humerus: MU 0358A, 0358B^a, 0358E, 0358F, 0358G, 0358H^a, 0358I, 0358J.

All specimens from the University of Missouri Zoological Collection (MU).

^aSpecimens lacked portions of measured features and therefore were not measured.

If the Cozumel fox does represent a unique taxon, it is likely among the rarest of the world's canids. Reports of Cozumel gray foxes are rare, consisting of occasional sightings or eyewitness accounts, but recent reports suggest a population may persist (Cuarón *et al.*, 2004). Taking a conservative tact, Cuarón *et al.* (2004) proposed the Cozumel fox be considered critically endangered (IUCN: CR A4bce B1abc C2b) based on IUCN criteria, despite the lack of a description of this population. Our evidence suggests that (like the other Cozumel dwarf carnivores, *P. pygmaeus* and *N. nelsoni*, and like the Channel Island fox, *U. littoralis*) the Cozumel *Urocyon* is phenotypically distinct from the mainland taxon, that this population may deserve a unique species or subspecies designation based on a long history of isolation, and thus that the critically endangered designation is justified.

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