

Why is the coyote (*Canis latrans*) expanding its range? A critique of the deforestation hypothesis.

Julián Monge-Nájera

Museo de Zoología, Universidad de Costa Rica

Bernal Morera Brenes

Escuela de Biología, Universidad de Costa Rica

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The current views hold that coyotes have dispersed from North America southwards to recently reach Panama (Keast 1972, Pielou 1979, Vaughan 1983). Gipson (1978) attributed invasion of southeast United States to forest alteration and diminishing populations of its competitors, the wolves *Canis lupus* and *Canis rufus*. Young and Jackson (1951) suggested that Spanish settlers, by deforesting Central America for cattle ranches, facilitated colonization by coyotes from Mexico. Presumably, concludes Vaughan (1983), a dense barrier limited the species for some 400 years at northwestern Costa Rica:

“Deforestation practices from 1940 to 1977 removed approximately 16000 km² of Costa Rica forest concentrated in the southwest and northeast sector of the country... This has given rise to large cattle farming operations.... favorable habitat for the coyote. Faced with no competitors in these deforested areas except perhaps the grey fox (*Urocyon cinereoargenteus*) and the smaller wild felids, the coyote rapidly increased its range” (citations deleted).

This paper challenges two assertions of the above scenario: the date of establishment of coyotes in northwest Costa Rica, and the role of deforestation in promoting dispersal.

When did coyotes arrive in northwest Costa Rica? A probable answer comes from the Spanish administrator and naturalist Gonzalo Fernández de Oviedo y Valdés, who visited southern Nicaragua, and Guanacaste, Costa Rica, in the year 1514. His observations were included in the monumental “Historia general

y natural de las Indias, Islas y Tierra-Firme del Mar Oceano”, finished in 1526 and published 330 years later (Fernández 1856). We think that his description leaves no doubt that he knew the canid:

“los lobos de la tierra firme... son... muy grandes é mayores que grandes alanos é tienen el pelo como de vaca, é los dientes como de perro, é son muy armados de colmillos, é toda la noche andan, dando muchos ahullidos que ponen terror grande á quien no ha acostumbrado á los oyr”.

“The mainland wolves... are... very big and larger than large mastiffs, and they have cow-like hair, and teeth like dogs, and are very well armed with eyeteeth, and they wander all the night, howling to the terror of those not accustomed to hear them”.

The above description could fit three canids in the Neotropics: wolves (*Canis lupus*, *Canis rufus*), coyotes (*Canis latrans*) and maned wolves (*Chrysocyon brachyurus*). The ancestors of the latter two appear to have reached the Central American isthm around the Pliocene, and Canids in general are known from Uquian (late Cenozoic) beds of South America (Patterson & Pascual 1972). Since there are no records of living or fossil wolves and maned wolves in Central America (Burton 1962, Keast 1972, Patterson & Pascual 1972, Dietz 1984), Fernández must have referred to coyotes. In another paragraph Fernández (1856) says:

“Lobos he visto en la gobernación de Castilla del Oro y en la de Nicaragua”

“Wolves I have seen in the realms of Castilla del Oro and Nicaragua”.

Another spaniard, the priest Francisco Ximénez (1967) confirmed in a manuscript of 1526 that the words "lobo", "adibe" and "coyote" were transposable:

"Lobo: Este animal que aquí llaman coyote, y antiguamente en España llamaban adibe, es muy común en aquestas tierras".

"Wolf: This animal that here they call "coyote", and that in old times was called "adibe" in Spain, is very common in these lands".

In conclusion, *Canis latrans* was established in southern Nicaragua, and probably in Guanacaste, in the year 1514, before any extensive deforestation had occurred (Fernández 1856, Cockburn 1962, Meléndez 1974).

Krebs (1972) has proposed a sequential approach to analyze distribution, based on Macan (1963). We follow the same series of questions to examine why coyotes were absent from most of Costa Rica and all of Panama for at least 400 years. Was the cause inability to disperse? That is improbable, since an individual can travel up to 323 km in 15 months (see Vaughan 1983), and routes such as the coast, riparian areas, and at least since 1858, the Puntarenas-San José road were available (Belly 1974). Was it feeding behavior? Coyotes eat a wide array of vertebrates, carrion of practically any type, and vegetable matter and invertebrates, a perfectly omnivorous and opportunistic diet (Burton 1962). Food constraints thus appear to be improbable barriers to colonization of areas southeast of the tropical dry forest. Was it interaction with other species such as predators, parasites, competitors or disease? We are aware of no studies of these factors in Central America, and they may repay further analysis. Vaughan (1983) cites the gray fox and the smaller wild felids, but in some areas they coexist with coyotes; so they are not promising candidates for barriers to coyotes. Were physical factors the barrier? Vaughan (1983) has suggested their possible role in preventing colonization of deforested areas of the Caribbean basin by coyotes: "the coyote does not seem to persist in the hot, humid, high rainfall climate which prevails on the Atlantic coast", whose altered habitats they visit during low rainfall periods. We doubt that climate is important as an impassible barrier to dispersal, because coyotes occur from zero to 3400 m altitude in Costa Rica (Vaughan 1983);

they thrive from Guanacaste, a hot area with two clearly defined seasons of drought and heavy rainfall, to areas of Paramo in the Talamanca Mountain Range, a chilly and moist habitat (Valerio 1980, Vaughan 1983). In conclusion, at least four hypotheses (or their combinations) remain to be tested: behavior in relation to habitat selection (Vaughan's favorite), predation, parasitism and disease.

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NOTE: Christopher Vaughan informed us that he will reply in a future publication.

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