The Factors for the Extinction of Jaguars and Cougars in El Salvador

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Abstract
The jaguar (Panthera onca, Linnaeus 1758) and cougar (Puma concolor, Linnaeus 1771) are the largest cats in the Americas and are listed as uniquely extinct in El Salvador, Central America. The contributory factors for this event are little understood and/or ignored. This omission hampers conservation planning for declining big cat populations in other countries. A thorough review and analysis of the literature reveals important gaps that impede assessment of the factors for big cat extinction, and also possible ameliorative efforts. The evidence questions the commonly blamed civil war and deforestation, and critically assesses a wider set of factors mostly not linked to big cat extinction; dense human population, small national territory, border porosity, cat adaptability to modified land cover and the actual importance of connecting forested corridors. The evidence from other countries shows possibilities of cat adaptability to all possible factors for extinction, but also hints at the possibility of the lack of connecting corridors as uniquely negative in El Salvador. Reintroductions of big cats in El Salvador must include internationalized assessments of their ecology and public tolerance of cat presence. It is imperative that generalized assumptions of cat extinction, e.g. the civil war and deforestation, and human population density are critically reviewed. Full conservation of big cats in the region requires reintroductions based on such critically acquired knowledge, rather than further debate.

Introduction
Human population increase, intensified land use and attitudes to wildlife, as well as habitat losses, hunting and pollution have devastated the global biodiversity, even in ecological “hotspots” such as Central America. Of all wild mammal species, half have declining populations and one quarter is threatened with extinction. Large carnivores are particularly affected, due to low population densities, human fear and attitudes, physical conflict, their mobility and requirement of large tracts of land and wide ranging prey species, and consequent difficulties of conservation. Consequently, the creation of reserves may be fruitless, due to land use conflicts with other pressing requirements, such as urbanization and agriculture, and the difficulty of restricting large carnivores to land inside the reserves. This situation exists in Europe, Asia, the Americas and Africa. Due to these issues, human action is seen as the main predictor of large carnivore existence and extinction in addition to the natural factors of prey abundance and habitat suitability. Both human action and prey availability are particularly relevant for large felids, the most carnivorous and feared mammalian predators and among the most threatened mammals globally. Although human population increase, cultural differences in carnivore tolerance and government attitudes are factors for carnivore depletion, adequate management even with high human density can preserve carnivore presence. Considering these issues, successful large carnivore conservation requires ecological information at species and population levels, and knowledge of relevant human behaviours, activities and attitudes [1-19].

Local extinction of large felids is common across the continents. Large extinct cats include: the Javan tiger (Panthera tigris sondaica, Temminck 1844), extinct in the 1970s in Java, one of the world's most heavily populated countries; the Caspian Tiger (Panthera tigris virgata, Illiger 1815); the Bali tiger and the North African lion (Panthera leo leo, Linnaeus 1758). In the Americas, the Eastern Cougar (Puma concolor, Linnaeus 1771) was declared extinct in 1923. The jaguar (Panthera onca, Linnaeus 1758) is largely extinct in the US, with occasional sightings in Arizona. In all these cases, contributory extinction factors are intensified land use, human extirpation of prey species and suitable habitat, and increased human populations, rather than competition from other species or migration. In terms of species extinctions, central America is a particularly interesting area, the location of the Mesoamerican Biodiversity Hotspot (Biodiversity Hotspots are areas considered extremely biodiverse but also highly threatened) which contains the third largest forested area in the world and constitutes a corridor between the ecological regions of North and South America. The region has experienced extreme environmental modifications, namely wars in El Salvador, Nicaragua, Guatemala and Panama; deforestation, partly associated with these upheavals; agricultural intensification; land use conflicts; and local mammal extinctions. The consequences for large carnivores, in this case the jaguar and the cougar, are unclear, but possibly pronounced, considering their environmental needs. The jaguar is currently recorded as extinct only in El Salvador in Central America, and also in Uruguay in South America. The puma is listed as almost extinct or extinct in El Salvador, the only central American country where it was not protected, at least in the 1990's [20-43].

The Situation of the Jaguar and Cougar
The jaguar is the largest felid in the Americas, the world's third largest cat, with a distribution from the southern borders of the US to northern Argentina. Jaguars are markedly less studied than other large cats such as lions, tigers and leopards and most studies neglect Central America in favor of South America, especially the Pantanal, and there are few countrywide studies of its status. This makes an international assessment of the status of the jaguar in Central America difficult.

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El Salvador (Figure 1, population 6,052,064 area 21,041 square kilometers, population density 288 per square kilometre; Central Intelligence Agency 2010) is the most densely populated country in Central and South America, and has the strongest reputation for environmental degradation in Central America, possibly also in Latin America. However, in common with other Latin American countries, there have been records of both deforestation and reforestation. The environment has been classified as highly changeable, due to war, hurricanes, floods, landslides and volcanic eruptions, and the very long period of human impact. The result is a mosaic of natural, secondary and anthropogenic forests, and farmland. Reforestation is based on:

a. The long civil war, which contributed to a retreat of cattle ranching and agriculture;
b. The local effects of economic globalization, which resulted in urbanization, rural to urban migration of farmers and diversified agriculture;
c. Structural adjustment policies which favoured more modern agricultural policies based on commercialization, trade

Habitat Requirements of Jaguars and Cougars

To consider the factors for extinction, a synthesis of the literature on adaptation is a reasonable starting point. Adaptability, the missing link in studies of these big cats, starts with assessments of their landscape ecology. Jaguars, very mobile, with low population densities and large ranges (up to 1,000 km²) generally avoid cultural landscapes. Both cats favour forest near water (especially for the jaguar) distant from roads, human settlements and steep slopes. However, there are disputes without resolution on the importance of proximate water. There is also no conclusion as to the degree of competition between the two species. Perhaps there is competition avoidance between the two species; the cougar taking a wider variety of prey species, and smaller prey. There is however unpredictability for adaptation in the dense forests, which may be less than predictable scenario than open grassland, with few water sources and greater visibility of large ungulates. Another uncertain factor is the introduction of livestock, which may wean both species off natural prey. Both species prey on livestock and the reduction of natural prey may encourage predation on livestock. Allegedly problem cats have been hunted and killed, but there is little documentation of how they may adapt to human reactions [64-84].

The identification of livestock killers is difficult, as other species may kill livestock, such as feral dogs (Canis lupus familiaris, Linnaeus, 1758), coyotes (Canis latrans, Say 1823) and ocelots (Leopardus pardalis, Linnaeus, 1758). Scat and DNA studies, using bile powder for DNA analyses, and animal remains may be used for predator identification purposes. Camera-based techniques differentiate cats by fur patterns. Limitations of these methods include the recording of more males than females, possibly due to the larger territories of males and the greater timidity of females on human-constructed trails. Species presence may also be assessed by interviewing relevant stakeholders. Who may provide real or anecdotal evidence of big cat presence [85-89].

The Case of El Salvador

The most problematic issue is big cat extinction in El Salvador. As the adaptability and human relations of these cats are not fully understood, and there is no consensus on the method of study, the way forward is to uncover any unique and relevant characteristics about El Salvador that may differentiate from other Latin American nations.

Recorded factors include habitat conversion under agriculture and urbanization, hunting and a decline, due to habitat losses and over-hunting from humans, of their natural prey. A quasi-religious and cultural icon in the past, jaguars are feared and therefore hunted, but this may be unjustified. Attacks on people are very rare, much rarer than those of tigers and leopards. The cougar is the second largest cat in the Americas, and the fourth largest in the world after the tiger, lion and jaguar, and usually slightly larger than the leopard. The cougar has a much wider range than the jaguar, appearing to be more adaptive than the other, larger cat. Throughout its range, the cougar is sympatric with other large or larger carnivores (brown and black bears, and wolves in North America, jaguars in North and South America). The cougar is generally considered less dangerous to people (there are few attacks, but possibly more than those of the jaguar) and a much more elusive cat than the jaguar, a possible factor for its survival. In some cases jaguars are blamed for livestock predation, where cougars are responsible. Although, possibly because of its wider range, the cougar is more studied than the jaguar, its very adaptability makes conclusions about its extinction difficult. It is hunted throughout its range, even where protected, but is extinct only in El Salvador [44-63].

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liberalization with foreign imports, cancellation of fiscal incentives, elitism and marginalization of poorer farmers;

d. Decentralization and democratization of political institutions, which were associated with the decline in agriculture and rural to urban migration and international emigration, enabling the rise of some ecological institutions and polices; and

e. Recent environmental programs, based on the greater support of international finance for environment conservation. These issues are documented and debated, but there is little documented connection with big cat, or even other wildlife presence in the literature. The borders of El Salvador do not prevent wildlife migration (Compare Figures 2-4) for the possibly of forest corridor migration). Possible factors for big cat extinction are assessed in turn [90-105].

**The Small Size of the Country and the Isolated Forests**

The area of El Salvador is only 21,040 km²; a small region considering that at least 2000 km² of forest are necessary to house at least 50 jaguars. By this logic, El Salvador could only house about 500 jaguars, even assuming all the land were forest and the forest was connected to the larger forested landscapes of Central America, neither of which is true. El Salvador has not only the smallest forested area of any Central American country, but its forest is also outside the mainstream forests of the region, with no clear corridors of sufficient size. The small size of the country, especially its location in the less forested western part of Central America is certainly a factor for the lack of connecting corridors. Complicating matters, the literature is unclear on the porosity of the borders and the modified landscapes between the forested areas. There is no available information on the capability of big cats to penetrate such substrates in El Salvador specifically. Certainly, both cats have been recorded as penetrating such land cover in other areas [106] (Figure 2).

**High Human Population Density**

El Salvador has the highest human population density in Central America (292 people per square kilometre), followed by Guatemala (129), Costa Rica (90), Honduras (67), Nicaragua and Panama (44 each) and Belize (13). This may be a factor for large carnivore extinction, although there is no conclusive link in the literature [2]. It may be difficult to discern links between human population and big cat numbers, as in many cases human-altered landscapes served as corridors “provided that other habitat components (cover, water, prey) are available and the landscape has not been severely altered or degraded by human activities” [28]. A study of the Panama Canal watershed showed a fivefold increase in the human population between 1950 and 1990, but no big cat extinction, possibly because of corridor forest [107]. Also, cougars are present in downtown areas of Canadian cities. This evidence contrasts with documented avoidance tendencies [73-74,107-109]. A contrast has been drawn between two, highly populated areas of Brazil; the Pantanal, with habitat loss mixed with corridors connected to Amazonian forest, and cattle herding; and the Atlantic coastal area, with habitat loss, hunting and reduced number of prey animals. Jaguars are commoner in the former than the latter, underscoring relevance of other factors apart from human population in their distribution [50] (Figure 5).

**Civil War**

The El Salvadoran civil war (1979 to 1992, up to 70,000 people killed) has been mooted as a factor for wildlife extinction, through the destruction by burning and bombing of potential habitats [110]. The war also encouraged forest regrowth, farming and livestock rearing were reduced through land abandonment and fear of old explosives and land mines [91]. Civil wars in Guatemala (a much longer war that killed more people-1960 to 1996, over 200,000 dead) and Nicaragua (also a longer war from the 1960’s to 1990) had similar effects on the
Nevertheless, jaguars were historically recorded in the open presence and encouraging the preference of such animals for dense dominated by farming and other human presence, inhibiting big cat interior Nicaragua and Honduras. The open savannas are largely coast, and the Central American tropical moist montane forest in of survival being the pine savannas and mangroves along the Caribbean highlands of Costa Rica and Panama, with the areas of low probability to northern Honduras. Areas of medium probability of survival are the a forested corridor from the Choco-Darien of Panama and Colombia habitat with high potential for the felids survival is the tropical lowland [83,89,115-116]. In Central America, the main area of perceived jaguar support more than 500 jaguars “may no longer exist in Central America” is unlikely that deforestation alone would result in cougar extinction; regions, such as the southwestern US and inter-montane Canada, it the distribution of cougars in arid, lightly vegetated habitats in other factors, beyond war, deforestation and human presence. Based on the distribution of cougars in arid, lightly vegetated habitats in other regions, such as the southwestern US and inter-montane Canada, it is unlikely that deforestation alone would result in cougar extinction; rather a combination of factors, perhaps stronger than for the less adaptive jaguar, may be more likely.

Deforestation

From the issues discussed above, would deforestation necessarily lead to the extinction of the big cats? For the cougar, the balance of probabilities hints at no. The cougar is plainly resilient to deforestation [75-78]. The extinction of this species in El Salvador points other factors, beyond war, deforestation and human presence. Based on the distribution of cougars in arid, lightly vegetated habitats in other regions, such as the southwestern US and inter-montane Canada, it is unlikely that deforestation alone would result in cougar extinction; rather a combination of factors, perhaps stronger than for the less adaptive jaguar, may be more likely.

The jaguar is more problematic. Forested areas of sufficient size to support more than 500 jaguars "may no longer exist in Central America" [83,89,115-116]. In Central America, the main area of perceived jaguar habitat with high potential for the felids survival is the tropical lowland forest, especially the Selva Maya of Guatemala, Mexico and Belize, and a forested corridor from the Choco-Darien of Panama and Colombia to northern Honduras. Areas of medium probability of survival are the highlands of Costa Rica and Panama, with the areas of low probability of survival being the pine savannas and mangroves along the Caribbean coast, and the Central American tropical moist montane forest in interior Nicaragua and Honduras [44]. The open savannas are largely dominated by farming and other human presence, inhibiting big cat presence and encouraging the preference of such animals for dense cover [2]. Nevertheless, jaguars were historically recorded in the open area of the southwest US [28]

Biodiversity and Prey Species

In Central America, El Salvador has lowest number of mammal species (137), followed by Belize (147), Nicaragua (181), Guatemala (193), Honduras (201), Costa Rica (232) and Panama (241). It also has the lowest number of animal species (birds, mammals, reptiles and amphibians), and vascular plants in Central America blame intensive agriculture, the destruction of the original vegetation, the small area of primary forest (2-5% of the national area), above average natural disasters for the area (landslides, earthquakes, river pollution, hurricanes, flooding and volcanic eruptions), and urban sprawl in a very small area for prey species extinctions. What is the link between these and big cat extinction? Intuitive judgement of the numbers quoted would probably hint; not much. Not all the species are prey for jaguars and cougars. However, few studies have attempted to make the link between prey species and the felids [117-118]

Excessive Hunting

Human hunting may either kill the carnivores themselves, or their prey species, as prey abundance is a predictor of predator density [5,14-17,60]. Most large felids, including jaguars and cougars have adaptive abilities for different prey. Prey selectivity is usually studied using indices that emphasize prey availability and abundance. Other studies go further, and explore reasons for selective foraging, mostly prey that maximizes the amount of energy gained and minimizes the amount of energy spent foraging [119-128]. Therefore, there must be a study of both the diet of the felid, and predator and prey ecology, behavior and population dynamics [14].

In El Salvador, herbivores that are prey species for large felids are of low conservation concern, despite the relatively low species diversity. These include the collared peccary (Pecari tajacu, Linnaeus, 1758), Red Brocket deer (Mazama americana, Erxleben, 1777) and White-tailed deer (Odocoileus virginianus, Zimmermann 1780). Baird’s Tapir, an occasional prey species, is extinct only in El Salvador among the Central America countries, possibly due to hunting by humans and deforestation. Tapir extinction is unlikely to be a factor for felid extinction, because adult tapirs are generally too large to be a common prey species [130]. A more relevant factor would be the preference for similar forest cover; hence, environmental factors for large felid extinction may also be factors for tapir extinction. Other smaller species have been described as more adaptive than both large felids and tapirs, hence their perseverance, even if decimated by hunting, may not be a factor in helping large felid conservation, while people still hunt the carnivores [2] (Figure 6).

Interactions with Other Predators

The jaguar and cougar have no natural enemies expect people. A possibility would be their competition, which might reduce their numbers due to the extinction of shared prey species, or the avoidance of the larger jaguar by the smaller cougar. However, there is little consistent evidence of either of these scenarios, although a few studies have examined the relations between these two species and some hint at avoidance tensions and others refute these possibilities [131-132]. As there are few such sympatric studies for areas of extreme environmental modification, questions remain whether in a modified environment such as El Salvador, the reduced numbers of prey species, substantially modified habitat and closer human proximity would increase tensions between the two species, to a result of local extinction of one or both species. Asserting such facts is very difficult, as both species are extremely elusive, and methods of assessment such as collection of scats do not indicate hunting locations. Jaguars and cougars could be using the same tracks, but be hunting in different areas [69,79].
The Way Forward

The assembled evidence compels the conclusion that there is no clear reason for the extinction of jaguars and cougars in El Salvador. Further debate would be pointless, without a testable example on the ground. Firstly, experimental reintroductions assume importance. With reintroductions, parallel studies indicate which factors are impediments [2]. In addition, despite the clear evidence of big cat adaptability, forested corridors are at least considered to be beneficial. The “Paseo del Jaguar” (Path of the Jaguar), is a proposed system of interconnected corridors and patches that will be distributed from the US to South America, that may allow the mobility of jaguars, while protecting them from land users, and including small preserves along the corridors, large enough for jaguar visitation. Although focused on jaguars, presumably this development may also benefit the more adaptive, elusive cougar [132].

Secondly, public support is an issue. There have been few assessments of public support for the scheme. Although studies have shown substantial sympathy for large cat reintroduction in El Salvador, more work is needed to determine the social impacts of predatory behaviour towards livestock or people, human fear in rural settlements and the impacts of human hunting on both prey and carnivore populations. These issues strongly exist in areas of big cat habitation in other countries [59-63,69]. Therefore, the extent of their relevance in El Salvador must be investigated.

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