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Jaguar (*Panthera onca*) in California: A History and a Future

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Reintroduction of large carnivores to regions they once inhabited has been considered or implemented for many species in North America, including gray wolf (*Canis lupus*), red wolf (*C. rufus*), grizzly bear (*Ursus arctos*) and others (Fritts et al. 1997; Merrill et al. 1999; Maehr et al. 2001; Phillips et al. 2003; Smith 2003). Reintroduction of large apex predators comes with significant potential risks—not only to the species being restored, but to the contemporary ecosystem (Smith and Peterson 2021; Baker et al. 2017) and to the public (Carroll et al. 2001). The counter argument is that such programs can in fact have beneficial effects on ecosystem health, ecotourism, and wide-ranging predator-prey interactions as well as other ecological processes (Ripple and Beschta 2003; Marshall et al. 2013; Martone et al. 2020; Smith et al. 2020). Additional consideration has been placed on peripheral populations, which would be classified as "non-essential experimental populations" by the United States Fish and Wildlife Service, that could be managed in the United States (Lesica and Allendorf 1995; Sanderson et al. 2021). Potential risks and benefits of restoring large predators in their ancient territories must be weighed very carefully (Baker et al. 2017; Maehr et al. 2001; Clark et al. 2005; Sanderson et al. 2021), and great consideration must be given to the anticipated welfare and success of the species itself.

A number of factors come into play: Is the habitat currently intact, and does it afford the species opportunities to grow in distribution and connect with other (reintroduced or naturally occurring) populations (Abbitt et al. 2000)? Are the risk factors associated with a large human population likely to result in negative outcomes (Clark et al. 2005; Lee et al. 2021)? Among myriad questions to be considered, the temporal scale of the proposed restoration is particularly critical. Is the intent of restoration to reintroduce keystone, preexisting species from a particular period (e.g., species present before European settlement)? Is the intent to restore an ecological unit (ecosystem, biological province, or other large-scale biotic unit) to a condition conducive to the reintroduced species? Or is it simply to restore a focal species and its prey base "because we can," without regard to the contemporary environment (Callicott 2011a)? Callicott (2011b) proposed that environmental timescale—that is, habitat- and condition-based restoration to a preexisting baseline—is the aspiration likeliest to succeed, laying as it does the groundwork for reintroduction of a species based on its known past occurrence and ecosystem needs. Restoration teams can then elect reintroduction goals based on evidence gleaned from historical or prehistoric presence. In such efforts, understanding the verifiable past range of a species assumes immense importance (Wolf and Ripple 2018).

Scientific literature has contributed significantly to establishing the known past occurrence and range of species; these data and observations are ideal for establishing goals for environmental restoration to conditions present at a particular period in the past (Redford et al. 2011). If a temporal framework is the goal, an understanding of the distribution during certain time events may be critical. Van Vuren and Deitz (1993) reported evidence of former occurrence of bison (*Bison bison*) in central and northeast Nevada, noting that such evidence can inform our understanding of the species' historical context. This, in turn, might suggest the likelihood of the species' successful reintroduction should conditions be reproducible for the long term.

Storer and Tevis (1955) reviewed the history of grizzly bears (*U. arctos horribilis*) in California, including information about occupied habitats and the historic distribution. Their well considered findings suggested the reproducibility of conditions conducive to grizzlies should the species be reintroduced. In an attempt to establish the historical range of the California condor (*Gymnogyps californianus*) on the Pacific Coast over time, D'Elia and Haig (2013) consulted 81 records, including anecdotal accounts, letters, journals, newspaper articles, the feathers on an indigenous costume, and museum specimens dating back to 1805. Their data pointed to a steep decline in condor populations after European settlement in the state, suggesting that a species restoration plan would need to give careful consideration not only to reproducibility of historical environmental conditions, but to protection from human activity. Such a program was initiated and is showing promising results in restoration and protection of *G. californianus* populations on the Central Coast (Kelly et al. 2015). Data can also be used to support or discourage species reintroduction and restoration. For example, Ripple and Beschta (2003) looked at the history of cougars (*Puma concolor*) in Wyoming's Yellowstone National Park, and determined, through an in-depth investigation of anecdotal records and letters, historical photographs, and trapping data, that current numbers of cougars were likely higher than historical numbers in that area. In such a situation, species restoration or population augmentation would presumably be unwarranted. It is important to note that indication of past and potential future occurrence of a species in an area is just that, support for assessing reintroduction. These data do not address the advisability of such reintroductions.

Reestablishment of jaguar (*Panthera onca*) in western North America has recently come under discussion. The species contemporary occupation of portions of Arizona and New Mexico (migrating individuals from Mexico) prompted the listing of *P. onca,* in the United States, as an endangered species under the Endangered Species Act (ESA)(USFWS 1997). The elevation in federal status precipitated discussions related to augmentation of colonizing populations, and potential reintroductions (Povilitis 2015; Sanderson et al. 2021). Although Povilitis (2015) has advocated for population restoration (both augmentation and reintroduction), others are in support of peripheral populations that can be managed in a different manner (Gittleman et al. 2001; Nielsen et al. 2001; Wolf and Ripple 2018) from that set forth by the Jaguar Recovery Plan (USFWS 2018). Hayward et al. (2007) noted that when introductions are planned, they should occur within the known historical range from which the species was extirpated.

It is also noteworthy that, although the historical data can provide a context for future management, research, or reintroductions, their reliability must be viewed with caution (Adams et al. 2023). Ripple and Beschta (2003) and D'Elia and Haig (2013) themselves noted that historical data, both pre– and post–European settlement in North America, are often anecdotal, highly imprecise, and narrative in nature, and commonly result in subjective or overly broad estimates of past occurrence or areas of distribution. McKelvey et al. (2008) cautioned that using these types of data may lead to large errors of commission or omission, with significant conservation implications. In some cases, in which anecdotal data provide the only available evidence, researchers must be careful to disclose the likely imprecision of the data set within their work. This may be particularly true when attempting to establish the known range of apex predators such as the grizzly (*U. arctos*) or the jaguar (*P. onca*).

Panthera onca is a species native to the Americas for which few historical data exist in the western United States. The available data, particularly in California, are almost all vague or anecdotal. Nonetheless, Povilitis (2015) stated that recovery, and any subsequent reintroduction or population augmentation of *P. onca* in the United States should be consistent with

historical records, however anecdotal. In other words, despite a very small historical sample size, incomplete and anecdotal data, and/or scant prehistoric evidence, understanding the historic distribution of *P. onca* in California—and the implications of that presence and distribution—should have bearing on any considered reintroduction of this top predator. To further explore the case for reintroducing *P. onca* into previously occupied territory, I reviewed historical records and paleontological evidence to augment the known natural history of *P. onca* in western North America and provide additional data to gauge whether reintroductions may be appropriate.

I conducted a search of the available online and archival documents, reports, journals, and other publications, searching *Panthera onca*, panther, jaguar, *onca*, leopard, spotted, and large cat. Search terms, and numerous combinations associated with California, Arizona, western United States, Alta California, and Baja California were used to identify relevant documents. I reviewed more than 32,000 pages from United States and California State archives on trapping, fur trading, exportation of animal products, and related fields for any report or mention of *P. onca* and associated search terms. Thirty-one books and personal journals (1856–1955), 51 scientific journals, 19 journals associated with the Spanish Missionaries in California, and 94 articles of gray literature were also carefully reviewed. One hundred eighty-six North American–based and 17 international museums of natural history, archeology, and paleontology were queried in the course of this research.

The prehistoric range of *P. onca* in North America has long been a matter of conjecture (Simpson 1941; Dagget and Henning 1974; Seymour 1989). There is relative accord among inferred range maps, which appear to derive from Simpson (1941). All include areas south of Spokane, Washington; eastward towards north central Nebraska; south towards northern Arkansas and central Tennessee; and northeast towards southeast Pennsylvania. This area would inferentially include all of California, however the past range of *P. onca* within present-day California *per se* is unclear and without consensus. Seymour (1989) suggested an area from approximately Santa Barbara County south to the border with Mexico. Hall and Kelson (1959) were more specific, including only the central core of the area suggested by Seymour (1989); their proposed range included the Tehachapi Range and eastern Mojave Desert southward, as well as the Colorado River drainage south of Nevada. When accounts of *P. onca* or similar predatory cats were encountered in conducting this research, I collected the entire excerpt of the account and/or recorded the museum data point, location, collector, and any other associated information that could be used to determine or verify the reported location. If precise, these data were entered on a map (i.e., dot); if imprecise, the data were converted to a shaded area on the map (Fig. 1). Combined, these data produced a hypothetical area of past *P. onca* occupation within California or immediately adjacent (the border regions of Arizona and Mexico). Currently available data suggest at least four areas in which *P. onca* were observed or for which anecdotal evidence suggests that the species was in the immediate area. These accounts were summarized by Merriam (1919), and an additional account was reported by Strong (1926), who claimed a *P. onca* had been killed in California *circa* 1860 (Fig. 1; Table 1). In the time since the reports by Merriam (1919) and Strong (1926), additional direct, verifiable evidence (i.e., bones) of *P. onca* in California has been collected from various sites, including Rancho La Brea in Los Angeles County, California (Jefferson 1983; 1991) (Table 1). The preponderance of evidence has been attributed to the Irvingtonian North American Land Mammal Age (LMA), approximately 0.25–1.6 million years Before Current Era (BCE), and represents fossil animals from that period. An additional *P. onca* fossil reported from Anza-Borrego Desert State Park in Southern California by Jefferson and

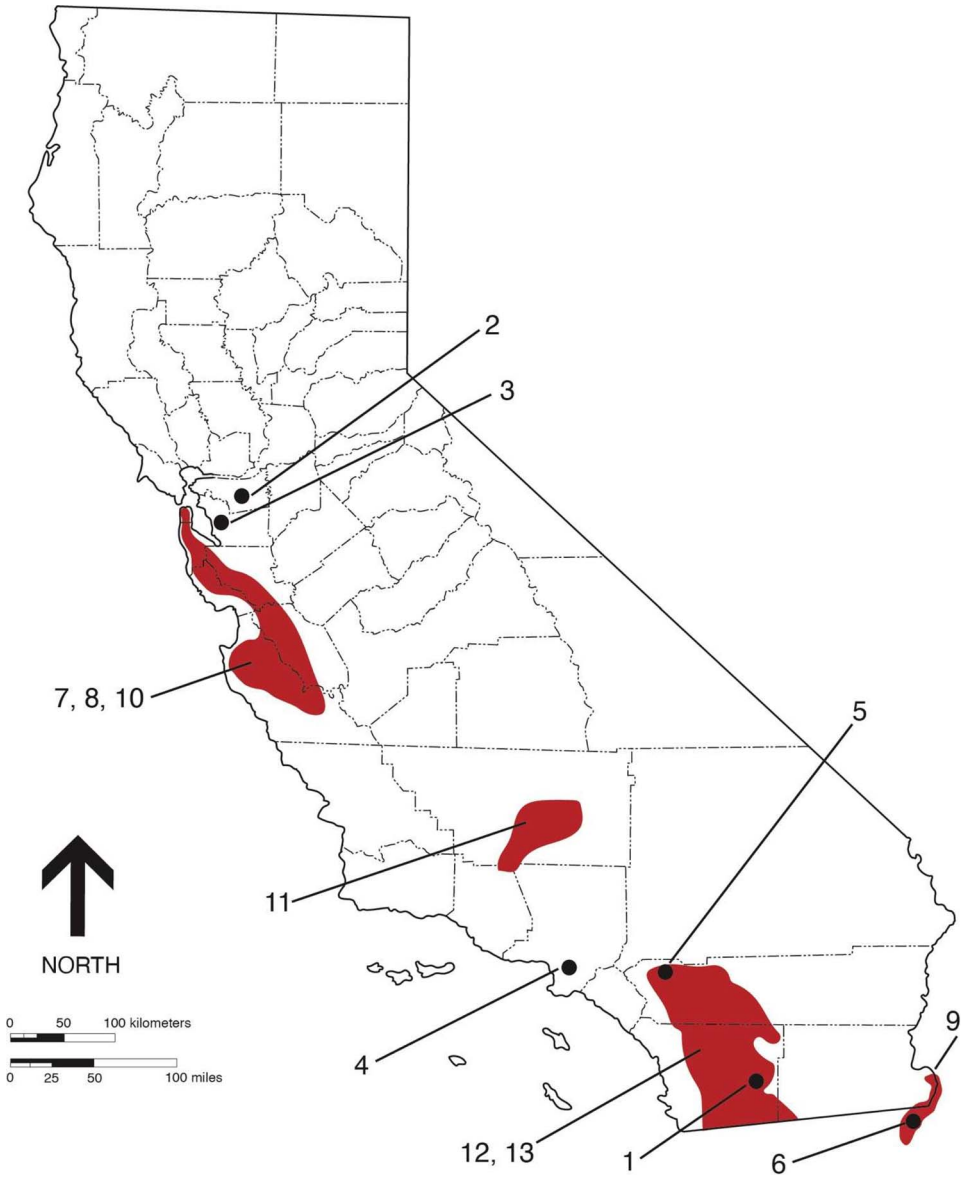

Fig. 1. Locations (dark dots) of prehistoric materials identified as *Panthera onca*, and general locations (red shade) of reported observations of *P. onca* in California from anecdotal reports. Numbers are associated with Table 1 details.

Lindsay (2006) was attributed to the Blancan North American LMA, approx. 4.75–1.6 million years BCE.

The accounts reported by Merriam (1919) and Strong (1926) suggest an area that exceeds that proposed by Seymour (1989) (and therefore also Hall and Kelson [1959]). These 1919 and 1926 accounts proposed an area from northern San Francisco County, southward; a discrete area in the Tehachapi Mountains; a second discrete range similar to that reported by Hall

Table 1. Prehistoric and historical accounts of jaguar (*Panthera onca*) in California. UCMP: University of California Museum of Paleontology, Berkeley, California; PBDB: Paleobiology Database. First-column numbers relate to locations shown in Fig. 1, below.

	Specimen	Age/Year	Location	Source
Prehistoric				
1	*Pathera onca* fossil	Blancan Land Mammal Age	Anza-Borrego State Park, San Diego County	Jefferson and Lindsay 2006
2	*P. onca* fossil	Irvingtonian LMA	Tassajara, Alameda County	UCMP 130468, 27308
3	*P. onca* fossil	Irvingtonian LMA	Fremont, Alameda County	UCMP 71237
4	*P. onca* fossil	Irvingtonian LMA	Rancho La Brea, Los Angeles County	Jefferson 1983, 1991
5	*P. onca* fossil	Irvingtonian LMA	Fort Irwin, San Bernadino County	PBDB 20335
6	*P. onca* fossil	Irvingtonian LMA	Colorado River Valley, Mexico	Arroyo-Cabrales 2002, Ruiz-Ramoni 2020
Historical				
7	*P. onca*	ca 1814	Monterey County area	Von Langsdorff 1814
8	*P. onca*	1826	San Francisco to Monterey	Beechey 1831
9	*P. onca*	mid-December 1827	Colorado River, Imperial County	Pattie 1831
10	*P. onca*	ca 1854	Presidio, San Francisco County	de Saint-Aman 1854
11	*P. onca*	ca 1860	Tehachapi Mountains, Transverse Range	Hittell 1860
12	*P. onca*	ca 1860	San Jacinto Mountains, San Bernadino County, and Santa Rosa Mountains, San Diego County	Strong 1926
13	*P. onca*	1800s (Year Unk)	Cuyamaca Mountains, San Diego County	Merriam 1919

Table 2. Excerpts of accounts from which observations of jaguar (*Panthera onca*) in California were inferred.

Excerpt	Source
"The American lion, *Felis concolor,* and the American tiger, *Felis onca*, stags, roes, wolves, foxes, bears, and pole-cats, *viverra putorius*, are very common here; the latter is called by the Spaniards *sorrillo*."	Von Langsdorff 1814
"The lion (*Felis concolor*) and the tiger (*Felis onca*) are natives of these woods [the area around Mission San Juan Bautista] but we never saw them; inhabitants say they are small, and the lion is less than the tiger, but more powerful."	Beechey 1831
"Of birds there are great numbers, and many varieties, most of which I have never before seen. We killed some wild geese and pelicans, and likewise an animal not unlike the **African leopard**, which came into our camp while we were at work upon a canoe. It was the first we had ever seen."	Pattie 1831
"There is also the **American tiger** in California, which is a **jaguar**. It lives in remote areas, and I have never had the opportunity to meet one. It is said to be more formidable than the cougar. Like him, he climbs trees. A French doctor (Jones) I knew found one in the Presidio, which almost devoured his dog. The Jaguar can carry a horse and an ox very long distances. It is mainly at night that it seeks its prey and makes its victims."	de Saint-Aman 1854 (translated from the French)
"Barely were my eyes closed, however, when a roar roused me and I started up and strained my eyes along the trail from the den to the trap, but could see nothing. In a few minutes the roar repeated, but in an apparently subdued tone; and directing my eyes in the direction from which it proceeded, I saw **a spotted animal, resembling a tiger in size and form**, with two young ones."	Hittell 1860
"...The male beast, as nearly as I could see, was twice as large as an ordinary cougar, and appeared to be covered with dark round spots of great richness and beauty."	
"...If they were not **jaguars,** which had strayed up beyond the usual range, I know not what to call them."	
"Still another bit of evidence comes from Indian tribes of Southern California. An old chief of the Kammei tribe (called by the Spanish 'Diegenos') told me the Cuyamaca Mountains region of San Diego County, the **'Tiger'**, while rare, was well known to the old Indians, who called it the **'Big-spotted Lion'**, Hut'te'kul' ".	Merriam 1919
"Francisco Nombre, an old clan chief of the Desert Cahuilla near Coachella, stated that in his youth an animal called tu'kwut, described as a **large cat with yellow brown skin marked with spots and having a long tail**, was well known in the mountains bordering the desert."	Strong 1926
"...The last animal of this species he remembers, was killed back of Palm Springs about 1860, by an Indian stalking deer with a deer head disguise. The **jaguar** attacked the man and was killed by a musket ball. Francisco saw the fresh spotted hide and the long claws which were used as a dog collar."	

and Kelson (1959) but shifted westward and expanded; and a fourth area comprising the Colorado River drainage between Arizona and California as well as portions of the river basin where it passes through Mexico (Fig. 1). Although it is conceivable that these four disjunct areas were in fact all connected at one time, constituting a range that included the South Coast

Range, the Tehachapi Mountains, the Peninsular Range of Southern California, and portions of the Imperial Valley and Colorado River drainages, no direct or indirect evidence suggests that this was a contiguous range.

Species reintroduction has gained some momentum in California, with current discussions related to reintroduction of grizzly bear (*U. arctos horribilis*), wolverine (*Gulo gulo*), and gray wolf (*C. lupus*) (Alagona 2013; Carroll et al. 2001; Lee et al. 2021). Although recent movements to reintroduce *P. onca* into its former range in the United States (Povilitis 2015; Sanderson et al. 2021) have not yet taken shape, discussion is increasingly likely to surface. Povilitis (2015) and Sanderson et al. (2021) concluded that reintroductions of *P. onca* should be considered as part of the recovery of the species, particularly in a region of Central Arizona, approximately 50 km from the California border. Although the USFWS has no current plans for reintroductions, support for rewilding carnivores is growing worldwide (Wolf and Ripple 2018). Augmentation of carnivore populations has been reported to be more publicly acceptable (Merrill 1999; Cassidy 2024), and may therefore be more likely to be considered for this species, particularly for Arizona and New Mexico, where the species is extant. Additionally, reports of *P. onca* in neighboring Arizona are on the increase, suggesting a potential future dispersal into California (McCain and Childs 2008).

Population growth of gray wolves (*C. lupus*) in the Pacific Northwest over the last two decades was likely the catalyst for natural recolonization of the species in California by individuals migrating from Oregon (Kovacs et al. 2016; Nickel and Walther 2019). In similar fashion, if *P. onca* continues to expand its range in Arizona, or if individuals from Mexico continue to disperse northward, we may well see migration of *P. onca* into California. Additionally, using a spatial prediction model, Jędrzejewski et al. (2018) have suggested a potential viable range that includes portions of Imperial, Orange, Riverside, and San Diego Counties, as well as the Colorado River Delta in Mexico, and reported a probability of future occurrence of up to 75%. Torres (2021) agreed with this potential range but extended it farther eastward into San Diego County and northward through Los Angeles and Ventura Counties. Furthermore, in 2018 the United States Fish and Wildlife Service (USFWS) provided modeling data suggesting the potential for measurable carrying capacities of available *P. onca* habitat that included southeast California.

Recolonization potential for top predators is not unknown for California. *Canis lupus* is well established, through ongoing immigration from Oregon, and at least two separate *Gulo gulo* individuals immigrated into California from other states (Moriarty et al. 2009; Kovacs et al. 2016). These successes may become relevant for *P. onca*, as it has been reported to disperse long distances. Leopold (1959) reported a *P. onca* in northern Baja California (San Pedro Martír, Mexico) that travelled at least 800 km. De la Torre and Rivero (2019) reported that jaguars in Mexico were capable of traveling up to 11 km per day. The nearest observation of *P. onca* to California comes from the Tumacacori Mountains, a range in Santa Cruz and Pima Counties in southern Arizona approximately 230 km southeast of the California border (Warshall 2013); a distance easily comparable to dispersal distances for *P. onca* coming from Mexico.

Ecological, physical, and existential barriers to migration from Arizona into California do exist, including (1) very low numbers of *P. onca* in Arizona (Brown and López-González 2001); (2) the physical barrier of the Colorado River between Arizona and California; and (3) recently erected sections of border wall along the United States-Mexico border. Nevertheless, it can be speculated that at least two of these obstacles could be overcome by migrating *P. onca*. First, Arizona populations may increase over time and produce enough offspring that

one or more individuals are able to move westward and cross into California, and second, given that *P. onca* is a highly proficient swimmer (Da Silveira et al. 2010), crossing the Colorado River would not likely be a true barrier. Undeniably, however, immense sections of the border between the United States and Mexico have been made impermeable by erection of the border wall; only small sections remain open in California and Arizona (Abhat 2011; pers. obs.). If completed, this wall may indeed prove the ultimate barrier to movement of *P. onca* (and other wildlife) across the border. It would take political will and public support to defeat plans for a continuous impenetrable barrier between the two countries.

Although predictive models by Jędrzejewski et al. (2018) and Torres (2021) suggest the possibility of natural recolonization, artificial reintroductions of *P. onca* should not be considered without extensive public input, habitat evaluation, a well-considered management plan, and proactive elevation of the species to endangered status under the California Endangered Species Act (Baker et al. 2017; Maehr et al. 2001; Clark et al. 2005; Sanderson et al. 2021). Reintroductions prompted by public opinion alone are not advisable. In order to be self-sustaining, *P. onca* requires large tracks of relatively undisturbed land (Seymour 1989; USFWS 2018). If the predictive models are accurate, *P. onca* would likely find suitable habitat in an area of California already populated by nearly 20 million people (https://www.california-demographics.com/counties_by_population). Such environments could reduce the availability of prey and compromise the safety of humans and their activities. Although attacks by *P. onca* on humans are very rare ($N = 28$ recorded in history), particularly in the wild ($N = 6$; Neto 2011; Iserson and Francis 2015), large predators can pose a threat to the public and to livestock and pets—interactions that, often as not, result in the precautionary or fear-driven killing of the animal by resource agencies or members of the public (Beier 1991; Carbyn 1989; Ferretti et al. 2015; Herrero et al. 2011).

Warshall (2013) suggested that female *P. onca* migration into Arizona might take 60 to 85 yr, which would push the species' natural establishment in California well into the future—at which time human settlement will presumably have grown significantly. Nevertheless, as mentioned above, a relatively high probability of recolonization of *P. onca* in California does exist (Jędrzejewski et al. 2018; Torres 2021), and State resource agencies should consider the species as potentially occurring naturally at some time in the distant future. Should this come to pass, or if human reintroduction of *P. onca* into California moves ahead after careful consideration of the risks and benefits discussed above, the species will logically warrant emergency listing as endangered, to accord colonizing individuals the greatest chance for survival (Quigley et al. 2017). It is incumbent on us to pave the way for species recolonization with care and deliberation.

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