Reintroduction programs are increasingly being used to save animals from extinction and aid in their recovery. The California Condor (Gymnogyps californianus), one of the most endangered birds in the world, is a remarkable example of how reintroduction programs can help rapidly increase a species’ population numbers and range following a population bottleneck. Despite these gains, condors remain a critically endangered species and are absent from the northern half of their historical range. Here I evaluated questions concerning the biological feasibility of reintroducing California Condors to their former range in the Pacific Northwest using a multidisciplinary approach, employing the fields of history, molecular ecology, and spatial modeling. A review of the historical evidence, including the archeological and paleontological record, use of condors in Native American culture, and early historical accounts of explorers and naturalists, suggest that condors were once widely distributed and likely abundant in the Pacific Northwest. It is also likely that they were breeding birds in the region, rather than seasonal migrants. Examination of 526 base pairs from the control region of mitochondrial DNA (mtDNA) harvested from California Condor museum samples (n = 67) and genetic founders of the captive population (n =14) revealed 18 haplotypes in the historical population, 14 of which have not been reported previously. Only three of these haplotypes survived the genetic bottleneck, indicating > 80% reduction in haplotype richness. This substantial loss of genetic diversity is consistent with the hypothesis that condor populations were relatively abundant at the time of Euro-American contact, but declined rapidly as a result of human causes. I found no spatial sorting of haplotypes in the historical population, which suggests historical gene flow between the Pacific Northwest and southern and central California. Therefore, conservation strategies should consider restoring rangewide metapopulation connectivity when planning future reintroductions. Finally, I developed and tested activity-
specific ecological niche models (nesting, roosting, and feeding) to identify areas in the Pacific Northwest that have retained ecological characteristics similar to those where condors have been observed in the last several decades. These models were integrated with information on condor movement ecology and biology to produce predictive maps of reintroduction site suitability across California, Oregon, and Washington. Ecological niche models were consistent with published knowledge of California Condor ecology, had good predictive performance when tested with data withheld from model development, and identified several candidate reintroduction areas. Results suggest that > 70% of the modeled nesting habitat and > 60% of the modeled roosting and foraging habitat in Washington, Oregon, and California is currently unoccupied. Thus, there are large unoccupied regions of the California Condor’s historical range in the Pacific Northwest that still possess relevant ecological features similar to currently occupied habitats, and therefore warrant consideration for future reintroduction efforts. In summary, this study provides foundational information to inform condor reintroductions to the Pacific Northwest. Key findings include: (1) extensive evidence that condors previously occupied the Pacific Northwest, likely in large numbers, prior to Euro-American expansion; (2) the lack of historical population structure, suggestive of historical gene flow between condor populations in the Pacific Northwest and elsewhere in the range; and, (3) identification of several candidate reintroduction areas in the Pacific Northwest that have retained environmental conditions that appear suitable for condor recovery.
California Condors in the Pacific Northwest: Integrating History, Molecular Ecology, and Spatial Modeling for Reintroduction Planning

by

Jesse D’Elia

A DISSERTATION

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degree of

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APPROVED:

_________________________________________________
Major Professor, representing Wildlife Science

_________________________________________________
Head of the Department of Fisheries and Wildlife

_________________________________________________
Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

_________________________________________________
Jesse D’Elia, Author
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<td>345</td>
</tr>
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<td>A3.1</td>
<td>California Condor occurrence datasets and number of data points by activity-type</td>
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<td>Wind power classes used to characterize the National Renewable Energy Lab’s average annual wind resource potential at 50 m above the ground for California Condor ecological niche models</td>
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DEDICATION

For Mason and Quinn

May you one day have the pleasure of gazing upward at a sky alive with
the splendid evolutions of the mighty California Condor
CHAPTER 1- INTRODUCTION

The California Condor (*Gymnogyps californianus*), North America’s largest avian scavenger and one of the largest flying birds in the world, is an iconic species by any measure (Figure 1.1). Although commonly depicted as a bird of southern California and the desert Southwest, condors once soared the skies of the Pacific Northwest and were deeply woven into the fabric of many Native American cultures in the region. Described by Captain Meriwether Lewis as the “beatifull Buzzard of the columbia [river],” condors were observed and collected by members of the Lewis and Clark Expedition and other explorers, trappers, fur traders, naturalists, and settlers in many parts of the Northwest during the nineteenth century. Soon after 1900, however, the condor disappeared from its northern haunts and its population and range continued to contract throughout the twentieth century until only a small remnant population remained in the mountains of southern California.

Despite the extensive volume of literature published on California Condors and the Herculean conservation struggle to bring the condor back from the brink of extinction (reviewed by Snyder and Snyder 2000), to date relatively little attention has been paid to the history of condors in the Pacific Northwest and opportunities for restoring them to the region (but see Koford 1953; S. Wilbur 1973; Moen 2008; Sharp 2012). With the acceptance of the Oregon Zoo into the California Condor recovery program in 2001, and increasing interest in restoration of condors from a number of Native American tribes and the general public throughout the Northwest (D’Elia and Haig 2013), the need for information to develop a reintroduction plan has been building.

Although not without limitations (see Snyder et al. 1996), when appropriately planned and designed, captive breeding and reintroduction programs can be effective conservation tools (Griffith et al. 1989, Seddon 2007, IUCN/SCC 2013, D’Elia 2010). Birds are among the most commonly reintroduced taxa with more than 200 avian species reintroductions and translocations documented around the globe (Lincoln Park Zoo 2014); and in several instances, these efforts have been instrumental in preventing the extinction of critically endangered birds (Butchart et al. 2006).

Perhaps one of the best known and most controversial efforts to prevent the extinction of a critically endangered species through reintroduction efforts is the saga of the California
Condor recovery program (Snyder and Snyder 2000). A little over two decades ago the California Condor population reached its nadir with only 22 individuals remaining worldwide. There are now over 200 wild birds as a result of reintroductions in the mountains of southern California, along the central California coast, near the Grand Canyon in Arizona, and in northern Baja California, Mexico (USFWS 2013). However, the condor is still entirely absent from approximately the northern half of its historical range (D’Elia and Haig 2013). Below, I review the evolution and life history of the California Condor, provide a brief history of the Condor Recovery Program, describe the origins of examining reintroductions in the Pacific Northwest, and outline the objectives and organization of this dissertation.

1.1. EVOLUTION AND LIFE HISTORY OF THE CALIFORNIA CONDOR

Condors are often defined by their remarkable size. They are the largest of the seven New World vultures that form the Cathartidae family (sometimes referred to as the Vulturidae family; Livezey and Zusi 2007). Although New World vultures look similar to Old World vultures (Accipitridae family), this resemblance is the result of convergent evolution rather than a close phylogenetic relationship (Seibold and Helbig 1995; Wink 1995; Hackett et al. 2008).

California Condors have a truly spectacular wingspan (2.74 m)—larger than any other North American land bird. This large wingspan gives them the ability to soar long distances in a single day (at up to 40–70 km per hour), expending minimal energy while searching for food along Pacific Ocean beaches (Figure 1.2) or inland over rivers, grasslands, and shrublands. However, their wingspan—and more specifically, the large surface area of their wings and weak wing musculature—limits their ability to sustain flapping flight for extended periods of time, as the immense amount of energy required to displace such a large amount of air quickly exceeds their metabolic output (H. Fisher 1946; Pennycuick 1969). This means that they are restricted to foraging over areas where there is enough upward air movement, or lift, to keep them aloft. Such upward air movement is typically generated by thermals, which form when the sun heats the ground and the heated area causes a pocket of warm air to rise, or through ridge lift, whereby air is pushed upward as winds collide with mountains or cliffs.

Condor movements are influenced by the location of nests and foraging habitat. Breeding birds are necessarily tied to nest sites but may travel up to 180 km from the nest in search of food. Nonbreeding birds can move over enormous home ranges. For example,
Meretsky and Snyder (1992) reported home ranges in southern California averaging approximately 7,000 km$^2$. California Condors do not undertake long-distance migrations but sometimes exhibit shorter seasonal movements to exploit traditional food resources or favorable atmospheric conditions.

Condors are obligate scavengers, feeding primarily on medium to large-sized mammal carcasses, often including those of domestic livestock as well as native terrestrial and stranded marine mammals. Obligate scavengers are an example of extreme specialization in the animal kingdom, with several adaptations critical for species that rely on finding carrion, a relatively unpredictable and highly transient resource:

1. large size and large crops, which are necessary to compete at carcasses and sustain individuals for relatively long periods between meals;
2. soaring flight and excellent eyesight, which help condors efficiently find food;
3. hooked bills, long necks, and largely naked heads, allowing condors to access muscle tissue deep within a carcass and to rip pieces of meat from a carcass, while minimizing the potential for feather fouling;
4. feet with short claws adapted for walking and running, which may provide a competitive advantage at carcasses;
5. intelligence, which is necessary for finding and competing for food in a complex social environment; and,
6. resistance to bacterial toxins, which is necessary for species that rely on carcasses.

Aerial scavengers can outcompete terrestrial scavengers for food because flight allows them to efficiently search a much larger area (Ruxton and Houston 2004). Soaring scavengers like the condor have an additional advantage over those that use primarily flapping flight because the energetic cost of soaring is so much less than that of flapping flight (Ruxton and Houston 2004). Condors do not have a well-developed olfactory tract or sense of smell (Stager 1967), so they rely on their keen vision to find food. In addition to locating food from a distance, condors will

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1 However, there was a recent case of a condor preying on an abandoned dying sea lion pup, and it is likely that condors occasionally take advantage of similar situations elsewhere (M. Tyner, Ventana Wildlife Society, pers. comm., 2011). Historical observations also suggest that condors once fed upon dead and dying salmon that were stranded as they attempted to move upstream toward spawning grounds (Audubon 1840). McGahan (2012) indicated that Andean Condors will apparently kill prey on rare occasions.
also use sentinel species, such as Turkey Vultures (*Cathartes aura*) or Common Ravens (*Corvus corax*), to help them find food. This communal searching for food allows condors and other avian scavengers to greatly improve the efficiency with which they find a meal (Houston 1985, 1988). It also means that condors can be found congregated in large groups at a carcass or water hole. Condors are typically the dominant avian species at a carcass unless Golden Eagles (*Aquila chrysaetos*) are present.² As a social foraging species, they develop a pecking order at carcasses, with juveniles subordinate to adults. This may be a mechanism to reduce intraspecific aggression, but it also means that juveniles depend on their parents for an extended period to obtain sufficient food.

Condors' massive wingspans dictate their need for open spaces, good winds, and high places from which to launch flights. These factors are particularly important in selecting nest sites, where fledglings must learn how to fly. Nests are generally placed on the floor of small caves on cliff faces, on rock ledges, or occasionally in a cavity or broken top of a large tree. Breeding pairs mate for life and are intensely devoted to the care of the single egg they lay and the resulting chick. Maximum productivity for a pair appears to be two surviving chicks in three years, as clutch size is always one, full nesting cycles take more than a year, and pairs are slow to reinitiate breeding when they still have a dependent fledgling (Meretsky et al. 2000). Condors will double clutch if their egg is removed or destroyed (Snyder and Hamber 1985).³ California Condors are long-lived (Mace 2014).⁴ Yet population growth rates are slow, as birds generally do not successfully breed until they are six to eight years old. Their slow maturation, slow breeding cycle, and low fecundity make condor populations sensitive to increases in adult mortality (Meretsky et al. 2000). These factors also make recovery of the species a relatively long and expensive proposition.

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² The Golden Eagle’s dominance at carcasses is not absolute. Condors will occasionally challenge Golden Eagles and aggressively displace them from carcasses.

³ Although apparent double clutching in condors was first reported by Harrison and Kiff in 1980, their paper showed only that two nesting events took place in the same year in the same cave. Because the adults were never identified, evidence from this paper was insufficient to get permission to take eggs from nests to start a captive flock. It was not until 1982 that conclusive evidence of replacement clutching was obtained (Snyder and Hamber 1985), allowing the start of egg removal operations to form a captive population the next year.

⁴ Topa-Topa (studbook #1), a male condor and the oldest condor in captivity, hatched in the wild in Ventura County in 1966. He was captured in 1967 and, as of 2012, was still alive at the Los Angeles Zoo (Mace 2014).
Readers looking for a more thorough review of the evolution and life history of the California Condor are directed to Koford (1953), Snyder and Snyder (2000, 2005), and Snyder and Schmitt (2002). For an overview of the evolutionary adaptations of scavengers, see Houston (1979, 1985, and 1988) and Ruxton and Houston (2004).

1.2 A BRIEF HISTORY OF THE CONDOR RECOVERY PROGRAM

The California Condor Recovery Program is one of the oldest and most renowned recovery efforts in the history of endangered species conservation. It is also one of the most controversial. In retrospect, it is remarkable that the California Condor did not end up as yet another entry in the long ledger of extinct birds (see Fuller [2001] for a detailed accounting of those birds that have been lost). At the time the first recovery plan for the California Condor was published in 1975—the first recovery plan for any species under the US Endangered Species Act of 1973—there were only about forty condors remaining (Wilbur 1978; see Table 1.1). By 1980 that estimate was reduced to twenty-five to thirty-five individuals (Wilbur 1980). Clearly the species was in jeopardy of going extinct if something was not done quickly to reverse the decline. The plan’s population objectives were modest, calling for the maintenance of “at least 50 California Condors, well distributed throughout their 1974 range” (USFWS 1975, 12). The recovery team noted the possibility that recovery efforts in the wild might fail and suggested developing a contingency plan that included captive breeding.

While the condors’ inherently low reproductive capacity makes it appear a less likely candidate for captive propagation than some other species, recent successes at the Patuxent Wildlife Research Center and elsewhere propagating South American condors (Vultur gryphus) gives some hope for the future of this technique. Patuxent personnel plan a continuing investigation of South American condor propagation and subsequent release to the wild, and this may have application to the California condor should current plans fail to improve its population status. (USFWS 1975, 11)

In 1976, the U.S. Fish and Wildlife Service California Condor Recovery Team, faced with continuing declines in condor population estimates and the very real possibility that the condor was vanishing, drafted a contingency plan that included provisions for initiating a captive-breeding program, with a view toward future reintroductions, a suggestion that was later
supported by a panel of ornithologists and the National Audubon Society (Ricklefs 1978), and by a report prepared for the U.S. Forest Service (Verner 1978). On November 2, 1978, the director of the U.S. Fish and Wildlife Service met with representatives of the National Audubon Society, who presented their recommendations for modifying the condor recovery strategy (USFWS 1979). This meeting resulted in the formation of a task force charged with charting a course for implementing a captive breeding program and identifying areas appropriate for future releases (USFWS 1979). Consequently, when the first revision to the condor recovery plan was published in 1980, it included the need to initiate captive breeding and identify potential reintroduction sites “in the states occupied by condors in the recent past (Oregon, Washington, California, possibly Arizona)” (USFWS 1980, 50).

Although captive breeding was initially meant to supplement the wild population (USFWS 1984), a catastrophic loss of 40 percent of the remaining population in the winter of 1984–1985 left only a single breeding pair in the wild. This led the recovery team and partners to reevaluate whether the wild population should be supplemented or integrated with the captive population to maximize genetic diversity (Snyder and Snyder 2000). Geneticists advising the Condor Recovery Team agreed that because of the limited number of individuals and family lines remaining, all remaining wild birds should be immediately added to the captive flock (Snyder and Snyder 2000). However, disagreements among the U.S. Fish and Wildlife Service, the Audubon Society, the Condor Recovery Team, and the California Fish and Game Commission; and ultimately, litigation brought by the Audubon Society, delayed that decision (Snyder and Snyder 2000).

Although capturing all remaining wild condors to form a captive breeding population was extremely controversial (Miller 1953; Pitelka 1981; Snyder and Snyder 2000; Alagona 2004), it was the only hope of preserving the species (Snyder and Snyder 2000). At the time the last

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5 The U.S. Fish and Wildlife Service, at the urging of the Audubon Society, did not support trapping all remaining birds at the beginning of 1985; instead, it advocated trapping only three birds and simultaneously releasing three captive birds. At the time, the USFWS apparently thought that mortality risks for the remaining birds could be significantly reduced through an intensive food provisioning program with lead-free carcasses (Snyder and Snyder 2000). Lead poisoning of a condor (AC-3) in December of 1985 on Hudson Ranch—where lead-free carcasses were being provided—ended the debate over the efficacy of food provisioning in reducing mortalities (Snyder and Snyder 2000). Litigation by the Audubon Society delayed the final trapping of all remaining birds until the spring of 1986.
wild condor was trapped, on Easter Sunday 1987, only twenty-seven California Condors remained in the world.

With all California Condors in captivity there was an urgent need to work out the most effective methods for minimizing mortality in future releases (Wallace 1989). Fortunately, Mike Wallace, curator of birds at the Los Angeles Zoo and a member of the California Condor Recovery Team, had completed a dissertation based on captive releases of Andean Condors (*Vultur gryphus*) in Peru from 1980 to 1984. Beginning in 1988, Wallace assisted with experimental releases of Andean Condors in southern California as surrogates for future California Condor releases.

Captive breeding and double-clutching protocols for California Condors were established by the early 1990s (Meretsky et al. 2000). In December 1991, the Condor Recovery Team recommended that releases also be conducted in northern Arizona in an area geographically separate from the southern California flock (USFWS 1996a).

Surveys of suitable habitat were never conducted in Oregon, Washington, or northern California, and subsequent revisions to the recovery plan dropped any mention of reintroductions to the Pacific Northwest (USFWS 1984, 1996b). Although significant progress had been made in captive breeding and release techniques through the early 1990s, there were only seventeen condors in the wild at the time of the last recovery plan revision in 1996. Furthermore, the plan did not address full recovery. Instead, its emphasis was on how to improve the species’ status to the point where it could be reclassified from “endangered” to “threatened” under the Endangered Species Act by maintaining a captive flock and establishing self-sustaining populations in southern California and Arizona (USFWS 1996b). Specifically, the recovery criteria for reclassification from endangered to threatened read:

The minimum criterion for reclassification to threatened is the maintenance of at least two non-captive populations and one captive population. These populations (1) must each number at least 150 individuals, (2) must each contain at least 15 breeding pairs and (3) be reproductively self-sustaining and have a positive rate of population growth. In addition, the non-captive populations (4) must be spatially disjunct and non-interacting.

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6 Although the recovery plan used the term “self-sustaining,” it also recognized (and allowed) that in some areas, reestablished condor populations might require continued artificial feeding to supplement natural food resources and/or to protect birds from exposure to contaminated carcasses.
Since the 1996 recovery plan, captive breeding efforts have proven extremely fruitful in boosting condor numbers. Since 1993, over three hundred condors have been raised in captivity and released into the wild and there are now five active release sites: Big Sur, California; southern California mountains; Pinnacles National Monument, California; northern Arizona; and Sierra San Pedro Mártir, Baja California, Mexico (Walters et al. 2010). With growing numbers of condors in captivity and in the wild, years of experience from several release programs, and a greater understanding of condor biology, population threats, and conservation needs, there is now growing interest by conservation organizations and Native American tribes in reestablishing the condor in the Pacific Northwest (Shepherdson et al. 2007; The Nature Conservancy, in litt. 2007; Yurok Tribe 2007; Walters et al. 2010).

1.3 Bringing Condors Back to the Pacific Northwest: The Birth of an Idea

As captive breeding techniques were worked out in the 1980s and 1990s, and the captive population began to grow, the capacity of zoos in the program to breed and house condors became a limiting factor. Consequently, in the late 1990s and early 2000s, the Condor Recovery Team began looking for additional zoos that were interested in joining the conservation breeding program. Adding another conservation breeding partner would have the benefits of spreading the risk to the captive population (e.g., containing a disease outbreak to only a portion of the population), increasing capacity to produce condors, and sharing the substantial costs associated with captive breeding and rearing. Several zoos expressed interest in joining the recovery effort, including the Bronx Zoo, the National Zoo, and the Oregon Zoo.

The Oregon Zoo’s interest in condor conservation and the notion of California Condor reintroductions to the Pacific Northwest stemmed from planning sessions for the Lewis and Clark bicentennial (Koch 2004). In preparation for the bicentennial, Jane Hartline, then marketing manager for the zoo, suggested reintroducing California Condors to Oregon. Jane’s idea was sparked by her recent trip to Ecuador, where she visited Hacienda Zuleta, a hotel on a colonial working farm that hosts an Andean Condor rehabilitation and educational facility.

As an outgrowth of the bicentennial planning sessions, the Oregon Zoo initiated discussions with the Condor Recovery Team in 2000 and presented a proposal to join the
recovery program as a captive breeding facility in February 2001, with hopes of eventually reintroducing condors to Oregon (Koch 2004). After considering proposals from a number of zoos, the Condor Recovery Team accepted the Oregon Zoo’s proposal later that year.

Upon acceptance into the recovery program, the zoo immediately began the process of selecting an offsite location for breeding condors. Because condors develop behavioral problems when they have contact with humans, the zoo sought a property that was out of view of the public. This ultimately led to the construction of a state-of-the-art condor breeding and veterinary facility at the Jonsson Center for Wildlife Conservation, in an undisclosed rural location near Portland, Oregon (Figure 1.3). The first pair of condors arrived at the facility on November 19, 2003, and the first egg hatched there the following spring (Koch 2004). It is now one of four facilities that breed condors for release into the wild.7

The Oregon Zoo is not the only organization interested in returning condors to the northern portion of their historical range. In 2007, the US Fish and Wildlife Service (USFWS) received a grant proposal from the Yurok Tribe in northwestern California to assess the feasibility of reintroducing condors to their ancestral lands (Yurok Tribe 2007). The Yurok believe that reintroduction of condors to the tribe’s ancestral territory will help restore spiritual balance to their world (Yurok Tribe 2007). The Yurok Tribe and the Oregon Zoo formed an informal partnership to promote the idea of reintroductions and in April 2010, the tribe and the zoo hosted a Pacific Northwest Condor Summit (with sponsorship from the Confederated Tribes of Grand Ronde), bringing together over 140 participants from other Northwest tribes, federal and state agencies, and conservation groups, as well as representatives from the California Condor Recovery Program.

With growing interest in returning condors to the Pacific Northwest, a number of questions remain: What was the historical distribution of condors in the region? Were they breeding here, or simply seasonal migrants? When did they disappear? What caused their extirpation? What is the potential for restoration (i.e., have the primary threats been identified and ameliorated and would ongoing management be necessary)? Where are the best places for a reintroduction in the Pacific Northwest? How much of their genetic diversity survived the population bottleneck, and are there lessons that might be learned from other vulture

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7 The others are the San Diego Wild Animal Park, Los Angeles Zoo, and the World Center of Birds of Prey, the latter operated by the Peregrine Fund in Boise, Idaho.
reintroduction projects throughout the world? In this dissertation I endeavor to provide answers to some of these questions.

1.4 OBJECTIVES
The three primary objectives of this study were: (1) to provide a comprehensive evaluation of the history of California Condors in the Pacific Northwest, (2) examine the historical population structure and genetic diversity of California Condors using ancient DNA from museum specimens, with particular attention to whether populations in the Pacific Northwest were historically isolated from populations to the south; and, (3) to develop spatial models to identify those areas of the Pacific Northwest most likely to support a California Condor reintroduction.

1.4.1 Historical Distribution, Abundance, and Causes of Regional Extirpation
Understanding the history of condors in the northern half of their historical range is more than a curiosity. It is vital to the U.S. Fish and Wildlife Service in defining recovery objectives and is a first step toward evaluating the potential for future reintroductions to the region. In its most basic sense, the history of a species’ distribution and range collapse establishes context and helps one gauge the magnitude of anthropogenic changes over the last several hundred years rather than shifting the species’ baseline condition to the current crisis situation (see Pauly 1995). It may also provide basic life history information of the species across its former range (e.g., historical breeding sites and movement patterns) that is important in setting appropriate recovery objectives. Finally, a species’ natural history provides insights into the timing, magnitude, and causes of range collapse or population decline—information that is fundamental to assessing the restoration potential of imperiled species.

Chapter 2 of this dissertation is taken from a book I coauthored with Dr. Susan Haig (D’Elia and Haig 2013), in which we document the California Condor’s history in the Pacific Northwest through a review of anthropological, archaeological, paleobiological, and other historical information from myriad sources. I consulted published literature, unpublished reports, museum records, historical photographs, newspaper archives, early American journals, and documents at museums and state and federal resource management agencies, including the U.S. Fish and Wildlife Service California Condor Recovery Office in Ventura, California, and the Santa Barbara Museum of Natural History. The primary goals of Chapter 2 are to: (1) provide
an integrated and comprehensive synthesis of the condor’s history in the region, establishing context for the species’ historical distribution and abundance, (2) address the timing and extent of the condor’s range collapse and population decline, and (3) analyze the veracity of the various hypotheses for the range collapse and population decline.

1.4.2 Evaluating Historical Population Structure and Population Declines through mtDNA

The revelation that DNA survives in old bones and tissue and can be extracted and amplified has revolutionized the field of molecular ecology (Wayne et al. 1999, Lee and Prys-Jones 2008, Rawlence et al. 2009, Haig et al. 2011). All major subdisciplines of taxonomy and population genetics benefit from the direct historical perspective provided by ancient DNA. Applications include evaluating the tempo and mode of evolution, estimating historical population sizes, understanding cryptic population histories, linking population histories with geological or anthropogenic events, and evaluating evolutionary relationships of extant and extinct birds and hypotheses regarding extinction processes (reviewed in Haig et al. 2011).

Reintroduction programs can benefit from application of ancient DNA by providing information on historical population structure, gene flow, and comparisons of historical and current levels genetic diversity (Leonard 2008). When reintroductions are accomplished through captive breeding aDNA can also be used to provide information regarding the relationship of founders if those relationships are unknown when the captive flock is formed (Leonard 2008). Such information can be critical to developing a breeding strategy that maximizes the retention of the remaining genetic diversity.

Chapter 3 analyzes the history of condors at the molecular level. This was the first study to analyze mtDNA from condor specimens across the historical range of the California Condor and across almost the entire historical temporal span of the available museum specimens, from 1825 to the genetic founders of the captive flock. Using the mtDNA from these specimens I investigate how much genetic variation has been lost and the timing and magnitude of that loss. I also examine whether or not condors in the Pacific Northwest had unique mtDNA haplotypes and test the hypothesis that Northwest condors were significantly differentiated in their mtDNA control region sequences than condors in other portions of the historical range.
1.4.3 Identifying Potential Reintroduction Sites

Understanding the relationship between biological and physical properties of the landscape and species’ ecological and geographic distributions is critical for conservation planning (Poirazidis et al. 2004, Davis et al. 2007, Elith and Leathwick 2009), prioritizing reintroduction sites (Schadt et al. 2002, Hirzel et al. 2004, Steury and Murray 2004, Munzbergova et al. 2005), and for evaluating spatially-explicit metapopulation structure (Akcakaya et al. 2004). Quantifying this relationship has become the core of predictive spatial modeling in ecology (Guisan and Zimmermann 2000). Although there are numerous methods available to predict species distributions (Guisan and Zimmermann 2000, Elith and Leathwick 2009), all rely implicitly or explicitly on the concept of the ecological niche (Grinnell 1928, Hutchinson 1957).

Predicting species distributions through ecological niche models can inform management decisions regarding prioritizing potential reintroduction sites for further evaluation (Osborne and Seddon 2012, Guisan et al. 2013). While ecological niche models have previously been suggested for identifying potential California Condor reintroduction sites (Martínez-Meyer et al. 2006), operational models that could be used in informing management decisions have not been developed prior to this study.

In Chapter 4, empirically-based ecological niche models were developed and tested to identify areas in the Pacific Northwest that have environmental conditions most similar to areas where condors currently exist; and, ostensibly areas that should be further evaluated through ground-based surveys in selecting reintroduction sites. While most ecological niche models simply assume all requirements for population persistence (nesting, breeding, and feeding) occur in a single environmental envelope, this is not the case for California Condors and modeling of these factors separately proved important in identification of potential reintroduction sites. This finding has implications for other species that use different ecological niches for survival and reproduction.

1.5 Synthesis

Chapter 5 provides a summary and synthesis of the findings of the dissertation and identifies areas of further research. Taken together, these chapters provide the foundational information for a reintroduction program for California Condors in the Pacific Northwest. It is my hope that this dissertation also provides a useful template for other reintroduction efforts for threatened
and endangered species that have endured a historical range collapse where there are captive individuals available for population reestablishment.

1.6 LITERATURE CITED


The Nature Conservancy, in litt. 2007. A proposal to explore the establishment of a California Condor (re)introduction program in the Lassen Foothills Project Area, California. Letter from Simon Avery (Dye Creek Preserve Manager) to Mark Weitzel (Hopper Mountain National Wildlife Refuge Project Leader). March 1, 2007.


Figure 1.1. Portrait of an endangered species icon: the California Condor. Photo by Michael Durham, Oregon Zoo.
Figure 1.2. California Condor soaring along the Big Sur coast, California. Photo by Jesse D’Elia, U.S. Fish and Wildlife Service.
Figure 1.3. California Condor at the Oregon Zoo’s Jonsson Center for Wildlife Conservation, just outside of Portland, Oregon. Photo by Susan Haig, U.S. Geological Survey.
Table 1.1. Timeline of events in the history and recovery of the California Condor.

<table>
<thead>
<tr>
<th>Year or time period</th>
<th>Event</th>
<th># of wild California Condors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pleistocene</td>
<td>Several species of <em>Gymnogyps</em> occur in North America. The California Condor is distributed from British Columbia to Baja California, and inland to Arizona, New Mexico, Texas, and central Mexico. It also occurs along the east coast from New York to Florida.</td>
<td>Unknown</td>
</tr>
<tr>
<td>Late Pleistocene</td>
<td>All species of <em>Gymnogyps</em> aside from the California Condor go extinct. The California Condor’s range contracts and it is now limited to the West Coast of North America from British Columbia to Baja California. Paleo-Indians begin populating North America.</td>
<td>Unknown</td>
</tr>
<tr>
<td>1602</td>
<td>First recorded sighting of a California Condor by European explorers—Father Antonio de la Ascension in Monterey Bay, California.</td>
<td>Unknown</td>
</tr>
<tr>
<td>1790s</td>
<td>Type specimen taken near Monterey, California, by Archibald Menzies. This condor skin is housed at the British Natural History Museum at Tring.</td>
<td>Unknown</td>
</tr>
<tr>
<td>1805</td>
<td>Lewis and Clark and the Corps of Discovery observe California Condors along the lower Columbia River from Celilo Falls to the coast.</td>
<td>Unknown</td>
</tr>
<tr>
<td>1849</td>
<td>California Gold Rush—massive influx of people to northern California.</td>
<td>Unknown</td>
</tr>
<tr>
<td>1850</td>
<td>California Condors no longer regularly reported from the lower Columbia River. Still sporadically collected and reported from elsewhere in the Pacific Northwest.</td>
<td>Unknown</td>
</tr>
<tr>
<td>1904</td>
<td>Generally regarded as the last reliable report of condors north of San Francisco, CA. However, there are a few other plausible reports of condors in the region into the 1920s.</td>
<td>Unknown</td>
</tr>
<tr>
<td>1905</td>
<td>Killing or collecting condors or their eggs is banned by the California Legislature and Fish and Game Commission.</td>
<td>Unknown</td>
</tr>
</tbody>
</table>
Table 1.1. (Continued)

<table>
<thead>
<tr>
<th>Year or time period</th>
<th>Event</th>
<th># of wild California Condors</th>
</tr>
</thead>
<tbody>
<tr>
<td>1906</td>
<td>William Finley and Henry Bohlman make the first study of a condor nest. Finley takes the chick captive and raises him as a pet in Oregon before transferring him to the New York Zoological Park.</td>
<td>Unknown</td>
</tr>
<tr>
<td>1939</td>
<td>Carl Koford begins his study of the California Condor.</td>
<td>150</td>
</tr>
<tr>
<td>1940s</td>
<td>San Diego Zoo is breeding Andean Condors successfully and demonstrates that pairs can produce more than one egg a year through replacement clutching.</td>
<td>150</td>
</tr>
<tr>
<td>1949</td>
<td>Belle Beachy of the San Diego Zoo proposes captive breeding of California Condors to the California Department of Fish and Game. Although the department approved the zoo’s proposal to capture two immature condors, trappers failed to catch any birds.</td>
<td>150</td>
</tr>
<tr>
<td>1953</td>
<td>Carl Koford completes the first major natural history study of the California Condor (Koford 1953).</td>
<td>150</td>
</tr>
<tr>
<td>1954</td>
<td>California Legislature expressly forbids taking any California Condors from the wild. San Diego Zoo trapping efforts cease.</td>
<td>150</td>
</tr>
<tr>
<td>1966</td>
<td>The U.S. Congress passes the Endangered Species Preservation Act on October 15, 1966.</td>
<td>60</td>
</tr>
<tr>
<td>1967</td>
<td>California Condor designated an endangered species under the Endangered Species Preservation Act.</td>
<td>60</td>
</tr>
<tr>
<td>1969</td>
<td>Locke et al. (1969) discover that Andean Condors are susceptible to lead poisoning and suggest that California Condors might also be susceptible.</td>
<td>60</td>
</tr>
<tr>
<td>1973</td>
<td>Endangered Species Act (ESA) of 1973 passed and additional protections given to species listed in 1967 under the Endangered Species Preservation Act.</td>
<td>35–60</td>
</tr>
<tr>
<td>Year or time period</td>
<td>Event</td>
<td># of wild California Condors&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>---------------------</td>
<td>------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td>-----------------------------------------</td>
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<tr>
<td>1976</td>
<td>Designation of California Condor critical habitat under the Endangered Species Act—all in southern California.</td>
<td>25–35</td>
</tr>
<tr>
<td>1980</td>
<td>First revision to the California Condor Recovery Plan adopted. Recommends captive breeding and identification of release sites by surveying areas of former occupation—including areas in the Pacific Northwest.</td>
<td>25–35</td>
</tr>
<tr>
<td>1982</td>
<td>Nadir of the California Condor population (considering both captive and wild birds, only 22 remain).</td>
<td>20</td>
</tr>
<tr>
<td>1983</td>
<td>Taking eggs from wild nests for artificial incubation and captive rearing initiated.</td>
<td>&lt; 20</td>
</tr>
<tr>
<td>1984</td>
<td>Second revision to the California Condor Recovery Plan adopted. The primary objective of the plan is to increase and maintain a self-sustaining population of 100 individuals, including 60 adults. Recommends captive breeding and multiple clutching of wild nesting pairs.</td>
<td>&lt; 20</td>
</tr>
<tr>
<td>1985</td>
<td>Catastrophic loss of 40 percent of the remaining wild condors (cause of death unknown). Discussions initiated regarding trapping all remaining wild condors.</td>
<td>&lt; 10</td>
</tr>
<tr>
<td>1987</td>
<td>Last wild California Condor (AC-9) trapped for captive breeding. The California Condor is extinct in the wild. At this time, 27 condors are in captivity (10 reared in the wild, 17 reared in captivity).</td>
<td>0</td>
</tr>
<tr>
<td>1988</td>
<td>Experimental releases of Andean Condors into southern California initiated.</td>
<td>0</td>
</tr>
<tr>
<td>1991</td>
<td>California Condor Recovery Team recommends releases in northern Arizona in addition to releases in southern California.</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 1.1. (Continued)

<table>
<thead>
<tr>
<th>Year or time period</th>
<th>Event</th>
<th># of wild California Condors</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>Third captive breeding facility established—World Center for Birds of Prey in Boise, Idaho, operated by the Peregrine Fund.</td>
<td>9</td>
</tr>
<tr>
<td>1994</td>
<td>California Condors retrapped due to behavioral problems.</td>
<td>3</td>
</tr>
<tr>
<td>1995</td>
<td>Release of California Condors that had undergone aversion training to reduce behavioral issues. The three condors that remained in the wild in 1994 were trapped to ensure they did not negatively influence the newly released birds that underwent aversion training.</td>
<td>14</td>
</tr>
<tr>
<td>1996</td>
<td>Second revision to the California Condor Recovery Plan adopted. Drops mention of identifying release sites in the Pacific Northwest. Focuses on building population levels to at least 150 birds in southern California and 150 birds in Arizona. Does not identify actions needed to achieve recovery and delisting; only provides downlisting criteria to threatened status under the ESA. The USFWS publishes a final experimental population rule designating northern Arizona, southern Utah, and a small corner of southeastern Nevada as a “non-essential experimental population.” Condor releases begin in December 1996 at Vermilion Cliffs, northern Arizona (second release area).</td>
<td>17</td>
</tr>
<tr>
<td>1997</td>
<td>Condor releases begin near Big Sur, Monterey County, California (third release area).</td>
<td>29</td>
</tr>
<tr>
<td>1998</td>
<td>Condor releases begin at Hurricane Cliffs in northwestern Arizona, 65 miles west of the Vermilion Cliffs release site (later discontinued due to logistical issues).</td>
<td>38</td>
</tr>
<tr>
<td>2001</td>
<td>Oregon Zoo presents its proposal to breed condors to the Condor Recovery Team with the ultimate goal of reintroducing them to Oregon. The proposal is accepted by the Recovery Team.</td>
<td>58</td>
</tr>
</tbody>
</table>
Table 1.1. (Continued)

<table>
<thead>
<tr>
<th>Year or time period</th>
<th>Event</th>
<th># of wild California Condors</th>
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<tbody>
<tr>
<td>2003</td>
<td>Condor releases begin at Pinnacles National Monument, California (fifth release area). First captive condors arrive at the Oregon Zoo’s Jonsson Center for Wildlife Conservation.</td>
<td>83</td>
</tr>
<tr>
<td>2004</td>
<td>First California Condor egg hatched at the Oregon Zoo’s Jonsson Center for Wildlife Conservation.</td>
<td>96</td>
</tr>
<tr>
<td>2007</td>
<td>The Yurok Tribal Council passes a resolution to develop a California Condor reintroduction site.</td>
<td>144</td>
</tr>
<tr>
<td>2008</td>
<td>The U.S. Fish and Wildlife Service provides funds to the Yurok tribe to study the feasibility of reintroducing California Condors to northern California.</td>
<td>167</td>
</tr>
<tr>
<td>2010</td>
<td>California Condor review panel commissioned by the American Ornithologists’ Union and the Audubon Society publishes its review of the recovery program (Walters et al. 2010).</td>
<td>181</td>
</tr>
<tr>
<td>2011</td>
<td>First meeting of the Pacific Northwest California Condor Coordination Team, an interdisciplinary and interagency team organized by the USFWS to evaluate remaining issues that need to be resolved prior to establishing a Pacific Northwest condor release site.</td>
<td>205</td>
</tr>
</tbody>
</table>

*Population estimates through the 1980s are based on Snyder and Snyder (2000). The numbers of wild condors from the 1990s through 2011 are based on California Condor Recovery Program records.*
CHAPTER 2—CALIFORNIA CONDORS IN THE PACIFIC NORTHWEST: A HISTORICAL PERSPECTIVE

Jesse D’Elia and Susan M. Haig

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2.1 HISTORICAL DISTRIBUTION OF CALIFORNIA CONDORS IN THE PACIFIC NORTHWEST

Fossil evidence suggests that California Condors were widely distributed in North America during the late Pleistocene,\(^8\) with records from Oregon, California, Nevada, Arizona, New Mexico, Texas, Florida, New York, and Mexico (L. H. Miller 1910a, 1910b, 1911; L. Miller 1957; Wetmore 1931a, 1931b; Parmalee 1969; Simons 1983; Steadman and Miller 1987; Emslie 1987; Steadman et al. 1994; Hansel-Kuehn 2003; Brasso and Emslie 2006). At that time, megaherbivores\(^9\) and megapredators\(^10\) likely provided significant food resources for large avian scavengers—including several condor species (\textit{Gymnogyps californianus}, \textit{G. amplus}, \textit{G. varonai}, \textit{G. kofordi}, \textit{Bregyps clarki})—that relied on the availability of large carcasses for survival (Emslie 1987, 1988).

The leading hypothesis regarding the California Condor’s range contraction and the extinction of all of its congeners at the end of the Pleistocene (with the possible exception of \textit{G. amplus} – see Syverson and Prothero 2012) is the loss of sufficient food resources away from coastal areas (Emslie 1987, 1990; Steadman and Miller 1987; Suárez 2000; C. Chamberlain et al. 2005; Fox-Dobbs et al. 2006). This hypothesis is consistent with available, albeit limited, radiocarbon-dated fossil condor evidence and stable isotope composition of bone collagen from museum specimens (Emslie 1987, 1990; Fox-Dobbs et al. 2006). Although prehistoric condors in Florida and Texas presumably had access to marine food resources, the lack of large salmon runs, pinniped rookeries, and haul-out sites, as well as the lack of offshore coastal upwelling (the wind-driven oceanographic phenomenon where cooler nutrient-rich water replaces warmer surface water, leading to increased productivity and food availability for large marine mammals), would have meant that food resources for scavengers may have become more limited there than along the Pacific coast in the wake of the terrestrial megafauna extinctions (Fox-Dobbs et al. 2006). However, other synergistic factors, including rapid climatic cooling and drought during the Younger Dryas (12,800 and 11,500 YBP)\(^11\), changes in the availability of

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\(^{8}\) circa 50,000–10,000 years before present (YBP)

\(^{9}\) e.g., ground sloths (\textit{Megelonyx jeffersonii}, \textit{Eremotherium laurillardi}, \textit{Nothrotheriops shastensis}, \textit{Glossotherium harlani}), camels (\textit{Camelops} spp.), wild horses (\textit{Equus} spp.), giant bison (\textit{Bison latifrons}), shrub oxen (\textit{Euceratherium} spp.), mastodons (\textit{Mammut americanum}), woolly mammoths (\textit{Mammuthus primigenius})

\(^{10}\) e.g., dire wolves (\textit{Canis dirus}), saber-toothed tigers (\textit{Smilodon} spp.), short-faced bears (\textit{Arctodus simus})

\(^{11}\) The cause of rapid cooling and drought during the Younger Dryas has been the subject of significant debate (see Broecker et al. 2010). The most pervasive hypothesis proposed that a catastrophic release of
thermal updrafts for soaring and finding food, and increased competition from other scavengers or mesopredators, may have also played a role and have not been sufficiently explored.

Along the Pacific coast there is no evidence that food was limiting for condors during the late Pleistocene or during the Holocene. Although the largest land mammals went extinct at the end of the Pleistocene, virtually all the surviving large herbivorous mammals (e.g., deer, elk) are wide-ranging species (Martin 1990) and were likely abundant in the Pacific Northwest, especially west of the Cascades and Sierra Nevada crest, where temperate forests looked much as they do today (Hansen 1947). Furthermore, beached whales, abundant salmon runs, and numerous pinniped rookeries and haul-out sites were also available to condors along the coast. In addition to food availability, the topographic complexity of the western United States provides extensive areas of slope lift that allow soaring avian scavengers to search vast areas for food, even in the absence of strong year-round thermals. Finally, the warming influence of the Pacific Ocean meant that climatic changes along the Pacific Northwest coast during the Younger Dryas were less dramatic than changes experienced in the Intermountain West and Great Plains (McCornack 1920; Hansen 1947). Whatever the reason, condors persisted in the Pacific Northwest for many millennia, alongside Paleo-Indians and Native Americans, prior to the arrival of early Euro-American and Russian explorers.

### 2.2 The Archaeological and Paleontological Record

Bones of two condor species—*Gymnogyps californianus* and *G. amplus*—have been found at fifteen prehistoric sites in the Pacific Northwest, ranging in age from about 200 to 25,000 YBP (Figure 2.1, Table 2.1). A larger condor-like species (*Teratornis woodburnensis*) with a 4.25 m wingspan was also present in the Pacific Northwest during the late Pleistocene (approximately 12,000 YBP), based on bones (humerus, parts of the cranium, beak, sternum, and vertebrae) from proglacial Lake Agassiz shut down the Atlantic Ocean’s circulation resulting in an extensive winter sea ice cover whose presence blocked the release of ocean heat, directed westerly winds to the south, and reflected solar radiation. More recently, largely as a result of dramatic recreations on television, the hypothesis that the Younger Dryas was triggered by the impact of an asteroid (or multiple asteroids, or airbursts over Laurentide Ice Sheet) has gained public attention, but has not gained traction in the scientific community. Broecker et al. (2010) argue that the Younger Dryas appears to simply be a stall in the processes that brought the last glacial period to a close and that no single catastrophic event is required to explain its existence.
unearthed from a buried bog in Woodburn, Oregon (northern Willamette Valley; K. Campbell and Stenger 2002; Figure 2.1).\(^{12}\)

Sites containing Gymnogyps fossils are distributed from San Francisco to southern British Columbia and from the Pacific Ocean beaches inland to the western slopes of the Sierra Nevada in California and along the Columbia River near The Dalles, Oregon (immediately east of the Cascade Range; Figure 2.1). The recent discovery of a broken California Condor tarsometatarsus\(^ {13}\) on South Pender Island, British Columbia (I. R. Wilson Consultants, Ltd. 2006; Figure 2.2), extends the northernmost paleontological record of condors by approximately 400 km. Although there was a report of bones possibly belonging to the California Condor at Smith Creek Cave in northeast Nevada (Howard 1952), paleontologist Steven D. Emslie later determined that those bones were from the extinct Clark’s Condor (Breagyps clarkii; Steadman and Miller 1987; Emslie 1988).\(^ {14}\) Most of the archaeological and paleontological evidence includes one or a few fragmentary bones (Table 2.1). In one case, however, a nearly complete, articulated skeleton—including the entire skull—was found preserved at a Berkeley, California, shellmound, suggesting a ceremonial burial (W. Wallace and Lathrap 1959). At several other sites around San Francisco and Sacramento, condor whistles and ornamented bone wands were found in association with human burials (Figure 2.3, Table 2.1). Over two hundred condor bones were unearthed at the Five Mile Rapids archaeological site near The Dalles, with approximately 20 percent of the bones (humerus, radius, and ulna) containing cut marks, signifying disarticulation and feather removal (L. Miller 1957; Hansel-Kuehn 2003), presumably for ceremonial regalia. At least one bone (the proximal end of a radius) also showed signs of being girdled (Hansel-Kuehn 2003), indicating that it may have been used as a primitive tool.

The archaeological and paleontological record establishes that condors occupied the region from the Cascade Range and Sierra Nevada to the coast for many millennia prior to Euro-

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12 Although Teratorns had large wingspans and several characteristics in common with Cathartid vultures (L. Miller 1909), more recent analyses of cranial morphology suggest that they were predators (likely piscavores) (K. Campbell and Tonni 1981, 1983; Hertel 1995). However, the abundant remains of Teratorns at the Rancho La Brea Tar Pits suggest that they may have also been facultative scavengers, similar to Bald Eagles (Haliaeetus leucocephalus; Hertel 1995).

13 A large bone in the lower leg of birds with which the toes connect, formed by fusion of the tarsal and metatarsal bones.

14 Although Howard (1952) tentatively identified six bones as Gymnogyps, she questioned this identification and suggested that they might be Breagyps.
American contact. Apart from the archaeological dig near The Dalles, evidence of ancient California Condor bones is currently lacking in the drier areas of the Pacific Northwest east of the Cascades and Sierra Nevada. However, additional evidence of condors from this area should be expected, as late Pleistocene California Condor bones have been found at dry inland sites to the south, and the Great Basin supported a diverse assemblage of large soaring scavengers and predators during this time period, including the Clark’s Condor, the Western Black Vulture (Coragyps occidentalis), the Incredible Teratorn (Aiolornis incredibilis), and Merriam’s Teratorn (Teratornis merriami) (Grayson 2011).

An evaluation of bones found in limestone caves in the lower McCloud River area near Mount Shasta in northern California indicates that a larger extinct condor (Gymnogyps amplus) was also once present in the Pacific Northwest (L. H. Miller 1911; Table 2.1). Syverson and Prothero (2010), noting that the larger size of the single condor skull found at the Five Mile Rapids site suggests that this specimen also belonged to G. amplus, stated: “The skull of UCMVZ 1337 falls well outside the range of sizes observed for G. californianus, and indeed at the large end of the spectrum of RLB [Rancho La Brea] specimens” (11). Unfortunately, Syverson and Prothero included only a small sample of the bones from the Five Mile Rapids site in their analysis. While they had access to the twenty-one condor bones from that site that are retained at the Museum of Vertebrate Zoology in Berkeley, California (at the request of L. Miller in a July 7, 1955, letter to L. Cressman, State Museum of Anthropology, University of Oregon, Eugene), the majority of bones from the Five Mile Rapids site are housed at the University of Oregon Museum of Natural and Cultural History (Hansel-Kuehn 2003) and were not included in their study.

Gymnogyps bones found at Galen’s Pit, near Mount Shasta (Table 2.1), were radiocarbon dated to 20,660±310 YBP and identified by Emslie (1990) as G. californianus. However, Emslie did not recognize G. amplus as a separate species (Emslie 1988), instead assigning the larger form as a possible temporal subspecies of G. californianus. As stated above, new information now suggests G. amplus may have been a distinct species (Syverson and Prothero 2010). Thus, reevaluation of Emslie’s assignment of the Galen’s Pit Gymnogyps bones is warranted.

Future work to reexamine the species-level identity of Gymnogyps bones from Galen’s Pit and the Five Mile Rapids site in light of Syverson and Prothero’s (2010) study may help clarify
the evolutionary relationships and temporal co-occurrence of these two condor species in the Pacific Northwest. Extraction of ancient DNA from these bones may provide another complementary avenue of inquiry. Whatever approach is taken, additional work in this area should be coupled with more direct radiocarbon dates from Pacific Northwest condor bones, as only two such dates are currently available (Table 2.1).

2.3 **California Condors in Pacific Northwest Native American Culture**

Condors were known to many Pacific Northwest tribes, who idolized them in their mythology, depicted them in their art, and used their feathers in ceremonies, medicine, and dances. Below, we review the ethnographic record of tribal relationships with the condor in the Pacific Northwest, by geographic region (Figure 2.4 is provided as a general guide to the distribution of tribes at the time of Euro-American settlement).

In the Sacramento Valley, along the north-central coast, and in the northern Sierra foothills of California, most Indian groups knew the California Condor by name and included it in their mythology (e.g., California Athapaskan, Yuki, Maidu, Patwin, Nisenan, Pomo, Wintun, Wappo, Coast Miwok, and Miwok Tribes; Barrett 1908; Merriam 1910; Kroeber 1925, 1929; Loeb 1933; Bates et al. 1993). Yuki Indians (present-day Mendocino County, California) had a myth that one of the two Great Spirits “took the shape of an enormous eagle or condor” (Hodgson 2007, 295). The Nisenans and Miwoks of the central Sierra foothills believed they descended from totem animals, including the condor (Merriam 1908, 1910). The Maidus of the north-central Sierra Nevada believed that condors were spirit animals capable of bestowing shamanistic power on humans and therefore condors were never eaten or caught (Loeb 1933).

Among the northern California tribes embracing the Kuksu religion (Patwin, Maidu, Miwok, Valley Nisenan, Yokut, and Pomo Tribes), condor dances were part of their annual dance cycle and tradition (Kroeber 1925). Pomo Indians, living in parts of present-day Sonoma, Lake, Mendocino, Colusa, and Glenn Counties, captured condors for their feathers and wings and may also have taken young and raised them in their villages (Loeb 1926). Some tribes in this area, including the Pomo, Maidu, Miwok, and Patwin, performed *moluku*, or condor dances, in which an entire feathered condor skin was worn (Loeb 1926, 1933; Gifford 1955). Gifford (1955) describes the process of preparing a condor skin for the dance.
When a condor is killed, the skin is kept for a dance. The hunters cut the skin from the mandible to the anus. They save the wings and the skin over the body, but not the feet or head. The body of the bird is burned, because, as the informant expressed it, the hunters feel sorry for him and do not want to see his body rot. They throw tuyu seed over the body while it burns and dance around the fire and sing. The skin is stretched on sticks, and when the hunters get back to the village, it is rubbed down with deer marrow to make it soft...

Assisted by the singer or drummer, the dancer puts on the condor skin in the chief's house, lacing it up the front of his body and sticking his legs through the skin where the bird's legs were. The condor's wings are tied to his arms and his head projects from the neck of the bird. The skin is usually so large that the tail drags on the ground. (288)

An excellent example of a condor dance costume has been preserved, collected by I. G. Voznesenskii in 1841 and housed in the Peter the Great Museum of Anthropology and Ethnography, Saint Petersburg, Russia (cat. no. 570-2; Figure 2.5). Other tribes in the region made headdresses adorned with condor feathers (Revere 1849; Collier and Thalman 1991). As Revere noted while traveling through Lake County, California (near Clear Lake) in early fall 1846:

In the evening . . . we had a visit from a party of Indians, both male and female, attired in head-dresses composed of the black feathers of the large Californian vulture, which fell down their backs. The men were painted all over with stripes and spots, and the women wore kilts or short petticoats made of flax or hemp hacked out and fastened round the waist, but so fashioned as not to impede the motions of their limbs. They wore besides, various articles of savage finery on different parts of their persons, and all were masked. (1849, 133)

Tribes in northwest California, along the southwest coast of Oregon, and in the mountains surrounding the upper Sacramento Valley were familiar with the California Condor. Condors figured in myths, tales, and religious beliefs handed down by the Yurok, Wintu, Chimariko, Wiyot, Hupa, and Karuk Tribes (Curtis 1924; Harrington 1932; Du Bois 1935; Kroeber 1976; Kroeber and Gifford 1980; Sapir 2001). Condors were principally noted for potent, and sometimes dangerous, spiritual strength (Du Bois 1935). Shamans believed that confronting a...

15 According to Gifford (1955), another informant stated that only a shaman would kill a condor. Beads and seed are scattered over the body, which is buried carefully, rather than burned.
condor in their dreams endowed them with spiritual power, and used condor feathers in their attempts to cure the sick (Kroeber 1908; Curtis 1924; Sapir 2001; Figure 2.6). In Wiyot mythology, the condor had a role similar to the Biblical Adam as the ancestor of all humanity (Curtis 1924). Farther inland along the Klamath River, condors were part of Karuk mythology and language (Harrington 1932).

Condor feathers were worn by Yurok, Wiyot, Hupa, Tolowa, and Chimariko people in dance rituals, such as the White Deerskin Dance, Jump Dance, and Kick Dance (Bates et al. 1993; Paterek 1996; Sapir 2001; Figure 2.7). Usually the condor feathers were spliced together along with flicker (*Colaptes auratus*) feathers on a rawhide strip to make especially long plumes (Drucker 1937; Bates et al. 1993; Figures 2.8 and 2.9). These plumes were attached to a wooden shaft and worn atop the dancer’s head (Figures 2.7 and 2.9). Condor feathers were used by *pegahsoy*, or clairvoyant Karuk doctors, to get rid of shadows that caused disease (Harrington 1932, 229–31). Condor feathers were also used by doctors of the Hupa and Kato Tribes (Loeb 1932; Sapir 2001). Some Kato doctors carried a stick called a *ketaltnes*, which was stripped of bark and adorned with condor feathers (Loeb 1932). For the Hupa Kick Dance (held at the conclusion of a new doctor’s training), the shaman held “a bunch” of condor feathers (Sapir 2001). Among the Yana Tribe, living between Mount Shasta and Mount Lassen, chiefs captured condors as pets (Sapir and Spier 1943).

In southwest Oregon, among the lower Rogue River Tribe, “buzzards” were considered guardian spirits with some of the most powerful curing powers (Drucker 1937). They were also believed to be patrons of hunters, who offered them the offal remaining after butchering their quarry (Drucker 1937). Farther north, Indian tribes along the lower Columbia River, the central and northern coast tribes, and Willamette River tribes were likely familiar with California Condors, but loss of cultural knowledge and traditions in this area prior to ethnographic research makes understanding the true role of condors in cultural traditions difficult. Nelson Wallulatum, a Wasco chief, reported that his people kept a condor chick in camp to keep away thunder and lightning (Schlick 1994). Condors, or condor-like figures, were also frequently depicted in basketry, handbags, beadwork, and stone sculptures of Columbia River tribes (Schlick 1994; Mercer 2005; Berg 2007; Figure 2.10).

Paleontological evidence suggests that the Columbia River tribes, at least several millenia, harvested condors for their feathers, and this practice appears to have taken place
over thousands of years (Hansel-Kuehn 2003). However, we failed to uncover more recent evidence that condor feathers were used in the ceremonial regalia of Columbia River tribes. Although Sharp (2012) asserted that a photo of a Wyam shaman (by Edward Curtis 1910, volume 7, folio plate 20) in the vicinity of Celilo Falls showed the shaman with condor wing feathers, careful investigation of that photo suggests that he is holding a wing of a much smaller bird (P. Trail, US Fish and Wildlife Service Forensics Lab, pers. comm., 2011). Despite searching the photographic collections of Edward Curtis and the extensive photography collections at the Oregon Historical Society, as well as contacting tribal museums and several anthropologists, we did not find any photographic evidence of condor feather use among the Columbia River tribes.

We found only a few ethnographic references to condors in Washington State away from the Columbia River. Along the Washington coast, the condor appears in Coast Salish mythology as a beneficent creature living in the hills (Curtis 1913). The Chehalis people of southwest Washington feared a monster bird—which an early twentieth-century ethnographer described as “possibly a condor”—that lived near the Black River Bridge, northwest of present-day Chehalis, because they believed it was able to bite off their heads (J. Miller 1999). Condors were also mentioned among the Chehalis as having strong warrior powers (J. Miller 1999). Sharp (2012) reported several additional references from Native American tribes in Washington to birds that may have been condors. Legends of condors are notably absent from the Olympic Peninsula (Swan 1870; Pettitt 1950; Wray 2002).

In coastal British Columbia, the Sechelt Indian Band, which inhabits an area northwest of Vancouver, incorporated condors into its mythology and totem poles (Peterson 1990). Condors (Tchass’-khain) were seen as creatures that could use their power only for good and could counteract evil creatures but not destroy them. This contrasted with Thunderbirds (Kwaht-kay’-ahm), which could use their powers for destruction (Peterson 1990). One of the stories in their oral history involved condors nesting high on a rock ledge near an impassable cliff (Peterson 1990), which is consistent with our modern understanding of condor nesting habits. The Sechelts would hunt eagles for their feathers, but not condors, which were considered protectors and guides above the hunter (Peterson 1990).

Little ethnographic evidence, and no physical evidence, of condors has been reported east of the Cascade Range apart from the archaeological dig at Five Mile Rapids, near The Dalles, Oregon. However, Klamath Indians may have been familiar with the California Condor, as they
had a word (tchuaish) meaning “black vulture of large size, head light-colored, or reddish” (Gatschet 1890, 446). This is contrasted with skólos, which clearly represented the Turkey Vulture (Gatschet 1890). Modoc and Achomawi Indians, in northeastern California, also had a name for the condor (úm-pni; Curtis 1924), and the Atsugewi people, also in northeastern California, had a special condor song and believed the condor brought food to the people at Ratstówni (the mythical village where the first people lived; Garth 1953). The Sahaptin-speaking tribes of north-central Oregon and south-central Washington (i.e., Yakima, Umatilla, Palouse, and Warm Springs Indians) had names for condors (čañahúu/pachañahú; Hunn 1990), as did the Okanogan Tribe in northeastern Washington and south-central British Columbia (sʔítn; Mattina 1987). Farther east, in present-day north-central Idaho, northeast Oregon, and southeast Washington, condors were part of the Nez Perce lexicon (i-stá-lamkt according to Curtis 1911; qúʔnes according to Aoki 1994). East of the Rocky Mountains, the Blackfeet Indians may have occasionally observed condors, according to their oral record (Schaeffer 1951). The Crow and Gros Ventre Indians of the northwestern Great Plains also referenced condors in their mythology (Boas 1916; Lowie 1918; Ehrlich 1937; Schaeffer 1951).

Physical evidence of condor feathers in tribal regalia in the Pacific Northwest is restricted to the tribes of northern California, leaving little question that condors were historically present there, and probably locally abundant, prior to Euro-American contact. The discovery of a large number of condor bones near The Dalles, Oregon, associated with human artifacts also suggests that condors were historically present along the mid-Columbia River and were likely harvested for their feathers. Language, artwork, and oral histories suggest that condors may have been encountered, at least on occasion, in other parts of the Pacific Northwest from California to southern British Columbia, and perhaps inland to the Rocky Mountains. However, trade, along with linguistic and material cultural diffusion among Indians in the Northwest, was extensive and centered around the mid-Columbia River and its enormous salmon runs (Winther 1950; Walker 1997). Thus, without additional physical evidence, it is not possible to know whether the stories of condors handed down through oral tradition represented familiarity with condors in a tribe’s home territory or knowledge gained from seasonal travels to the great salmon runs on the mid-Columbia River, where we have physical evidence of condor occurrence.
It is important to consider that in some Native American cultures, the lack of physical evidence would be expected; for example, when killing condors was taboo due to their totemic status (Peterson 1990), when feathers or other parts of a spirit animal were considered great medicines not to be seen by anyone except the possessor (Swan 1870), or when burial customs of the tribe dictated that all of a person’s property should be destroyed when he or she died, as was the case with several Northwest tribes (Wickersham 1896). The lack of evidence of condors in tribal religion and rituals may also be expected in those areas where ancient traditions were lost when large numbers of Native Americans were converted to Christianity or when diseases and war ravished populations in advance of detailed ethnographic studies (Okladnikova 1983), as they did in many areas of the Pacific Northwest, especially in western Oregon and Washington (Boyd 1999).

In summary, most tribes in the Pacific Northwest had a name for the condor in their native language, and many, especially in northern California, revered them in their mythology and used their body parts for ceremonial, medical, and religious purposes. Some even believed that all living animals, including humans, were direct descendants of the condor. Given physical evidence in the form of bones and feather regalia, there is little doubt that tribes in northern California and along the mid-Columbia River had an association with California Condors. Because condors were present in their language, mythology, and art, other tribes distant from these areas may have been familiar with condors, but given the extensive trade and cultural diffusion in the region it is not possible to discern between those cultures that observed condors and those that simply knew of them from their travels to the mid-Columbia River to trade and fish for salmon.

2.4 Observation and Collection of California Condors by Naturalists, Explorers, and Settlers

Documented observations of California Condors in the Pacific Northwest by early European, American, and Russian explorers and naturalists began with William Clark, Meriwether Lewis, and other members of the Corps of Discovery in 1805 and 1806 (Figure 2.11; Table 2.2; Members of the Corps of Discovery often copied journal entries from one another. Meriwether Lewis’ sketch of a condor head is shown in Figure 2.12. William Clark copied Lewis’ condor head sketch in his...
Appendix 1). During their travels along the lower Columbia River, they killed at least five condors and observed them on numerous occasions from around Celilo Falls (near The Dalles, Oregon) to the coast (Lewis et al. 2002; Figure 2.12).

In the wake of Lewis and Clark’s expedition, trappers and fur traders in support of the Pacific Fur Company, American Fur Company, North West Company, and the Hudson’s Bay Company were all seeking their fortunes in the region (Schafer 1909). Among these individuals, Alexander Henry, David Thompson, and Donald McKenzie reported seeing condors along the Columbia River and in the Willamette Valley in the early 1800s (Figure 2.11; Table 2.2; Appendix 1). As fur trapping became increasingly competitive along the Columbia River and its tributaries, new trapping grounds were sought by enterprising mountain men like Jedediah Smith. Smith pioneered a route over the Sierra Nevada and up the California coast to reach the Oregon Country (Sullivan 1934; Davis 1989). On his journey through northern California in 1828, he observed “large & small buzzards,” which he differentiated from eagles, ravens, and hawks (Sullivan 1934, 92). Around the same time, the Hudson’s Bay Company was starting to send trapping brigades south from Fort Vancouver, along what became known as the Siskiyou Trail, into northern California as far south as San Francisco Bay.17

With the opening of the West to trade and travel, a few adventure-seeking naturalists, including David Douglas, John Scouler, John Kirk Townsend, and Titian Ramsay Peale, ventured into the region in the early 1800s (J. Townsend 1839; Scouler 1905; Young 1904; Douglas 1914; Poesch 1961). They collected specimens for natural history museums and herbaria and recorded their observations in journals (Figure 2.13). West of the Cascades and Sierra Nevada, condors were observed by these naturalists with some regularity in the first half of the nineteenth century. David Douglas described them as “common on the shores of the Columbia” and “plentiful” in the Umpqua River region in southern Oregon, observing nine in a single flock (Douglas 1914). In his letters to John James Audubon, Townsend mentioned seeing condors in Oregon on a number of occasions (Audubon 1840). Titian Ramsay Peale described condors as

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17 The trespasses and atrocities committed by the Hudson’s Bay Company and other early pioneers on the Native Americans of the Rogue River Valley, along with the spread of deadly diseases, resulted in considerable friction among the natives and newcomers. Increasing use of the Siskiyou Trail by fur traders and settlers resulted in escalating violence and ultimately the Rogue River Wars, described in detail by Schwartz (1997).
uncommon in Oregon in 1841, but “much more numerous” in northern California at the time (Peale 1848).

As reports of the Oregon Country reached the eastern United States, churches sent missionaries to convert the Indians to Christianity and Euro-American settlers began to arrive overland via the Oregon Trail starting in the late 1830s (Doherty 2000). California was a less popular destination for settlers at that time, but by 1840 a new inland center began to emerge in the Sacramento Valley, near the nexus of the California and Siskiyou Trails, where John Sutter received a large land grant from the governor of Monterey and built a thriving trade center, ranch, and fort (Meinig 1998). Sutter provided accommodations to many travelers, at least one of whom observed condors somewhere between Sutter’s Fort and Suisun Bay (M. Wilbur 1941); however, most of northern California remained only lightly populated and remote up until the California Gold Rush of 1849 (Caughey 1948).

Although most of the early fur trappers, settlers, and explorers were European or American, Russia had also been vying for a share of the Pacific Northwest fur trading industry since the early 1800s. It had established an outpost in northern California—Fort Ross—near Bodega Bay in 1812 as an agricultural base to supply its operations farther north (Alekseev 1987). By the 1830s, the Russian-American Company was winding down its operations at Fort Ross, but between 1840 and 1841, Russian scientist I. G. Voznesenskii visited the fort and surrounding areas as part of an expedition to make scientific collections for the Russian Academy of Sciences (Lipchitz 1955; Alekseev 1987). Voznesenskii’s California collections are widely recognized as important to science because he was one of the last interested witnesses to provide a detailed account of California Indian life prior to the California Gold Rush and the last collector of unique objects of their material and artistic culture (Okladnikova 1983). Voznesenskii collected four California Condor specimens for the academy around San Francisco Bay and the Sacramento Valley, all of which were shipped back to Russia (see Appendix 1; Bates 1983). With the assistance of John Sutter, he also procured a cape made from condor and eagle feathers and an entire condor feather costume from the Native Americans around Sacramento, perhaps the only one of its kind still in existence (Figure 2.5; Bates 1983).

American immigrants continued to arrive in northern California overland via the California and Siskiyou Trails through the 1840s, but the population remained small. With the January 1848 discovery of gold in Sutter’s millrace along the South Fork of the American River in
the Sierra foothills, there was a surge of immigrants that would forever transform California (Caughey 1948). The sudden influx of immigrants created enormous demand for provisions and those who could provide them (Caughey 1948). With large numbers of miners and settlers infiltrating interior northern California, the entire gold-bearing region was thoroughly explored and the increasing number of local newspapers began to run stories of encounters with enormous birds with wingspans of “9 feet [and larger] from tip-to-tip,” several of which were shot out of curiosity (see Appendix 1).

By the time of the California Gold Rush, the United States and England had agreed to separate their interests in the Oregon Territory by dividing it at the forty-ninth parallel, and the Mexican government had ceded control of California to the United States. The confluence of these events, and the need for the United States to protect its newly acquired territory, created heightened interest in providing a safer, more efficient means of transportation and trade to connect the eastern and western seaboards (Albright 1921). Meinig (1998, 5) noted that by 1852 relatively few questioned either the necessity or the practicality of [a transcontinental railroad]. A railroad to the Pacific was the main theme of commercial conventions, orations, pamphlets, newspapers, and national periodicals, and Pacific railroad bills became the staple of every session of Congress. From this time on the basic questions were not could and should we build a trans-continental band of iron but how and where to do so.

From 1853 to 1854, Senator William M. Gwin of California got an appropriation into the War Department budget to allow the secretary of war (Jefferson Davis) to send out surveying parties along four potential transcontinental railroad routes to determine which would be best (Albright 1921). North–south routes from California to Washington were also surveyed (Baird et al. 1858; Cooper and Suckley 1859). Upon completion of the surveys, twelve illustrated volumes were published between 1854 and 1859 (Albright 1921), including detailed accounts and illustrations of the birds observed and collected along the various survey routes compiled at the Smithsonian Institution (Baird et al. 1858).

At the time of the railroad surveys, condors were apparently still regularly observed in northern California but were a rare occurrence north of California (Cooper and Suckley 1859; Jobanek and Marshall 1992; Gabrielson and Jewett 1970). Newberry (1857, 73) reported, quite
poetically, seeing condors every day in the summer of 1855 while traveling through the Sacramento Valley on his way to Oregon:

A portion of every day’s experience in our march through the Sacramento valley was a pleasure in watching the graceful evolutions of this splendid bird [the California Condor]. Its colors are pleasing; the head orange, body black, with wings brown and white and black, while its flight is easy and effortless, almost beyond that of any other bird. As I sometimes recall the characteristic scenery of California, those interminable stretches of waving grain, with, here and there, between the rounded hills, orchard-like clumps of oak, a scene so solitary and yet so home-like, over these oat-covered plains and slopes, golden yellow in the sunshine, always floats the shadow of the vulture.

However, Newberry’s party reported seeing only a few condors in the Klamath Basin of California and none in Oregon (Newberry 1857). Matteson (1886) stated they were sometimes seen in southern Oregon and up along the coast. Despite the substantial increase in the number of potential observers and outlets for reporting observations in the late 1800s, the number of condor observations continued to decline across the Pacific Northwest, with most being brief newspaper reports of condors being killed or captured in northern California, or recollections of condor observations in ornithological compendiums (Figure 2.14; Appendix 1). James Graham Cooper—appointed surgeon on the western Pacific Railroad Surveys through Idaho and Washington, and after which the Cooper Ornithological Club was named (Emerson 1899)—first observed condors in northern California in 1855. He also noted that he had seen fewer every year since then and that unless protected they appeared, “doomed to rapid extinction” (Cooper 1890). After 1900, there were only a handful of condor observations in the Pacific Northwest, and the birds were completely gone from the region sometime in the early twentieth century.

18 Newberry actually used the common name “Californian Vulture” to describe the California Condor. Although the species had been described as a representative of the Condor in the northern hemisphere (the term condor originally reserved for the Andean Condor) as early as 1829 (Douglas 1829), the common names of Californian Vulture or California Vulture persisted through most of the nineteenth century among those who knew the bird. The name California Condor didn’t take over in popularity until late in the 1800s.
19 Cooper (1890) gave three reasons for the condor’s decline: secondary poisoning, conversion of grazing land to cropland, and wanton shooting. In chapter 4 we discuss these and other possible reasons for the condor’s decline.
2.5 **Summary of Historical Distribution**

The occurrence records indicate that condor observations in the Pacific Northwest appear to have been concentrated in a few areas (i.e., the Sacramento Valley, central and northern California coast, Oregon coast, Sierra Nevada foothills, Columbia River, and Umpqua foothills; Figure 2.11). Although the distribution of these records is undoubtedly biased by the spatially concentrated distribution of observers at that time (S. Wilbur 1973; Jobanek and Marshall 1992), more than half the records were within 75 km of the Pacific coast and three-quarters were within 150 km (Figure 2.15). This may be a result of higher food availability along the coast than in the drier intermountain basins, more favorable climatic conditions for nesting, roosting, and foraging in coastal areas, or simply an artifact of the concentration of people in areas closer to the coast. Whatever the cause, the dearth of observations farther east is probably not solely a reflection of observer bias, because the Corps of Discovery, John Kirk Townsend, and others either noted their absence east of Celilo Falls or failed to record them. Furthermore, there were several east–west travel corridors—including the Oregon and California Trails—that were used by numerous trappers, settlers, gold seekers, and naturalists throughout the 1800s (Gerlach 1970). The extensive Pacific Railroad Surveys also traversed the continent from east to west along several routes (Albright 1921). Despite the number of potential observers in the area, there were very few reliable condor observations east of the Cascade Range and Sierra Nevada, and no specimens collected from this area (Figure 2.16, Table 2.2). In addition to the condor occurrence data reported in Table 2.2, there are a small number of other purported condor observations east of the Cascade Range and Sierra Nevada, but these lack credibility or sufficient details to determine their reliability:

- Several Blackfeet Indians reported seeing large birds in current-day Montana during the 1800s, some of which could have been condors, but others of which clearly were not (Schaeffer 1951).

- Lewis and Clark may have seen condors in Idaho, but the record is unclear. While traveling back East near present-day Weippe, Idaho, in June 1806, Meriwether Lewis indicated that “Labuish and Cruzatte returned and reported that the buzzards has eaten up a deer which they had killed butchered and hung up this morning” (Lewis et al. 2002; Lewis’s journal, Friday, June 13, 1806). Other authors have referred to this observation
as a Turkey Vulture (Jollie 1953; Lewis et al. 2002), although it is impossible to be sure given that the term “buzzard” was used by Lewis and Clark for both condors and Turkey Vultures.

- A published report of two condors near Calgary, Alberta, in September 1896 (Fannin 1897) appears to be a misidentification of immature Golden Eagles (Brooks in litt. 1931).
- Moen (2008) reported oral history accounts of condors along the Yakima River (Washington), near Celilo Falls, at the eastern rim of Hell’s Canyon (Idaho), and in the Clearwater River Valley (Idaho). Sharp (2012) also reported oral history accounts in the Hell’s Canyon–Seven Devils area along the Snake River. However, these records are based on stories passed down as oral histories and are secondhand accounts from observers with unknown familiarity with condors; without additional evidence, their reliability is questionable (especially the later records that fall well outside of the time period of the last specimen collected in the Pacific Northwest).

The northernmost condor occurrence records are from southern British Columbia, near the mouth of the Fraser River (Lord 1866; Fannin 1891; Rhoads 1893). M. Chamberlain (1887) reported that condors were taken at the mouth of the Fraser River but provided no details on the disposition of the specimens. Bendire (1892) stated that condors were observed on Vancouver Island by early ornithologists but did not say where or when. Although there are no definitive reports of condor specimens taken in Canada during early settlement and exploration, a single broken condor tarsometatarsus (radiocarbon dated to 2,915±15 YBP) was recently unearthed during an archaeological excavation on South Pender Island (in the Strait of Georgia, near the southern tip of Vancouver Island; I. R. Wilson Consultants, Ltd. 2006; Figures 2.1 and 2.2), lending additional credibility to the Fraser River observations and Bendire’s comment that condors were observed on Vancouver Island. The southern British Columbia observations are also consistent with the northern extremes of other vulture ranges worldwide (Mundy et al. 1992) and are within the northern distribution of Turkey Vultures in British Columbia (R.
There are three other reports that may reference condors farther north, but these lack sufficient details to determine their reliability:

- In 1834, near Fort McLoughlin, along the central British Columbia coastline, William Fraser Tolmie observed “what I supposed a large species of vulture at the northern end [of a lake], along with some white-headed eagles (Bald Eagles \( \text{Haliaeetus leucocephalus} \)) attracted probably by the dead salmon” (1963, 293). This record is questionable, although not implausible given (1) its location approximately 500 km north of other accepted observations along the Fraser River, (2) the uncertainty of Tolmie’s phrasing, since he had already seen condors along the Cowlitz River in Washington the year before, and (3) the association with Bald Eagles, which may indicate that Tolmie was actually observing juvenile Bald Eagles and simply did not realize that they would have had dark heads.

- Ross Cox, a fur trader and writer, noted shooting “a bird of the vulture tribe” northwest of the Canoe River in British Columbia in September of 1817. Although this would be farther north than Turkey Vultures are typically observed (R. Campbell et al. 1990), lack of identifying details makes it unclear whether Cox was referring to a California Condor, Turkey Vulture, or something else.  

- Sharp (2012) cited a personal communication with a Sto:lo Salish tribal biologist relating a 1935 observation of a “condor-sized bird” on the Fraser River near Spuzzum, British Columbia. In an appendix to his work, Sharp (2012) admitted that details for this record were “sparse.” Given that this was approximately thirty years after the last reliable sighting in the entire Pacific Northwest, there was no definitive identification, and it was second- or third-hand information, this observation is unreliable (although not impossible).

Records of condors are noticeably absent from the Olympic Peninsula. This could reflect their actual absence, or may simply a reflection of the difficulty early settlers had accessing this

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20 Vultures are limited to those latitudes where there is enough daylight in winter for them to find sufficient food resources.
21 Early explorers included many other birds in the “vulture tribe”, including corvids (e.g., Lewis et al. 2002; journal entry of September 18, 1805).
remote area. The first white settlers did not arrive on the Olympic Peninsula until 1845, and in the early 1900s there were only two wagon roads in the entire western half of the peninsula (Pettitt 1950; Wood 1995). As Wood (1995, 20) put it:

While the overland migrations [to the Oregon Country] were occurring during the first half of the nineteenth century, the Olympic Peninsula remained an isolated, unsought corner, a land wild, remote, and untraveled.

Historically, food resources were likely abundant for avian scavengers on the peninsula, with numerous salmon runs, pinniped rookeries, populations of elk and deer, and whale carcasses harvested by the whaling tribes in the region (Reagan 1909; M. L. Johnson and S. Johnson 1952; Kenyon and Scheffer 1961). Furthermore, the rugged terrain and coastal winds would likely have provided consistent slope lift for large soaring birds. However, we found no evidence of condors inhabiting the peninsula in archaeological, paleontological, ethnographic, or historical literature.

Records are also absent from the Puget Trough and San Juan Islands, despite the fact that several explorers who recorded condors along the Columbia River traveled there (Cooper and Suckley 1859; R. Miller et al. 1935; Tolmie 1963). Condors may have been rare or absent in these areas because the Puget Trough and San Juan Islands do not provide ideal soaring conditions, being relatively flat and containing large water bodies that are not conducive to thermal updrafts. The physical evidence of condors in this area is limited to the single condor tarsometatarsus found just north of the San Juan Islands, on South Pender Island (Figures 2.1 and 2.2). Because this bone was found in association with cultural artifacts, it is unclear whether it was taken from a bird inhabiting the island or obtained during an excursion by Native Americans to the mainland or Vancouver Island. Cooper (1890) stated that condors ranged from “Lower California to Puget Sound” but provided no further details on specific observations within Puget Sound (Cooper 1870, 1890). In an early work, Cooper had reported that he had neither seen California Condors nor heard of their occurrence at Puget Sound (Cooper and Suckley 1859).

There are no records of California Condors in the Cascade Range. This may be the result of surveyor bias, as few early explorers ventured into the high mountains, and the Barlow wagon road over the Cascades (created to circumvent the dangerous descent of the Columbia
River rapids) was not used by immigrants on the Oregon Trail until 1845 (Barlow 1902), just a few years before the last reliable observation of condors along the lower Columbia River. Those few explorers that did venture into the Cascades found rugged mountains and difficult travel, with nearly impenetrable primeval forests with dense undergrowth or canopies (Hines 1894; R. Sawyer 1932). The only report of condors in the Cascades is a secondhand account relayed in a letter from John Kirk Townsend to John James Audubon that seems dubious given the claim that condors were nesting in swamps under pine forests.

The Indians of the Columbia say that [the California Vulture] breeds on the ground, fixing its nest in swamps under the pine forests, chiefly in the Alpine country. The Wallameet Mountains [Cascade Range], seventy or eighty miles south of the Columbia [River], are said to be its favourite places of resort. I have never visited the mountains at that season, and therefore cannot speak from my own knowledge. (Audubon 1840, 13)

The last record of a condor killed in the Pacific Northwest is from the mountains north of San Francisco sometime between 1900 and 1905 (Table 2.2). A few observations of condors by individuals familiar with the species were made several years after that specimen was taken, but the lack of other corroborating evidence during this time period makes these observations less reliable. One purported observation was in 1912 on the remote Lost Coast of California and another was of six condors in 1925 by Henry Frazier in Siskiyou County (Table 2.2). A report of condors at the mouth of the Columbia River was published in the Wellsboro Gazette (a Pennsylvania newspaper) on June 8, 1922.

The belief that the west coast or California condor, North America’s largest bird is practically extinct, must be revised, for

22 However, it is possible that some of the conversation that Townsend had with the locals got lost in translation. In Chinook jargon, the common language used among the lower Columbia River tribes, where Townsend was traveling, the word for swamp was *klimin ilēhi*, which also means mud, or soft ground. However, *klimin* is also the word for “broken.” Is it possible that the Indians were trying to tell Townsend that condors nested in the broken trees of the pine forests in the Alpine Country? The notion that condors nested in the Alpine Country of the Cascade Range seventy or eighty miles south of the Columbia River is entirely plausible, as is the notion that Townsend’s translation was not entirely accurate.

23 Townsend (1848) also related that condors were “reputed (almost certainly by David Douglas (1829)) to breed in the Umptqua [Umpqua] country, about fifty or sixty miles south of the Oregon Rion [?] and it is said to lay two eggs, which are entirely black!” Although it is certainly possible that condors were breeding in the vicinity of the Umpqua River, they lay only one egg at a time and the notion that their eggs were black is clearly erroneous.
several recent news stories from towns at the mouth of the Columbia river report two pairs of the big birds are frequently seen on the rocky bluffs there. They are evidently preparing to nest later on.

The condors noticed soaring above the extensive stretch of bluffs and sandbars are very large with a wing spread of eight or nine feet. They are as black as the traditional German eagle.

However, searches of local newspapers from January to June 1922 in the archives at the Columbia Pacific Heritage Museum and in other newspaper databases failed to uncover the source of that report.

Anecdotal data can be notoriously unreliable, and evidentiary standards should become more stringent as observations move farther away from direct physical evidence in time and space (McKelvey et al. 2008). Moen (2008) and Sharp (2012) described several oral history accounts of condors in Oregon, Washington, and Idaho up until the mid-twentieth century, including a firsthand account of James Selam, who claimed to have seen two condors at Celilo Falls on the Columbia River while fishing in the 1920s. While sightings in the 1920s along the Columbia are not inconceivable, the fact that there were no other credible observations there after 1897 makes them suspect. We find the later accounts from the 1940s to the 1970s, described in Moen (2008) and Sharp (2012), to be unreliable in light of the extreme rarity and declining population trend of the condor at the time, the physical distance between the known population in southern California and the alleged sightings, and the fact that no ornithologist or birder in the region reported any sightings of this extremely rare, large, soaring species anywhere north of San Francisco after the early 1900s.

2.6 Historical Movement Patterns

Whether or not condors historically were migratory or resident in the Pacific Northwest has been a matter of debate (Koford 1953; S. Wilbur 1973, 1978) and has implications for planning future reintroductions and establishing connectivity between populations. In his seminal work on the California Condor, Carl Koford (1953) hypothesized that all condor records north of San Francisco Bay may have represented seasonal or sporadic migrants from the southern California population in search of seasonally abundant food resources. He offered an alternative hypothesis that condors were a resident species that formerly had a much larger range, but he
found this hypothesis wanting due to the lack of known fossil evidence of condors at the time (Koford 1953). New information has, indeed, revealed fossil evidence in the region, ranging from San Francisco to British Columbia (Table 2.1). Ethnographic evidence of condors inhabiting the Pacific Northwest was also unknown to Koford—although he suggested that evidence of the former occurrence of condors in Oregon might be obtained through anthropological investigations.

The migratory hypothesis was an extension of the observations and speculations of several early explorers. Douglas saw them in “great numbers on the woody part of the Columbia” but observed that they were less abundant there in winter (Douglas 1914). Douglas also stated, “I think they migrate to the south, as great numbers were seen by myself on the Umpqua River, and south of it by Mr. McLeod, whom I accompanied” (241).

Townsend reported that condors were seen on the Columbia River only during summer, “appearing about the first of June, and retiring, probably to the mountains, about the end of August” (Audubon 1840, 13). However, in a previous letter to Audubon he described the condor as “most abundant during the spring, at which season it feeds on the dead salmon that are thrown upon the shores in great numbers.” This confusion is not cleared up by the occurrence records, as the only condor occurrence record from Townsend that has a definite date was the condor he shot at Willamette Falls, along the Willamette River, in April, 1835.

Gambel (1847, 25) observed that condors appeared to be more numerous in California in the winter.

[The California Vulture] is particularly abundant in California during winter; when they probably come from Oregon, as they are said to disappear from the region of the Columbia at that time.24

Koford (1953) acknowledged problems with the migratory hypothesis because the known records of observations in the region were asynchronous with the main salmon runs

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24 Gambel’s travels were limited to southern and central California (from about San Diego to Sonoma County; Beidleman 2006), so he may have observed condors becoming more abundant in California in winter, but he did not travel north of Sonoma County, California, or to Oregon, so his supposition that condors disappeared from Oregon in winter is hearsay.
along the Columbia River, the only significant source of food that he felt could have drawn condors north.

The only difficulty with this supposition [the migratory hypothesis] is that all of the definite records of condors in the region of the Columbia River are included between the months of September and March, the opposite of the season of the salmon run. Possibly the population of condors was so scattered in summer, when there was an abundance of food for 100 miles or more along the river, that the explorers did not notice them.25

A review of the timing and distribution of known historical condor records led S. Wilbur (1973, 1978) and Sharp (2012)26 to conclude that condors were likely a resident species in the Pacific Northwest. In the next section, we more thoroughly review migratory versus resident strategies for vultures of the world, reassess the timing of condor sightings in the Pacific Northwest with a more extensive data set of historical occurrences, and weigh the evidence for and against historical seasonal migration in California Condors. Although there are several types of migratory movements in birds (e.g., latitudinal versus altitudinal), this chapter focuses on seasonal latitudinal migration (migrating from the Pacific Northwest to southern or central California), as this has the most obvious and significant implications for reintroducing condors to the Pacific Northwest. Other forms of migration (e.g., altitudinal migration), wanderings, and dispersal movements are mentioned below, but our primary aim in this chapter is to explore whether or not at least a portion of the condors in the Pacific Northwest were resident birds.

### 2.7 Evolution of Migration in Vultures of the World

There are numerous factors that influence the evolution and extent of migratory behavior, including seasonality of resources, barriers, population density, historic and genetic factors,  

25 Although Koford (1953) relied on salmon runs as the basis for his migratory hypothesis, he also expressed doubt about salmon really being a significant condor food resource. Also, he suggested that the peak of the salmon run was during the summer; actually the peak of the chinook salmon run was in September, when steelhead were also abundant. Salmon and steelhead numbers were lower from November to March (Schoning et al. 1951). However, between the various species and populations, there were salmon-steelhead runs in the Columbia almost every month of the year.  

26 Sharp’s (2012) analysis included a number of records that are questionable given their lack of supporting evidence and distance in time or space from locations corroborated by physical evidence or firsthand accounts of trained naturalists or ornithologists.
competition, mortality costs, and transportation costs (reviewed by Alerstam et al. 2003). Many of the twenty-three vulture species undertake seasonal movements, although distances traveled and the proportion of the population that migrates vary widely (Eisenmann 1963; Stewart 1977; Bernis 1983; Houston 1983; Mundy et al. 1992; Rowe and Gallion 1996; Meyburg et al. 2004; Kim et al. 2007; Mandel et al. 2008; Bildstein et al. 2009; García-Ripollés et al. 2010). Often, migration is simply an adaptation to exploiting seasonal peaks of resource abundance and avoiding seasonal resource depletion (Alerstam et al. 2003), but such movements are constrained by the length of the breeding season and barriers to soaring flight. These constraints are magnified in large-bodied vultures, which have longer breeding seasons and are unable to sustain flapping flight for more than a few minutes (Pennycuick 1968; Mundy et al. 1992).

Food availability may be the ultimate determinant in shaping movement patterns in large avian scavengers. Small vultures, which tend to be extremely flexible in their diet—an adaptation to being weaker competitors at carcasses—can exploit large and small food items and can rely primarily on small food items when necessary (e.g., Paterson 1984; Ceballos and Donázar 1990; Prior 1990). Large size in vultures is selected for only when carrion is available in large packages (Ruxton and Houston 2004), meaning that seasonal movements of large-bodied or abundant food resources, or seasonal differences in mortality rates among these food resources, are likely to be key determinants of movement patterns of large vultures (Houston 1983). However, regular seasonal movements are likely to evolve only when vultures are not physiologically constrained from being able to keep up with, or move between, seasonal food resources, and when changes in food resources are predictable (Houston 1983).

Although food availability is a strong driver of avian scavenger movements, it is not the only mechanism that can drive seasonal movement patterns. Traditional movements, possibly reflective of other physical or biological properties of the landscape (e.g., preferred roosting locations or areas with exceptional soaring potential), may also drive condor movements and may be asynchronous with food density, as S. Wilbur (1972, 1978) observed in the wild condor population of the 1960s and 1970s.

Even when predictable seasonal differences in food availability or other landscape properties exist, the evolution of long-distance seasonal migration requires that breeding individuals complete their entire breeding and rearing cycle between long-distance movements.
Large birds tend to have more extended breeding and rearing periods than small birds (Blueweiss et al. 1978; Meiri and Yom-Tov 2004), making it difficult or impossible for some large birds to migrate long distances from nesting grounds on an annual basis. For those species with breeding periods longer than a year, long-distance seasonal migration is possible only for nonbreeders or juveniles. Juvenile vultures can, and often do, make long-distance movements (e.g., Arizona Condor Review Team 2002; Urios et al. 2010); apart from searching vast areas for food, juveniles may be particularly prone to wandering as they are typically outcompeted at carcasses by adults and may be seeking information about future breeding territories or location of mates. These movements may also represent attempts at dispersal, an evolutionary mechanism that may help reduce inbreeding in wild populations (Szulkin and Sheldon 2008).

The condor’s breeding cycle is one of the longest among all birds (Amadon 1964; Figure 2.17), with courtship in the late fall, egg laying from February to April, hatching from March to June, and young in nests from March to December (Koford 1953). In fact, the breeding cycle is so long that only condors that breed early in the season can breed late in successive years (Snyder and Hamber 1985). This is an extremely rare occurrence because fledgling condors remain partially dependent on their parents well into the spring after hatching. Thus, at a maximum, breeding pairs can breed two out of three years (Snyder and Hamber 1985) and chicks are dependent on parents for an extended period. Therefore, such long-distance seasonal migration among the entire population is not likely. However, nonbreeders and immature individuals are not limited in this respect, meaning that it is possible that a portion of the population could migrate (partial migration) while adult breeders remain resident.

Topography and weather, in combination with body size, can also play a role in determining whether a migratory life-history strategy is likely to evolve in soaring birds (Houston 1975). Small-bodied vultures such as Egyptian Vultures (Neophron percnopterus) and Turkey Vultures can travel thousands of miles seasonally and cross large expanses of water or flat terrain using flapping flight or soaring on weak thermals (Meyburg et al. 2004; Mandel et al. 2008). However, large-bodied birds, like condors, which have relatively high wing loading (a bird’s weight divided by its wing area—a measure of how much lift or rising air is required to
maintain soaring flight; see Table 2.3) and weak wing musculature,\textsuperscript{27} cannot sustain flapping flight for very long and are more reliant on areas with consistent upward air flow (e.g., mountain ridgelines) to stay aloft (H. Fisher 1946; Koford 1953; Pennycuick 1972; McGahan 1973; Houston 1975). Therefore, terrain features and weather patterns can limit seasonal movements of large soaring birds (Pennycuick 1972; Houston 1975, 1983). For example, Andean Condors are altitudinal migrants, regularly traveling large distances from mountainous nest sites to lowland feeding sites on a seasonal basis (Bildstein 2004). However, their distribution is tied to the Andes mountain chain and coastal areas where there is sufficient slope lift along mountain ridges or sea cliffs (Pennycuick and Scholey 1984; Lambertucci 2007). This constraint is consistent with available genetic data for Andean Condors showing detectable differences in gene distributions among populations on either side of a break in the Andes at the Northern Peruvian Low\textsuperscript{28}, which suggests a potential dispersal barrier (Hendrickson et al. 2003). Bildstein et al. (2009) noted that Griffon Vultures (\textit{Gyps fulvus}), another large-bodied vulture with high wing loading, had difficulties making a short (14 km) water crossing over the Strait of Gibraltar between Europe and Africa, with many attempts to cross the strait aborted. Houston (1983) also noted the dependence of Himalayan Vultures (\textit{Gyps himalayensis}) on reliable areas of slope lift in mountainous terrain. Thus, long-distance movements of large vultures are limited to areas where slope-lift or thermals provide reliable upward air currents. Mountainous regions may also be attractive to large soaring birds that have difficulty taking off over flat ground because these birds can jump off some eminence rather than struggle to reach the minimum takeoff speed necessary for flight (Pennycuick 1968).

\subsection*{2.8 Modern California Condor Movement Studies}
Biologists have long sought to describe California Condor movement patterns in southern California (Koford 1953; A. Miller et al. 1965; USFWS 1975; S. Wilbur 1978; USFWS 1980; E. Johnson et al. 1983). However, these early studies were hampered by a lack of radio-tracking technology, the inaccessibility of large portions of the condors’ range, and the capability of

\textsuperscript{27} California Condors have the weakest wing musculature of all New World vultures in relation to body weight (H. Fisher 1946).
\textsuperscript{28} The Andes form a largely unbroken, high elevation mountain chain for over 7,500 kms along the Pacific coast of South America. However, there is a pronounced discontinuity in the Andes in northern Peru where the mountain range changes direction. This region, which is about 100 km wide, is variously called the Northern Peruvian Low, Huancabamba Depression, Piura Divide, or Depression de Huarmaca.
condors to make extensive movements in short periods of time. With the advent of a photographic archive of condor primary feather patterns (allowing individual identification; Snyder and Johnson 1985) and the development of lightweight patagial-mounted radio transmitters, the first quantitative study of condor movement patterns was undertaken from 1982 to 1987 (Meretsky and Snyder 1992). This study found, among other things, that (1) breeding pairs in California tended to restrict their movements to within 50–70 km of their nesting site, (2) unpaired and immature condors made the longest observed daily movements, (3) foraging zones varied seasonally in accord with recent and historical patterns of food availability, and (4) most birds traveled widely among feeding zones throughout the year, probably in an attempt to maintain familiarity with unpredictable food supplies.

The analysis of spatial relationships between animals and their environment became increasingly accessible in the 1980s and 1990s with increased computing power and the commercial development of Geographic Information Systems (GIS). In conservation biology, GIS is routinely used to overlay information on the occurrence of species and the environmental variables that might explain the species’ presence or absence. Using this technology and condor occurrence data from the 1980s studies, Stoms et al. (1993) evaluated condor occurrence data through time and found that the species was non-randomly associated with mapped land cover types, and the precipitous decline in the population in the twentieth century resulted in only a small reduction of the species’ overall range (in southern California), as birds continued to forage over most of the range.

As captive birds were reintroduced to the wild through the 1990s and 2000s, advances in combining Global Positioning System (GPS) receivers and satellite tracking technology provided the means for more detailed studies of condor movements. Hunt et al. (2007) described the movements of condors released at Vermilion Cliffs in northern Arizona from 1996 to 2005 based on very high frequency (VHF), GPS-equipped, satellite-reporting transmitters. They found that early in the release program condors moved in an unpredictable manner. During the summer months, when thermals were strong, some individuals ventured hundreds of kilometers away from the release area. For example, in July 1997 a female condor traveled 301 km to Arches National Park in Utah. In 1998, three condors traveled 387 km to Grand Mesa, Colorado, and one individual traveled 516 km to Flaming Gorge, Wyoming. Yet another long-distance flight occurred when one bird roamed as far as the Arizona-California border south of
Lake Havasu City. All of these birds eventually returned to the release site. These long-distance movements were primarily by young birds (four years old or less) and apparently followed major river corridors (i.e., Colorado, Green, and San Juan Rivers; Arizona Condor Review Team 2002). As birds in the released flock became more experienced, they started to develop more predictable movement patterns, seasonally exploiting areas of higher food density during the warmer months (e.g., the Kolob region of Utah, where thousands of sheep are seasonally grazed in high-elevation meadows) when thermal updrafts were most reliable, and staying closer to the release site during the winter when thermals were less reliable and the risk of being grounded was greater.

M. Johnson et al. (2010) analyzed space use of reintroduced California Condors in southern California based on GPS transmitter location data from 2004 to 2009. They found that condors were beginning to recolonize the eastern portion of their historical range in the southern Sierra Nevada and were reestablishing traditional movement and foraging patterns. Unpublished data from condors being tracked with GPS transmitters in southern and central California also demonstrate that condors are reoccupying portions of their historical range, with occasional movements between the central and southern California flocks (approximately 400 km) and occasional exploratory movements from southern California into the southern Sierra Nevada (approximately 250 km; USFWS California Condor Recovery Office, unpublished data).

2.9 Seasonality of Occurrence Records in the Pacific Northwest

If condors historically expressed a seasonal migration pattern in the Pacific Northwest we would expect to see differences in the number of occurrence records across seasons. However, we found no clear north–south pattern of condor occurrence records by season (Figure 2.18), and the occurrence records do not support Douglas’s (1914) hypothesis that condors migrated south in the winter.

Condors were observed in all seasons in the Pacific Northwest (Figure 2.19). Specific summer records in Oregon and Washington are sparse; however, John Kirk Townsend described condors variously as most abundant in the summer or spring along the Columbia. David Douglas reported them in the “summer and autumn months” as far north as the Canadian border east of the Cascades (Douglas 1914), and John Scouler obtained a condor specimen from the Native Americans along the Columbia in September 1825 (Scouler 1905). Finally, two condors were
observed near Drain, Oregon, in the summer of 1903 (Peck 1904; W. Finley 1908b; Gabrielson and Jewett 1970). The rarity of summer occurrence records in Oregon and Washington is consistent with modern observational studies of Andean Condors and is possibly the result of condors migrating to more inaccessible, higher elevations in the summer in pursuit of better soaring conditions (Lambertucci 2010). Summer is also the season when some large mammal populations migrate upslope following the wave of nutrient-rich vegetation that moves up the elevation gradient through the growing season—potentially providing a more accessible and concentrated food resource for scavengers. Andean Condor movements into higher elevation sites during the summer may also be the result of the birds seeking out traditional, but only seasonally available, roosting sites, as was observed in the nonbreeding wild California Condor population in the 1960s and 1970s (S. Wilbur 1978).

The outer boundaries of condor occurrence records to the north and east are formed by fall and summer records. This is likely the result of the predominant high pressure weather patterns and high temperatures that typify the Pacific Northwest from June to September (Maunder 1968). These bring stronger thermals that facilitate long-distance movements in soaring birds. This pattern is similar to the seasonality of long-distance movements observed in condors released in northern Arizona (Hunt et al. 2007).

No historical nests of California Condors have yet been confirmed in the Pacific Northwest.29 However, two condor specimens collected in the Pacific Northwest (one held at Eureka High School, California, and the other at the US National Museum) were juveniles (Figure 2.20). Because young condors often stay in close proximity to their nest site for the first year or two of life, it is possible that these birds were hatched in the region and that at least a portion of the condor population was resident.30

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29 Aside from the second- and third-hand accounts reported by John Kirk Townsend (Audubon 1840; J. Townsend 1848). Townsend reported to Audubon that the Indians thought they nested on the ground in the central Cascades (Audubon 1840). Townsend (1848) also reported hearsay (almost certainly from David Douglas’s interactions with the Indians) that they nested in trees in the Umpqua region of southwest Oregon. Cooper and Suckley (1859) stated that “Townsend supposed he saw its nests along the Columbia.”

30 While the presence of young birds in the Pacific Northwest is suggestive of breeding in the Pacific Northwest, taken alone, it is not conclusive. Condors in their third year, when they usually begin to move long distances from their natal territory, are still dark headed and often retain some down on their heads.
2.10 **SUMMARY OF HISTORICAL MOVEMENT PATTERNS**

Reconstructing historical movement patterns of condors in the Pacific Northwest is not possible given the limitations of the available data. However, we can draw the following general conclusions from the historical record, our review of migration in other vultures of the world, and data from modern condor movement studies:

1. Few vultures exhibit long-distance seasonal latitudinal migrations, but many vultures exhibit shorter seasonal movements (e.g., altitudinal migration or movements associated with seasonal shifts in food supply).

2. Breeding condors cannot migrate and successfully raise young due to their extended breeding cycle, which can last for more than a year. Immature and other nonbreeding birds are not limited in this respect.

3. Condors, as large soaring obligate scavengers with high wing loading, are adapted for traveling long distances in search of food but are physiologically limited to areas with upward-moving air in the form of thermals or slope lift (Ruxton and Houston 2004). Condors attempting to cross areas of inconsistent patterns of lift risk becoming grounded and subject to mortality from predators or starvation. Thus, as long as food is available, it is generally advantageous for condors to restrict movements to areas with consistent lift.

4. Modern studies of condor movements using GPS and satellite technology have documented long-distance exploratory movements of more than 500 km, but no regular long-distance seasonal latitudinal migration has evolved in released birds. Shorter seasonal movements in relation to food availability and accessibility, however, have been observed, but there are no discrete seasonal movements between breeding and nonbreeding areas. This is consistent with movement patterns seen in Andean Condors, a good ecological surrogate because of their size, breeding and rearing duration, and presence in a large north–south mountain chain that could facilitate migratory movements.

5. Condors were historically observed throughout the year in the Pacific Northwest and, based on anecdotal observations, do not appear to have been migratory. Exploratory movements east of the Cascades and north to British Columbia likely occurred when weather patterns were favorable.
6. Two young condor specimens were collected by naturalists in the Pacific Northwest, providing physical evidence that breeding likely occurred in the region.

2.11 TIMING AND CAUSES OF THE CONDOR’S RANGE COLLAPSE

The extinction problem has little to do with the death rattle of its final actor. The curtain in the last act is but a punctuation mark—it is not interesting in itself. What biologists want to know about is the process of decline in range and numbers. (Soulé 1983, 112)

The California Condor has sometimes been portrayed as a Pleistocene relict or a senescent species that has been in a state of population decline for thousands of years (e.g., L. Miller 1942; Pitelka 1981). Despite a significant range contraction and the concurrent extinction of several large avian scavengers (including several condor species) at the end of the Pleistocene, the ethnographic, paleontological, and early observational record of California Condor populations along the West Coast of North America suggests that they were not rare at the time of Euro-American contact. While the exact population size of condors at Euro-American contact is unknown, a number of early explorers and settlers considered them common or numerous, especially in California. Bryant (1891, 52) noted that

[the California Vulture] is better known in California than elsewhere, where, previous to the civilization of that country, it was very abundant, approaching in large flocks the near vicinity of the Missions, where it contended with the coyote for the offal and carcasses of cattle slaughtered for their hides and tallow.

In the fall of 1826, David Douglas observed condors in “great numbers” along the lower Columbia River (1914). Townsend said he would not consider them numerous along the Columbia in the 1830s (Audubon 1840) but also stated, “during the spring, I constantly saw the [California] Vultures at all points where the Salmon was cast upon the shores” (J. Townsend 1848, 266). Clyman (1926) described them as being in “greate abundance” in Napa Valley, California, in 1845. John Strong Newberry (1857, 73) saw them “every day” on his travels in the Sacramento Valley in 1855. Joseph Lamson observed “upwards of fifty” condors flying over the mountains east of San Francisco in the 1850s (Monteagle 1976).
Snyder and Snyder (2005) calculated that if the 5 percent annual population decline estimated for 1950 to 1968 was extrapolated backward in time, there could have been one thousand condors alive at the beginning of the 1900s, although they recognize the possibility of differential mortality rates through time and do not consider this to be a reliable estimate of the population at the turn of the century.

While we may never know the true historical population size, the abundance of ungulates and marine mammals prior to Euro-American expansion into the region would likely have once supported several thousand condors in the western United States. A. Taylor (1859) reported that in July 1859, his friend had observed as many as three hundred condors feeding on dead sea lions in Monterey, California, but Taylor’s facts were sometimes inaccurate and the identity and reliability of his source are unknown. Nevertheless, it is not beyond the realm of possibility, as flocks of several hundred vultures are not uncommon when food is abundant (e.g., Prather et al. 1976; Mundy et al. 1992; Bildstein et al. 2009).

Andean Condors—which also have high wing loading, are long lived, have slow rates of maturation, and are restricted to more mountainous regions of South America—are estimated to number at least 10,000 individuals (BirdLife International 2014). Using mark-recapture techniques, Lambertucci (2010) estimated that there were 260–332 Andean Condors in just one area of northwestern Patagonia measuring 6,300 km² (smaller than the Olympic Peninsula). This estimate may represent a reduced number of birds from the historical population size due to ongoing threats such as persecution, poisoning, and electrocution (Lambertucci 2010). Given the similarities in body size, diet, reproductive output, and mobility between California and Andean Condors, it seems plausible that California Condors, which once occupied an area from Baja California to British Columbia, may also have historically numbered several thousand individuals rangewide. However, without additional information, this remains a tentative, untested hypothesis. Analysis of genetic data in museum specimens may provide one avenue of inquiry to evaluate this hypothesis (see Chapter 3).

A number of hypotheses have been proposed for why condors disappeared from the Pacific Northwest. However, there has been no systematic and thorough accounting of the likelihood of each hypothesis for the region given the facts regarding the timing and magnitude of the threats, population decline, and range contraction (but see S. Wilbur 1978, 2004; and Snyder and Snyder 2005 for a more general discussion of reasons for the condor’s historical
decline). Here we assess the plausibility of each hypothesis with respect to timing, magnitude, and extent, in the hope of narrowing the range of proposed explanations.

2.11.1 Secondary Poisoning

The use of poison to kill predators and other mammalian pests was largely an outgrowth of the expanding fur trade and livestock industries throughout the West. Livestock expansion started during the late 1700s in the Southwest in order to provide a reliable food supply for early explorers and missionaries (Love 1916), and it reached the Pacific Northwest on the heels of the fur trading industry, which rapidly expanded in the Pacific Northwest in 1821 when the Hudson’s Bay Company gained access to trapping grounds in Oregon, Washington, and British Columbia (Hammond 2006). The Hudson’s Bay Company viewed competition from predators as counter to the company’s interests and actively promoted wolf poisoning (Hammond 2006). It also sought to protect the small but growing number of livestock it and its workers owned. In 1839, Dr. John McLoughlin, chief factor in charge of the Columbia District for the Hudson’s Bay Company, requested poison to use on the company farms in the Pacific Northwest and to sell to settlers (Hammond 2006). The company responded by sending

a small quantity of Strychnine made up in dozes for the destruction of Wolves; it should be inserted in pieces of raw meat placed in such situations that the shepherd’s dogs may not have access to them, and the natives should be encouraged by high prices for the skins to destroy wolves at all seasons. (Rich 1943, 164)

Strychnine was offered for sale by the Hudson’s Bay Company (Rich 1943) and was likely used around company farms at Nisqually, Cowlitz, and Fort Vancouver in Washington. Titian Ramsey Peale reported that it was used to destroy wolves near Puget Sound in 1841 (Peale 1848). Missionaries also used poison to kill wolves around missions in the region as early as 1839 (Marshall 1911; Gibson 1985). In the fall of 1839, following a series of wolf and Indian dog attacks on livestock and horses near present-day Lewiston, Idaho, missionary Henry Spalding requested that the American Board of Commissioners for Foreign Missionaries send enough poison to kill one thousand wolves (Gibson 1985). The following spring he requested enough poison to kill twenty thousand wolves (Gibson 1985).

31 More formally known as *nux vomica* on some Hudson’s Bay Company inventories.
As the number of settlers to the region increased, so did interactions between livestock and predators. Following widespread wolf depredations on valuable imported livestock, predator bounties were enacted by the first provisional government in the Oregon Territory in 1843 (Brown 1892; Hampton 1997). Thomas Cox, who operated a trading post in Salem, Oregon, imported large amounts of strychnine to the Willamette Valley starting in 1847 (Minto 1905). John Minto, an early pioneer (and later a prominent sheep farmer and Oregon state representative) who arrived in the Willamette Valley in 1844, wrote:

The chief enemies of early home building were the carnivori, of which the large wolf was the most destructive, attacking all kinds of stock, colts being their most easy prey, next calves and young cattle. They kept range cattle wild and made swine band together in self defense. They ate up the first two swine I owned, and all their young but one. They ran in families most of the year, I think. I never saw more than seven or eight together, and were so voracious that they were easily poisoned, leaving the small wolf, or coyote, the most cunning and active pest. (1908, 149)

Strychnine use expanded throughout the American West during the Gold Rush of 1849, when jars of it in crystalline-sulphate form quickly became a familiar feature on the shelves of trading posts (Coates 1999; Jones 2002). Roselle Putnam, daughter of Oregon pioneer Jesse Applegate, offers the following firsthand account from a settlement in southwest Oregon in 1852:

The wolves of this country are very large and numerous[—]there has been a great many of them killed this winter, in this neighborhood with strychnine, Charles put out upwards of thirty doses of it, and I suppose every one killed a wolf at least the physician from whom we got it said it would—we have seen two die near the house—notwithstanding the quantity of poison they have taken—they are still to be heard every night or two howling round us & one impudent fellow has been in the habit of coming every night to pick up the scraps about the house & even in the porch a couple of nights ago—we gave him a dose of poison and he has not been back since. (1928, 256)

Over the course of the latter half of the century, poison would decimate wolf populations across North America, with an untold impact on other scavengers (Hampton 1997).
It was also used by farmers to kill smaller agricultural pests such as ground squirrels and rabbits (*Willamette Farmer* 1872).

The prevailing opinion among those commenting on the condor’s status was that poisoning was to blame for the condor population decline in the late 1800s (A. Taylor 1859; H. Henshaw 1876; Cooper 1890; Lucas 1891; Streator 1888; Bendire 1892; Shufeldt 1900; *New York Times* 1906; W. Finley 1908b; W. Finley and I. Finley 1915; Lyon 1918; Tyler 1918; W. Fry 1928), yet some believed that condors and other vultures possessed some natural immunity to poisons or could disgorge the poison before it was absorbed (Scott 1936b; Harris 1941; D. Smith 1978). Opponents of the poisoning hypothesis noted the scarcity of historical accounts of California Condors actually being killed by poison.

If poisoning had been a significant factor in the condor’s population decline and range contraction, one might expect more reports of condor deaths from poisoning in the historical record, as a dead bird with a nine-foot wingspan was newsworthy in the 1800s (Scott 1936b; S. Wilbur 1978, 2004). However, the absence of evidence is not evidence of absence. It is entirely plausible that poisoned birds were significantly underreported because they died in inaccessible areas, decomposed before being found, or were scavenged themselves. Moreover, those putting out the poison may have been uninterested in its side effects on what they viewed as economically unimportant birds, or they may have been misinformed and thought that condors were detrimental to livestock interests—a common misconception at the time. One trapper described the animals impacted by predator poisoning: “Magpies, buzzards, porcupines, wildcats, skunks; Did not count them as was glad to see them dead.” (Linsdale 1932, 126)

Adverse impacts on other avian scavengers with higher reproductive rates and less parental care than condors were noted. One wolf hunter in Texas reported, “Many, many hundreds of ravens were killed by eating the carcasses of poisoned wolves.” Another wolf hunter in Kansas claimed that ravens disappeared entirely from the central plains from eating poisoned baits (Hampton 1997, 110).

If California Condors congregated at a poisoned carcass, something that would not be unexpected (John Pemberton documented thirty condors at a single [untainted] carcass [Koford 1953]), a large number of condors could have been wiped out in a very short time. Assuming an average of ten condors at a medium-sized carcass, and a hypothetical condor population in the Pacific Northwest of one thousand individuals, just one hundred poisoned carcasses could have
contaminated the entire population. The number of poisoned carcasses was actually much higher, based on accounts of settlers and travelers indiscriminately lacing carcasses with poison along trails and around homesteads. Over just a four-year period in one small area of Humboldt County, California, government trappers, farmers, and ranchers reported the loss of fifty “buzzards” (presumably Turkey Vultures) from secondary poisoning (Linsdale 1932). Linsdale (1932) also received thirteen other reports of Turkey Vultures or “buzzards” being killed by poison in California.

In parts of the world where predator poisoning is still a common practice, vulture deaths and population declines from secondary poisoning have been well documented. For example, predator poisoning is one of the primary causes of Egyptian Vulture declines in Spain (Carrete et al. 2007; Hernández and Margalida 2009). A total of 241 poisoning incidents were recorded in Spain, killing 456 Cinereous Vultures (*Aegypius monachus*) from 1990 to 2006 (Hernández and Margalida 2008) with as many as thirty-eight vultures poisoned in a single incident; carbofuran, aldicarb, and strychnine accounted for 88 percent of the deaths from poisoning. Reports of mass vulture poisonings within Africa are numerous (reviewed by Ogada and Keesing 2010). Mundy et al. (1992) reported 293 poisoned vultures (including White-backed Vultures [*Gyps africanus*], Cape Griffons [*Gyps coprotheres*], and Lappet-faced Vultures [*Torgos tracheliotos*]) in just a two-year period in Kruger National Park, South Africa (purposely poisoned to be sold for medical purposes on the black market). An estimated one hundred vultures were killed at a single cow carcass poisoned with strychnine near Mochudi, Botswana, in December 1984 (Mundy et al. 1992). Simon Thomsett reported 187 vultures at a single poisoned carcass in Kenya (Virani et al. 2011).

In Europe, strychnine poisoning has likely resulted in the disappearance of the Egyptian Vulture from most of the mountainous parts of the Midi in France, the loss of Bearded Vultures (*Gypaetus barbatus*) from southern Spain as well as Bosnia and Herzegovina, the decimation of several vulture species from Sardinia, the loss of Griffon Vultures from Sicily, and the extermination of Bearded Vultures and Griffon Vultures from Romania (reviewed by Bijleveld 1974).

In Africa, the use of carbofuran (which also goes by the trade name Furadan) by livestock owners to kill lions and other predators is widespread, and this powerful and toxic insecticide may be a factor in the decline of several vulture species in that region (Thiollay 2006;
This poison is particularly dangerous because it is odorless, tasteless, cheap, and readily available. In Kenya, Otieno et al. (2010) reported the deaths of twenty White-backed Vultures related to predator poisoning at a single bait site. Mineau et al. (1999) documented hundreds of cases of raptors being poisoned by the use and abuse of organophosphorus and carbamate pesticides in Canada, the United States, and the United Kingdom from 1985 to 1995. This included 125 cases of Golden Eagle mortalities from pesticide abuse related to attempts to poison coyotes or eagles. A study of secondary poisoning of eagles over a ten-year period (from 1993 to 2002) in Saskatchewan, Canada, resulted in fifty-four putative poisoning incidents involving seventy Bald Eagles and ten Golden Eagles (Wobeser et al. 2004).

The recent catastrophic collapse of Asian vulture populations demonstrates how poisoned carcasses can quickly decimate populations of once-common avian scavengers (in this case the poison was a veterinary drug given to cattle, rather than an attempt to deliberately poison predators; Gilbert et al. 2002; Prakash et al. 2003; Green et al. 2004; Oaks et al. 2004; Shultz et al. 2004). In less than ten years, two species of Gyps vultures declined by over 90 percent in India (Prakash et al. 2003) due to diclofenac poisoning (Oaks et al. 2004; Shultz et al. 2004). The sociality and large range size of many vultures means that massive population declines can occur with seemingly small percentages of carcasses poisoned. For example, Green et al. (2004) reported annual mortality rates of 22–50 percent in Gyps vultures in Southeast Asia, which could be explained by diclofenac poisoning in less than 1 percent of carcasses.

Although direct evidence linking poisoning and California Condors is limited, the circumstantial evidence that condor declines may have been caused by poisoning is significant. Most notably, vulture declines in other parts of the world have been directly linked to predator poisoning campaigns or inadvertently poisoned carcasses, something that was not known at the time this hypothesis was roundly criticized by Scott (1936b), Harris (1941), Koford (1953), and S. Wilbur (1978). Socially foraging vultures are particularly susceptible to secondary poisoning because a large portion of the flock can be poisoned at a single poisoned carcass. Given the evidence now available, it seems plausible that poisoning played a significant role in the condor’s range contraction. The dearth of reasonable alternative hypotheses (aside from direct persecution through shooting, and possibly lead poisoning [see below]) lends further support to this idea.
2.11.2 Lead Poisoning

Lead toxicosis is currently considered to be the anthropogenic threat of primary concern for reestablishing viable self-sustaining condor populations (Wiemeyer et al. 1988; Pattee et al. 1990; Meretsky et al. 2000; Snyder and Snyder 2000; D. Fry 2003; Cade et al. 2004; Cade 2007; Woods et al. 2007; Finkelstein et al. 2010; Walters et al. 2010; Finkelstein et al. 2012; Rideout et al. 2012). The most likely pathway for lead ingestion is through gut piles left in the field by hunters after they remove the meat, or through animals that are shot and unrecovered (Church et al. 2006). Gut piles and carcasses can contain significant quantities of lead fragments from spent ammunition (Hunt et al. 2009), and numerous studies have shown elevated lead levels in avian scavengers, including condors, vultures, eagles, and ravens, with the most likely source being lead ammunition (Janssen and Anderson 1986; Pattee et al. 1990; Church et al. 2006; Cade 2007; Craighead and Bedrosian 2008; Bedrosian and Craighead 2009; Helander et al. 2009; Stauber et al. 2010; Lambertucci et al. 2011).

Although lead is a well-known neurotoxin and nephrotoxin (a toxin having specific destructive effects on kidney cells), the threat of lead toxicosis to California Condors from spent ammunition became recognized only after Locke et al. (1969) discovered that Andean Condors were susceptible to lead poisoning and suggested that California Condors might also be susceptible. Additional research in the 1980s confirmed that California Condors were ingesting lead in the wild and were susceptible to its effects (Janssen and Anderson 1986; Snyder and Snyder 1989). Given the relatively recent realization that lead ammunition is a threat, the extent of its historical impact is not well understood.

Changes in bullet construction and concomitant changes in bullet velocity may have changed the bioavailability of lead to scavengers beginning in the 1890s with the invention and mass production of smokeless powder cartridges to replace the slower burning and less powerful black powder cartridges. Smokeless powder rounds and the rifles designed specifically to use these new rounds were immediately popular. The Winchester Model 1894, the first commercial rifle designed to chamber smokeless powder rounds—specifically, the .30-30 Winchester, or .30 WCF, which is still a popular round—was a sensation, with over one million sold by 1927 (T. Henshaw 1993). Numerous other arms and ammunition manufacturers were also developing smokeless powder munitions and guns to shoot them by the time of the First
Annual Sportsman’s Exposition at Madison Square Garden, New York, in 1895 (Forest and Stream 1895).

Aside from the obvious advantage of making less smoke, smokeless powder rounds also generated significantly more force than black powder (Kneubuehl et al. 2006). Maximum muzzle velocities for black powder rifles were restricted to about 1,850 feet per second (ft/sec) and typically fell within the range of 1,250–1,450 ft/sec (Walter 2006). The significant increase in energy created by smokeless powder was not effectively harnessed by conventional solid lead bullets, which led manufacturers to quickly develop a jacketed bullet, consisting of a lead core encased in a “jacket” of copper, cupronickel, tin-plated copper, or mild steel. Jacketing the lead bullets decreased the friction of the bullet as it traveled down the barrel, reduced leading of the rifle barrel, and greatly increased muzzle velocities (i.e., resulting in loads exceeding 2,500 ft/s; Whelen 1918). With greater velocities, bullets could be made longer and thinner to fly faster and stay true at greater distances. Early full-metal jacket bullets (where the lead core was fully encased in another metal) were found to be unsatisfactory for big game hunting because they tended to penetrate straight through the animal without causing sufficient damage, expending most of their energy beyond the target. To rectify this problem the cartridge companies soon developed the soft point bullet, a jacketed bullet with a small amount of exposed lead at its tip. These bullets expanded in animal tissue, causing serious wounds (Whelan 1918).

Despite their advantages, higher velocity jacketed and soft tip bullets have a much greater rate of fragmentation than solid lead bullets fired from a black powder rifle (Whelan 1918). The fragmentation of bullets into a cloud of small particles increases the surface area of metallic lead and its uptake by animals that consume the fragments (Pauli and Buskirk 2007; Hunt et al. 2009). Conversely, when bullets remain largely intact (as the lead bullets from black powder rifles likely did), they may exit the animal without significant fragmentation, thus leaving little to no lead for uptake by scavengers (Pauli and Buskirk 2007), or the intact bullet may be large enough for scavengers to detect and avoid while feeding (e.g., Stendell 1980).

If bullets shot from historical firearms did fragment and contaminate carcasses, lead poisoning could have been a significant cause of condor mortality in the late 1800s due to intensified market hunting at that time on native ungulates and pinnipeds (see “Reductions in Food Availability”, below), as well as increased subsistence hunting from the growing human population. Shotgun pellets from the extensive market, recreational, and subsistence killing of
waterfowl (especially in and around the Central Valley of California) and other small game may also have been a source of lead contamination, but condors are rarely observed feeding on bird carcasses due to their small size. Shotgun pellets have been implicated in some modern condor deaths (Rideout et al. 2012), but the source of that lead shot is unknown (some possibilities include upland game bird hunting; plinking small mammals; dispatching sick or injured livestock or pets; or depredation kills). Regardless of whether additional research clarifies the role of lead poisoning in the early decline of the condor, the overwhelming evidence that modern lead ammunition is the primary threat to reestablishing self-sustaining condor populations (Walters et al. 2010; Finkelstein et al. 2012; Rideout et al. 2012) means that reducing the threat of lead-contaminated carcasses is essential for a successful reintroduction program in the Pacific Northwest.

2.11.3 DDT, DDE, and Eggshell Thinning

DDT was first developed by an Austrian graduate student in 1873, but its properties as an insecticide were unknown until around 1940, when a Swiss chemist, Dr. Paul Hermann Müller, discovered that it was effective at killing insects—a discovery that later won him the Nobel Prize in medicine (see http://nobelprize.org/nobel_prizes/medicine/laureates/1948/muller-bio.html). DDT was widely used as a pesticide during World War II, with peak US production in the 1960s (Woodwell et al. 1971). Following the war, the Montrose Chemical Corporation of Los Angeles, California, the largest manufacturer of DDT in the world, developed a waste disposal system that funneled DDT and the plant’s processing wastes into the county sewer system, which drained into the ocean and contaminated the Southern California Bight (Kehoe and Jacobson 2003).

DDT and its metabolite DDE are known to bioaccumulate through the food chain and cause eggshell thinning, increased incidences of breakage, and resultant declines in productivity in birds. High levels of DDE were reported from condor eggshells in the 1960s, and DDE was suspected as a possible cause of decreased productivity in the historical population (Kiff et al. 1979; Kiff 1989; but see Snyder and Meretsky 2003). Recent data from condors feeding on migratory sea lions along the California coast near Big Sur, California indicates that they are ingesting sufficient DDE to induce eggshell thinning (Burnett et al. 2013).

DDE was not present in the environment when condors inhabited the Pacific Northwest and therefore was not associated with their historical decline and range contraction throughout
the nineteenth century. However, given eggshell abnormalities in condors feeding on marine mammals, future reintroduction efforts should consider the scope and magnitude of DDE and other potential contaminants (e.g., mercury, polychlorinated biphenyls [PCBs]) in marine mammals and surrogate coastal scavengers when evaluating potential reintroduction sites in the Pacific Northwest.

2.11.4 Collecting and Shooting
Collecting condor specimens, as well as wanton shooting, has been suggested as a major cause of the condor population decline in the 1800s and early 1900s (Dawson 1923; Scott 1936a, 1936b; Koford 1953; McMillan 1968; S. Wilbur 1978). Reasons for shooting condors were varied and included general curiosity, target practice, perceived protection of livestock, use of quills as gold-dust containers or for making tobacco pipes, and the desire to obtain specimens for private or institutional museum collections (reviewed by S. Wilbur 1978; also see Cooper 1890; Bidwell 1890; Anthony 1893; Douglas 1914; Scott 1936a; Harris 1941; Koford 1953). David Douglas noted that in the Oregon Territory, circa 1826, condor quills were “highly prized by the Canadian voyageurs for making tobacco pipe-stems” (1914, 154–55). However, the extent of killing to obtain these pipe stems is unknown.

Condor skins were collected in the Pacific Northwest for museums, beginning with Dr. John Scouler in 1825.32 By the dawn of the twentieth century, condor skins were extremely valuable and regularly sought by collectors (Blake 1895; S. Wilbur 2004). Koford (1953) estimated that approximately two hundred condors and condor eggs had been taken as specimens from the late 1700s to the mid-1900s. S. Wilbur (1978) used an extensive survey of museum collections and early diaries and journals to document 177 condors killed and 71 eggs taken for collections. Additional research since 1978 has revealed an additional 18 condors killed, for a total of 195 (S. Wilbur, pers. comm., 2011).

With the rise of zoological institutions, there was also a growing demand in the late 1800s and early 1900s for live specimens. Thus, condors were captured and shipped to zoos in

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32 Lewis and Clark’s party killed a number of California Condors but apparently preserved only a few parts, which were deposited in Peale’s Museum in Philadelphia. The museum was disbanded in the late 1840s and the collections were sold off, and it is unknown if these parts are still in existence (S. Wilbur, pers. comm.).
London, New York, Philadelphia, and Washington, DC (Sclater 1866; W. Finley 1910; J. Dixon 1924). Condors were also live-captured as curiosities to display in hotel courtyards, or even to be kept as personal pets (Daily Union 1857; Gassaway 1882; Holmes 1897; Daggett 1898; Rising 1899; Stephens 1899; Millikan 1900).

In addition to shooting for collections, shooting without any apparent purpose was also a relatively common occurrence. S. Wilbur (1978) documented forty-one condors shot for no apparent reason between 1806 and 1976. As W. Finley (1941) noted: “because of its size, it is a mark for wanton hunters with long-range rifles who often penetrate the wilder mountain regions where this bird lives.” J. G. Cooper (1890) stated:

> The other [reason for the condor’s population decline, in addition to poisoning and reduction in livestock abundance in southern California] is the foolish habit of men and boys, who take every opportunity of shooting these birds, merely because they are so large and make good marks for their rifles when they want to practice at vultures’ heads as a preparation for the annual turkey shooting in the fall. Some may even believe that the vultures may injure their live stock, but with little reason.

Some killing may have been done as retribution for appropriating game. Andrew Jackson Grayson noted that prior to 1847, the condor was “much disliked by the hunter for its ravages upon any large game he may have killed and left exposed for only a short length of time” (Bryant 1891, 52–53). Although not specifically stated, this suggests that some hunters around that time killed condors in retribution for taking their game. Many of these killings likely went unreported.

In the Pacific Northwest, we documented thirty-nine condors killed for museum collections or shot for no apparent purpose from 1804 to 1905 (Table 2.2). In addition, two condors were live-captured and kept as pets.33 This is a relatively small number of individuals over the course of a century, even for a long-lived vulture. However, there are surely many shooting deaths that went unreported. Shooting animals for entertainment or target practice was not considered morally objectionable at the time. As noted by John Work, who led a Hudson’s Bay Company fur brigade through northern California in 1832–1833:

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33 A third condor was injured and kept as a pet for some time, escaped once, was found “more dead than alive,” later escaped again, and was never found. See Millikan (1900) for this fascinating account. An abbreviated version of this account is also provided in Appendix 1, record 45.
When the most of the people have ammunition and see animals they must needs fire upon them let them be wanted or not. (Maloney 1945, 31)

Therefore, while we can document only a small number of condors actually killed in the Pacific Northwest, our imperfect knowledge regarding actual numbers taken and our recognition of the lack of moral impediments to killing condors leaves the possibility open that this was a significant threat to the population and a primary factor in the extirpation of the condor from the Pacific Northwest.

2.11.5 Egg Collecting

Egg collecting did not take hold in North America until the 1860s and reached its zenith from 1885 to the 1920s (Kiff 2005). In combination with shooting, egg collecting may have had an impact on California Condor populations in southern California (S. Wilbur 1978). However, given that condors will double clutch if the first egg is removed or destroyed (Snyder and Hamber 1985), the extent of this impact on population demographics is unclear.

Regardless of the extent of the impact of egg collecting in southern California, there are no certain records of condor nests or eggs collected in the Pacific Northwest. In 2003, the Napa-Solano Audubon Society published a note in their book Breeding Birds of Napa County, indicating that a condor egg was collected in Napa County on August 16, 1845. However, the veracity of this report is questionable given the late summer collection date. Other than this dubious record no condor eggs are known to have been collected from the Pacific Northwest. Thus, egg collecting was not a factor in the condor’s extirpation from the region.

2.11.6 Loss of Nesting Habitat

California Condors, and New World vultures in general, have variable nesting habitats, using large tree cavities, caves, crevices in rock faces, and rock ledges (Snyder et al. 1986). Although historical nesting sites of condors in the Pacific Northwest were not documented,34

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34 Aside from the second- and third-hand accounts reported by John Kirk Townsend (Audubon 1840; J. Townsend 1848). Townsend reported to Audubon that the Indians thought they nested on the ground in the central Cascades (Audubon 1840). Townsend (1848) also reported hearsay (almost certainly from David Douglas’s interactions with the Indians) that they nested in trees in the Umpqua region of southwest Oregon. Cooper and Suckley (1859) stated that “Townsend supposed he saw its nests along the Columbia.”
they are known to nest in coast redwoods (*Sequoia sempervirens*) near Big Sur, California (Ventana Wildlife Society, unpublished data), and historically nested in giant sequoias (*Sequoiadendron giganteum*) in the southern Sierra Nevada (Snyder et al. 1986). Accordingly, they may have used cavities in the large trees from northern California to southern British Columbia. Therefore, it is worth considering whether early logging of old-growth forests may have substantially reduced the number and distribution of suitable tree nesting sites for condors at the time condor populations were declining in the region.

The earliest logging of redwood forests was by the Spaniards near San Francisco Bay, but these were small operations (Browne 1914). Up until the Gold Rush era, starting in 1849, most lumber for southern California was still shipped from New England; Oregon and Washington had only a few small mills that supplied lumber locally and to the Hawaiian Islands (Ficken 1987). Commercial logging of the coast redwoods started around 1850 with the increasing demand for lumber associated with the Gold Rush, first near San Francisco and soon thereafter around Humboldt Bay. Redwood groves around San Francisco were heavily impacted by logging following the Gold Rush, and few remained south or east of San Francisco Bay by 1880 (Schrepfer 1983).

Outside of the San Francisco Bay area, logging in the Pacific Northwest was highly localized through the mid-1800s due to limited transportation infrastructure and technology (McKelvey and Johnson 1992; Rajala 1998). Early logging operations relied on handsaws and axes to fell trees and oxen to move logs along primitive skid roads (Pomeroy 1965). Loggers were selective, restricted to areas in close proximity to a waterway or sawmill, and largely limited to supplying local markets (Rajala 1998). Large-scale mechanized clear-cut logging operations and the expansion of the forest industry into continental and Pacific Rim markets were not in place along the Pacific Northwest coast until transcontinental railroad lines were completed (the Northern Pacific line was completed in 1883, and the Great Northern was completed in 1893; Rajala 1998; Hessburg and Agee 2003), and by this time, condor sightings in the region were exceedingly rare. Moreover, the trees that condors selected to nest in were not the trees that lumbermen preferred because condors require large cavities or broken tops in which to nest and nurture their eggs and young.

We cannot rule out the possibility that some nest trees were harvested with eggs or young in them, especially in the redwoods south and southeast of San Francisco—where there is
evidence that condors were nesting. However, condors are known to renest if they lose their first egg early enough in the breeding season (Snyder and Hamber 1985), are not bound to a specific nest site from year to year (although some sites are used year after year), and invest virtually no energy in nest site preparation (Snyder et al. 1986). Moreover, alternative nest sites, including remnant stands of large trees, rock ledges, and caves, are locally abundant in the region, especially in the more remote mountainous areas that are typical of condor nesting habitat. Finally, condors are long lived and could have persisted in the region for decades despite decreased productivity as long as adult mortality was not too high. Thus, even if a number of tree nests were lost to early logging in the region, we would not expect this loss to have caused a dramatic population decline or local extirpation.

2.11.7 Native American Ritual Killings
Condor feathers, bones, and parts were used by many tribes in the western United States for ceremonial or spiritual purposes (see chapter 2). While some tribes sacrificed condors to adorn dancers in entire condor cape suits (Loeb 1926; Gifford 1955), others believed that killing a condor was taboo (e.g., Peterson 1990). Despite Native American ritual use by some tribes, condors persisted in the region for millennia prior to Euro-American immigration. The question then is whether ritual killings were increasing around the time of the condor declines in the mid-1800s to such an extent that they could have substantively contributed to the extirpation of condors from the Pacific Northwest, as has been suggested by some (McMillan 1968; Snyder and Snyder 2000).

In 1825 there may have been as many as 180,000 Native Americans inhabiting the Pacific Northwest, with 30,000 below the confluence of the Columbia and Snake Rivers (Carey 1935; Winther 1950) and 70,000 along the north coast of California (Cook 1956). But between 1829 and 1832, a series of fatal epidemics had a devastating effect on the native people, especially along the lower Columbia River (90 percent population decline from 1805 to 1855) and the Sacramento Valley—such that families, whole villages, and even entire tribes were destroyed or so depleted that they lost their identity and became merged with others (New York Times 1874; Carey 1935; Boyd 1999).

In addition to disease, battles in northern California and southwestern Oregon between Native Americans and settlers and miners culminated in the death or forcible removal of most
Native Americans from this region to reservations in 1856 (Bledsoe 1885; Mark 2006). Those tribes that remained in scattered villages or rancherias had been greatly diminished by wars with settlers and disease epidemics (Bledsoe 1885; Nomland 1938; Boyd 1999; Mark 2006). By the 1870s, the majority of survivors had been moved to reservations, sometimes well outside of their historic environment, and pooled with the remnant members of other near-extinct groups (Suttles 1990).

By 1900, only a few thousand Native Americans remained in the entire Pacific Northwest (Boyd 1999). Little information on interactions with wildlife survived the drastic reduction in Indian numbers and the disruption of traditional activities. Although we do not have data on exactly how many condors were killed for ritual purposes through time, given the backdrop of disease, wars, massive population reductions, and the forcible removal of Native Americans from their homelands, it seems highly unlikely that condors in the Northwest were experiencing increased mortality from ritual killings in the mid-1800s that would have substantively contributed to their extirpation from the region.

Even if the remnant Native American populations wanted to use condors in their ceremonies, condors were becoming increasingly rare, making them harder to find and kill. Loeb (1926) reported that the Pomo Indians in California, who traditionally killed condors and used the entire skin in their condor dance, had stopped using condor skins in the early 1900s and instead merely imitated their appearance with other materials.

Although some have asserted that Native American ritual sacrifice substantially depressed condor populations, leading to continuous overall population declines long before the arrival of Europeans (McMillan 1968; Snyder and Snyder 2000), the magnitude and extent of this impact is unclear. A review of the ethnographic and archaeological record indicates that condors were killed in annual rituals in some areas—most notably in and around the Sacramento Valley and in southern California (Harris 1941; S. Wilbur 1978; Simons 1983). However, tribes in other areas revered the condor, and killing it was taboo (S. Wilbur 1978).

### 2.11.8 Food Increases in Central and Southern California

In 1769 Spain sent Friar Junípero Serrá and a small band of Franciscan monks to settle Alta California, establish missions, convert the natives to Christianity, and claim the land in advance of the Russians, who from 1741 to 1767 had been sending expeditions from Alaska southward
along the coast (McRoskey 1914). By 1804, nineteen missions had been established from San Diego to San Francisco, with two more missions constructed by 1830 (McRoskey 1914). In 1834, only sixty years after the friars came north from Baja California with two hundred head of cattle, there were at least twenty thousand Native Americans at the missions and approximately eight hundred thousand cattle, horses, sheep, and mules (McRoskey 1914). The main industry of the missions was the tallow and hide trade, which resulted in an abundance of offal for scavengers.

The hides and tallow are the only parts exported, the dried beef being consumed in the country as well as the finer quality of tallow or “manteca,” made from the fat of the intestines. The heads, horns, hoofs, bones, &c., are utterly wasted and thrown away; and, indeed, until within a few years, immense numbers of cattle were slaughtered for their hides alone, the entire carcass being left to corrupt, or feed immense numbers of wild beasts and large vultures, which were thus greatly encouraged and augmented. (Revere 1849, 100)

The Mexican government’s threat to secularize the Spanish missions caused the slaughter of about one hundred thousand cattle in 1834 (Cronise 1868). Koford (1953, 68) noted that “this was the year that the last specimen of the condor was taken on the Columbia River. If condors had migrated northward in search of food, they no longer had to do so.”

Koford’s quote suggests that the massive slaughter of cattle in 1834 might have resulted in condors abandoning traditional foraging grounds in the Columbia River region. However, evidence now suggests this hypothesis should be rejected for the following reasons:

1. At least a portion of the population was likely resident in the Pacific Northwest (see Historical Movement Patterns section, above).
2. John Kirk Townsend killed a juvenile condor (suggestive of breeding nearby) near Willamette Falls (approximately 20 km south of the Columbia River) in the spring of 1835, a year after the slaughter.
3. A juvenile condor was killed near Eureka, California, in the fall of 1892.
4. Numerous reliable condor observations were documented throughout the Pacific Northwest in the second half of the nineteenth century (see Table 2.2), including an observation along the mid-Columbia River in 1850 (Cooper and Suckley 1859) and an observation near Coulee City (which is on the Columbia River in Washington State) in 1897.
2.11.9 Reductions in Food Availability

The leading hypothesis for the prehistoric range contraction of condors is that food resources became limited in the interior of the continent and farther east at the end of the Pleistocene, causing condors to become restricted to the West Coast (see chapter 2). Although some have speculated that food reductions may have been a major cause of the species’ population decline and range contraction in the nineteenth and twentieth centuries (Grinnell 1913; Sheldon 1939), others have suggested that food limitations did not provide a compelling explanation for the historical decline of the species (A. Miller et al. 1965; McMillan 1968), and Snyder and Snyder (2000) found no evidence for food limitations in the remnant population in the 1980s. Koford (1953, 72), one of the few authorities on condors and changes to their historical food supply in southern California, stated:

> With the exception of the killing and molesting of condors by man, the change in the supply of food has been the most important factor determining the distribution and numbers of condors within the last century.

However, Koford did not extend this rationale to explain the disappearance of condors from the Pacific Northwest.

> No evidence has been discovered which suggests that condors were driven from Oregon or northwestern California by a shortage of food there. It is probable that some factor other than lack of food caused them to disappear from these areas. (67)

Koford’s analysis of the issue of food supply revolved almost entirely around changes in food availability in southern California, with no details regarding changes in food resources in the Pacific Northwest. Here, we specifically address changes in food resources in the Pacific Northwest and whether or not particular food items may have been increasing or decreasing during the nineteenth century, when condors disappeared from the region.

Salmon

The importance of salmon as a dietary component of condors in the Pacific Northwest is unclear. We know that there were millions of chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*) in the
Columbia River, Fraser River, Sacramento River, and coastal rivers of northern California and Oregon in the 1800s (Chapman 1986; Northcote and Atagi 1997; Yoshiyama et al. 1998; Meengs and Lackey 2005). Because most species of *Oncorhynchus* die after spawning, a large spawning run would, at least seasonally, produce a significant number of carcasses (Cederholm et al. 1999). Moreover, salmon attempting to swim upstream to spawn occasionally become stranded around waterfalls and barriers as they attempt to leap these barriers. Finally, Indian fishing villages that relied on salmon for sustenance would have produced a significant amount of concentrated fish offal as they cleaned the salmon and hung them out to dry. As John Kirk Townsend noted in a letter to John James Audubon in the 1830s:

> The Californian Vulture inhabits the region of the Columbia River, to the distance of five hundred miles from its mouth,\(^{35}\) and is most abundant in spring, at which season it feeds on the dead salmon that are thrown upon the shores in great numbers. It is also often met with near the Indian villages, being attracted by the offal of the fish thrown around the habitations. . . . On the upper waters of the Columbia the fish intended for winter store are usually deposited in huts made of the branches of trees interlaced. I have frequently seen the Ravens attempt to effect a lodgement in these deposits, but have never known the Vulture to be engaged in this way, although these birds were numerous in the immediate vicinity. (Audubon 1840, 12)

In a subsequent note to Audubon, Townsend continues:

> [The Californian Vulture] is particularly attached to the vicinity of cascades and falls, being attracted by the dead salmon which strew the shores in such places. The salmon, in their attempts to leap over the obstruction, become exhausted, and are cast up on the beaches in great numbers. Thither, therefore, resort all the unclean birds of the country, such as the present species, the Turkey-Buzzard, and the Raven. . . . Their food while on the

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\(^{35}\) Townsend (1848, 265) stated, “In my journey across the Rocky Mountains to the Oregon [Territory] in 1834, I kept a sharp look-out for this rare and interesting bird [the California Condor] in all situations on the route, which I thought likely to afford it a congenial dwelling place; but not one did I see. It was not indeed until my return to the coast in the spring from the Sandwich Islands [Hawaiian Islands], where I spent the winter, that I was gratified by a sight of the great Vulture”. Upon returning from Hawaii, Townsend traveled as far east as the Blue Mountains, only about 350 miles from the mouth of the Columbia (but makes no specific mention of seeing condors in the Blue Mountains). It is possible that the distance of five hundred miles was based on David Douglas’s account that they were observed east of the Cascades up to 49°N latitude (what would become the Canadian border).
Columbia is fish almost exclusively, as in the neighbourhood of the rapids and falls it is always in abundance; they also, like other Vultures, feed on dead animals. (13)

Townsend also mentioned seeing condors “constantly” in areas where salmon were “cast upon the shores” and observed a condor alighting on a salmon that had had become stranded after trying to leap over Willamette Falls, near current-day Oregon City, Oregon (1848). Townsend’s are the only firsthand historical accounts we are aware of that mention condors feeding on salmon,36 although the Corps of Discovery observed them feeding on unidentified fish that had been “thrown up by the waves on the Sea Coast” near Fort Clatsop (Lewis et al. 2002). Peale (1848, 58) stated that condors were “much more numerous in California, from the fact that the carcasses of large animals are more abundant, which they certainly prefer to the dead fish on which they are obliged to feed in Oregon, and all the countries north of the Spanish settlements in California.” However, Peale makes no specific mention of observations of condors feeding on salmon. Macoun (1903, 219) reviewed the history of condor observations in British Columbia and described them as “a rare visitant at the mouth of the Fraser River, B.C., apparently attracted by the dead salmon,” but no details were provided that can ascertain whether Macoun actually observed them feeding on salmon. Cassin (1856a) described them as occurring in the vicinity of rivers, “living principally on dead fishes.” In a separate publication of the same year in The United States Magazine, Cassin (1856b, 24) stated:

The [California Vulture] is frequently seen on the rivers during the fishing season, particularly in the period at which the salmon ascend the streams of fresh water. Many are killed in attempting to pass rapids, and afford food for this Vulture, which, like its smaller relatives, possesses by no means a fastidious appetite. It devours all descriptions of animal refuse, following a deer wounded by the hunter until it sinks in death, or is satisfied with the rejected parts of slaughtered cattle, fresh or in any state of putridity.

36 Thomas Nuttall, a botanist and traveling companion of John Kirk Townsend, also noted condors feeding on salmon, “which [the condors] find wrecked and stunned to death in their unceasing attempts to ascend the rapids of the Oregon [Columbia River] and Wahlamet [Willamette River]” (1840). However, because Townsend and Nuttall were traveling together, we do not consider these to be independent observations, and it is likely that Nuttall was simply repeating what he had heard from Townsend or what he had read from David Douglas (1829).
However, Cassin did not visit the western United States, and his secondhand account was likely derived from communications with his contemporary and associate at the Philadelphia Academy of Natural Sciences in the 1840s—John Kirk Townsend. Cassin (1856a) also relayed a report of a condor that was allegedly dissected by A. S. Taylor, who described the stomach contents as containing “fish, meat, and muscles [sic] with the shells on—the latter in a half-digested condition.”

The paucity of the historical record regarding condors feeding on salmon might be an artifact of the fragmentary nature of historical observations in the region, or it may be that salmon were consumed infrequently or seasonally. Given the accounts of Townsend, Macoun, and the Corps of Discovery that indicated fish were the primary food resource for condors along the Columbia and Fraser Rivers, we cannot rule out the possibility that salmon carcasses around falls and cascades, spawning areas, and Indian villages may have provided an important food resource for condors in the Northwest. Because there were multiple salmon runs in many rivers that occurred at different times of the year, this food resource was not limited to a single season, although it was less abundant in the mid-Columbia River from November to March. In late April or May the spring chinook salmon run peaked in the Columbia River Gorge just before the annual spring freshet on the Columbia reached its peak (Schoning et al. 1951). This was followed by the peak of the sockeye salmon run in July. Chinook salmon were present throughout the summer and became extremely abundant in early September during the fall run, at which time steelhead and silver salmon were also present. Steelhead were also present in significant numbers from July to October (Schoning et al. 1951).

Contemporary observations of condors eating fish are rare, but they readily consume fish provided in captivity. Other Cathartid vultures appear to be quite adaptable to local foraging conditions, in some situations focusing foraging efforts in areas where humans discard undesirable or injured fish, and even taking live fish under certain circumstances (e.g., Jackson et al. 1978). Among the Karok Tribe, vultures (it is unclear whether they were California Condors or Turkey Vultures) were also known to appear along the Klamath River at the site of smoke that signaled the First Salmon Festival because, as one informant put it, “They know they are going to eat salmon” (Kroeber and Gifford 1949).

At the time that condor observations were in noticeable decline in the region (mid-1800s), salmon runs may have been larger than at just about any other time in postglacial
history because Native Americans had experienced massive population declines from introduced diseases and were no longer harvesting large quantities of fish (reviewed by Meengs and Lackey 2005). Local declines in salmon populations were quickly noticed in northern California and southwest Oregon in the 1850s following the development of hydraulic mining, where miners used pressurized water to blast away hillsides, washing excess sediment into streams and rivers and suffocating spawning fish and their offspring (Schaeffle 1915; Meengs and Lackey 2005). Around the same time, intensive commercial fishing for Pacific salmon was taking hold with the development of an effective method of canning fish (Cobb 1921; Lichatowich et al. 1999). However, in northern California, more than ten million pounds of salmon were still being harvested from the Sacramento River in 1880 (Porter et al. 1882), and the maximum yield of chinook salmon in the Columbia River was not attained until around 1880 (McKernan et al. 1950), when there were still several million adult salmon returning to the Columbia and other Northwest rivers each year (Chapman 1986; Yoshiyama et al. 1998; Meengs and Lackey 2005). In the Fraser River system of British Columbia, it is estimated that there were more than fifty million salmon in the late 1800s and early 1900s, prior to a series of landslides in 1913 caused by railroad construction, which blocked salmon from the entire upper basin (Northcote and Atagi 1997). Thus, although localized salmon declines began in the 1850s, salmon remained relatively abundant in northern California, Oregon, Washington, and British Columbia until the 1880s, when condor observations had become rare in the region, arguing against the hypothesis that declines in salmon populations caused condor declines in the region.

Whales

Beached whales represent a potentially substantial food resource for condors; however, documented historical observations of condors feeding on whale carcasses are rare. We are aware of only three historical accounts of condors feeding on whales:

1. A condor was killed on a Cape Disappointment, Washington beach next to a whale carcass by the Corps of Discovery on November 18, 1805 (Lewis et al. 2002).  

37 A bronze statue of a California Condor perched on whale bones now commemorates that observation. It is located at the southern end of the Discovery Trail at the Port of Ilwaco, Washington.
2. Gambel (1847, 25) reported: “It is not uncommon to see them assemble with the gulls, and greedily devour the carcase of a whale which had been cast ashore,” but it is unclear whether this was based on a firsthand observation.

3. A. Taylor (1859) observed “a number of” condors feeding on a whale carcass in 1859 near Monterey, California.

More recently, in 2006 and 2008, condors were documented feeding on gray whale (Eschrichtius robustus) carcasses near Big Sur, California (J. Burnett, Ventana Wildlife Society, pers. comm., 2011; Figure 2.21).

Harry Harris (1941, 3-4) gave a colorful, embellished account of the first European encounter with condors, as they feasted on a whale carcass.

The record [of condor observations] begins with the published diary of a barefoot Carmelite friar, Fr. Antonio de la Ascension, who in 1602, from the tossing deck of a tiny Spanish ship, observed on a California beach the stranded carcass of a huge whale (conceivably and probably)38 surrounded by a cloud of ravenous condors. Here indeed is material with which to stir the most dormant imagination; civilized man for the first time beholding the greatest volant bird recorded in human history, and not merely an isolated individual or two, but an immense swarm rending at their food, shuffling about in crowds for a place at the gorge, fighting and slapping with their great wings at their fellows, pushing, tugging at red meat, silently making a great commotion, and in the end stalking drunkenly to a distance with crop too heavy to carry aloft, leaving space for others of the circling throng to descend to the feast!

While Ascension did see a whale carcass at Monterey Bay (being fed upon by bears), he never reported condors feeding on a whale carcass—something that Harris simply thought was conceivable and probable.

The documented evidence of condors feeding on whales is sparse; however, isotopic data from Pleistocene condor bones suggest that marine resources were an important component of their diet in Pacific coastal regions (C. Chamberlain et al. 2005; Fox-Dobbs et al. 2006). Commercial whaling practices caused large population declines for many whale species, leading some to suggest that this may have caused or contributed to California Condor

38 Harris notes that he was using his imagination here, not reporting a fact.
population declines in the nineteenth century (C. Smith 2006). Below, we review Native American and commercial whaling practices in the region to see how they might have influenced whale populations and the historical availability of whale carcasses for condors.

Several Pacific Northwest tribes practiced whaling, a hunting tradition that appears to have been limited to tribes on the west side of the Olympic Peninsula, including the Quileute, Quinault, and Makah Tribes, as well as tribes on the west coast of Vancouver Island (Curtis 1915; Waterman 1920; Pettitt 1950; Monks 2001). Although other coastal tribes in the Pacific Northwest south of the Olympic Peninsula did not typically kill whales at sea (Waterman 1920), they would harvest the blubber of beached whales for food and oil (Meany 1907; Waterman 1920; Kroeber 1925). According to Kroeber (1925, 84), among the Yurok Tribe of northern California,

> the stranding of a whale was always a great occasion, sometimes productive of quarrels. The Yurok prized its flesh above all other food, and carried dried slabs of the meat inland, but never attempted to hunt the animal.

Whale strandings, although sporadic, were likely a more common event prior to stock depletions. Mrs. Sarah Ruhamah De Bell observed twenty large whales on one stretch of beach at Clatsop, Oregon, in 1840.

> Some of these monsters took a long time to die, but all of them furnished food for the Indians. The white folks saved as much as they could of the oil. (Meany 1907, 14)

Among the Makah Indians, who were some of the most adept native whalers, whale blubber was highly valued for the oil it contained and for its ability to be dried and stored for food (Waterman 1920). The flesh was also taken for food; ligaments were prepared and made into ropes, cords, and bowstrings; and the stomach and intestines were dried and used to hold oil (Swan 1870; Curtis 1913). However, on some occasions whales killed at sea could take one to two days to bring to land for butchering. During that time the intestines, stomach, and flesh would begin to rot, leaving food for scavengers. As Waterman (1920, 46) noted:

> The process of decay goes on much more rapidly in the flesh than in the blubber, which keeps for an indefinite period, even if not removed from the whale. The flesh can only be removed from the bones only after stripping off the blubber, which
requires time. Possibly that is the reason the flesh of the whale is not more generally utilized. Blubber which has become rancid, through overmuch delay, is tried out\(^{39}\), and the oil is used for various technological purposes, not for food. The bones, with the muscles and ligaments, are left on the beach for the birds and other scavengers. All of the blubber, however, down to that on the flukes, is carefully preserved.

Gray whales and humpback whales (*Megaptera novaeangliae*) were the preferred quarry of the whaling tribes, although other whale species were taken when available (Swan 1870; Monks 2001). Precise records of the number of whales historically harvested by the tribes of the Olympic Peninsula and Vancouver Island are not available. Nicolay (1846) reported that about twenty whales were killed annually in the Strait of Juan de Fuca, with most of the whales appearing in the North Pacific from May to November. The timing of the harvest is consistent with our current knowledge of the timing of the gray whale migration through the region (Sumich 1984) and the movements of humpback whales to nearshore coastal feeding grounds (National Marine Fisheries Service 1991; Clapham et al. 1997; Calambokidis et al. 2001). By the 1860s, the number of whales killed by the Makah had declined (Swan 1870), but it is not clear whether the decline in harvest was due to the availability of whales or a shift to harvesting northern fur seals (*Callorhinus ursinus*), which were easier to take and whose skins and oil could be traded with the Euro-American settlers (Swan 1870; *Puget Sound Argus* 1882). Despite this lack of clarity, we do know that the decline in Native American whale harvest occurred at the same time gray whales were in serious decline in the eastern Pacific due to intensive commercial harvest.

The first commercial whaling vessel reached the Pacific (off the coast of Chile) in 1791 (Tower 1907). By 1808, whalers were hunting sperm whales along the coast of Baja California, and by 1834 there were so many whalers off the coast of California that the Hudson’s Bay Company considered opening another trading post to provision them (Busch 1998). In 1838, the great Northwest coast whaling grounds were discovered and by 1850, almost all the Atlantic whale fleets had moved to harvesting whales in the Pacific (Tower 1907; Tønnessen and Johnsen 1982). In 1851, shore whaling was first tried at Monterey, California, and over the course of the next twenty years this practice was carried out from Monterey to Baja California (Tower 1907).

\(^{39}\) Trying out is a technical term for extracting oil from the fat of an animal through boiling.
Particularly devastating to the gray whale population was the practice of killing whales in their breeding lagoons in Baja California, starting in earnest in 1858 (Tønnessen and Johnsen 1982; Busch 1998). The rapid depletion of stocks soon followed (between 1845 and 1874 over eight thousand gray whales were killed [Busch 1998]), and some believed the gray whale was headed toward extinction (Tønnessen and Johnsen 1982; Busch 1998). 40 As the whales along the California coast were depleted, whalers moved north to Oregon, Washington, and British Columbia, with nearshore commercial whale harvesting continuing well into the twentieth century. Unlike native whaling practices, which sometimes resulted in rotten portions of the carcass being left on the beach, commercial whalers rendered all fleshy parts of the carcass (Webb 1998), leaving nothing for the scavengers. This shift from a limited Native American harvest that left rotting meat on beached carcasses to industrial whaling practices that decimated the whale population occurred around the same time as condor observations in the region were in decline. However, the importance of whales in the condor’s historical diet is unclear, as there are only a few known observations of condors feeding on whales.

Seals and Sea Lions

Pinnipeds along the coast of northern California, Oregon, Washington, and British Columbia (most notably, harbor seals [Phoca vitulina]), northern fur seals, California sea lions (Zalophus californianus), and Steller’s sea lions (Eumetopus jubatus) may once have provided a substantial coastal food resource for condors. Pinnipeds may have also provided a minor food resource for condors farther inland, as some occurred in the major Pacific Northwest river systems (Paulbitski 1974; R. L. Lyman et al. 2002) and were occasionally taken by Native American nets and traps (R. L. Lyman et al. 2002). Although historical accounts of condors feeding on pinnipeds are uncommon, condors released in central California are regularly observed feeding on beached carcasses of California sea lions at one of their haul-out sites near Big Sur, California (J. Burnett, Ventana Wildlife Society, pers. comm., 2011). In one case a condor was even observed killing a weak and abandoned sea lion pup (M. Tyner, Ventana Wildlife Society, pers. comm., 2011).

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40 The International Whaling Commission has prohibited the killing of gray whales in the Pacific Ocean since 1947 and the gray whale was protected under the Endangered Species Act from 1973 to 1994, when it was one of the first species to be removed from the list due to recovery. The eastern North Pacific gray whale has now recovered to a level near its estimated pre-exploitation size and is considered one of the world’s great conservation success stories (Gerber et al. 2000).
Below we review observations of seal and sea lion abundance and practices of harvesting pinnipeds to see if shifts in relative abundance and harvest practices were coincident with the condor’s range contraction in the nineteenth century.

Native American tribes in the Pacific Northwest killed seals and sea lions, usually by sneaking up on them at rookeries or haul-out sites, although specific hunting practices varied regionally (Braje and Rick 2011). Prehistoric impacts to mainland rookeries may have been significant, especially those situated on accessible shorelines (Hildebrandt and Jones 1992). However, accounts of explorers and settlers suggest that sea lions and seals were relatively abundant throughout the coastal Pacific Northwest through the mid-1800s (Newberry 1857; Chase 1869; Swan 1870; Murphy 1879), where, except for limited Native American harvest, they remained largely unmolested (Murphy 1879). Significant commercial harvest of pinnipeds, particularly California sea lions and northern fur seals, began in the 1850s, when thousands of individuals were killed for their skins, whiskers, testicles, and blubber (Scammon 1874; Cass 1985). In 1880, over six thousand fur seals were harvested off the northwest coast of the United States (Swan 1887), and over twelve thousand were harvested in Oregon and Washington in 1892 (Wilcox 1895).

Around the turn of the century, government agents began to kill seals and sea lions in Oregon at the mouth of the Columbia River and at their breeding grounds at the mouth of Elk Creek in hopes of protecting dwindling salmon runs (Oregon Fish and Game Commissioner’s Board 1901). During the spring and summer of 1900, government agents killed 288 seals and 670 sea lions (Oregon Fish and Game Commissioner’s Board 1901). They were also being slaughtered by recreational shooters who viewed them as a nuisance species because of their predatory habits on salmon (Wild 1898). These practices escalated through the early 1900s, greatly depleting seal and sea lion populations along the Oregon coast (Scheffer 1928), but these killings would have also provided a temporary abundance of carcasses for scavengers during the time period when condors disappeared from the Pacific Northwest.41

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41 This also raises the possibility that a significant number of lead-contaminated carcasses were available to condors during this time—see “Lead Poisoning” section, above.
Native Ungulates

The principal native ungulates that were available to condors in the Pacific Northwest included Rocky Mountain elk (*Cervus canadensis nelsoni*), Roosevelt elk (*C. c. roosevelti*), tule elk (*C. c. nannodes*), black-tailed deer (*Odocoileus hemionus columbianus*), and white-tailed deer (*O. virginianus*). Bison (*Bison bison*) once occurred in some areas of the Pacific Northwest (east of the Cascades) but were scarce by the time early Euro-American explorers entered the region (Wilkes 1849; Kingston 2010).

In northern California, tule and Roosevelt elk were abundant in the early 1800s, but populations declined with the discovery of beaver (*Castor canadensis*) in the northern Sacramento Valley by Jedediah Smith and party (McCullough 1969). This discovery led to Hudson’s Bay Company fur brigades frequenting these grounds and harvesting large numbers of animals for food up until the mid-1840s (Harper et al. 1967; McCullough 1969; Phillips 1976). In the 1830s, Peale (1848) noted an abundance of large ungulate carcasses in northern California and suggested this was the reason condors were more prevalent in northern California than in Oregon. Sage (1846) also noted that game was plentiful in northern California in the early 1840s, especially in the vicinity of the Tulare and Sacramento Rivers. Newberry (1857) found elk to be common in the valleys of northern California, but not as common as in the early 1800s, when herds of game in the Central Valley rivaled the bison herds on the Great Plains and the antelope herds of South Africa. Despite apparent reductions from historical numbers and the extirpation of tule elk from northern California shortly after the Gold Rush (McCullough 1969), deer and Roosevelt elk were still considered plentiful in many areas of northern California up until the 1870s (Doney et al. 1916).42

In Oregon and Washington, elk and deer were widely distributed and relatively abundant during the early Euro-American settlement period, especially west of the Cascade crest (Wilkes 1849; Victor 1872; Merriam 1897; Bailey 1936; S. Dixon and Lyman 1996; Harpole and Lyman 1999; R. E. Lyman 2006). Game populations in the region were likely increasing at

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42 In contrast to Roosevelt elk (of coastal northern California, Oregon, and Washington), tule elk (historically inhabiting the Central Valley and central Coast Range of California) were driven close to extinction by the 1850s due to market hunting as well as the spread of agriculture and the concomitant destruction of elk habitat (McCullough 1969).
the time as a result of decreased hunting pressure from Native Americans (Martin and Szuter 1999; R. L. Lyman and Wolverton 2002; Kay 2007), who were in the midst of massive population declines resulting from a series of fatal epidemics. In 1826, David Douglas found elk to be “plentiful in all the woody parts of the country” and “particularly abundant near the coast” (1914, 155).

Significant impacts to native ungulate numbers began during the Gold Rush era. During this time many mining camps were established in northern California and southwestern Oregon. These mining camps depleted local deer and elk populations, as hunting was unregulated and occurred year-round to supplement what the mining camps could purchase from nearby farmers (Longhurst et al. 1952; Mark 2006). Ranching and grazing operations were also established, and as early as 1851, cattle began replacing elk in some areas (Harper et al. 1967; J. Sawyer 2006). Elk and deer populations were declining in the 1860s around settlements and mining camps, but these ungulates were still considered common in areas that were lightly populated or inaccessible (Cronise 1868). However, from 1870 to 1900, market hunting for deer and elk hides seriously depleted wild ungulate numbers throughout the region as roving commercial hunting outfits penetrated more remote areas (Doney et al. 1916; Hessburg and Agee 2003). In 1880, thirty-five thousand deer hides were shipped from Siskiyou, Trinity, and Shasta Counties in California, with the meat left to rot on the ground (Doney et al. 1916). Similar slaughter was also occurring in Oregon, with thousands of deer hides shipped from southern Oregon to San Francisco in the 1870s and 1880s (Willamette Farmer 1887; Doney et al 1916). Increasing competition from livestock, a series of hard winters from 1879 to 1907, logging practices, and development also contributed to native ungulate declines in the late 1800s (Longhurst et al. 1952).

At the turn of the twentieth century, ungulate numbers were severely depleted (Barnes 1925; Longhurst et al. 1952). Some herds persisted in areas away from settlements, albeit at reduced numbers and distribution (Merriam 1897; Bailey 1936; Longhurst et al. 1952). Deer populations did not begin to stabilize and increase until the early 1900s, following the establishment of hunting seasons, bag limits, and a ban on selling wild game (W. Taylor 1916; Bailey 1936; Longhurst et al. 1952). Elk populations were slower to recover and began to return to significant numbers only in the 1950s and 1960s (Harper et al. 1967; McCullough 1969).
While hunting, hard winters, and other factors ultimately resulted in severe depletion of
deer and elk numbers, the quantity of carcasses left in the field for scavengers during this period
would have been locally significant, albeit ephemeral (e.g., Doney et al. 1916). 43 Furthermore, in
areas around settlements, where ungulates became scarce in the late 1800s, they were being
replaced on the landscape with livestock, which would have provided an alternative, and more
predictable and reliable, food resource for condors.

Livestock
In California, early settlers maintained a few cattle ranches in the northern part of the state
during the early 1800s, but at that time, the cattle industry was run largely by Spanish missions
and the hide-and-tallow trade of southern California. Only about 3,700 sheep and 55,000 cattle
resided in northern California in 1850 (US Department of the Interior 1853; Burcham 1957).
Following the Gold Rush, demand for beef instigated enormous cattle drives from southern to
northern California to feed the burgeoning mining towns along the Sierra foothills (Cleland
1951; Burcham 1957). Some southern ranchers leased grazing rights in the vicinity of San Jose,
Sacramento, or San Francisco Bay, where the stock was fattened after the long journey north
(Cleland 1951). Tens of thousands of cattle were also imported from the Midwest via overland
trails around this time due to the high price of beef in northern California (Cleland 1951;
Burcham 1957). Cattle numbers peaked in California around 1860, when there were 1.1 million
head, then declined to about 800,000 in 1880 following a succession of droughts that
devastated the cattle industry (Porter et al. 1882; Burcham 1957). However, cattle numbers
recovered to more than 1.3 million by 1890 (US Department of the Interior 1895; Burcham
1957). Cattle numbers were much higher in southern and central California through the late
1800s, but there were over 100,000 cattle in northern California by 1860 and more than 175,000
cattle there by 1880 (Burcham 1957).

Sheep populations also increased rapidly in California following the first wave of the
Gold Rush. First introduced to California in 1773 by Spaniards, there were only about seventeen
thousand sheep in California in 1850 (Burcham 1957). By 1860 there were more than one million
sheep in California, a number that more than doubled by 1870 and surpassed four million by

43 This also raises the possibility that a significant number of lead-contaminated carcasses were available
to condors during this time—see “Lead Poisoning” section, above.
1880 (Burcham 1957). Although a large portion of the sheep were in central and southern California prior to 1900, there were over eight hundred thousand sheep in northern California by 1880 (Burcham 1957).

In the Oregon Territory, livestock introductions began with the importation of hogs and sheep by the Astor party in 1811 (Carey 1922), and cattle from California were imported by the Hudson’s Bay Company starting in 1830 (Gaston 1912). The initial quantity of livestock was modest and largely meant for the subsistence of settlers, who kept small herds of dairy cows, goats, oxen, sheep, horses, and beef cattle on family farms (Hessburg and Agee 2003). In 1841 there were approximately three to ten thousand cattle in the Willamette Valley, five hundred horses, and a “multitude of hogs” (Bancroft 1886). The mass influx of immigrants following the Gold Rush in 1849 brought large numbers of livestock to the region (Carey 1922), and cattle and sheep herds expanded well beyond family farming into an industry. In Oregon, by the 1860 census, there were approximately 147,000 cattle and over 1.6 million sheep (US Department of the Interior 1864); by 1890 there were over 520,000 cattle and 1.7 million sheep (US Department of the Interior 1895); and by 1900 there were 532,000 cattle and approximately 2.8 million sheep (US Department of the Interior 1902).

Livestock numbers also increased in Washington during the latter part of the nineteenth century, although not in the numbers seen in Oregon and California. In 1860, there were only 25,888 cattle and 10,157 sheep in the Washington Territory (US Department of the Interior 1864). At the time of the 1890 agricultural census, there were 255,134 cattle and 265,267 sheep (US Department of the Interior 1895), and by 1900, there were 290,000 cattle and 864,480 sheep (US Department of the Interior 1902).

Although most of the livestock industry in Oregon and Washington was situated east of the Cascades in Oregon (and therefore east of most of the known condor occurrence records), there were still large numbers of livestock being imported to the western portions of the two states, especially Oregon. According to the 1890 census there were over two hundred thousand cattle and three hundred thousand sheep in western Oregon and approximately seventy-five thousand cattle and thirty thousand sheep in western Washington (US Department of the Interior 1895).

Early livestock drives sometimes resulted in large losses, which would have meant increased food availability for condors. For example, after buying eight hundred head of cattle in
San Francisco and San Jose in 1837, Ewing Young and others drove the herd north to Oregon (Dillon 1961). By the time they reached the Willamette settlements in western Oregon, they had lost 168 cattle (Dillon 1961).

The number of domestic livestock increased rapidly in the Pacific Northwest following the California Gold Rush, with millions of animals present by the late 1800s. Even if only a small fraction of these animals died and were accessible to condors annually, there would have been thousands of carcasses to feed on. In reality, mortality, especially among sheep, was sometimes extremely high. For example, the 1890 census reported five hundred thousand sheep in Oregon dying from disease and weather in 1889 (a mortality rate of approximately 20 percent; US Department of the Interior 1895), with more than thirty-one thousand dying in western Oregon alone (a mortality rate of approximately 10 percent).

Declines in condor observations were noted following introduction and proliferation of livestock to the region. An exponentially expanding livestock industry at the time of condor population declines is inconsistent with the hypothesis that food limitations were the cause of the decline.

**Summary of Changes to the Condor’s Food Supply**

Our review of the historical record indicates that the lack of food does not appear to have caused the condor’s nineteenth-century population decline in the Pacific Northwest. There were diverse and abundant native food resources in the region through the 1850s, including salmon, whales, pinnipeds, and ungulates (Figure 2.22). Although declines in some native food resources were observed in the region in the mid to late 1800s, it is unlikely food was becoming limited for condors in the Pacific Northwest for a number of reasons:

1. Obligate scavengers have evolved mechanisms to cope with cyclic or temporary food shortages. As large soaring birds with keen eyesight, condors are adapted to searching enormous areas for food while expending little effort. With the ability to travel long distances and soar at high altitudes, condors can search several hundred square kilometers for food on days when soaring conditions are favorable. Furthermore, they have an extremely flexible diet, which includes fish, small mammals, livestock, native ungulates, and marine mammals. Their ability to switch between food resources and soar long distances are effective adaptations to
exploiting seasonal, migratory, or temporary food resources and an effective buffer against local or temporary food shortages.

2. Hunting practices resulted in temporary increases in carcass availability in the mid to late 1800s. Market hunters were shooting thousands of elk and deer for their hides in northern California and southern Oregon in the late 1800s and leaving the meat and viscera in the field. Seals and sea lion carcasses would also have been abundant from commercial harvest operations. Furthermore, the lack of regulated hunting seasons in the 1800s meant that carcasses would have been available throughout the year. While this ultimately resulted in lower numbers of ungulates and pinnipeds at the turn of the twentieth century, for a number of years there would have been a superabundance of carcasses for condors and other scavengers. Many of these carcasses may have been contaminated with lead bullet fragments, which could have played a role in the condor’s decline (see “Lead Poisoning” section, above).

3. Around the time that native ungulates, whales, and pinnipeds were in decline in the region, there were massive increases in livestock, numbering hundreds of thousands of individuals, many of which roamed freely in the mountain ranges prior to grazing restrictions. Mortality rates of these livestock herds were relatively high, sometimes exceeding 20 percent, due to the inferior animal husbandry practices at the time.

2.12 SUMMARY OF THE PLAUSIBLE CAUSES OF EXTINCTION IN THE PACIFIC NORTHWEST

Identifying and eliminating, or sufficiently reducing, the original causes of local extinction are critical aspects of successful reintroduction planning (Griffith et al. 1989, IUCN/SSC 2013). However, extinction processes are often the result of interactions between multiple causes that are difficult to disentangle (Carrete et al. 2007). This can be especially problematic when working with data sets assembled from historical observations that have inextricable statistical biases. Despite these problems, a careful review of the range of plausible hypotheses can be helpful in rejecting those that do not align with the scope, magnitude, or timing of the decline of the subject species. It can also identify areas where additional research may help reject other hypotheses. Contemporary information regarding the causes of decline in ecological surrogates can also be helpful in such reviews.
Based on our review, there is limited direct observational evidence—but significant circumstantial evidence—that secondary poisoning could have been a primary factor in the condor’s extirpation from the Pacific Northwest (Table 2.4). Strychnine-laced carcasses were locally abundant near homesteads, trapping sites, and travel corridors during the period of the condor’s population decline, and the social feeding habits of condors predispose them to mass die-offs when their food is contaminated. Moreover, contemporary studies show that predator poisoning is a major factor in population declines for many vulture species around the world. Lead poisoning may also have played a role in the condor’s range contraction, but there is uncertainty regarding the bioavailability of lead to condors during this time period due to changes in firearms and ballistics. Collecting and shooting resulted in some direct loss to the condor population and may also have played a role in the condor’s range contraction. Loss of nesting habitat, egg collecting, and Native American ritual sacrifice are not likely causes of the condor’s disappearance from the region.

Although declines in some native food resources were occurring around the time that condor occurrence records were in decline, particularly coastal food resources, it is unlikely that food was ever limiting for condors in the Pacific Northwest. Market hunting ultimately reduced native ungulate and pinniped populations in the late 1800s but also temporarily produced a significant amount of offal in some areas. Furthermore, there was a massive importation of livestock to the Pacific Northwest by the time these native food resources were significantly depleted.

It should not be surprising that anthropogenic causes were almost certainly responsible for the decline and extirpation of condors from the Pacific Northwest. Human influence is highly correlated with range contractions for many North American species (Laliberte and Ripple 2004). But the question remains: Why did populations go extinct in the Pacific Northwest while they persisted in southern California (albeit in a rapidly declining state)? Is it possible that the habitat conditions in the Northwest were marginal, contributing to their early demise compared with the core range in southern California?

It seems intuitive that populations at the periphery of a species’ range (such as condors in the Pacific Northwest) might be innately more susceptible to extinction events than those populations at the core of the range. This is because peripheral populations often represent the extremes of the species’ ecological niche, where species should be expected to occur in lower
densities or lower quality habitats (G. Caughley et al. 1988). However, populations at the edge of a species’ range are not always less dense, and in many cases peripheral populations persist despite range contractions (Channell and Lomolino 2000).

Given its extensive historical range, it is likely that the California Condor was once divided among a number of interacting populations. If populations in the Pacific Northwest were indeed on the periphery of the condor’s ecological niche, they may have been more susceptible to increases in mortality or declines in productivity than those populations at the core of the species’ range in southern California. However, it is also possible that threats were unevenly applied to the landscape (see Rodríguez 2002), whereby the northern populations were subjected to more shooting and poisoning early in the settlement of the West than were condors in the mountains of southern California, and thus they declined and went extinct faster. Both scenarios are plausible, as is the scenario that the asynchronous distribution of threats and the location of populations at the periphery of the range were factors contributing to the extinction of condors in the Pacific Northwest. Thus, it is unclear whether the peripheral position in the species’ range was part of the reason condor populations in the Pacific Northwest went extinct first. Nevertheless, peripheral portions of the California Condor’s historical range may be important to their recovery, because the location of a reintroduction site with respect to the core or periphery of the species’ historical range is not always a good predictor of reintroduction success (White et al. 2012). This is especially true when the reasons for local extinction are anthropogenic causes that have since evaporated or been significantly dampened, or in circumstances (as with the condor) when threat factors have since been completely reshuffled in form and space.

2.13 LITERATURE CITED


Barnes, E. P. 1925. Elk in Del Norte County. California Fish and Game 11:90.


Bulletin (San Francisco newspaper). 1856. The California Condor. 16 May.


Bulletin (San Francisco newspaper). 1880. State news in brief. 5 April.


Cooper, J. G., and G. Suckley. 1859. The Natural History of Washington Territory, with Much Relating to Minnesota, Nebraska, Kansas, Oregon, and California, Between the Thirty-Sixth and Forty-Ninth Parallels of Latitude, Being Those Parts of the Final Reports on the Survey of the Northern Pacific Railroad Route, Containing the Climate and Physical Geography, with Full Catalogues and Descriptions of the Plants and Animals Collected from 1853 to 1857. Baillière Brothers: New York.


Cronise, T. F. 1868. The Natural Wealth of California: Comprising Early History; Geography, Topography, and Scenery; Climate; Agriculture and Commercial Products; Geology, Zoology, and Botany; Mineralogy, Mines, and Mining Processes; Manufactures; Steamship Lines, Railroads, and Commerce; Immigration, Population and Society; Educational Institutions and Literature; Together with a Detailed Description of Each County; Its Topography, Scenery, Cities and Towns, Agricultural Advantages, Mineral Resources, and Varied Productions. H. H. Bancroft & Company: San Francisco.


Feranec, R. S. 2009. Implications of radiocarbon dates from Potter Creek Cave, Shasta County, California, USA. Radiocarbon 51:931–936.


Oregon Fish and Game Commissioner’s Board. 1901. Annual Reports of the Department of Fisheries of the State of Oregon to the Legislative Assembly, Twenty-first Regular Season. W. H. Leeds: Salem, Oregon.


Revere, J. W. 1849. A Tour of Duty in California, Including a Description of the Gold Region: and an Account of the Voyage Around Cape Horn; With Notices of Lower California, the Gulf and


Rowe, S. P., and T. Gallion. 1996. Fall migration of Turkey Vultures and raptors through the southern Sierra Nevada, California. Western Birds 27:48–53.


Sage, R. B. 1846. Scenes in the Rocky Mountains, and in Oregon, California, New Mexico, Texas, and the Great Prairies; or Notes by the Way, During an Excursion of Three Years, with a Description of the Countries Passed Through, Including Their Geography, Geology, Resources, Present Condition, and the Different Nations Inhabiting Them. By a New Englander. Cary & Hart: Philadelphia.


Swan, J. G. 1870. The Indians of Cape Flattery, at the Entrance to the Strait of Fuca, Washington Territory. Smithsonian Contributions to Knowledge 220. Smithsonian Institution: Washington, DC.


The Nature Conservancy, in litt. 2007. A proposal to explore the establishment of a California Condor (re)introduction program in the Lassen Foothills Project Area, California. Letter from Simon Avery (Dye Creek Preserve Manager) to Mark Weitzel (Hopper Mountain National Wildlife Refuge Project Leader). March 1, 2007.


Townsend, J. K. 1839. Narrative of a Journey Across the Rocky Mountains, to the Columbia River, and a Visit to the Sandwich Islands, Chili, &c, with a Scientific Appendix. Henry Perkins: Philadelphia.


Wetmore, A. 1931b. The Avifauna of the Pleistocene in Florida. Smithsonian Miscellaneous Collections  85(2). Smithsonian Institution: Washington, DC.


Williamette Farmer (Salem, Oregon). 1872. Highland Farmers’ Club. 6 July.

Williamette Farmer (Salem, Oregon). 1887. State and territorial news. 25 March.


Figure 2.1. (•) = Archaeological and paleontological sites containing Gymnogyps bones (see Table 2.1 for additional details); (x) = Woodburn archaeological site, where bones of the extinct condor-like Teratornis woodburnensis were found; (*) = Smith Creek Cave, where remains of extinct large avian scavengers (Aiolornis incredibilis [formerly Teratornis incredibilis], Breagyps clarki, and Coragyps occidentalis) were found.
Figure 2.2. Partial California Condor tarsometatarsus unearthed from Poets Cove archaeological site (DeRt-4), Bedwell Harbour, South Pender Island, British Columbia, Canada. Image B-01601 courtesy of the Royal British Columbia Museum, British Columbia Archives, Victoria, British Columbia, Canada. This bone was radiocarbon dated to 2,920±15 YBP (I. R. Wilson Consultants, Ltd. 2006).
Figure 2.3. Bird bone tubes and whistles from an archaeological site in Watsonville, California (CA-SCR-44). The bottom whistle was made from the left ulna of a California Condor (Breschini and Haversat 2000). The other bones are from Bald Eagles (*Haliaeetus leucocephalus*; the two above the condor bone) and Great Blue Herons (*Ardea herodias*; the four bones at the top). Photo by Trudy Haversat and Gary S. Breschini. Used with permission of Gary S. Breschini, Archaeological Consulting, Salinas, California. Scale in centimeters.
Figure 2.4. Approximate tribal boundaries in the Pacific Northwest at the time of European contact. Boundaries and names based on Sturtevant (1967) and a map of historical First Nations languages of British Columbia developed by the University of British Columbia’s Museum of Anthropology in coordination with the First Peoples’ Heritage, Language and Culture Council. These boundaries were diffuse and dynamic but are shown here to give the reader a general sense of the geographic extent of Native American tribes at the time of European contact.
Figure 2.5. California Condor feather costume collected by I. G. Voznesenskii (1841). From the collection of the Peter the Great Museum of Anthropology and Ethnography (Kunstkamera), Russian Academy of Sciences, catalog number 570-2.
Figure 2.6. Nora Coonskin, last shaman of the Bear River Tribe in northern California (near Cape Mendocino) holding what appear to be California Condor primaries, circa 1930 (from Nomland 1938, plate 8).
Figure 2.7. Panamenik (Karuk) White Deerskin Dance, northern California, 1910. Feather plumes in the headdresses of the deerskin dancers are made from California Condor feathers that were spliced together on a rawhide strip. Courtesy of the Phoebe A. Hearst Museum of Anthropology and the Regents of the University of California, California Indian Library Collections Siskiyou County book 4, number 1.
Figure 2.8. (top) Hupa California Condor feather plume for White Deerskin Dance, circa 1880. Courtesy of the National Museum of the American Indian, Smithsonian Institution; catalog number 001209.000. (bottom) Karuk California Condor feather wands, collected 1927. Courtesy of the National Museum of the American Indian, Smithsonian Institution catalog number 151922.000.
Figure 2.9. California Condor feather plume (top, center) in a Hupa headdress. Courtesy of the National Museum of the American Indian, Smithsonian Institution catalogue number 4/1439. Photo by Ernest Amoroso.
Figure 2.10. Cylinder basket with condor motif, lower Columbia River, circa 1880. 9 x 5 1/4 inches diameter. Private collection. Courtesy of the Portland Art Museum, Portland, Oregon (catalog number 107). Photo by Bill Mercer.
Figure 2.11. California Condor occurrence records in the Pacific Northwest.
Figure 2.12. California Condor drawing from Meriwether Lewis’s journal (Codex J, p. 80), February 17, 1806. Courtesy of the American Philosophical Society.
Figure 2.13. Excerpt from Dr. John Scouler’s journal, September 22, 1825. “I obtained specimens of *Pelecanus onocrotalus, Falco*—& a species of *Vultur*, which I think is nondescript. My birds were principally obtained from the Indians, who would go through any fatigue for a bit of tobacco.” The specimen referred to is now housed at The Netherlands National Natural History Museum in Leiden. Courtesy of the Oregon Historical Society.
Figure 2.14. California Condor occurrence records and human population growth in the Pacific Northwest, 1800–1920.

1 Based on U.S. Census data for Washington, Oregon, and the counties of northern California (north of San Francisco). Census data represent counts at the mid-points of time periods. Due to limitations in census data, human population numbers for 1850 did not include data for the following counties in California: Alpine, Amador, Contra Costa, Del Norte, Glenn, Humboldt, Lake, Lassen, Modoc, Mono, Nevada, Placer, Plumas, San Francisco, Sierra, Siskiyou, Tehama. Due to limitations in census data, human population numbers for 1870 did not include data for Glenn or Modoc counties in California.

* Census data are not available for 1800-1840; however the human population was sparse during this time period.
Figure 2.15. California Condor occurrence records and distance (km) from the Pacific coastline. Average movement distance of breeding California Condors in southern California from 1982 to 1987 was 50–70 km (Meretsky and Snyder 1992). Vertical dashed lines represent quartiles.
Figure 2.16. Reliability of California Condor occurrence records in the Pacific Northwest. Color represents reliability class, as described in Table 2.2 (black = 1, gray = 2 or 3, and white = 4 or 5).
Figure 2.17. (a) Combined incubation and fledging periods (days) and mass (g) for large (> 2000 g) birds of prey (both migratory and nonmigratory) with known development times (based on data in Meri and Yom-Tov 2004; Turkey Vulture data based on Kirk and Mossman 1998). (b) Frequency of combined incubation and fledging periods (days) for all large (> 2 kg) migratory bird species that have known development times (based on data in Meri and Yom-Tov 2004). Abbreviations of New World vultures (Cathartidae) given for reference (ANCO = Andean Condor; BLVU = Black Vulture, CACO = California Condor; KIVU = King Vulture; TUVU = Turkey Vulture). The longest development time (incubation and fledging period) reported for any large migratory bird was 171 days (Mute Swan [Cygnus olor]; dashed line), more than two months shorter than the California Condor, at 239 days.
Figure 2.18. Seasonal density of California Condor occurrence records in the Pacific Northwest, with annotations: (1) John Kirk Townsend variously described condors as most abundant along the Columbia River in spring or summer (Audubon 1840); (2) David Douglas reported them from the summer and fall as far north as the Canadian border (Douglas 1829); (3) John Strong Newberry reported seeing condors “every day” in the Sacramento Valley in the summer of 1855, on his journey to Oregon (Newberry 1857); (4) In the summer of 1847 Andrew Jackson Grayson observed more than a dozen condors coming to a carcass in Marin County, California (Bryant 1891); (5) In October 1826, David Douglas reported condors “in great numbers” in the Umpqua River region of Oregon, and south, observing nine in one flock (Douglas 1914).
Figure 2.19. California Condor occurrence records by season in the Pacific Northwest.

1 Spring = March-May; Summer = June-August; Fall = September-November; Winter = December-February.
Figure 2.20. Juvenile California Condor (US National Museum Specimen 78005) shot by John Kirk Townsend at Willamette Falls, Oregon, 1835. Gray down on the neck and head along with dark coloration on the bill and head indicate that this bird was a juvenile (≤ 3 years old), contrary to the specimen tag, which described it as an adult. Courtesy of James Dean, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, DC.
Figure 2.21. California Condors feeding on a gray whale near Big Sur, California, 2006. Photo by Ryan Choi. Courtesy of Ventana Wildlife Society.
Figure 2.22. Relative changes in California Condor food resources and associated threats (top panel) in relationship to the number of California Condor occurrence records, human population, and numbers of condors killed or captured and removed from the wild (bottom panel), 1800–1920.
Table 2.1. The fossil record of *Gymnogyps* in the Pacific Northwest.\(^a\)

<table>
<thead>
<tr>
<th>Site letter</th>
<th>Site name</th>
<th>Location</th>
<th>Minimum # of bones</th>
<th>Species</th>
<th>Site type(^b)</th>
<th>Years before present(^c)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Potter Creek Cave</td>
<td>Shasta County, CA</td>
<td>10</td>
<td><em>G. amplus</em></td>
<td>N</td>
<td>25,000–14,100</td>
<td>Sinclair 1904; L. Miller 1911; Payen and Taylor 1976; Feranec 2009</td>
</tr>
<tr>
<td>B</td>
<td>Samwel Cave</td>
<td>Shasta County, CA</td>
<td>2</td>
<td><em>G. amplus</em></td>
<td>N</td>
<td>21,010–15,980</td>
<td>L. Miller 1911; Feranec et al. 2007</td>
</tr>
<tr>
<td>C</td>
<td>Galen’s Pit</td>
<td>Shasta County, CA</td>
<td>3</td>
<td><em>G. californianus</em>?</td>
<td>N</td>
<td>20,970–20,350*</td>
<td>University of California Museum of Paleontology specimen 131552; Emslie 1990</td>
</tr>
<tr>
<td>D</td>
<td>Five Mile Rapids (ORE-WS-4)</td>
<td>Wasco County, OR</td>
<td>212</td>
<td><em>G. amplus</em>?</td>
<td>C</td>
<td>11,970–6,750</td>
<td>L. Miller 1957; Simons 1983; Hansel-Kuehn 2003; Syverson and Prothero 2010</td>
</tr>
<tr>
<td>E</td>
<td>Old Bridge site</td>
<td>Calaveras County, CA</td>
<td>2 humeri wands</td>
<td><em>G. californianus</em></td>
<td>B</td>
<td>3,930–3,330</td>
<td>J. Johnson 1967; R. Taylor 1975; Simons 1983</td>
</tr>
<tr>
<td>Site letter</td>
<td>Site name, Location</td>
<td>Minimum # of bones</td>
<td>Species</td>
<td>Site type</td>
<td>Years before presentc</td>
<td>References</td>
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</tr>
<tr>
<td>F</td>
<td>West Berkeley shellmound (CA-Ala 307)</td>
<td>1 articulated skeleton</td>
<td>G. californianus</td>
<td>B</td>
<td>3,510–2,400</td>
<td>Wallace and Lathrap 1959; Crane 1956; Wallace and Lathrap 1975; Simons 1983</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>Windmiller mound (CA-Sac-107c)</td>
<td>1 mandible</td>
<td>G. californianus</td>
<td>B</td>
<td>3,180–2,540</td>
<td>Gifford 1940; Ragir 1972; Simons 1983</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>Poet's Cove, Bedwell Harbour (DeRt-4)</td>
<td>1</td>
<td>G. californianus</td>
<td>C</td>
<td>2,935–2,905*</td>
<td>I. R. Wilson Consultants, Ltd. 2006; Royal British Columbia Museum Archeology Collection</td>
<td></td>
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<tr>
<td>J</td>
<td>Stevenson Street (CA-SFR-112)</td>
<td>1</td>
<td>G. californianus</td>
<td>C</td>
<td>1,790–1,240</td>
<td>Lieberson 1988; Broughton et al. 2007</td>
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Table 2.1 (Continued)

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<th>Site letter</th>
<th>Site name</th>
<th>Location</th>
<th>Minimum # of bones</th>
<th>Species</th>
<th>Site type</th>
<th>Years before present</th>
<th>References</th>
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<tbody>
<tr>
<td>K</td>
<td>McCauley mound</td>
<td>San Joaquin County, CA</td>
<td>4 bone whistles</td>
<td><em>G. californianus</em></td>
<td>C</td>
<td>1,500–500</td>
<td>Schenck and Dawson 1929; Simons 1983; Maniery 1991</td>
</tr>
<tr>
<td></td>
<td>number 3 (CA-Sjo-43)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>L</td>
<td>Hotchkiss mound</td>
<td>Contra Costa County, CA</td>
<td>3 bone whistles</td>
<td><em>G. californianus</em></td>
<td>C</td>
<td>1,429–350</td>
<td>Libby 1954; Crane and Griffin 1960; Simons 1983</td>
</tr>
<tr>
<td></td>
<td>(CA-Cco-138)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>N</td>
<td>Filoli site (CA-SMA-125)</td>
<td>San Mateo County, CA</td>
<td>4 bone whistles</td>
<td><em>G. californianus</em></td>
<td>B</td>
<td>ca. 1,000</td>
<td>Morejohn and Galloway 1983; Griffin et al. 2006</td>
</tr>
<tr>
<td>O</td>
<td>Berryessa Valley Adobe</td>
<td>Napa County, CA</td>
<td>1 bone whistle</td>
<td><em>G. californianus</em></td>
<td>C</td>
<td>ca. 200</td>
<td>Simons 1983</td>
</tr>
</tbody>
</table>

* See Figure 2.1 for a map of the sites.

b B = Burial; C = Cultural Deposit; N = Natural Deposit

*asterisk indicates direct radiocarbon date of a condor bone.
Table 2.2. Records of California Condors in the Pacific Northwest, based on a review of published literature, newspaper articles, journals of early explorers and settlers, and museum records. See Appendix 1 for additional details regarding each record of early explorers and settlers, and museum records. See Appendix 1 for additional details regarding each record.

<table>
<thead>
<tr>
<th>Record number</th>
<th>Location</th>
<th>Observer/collector</th>
<th>Obs. type(^a)</th>
<th>Positional accuracy(^b)</th>
<th>Reliability score(^c)</th>
<th>Year</th>
<th>Season(^d)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Near confluence of the Wind River and Columbia River, Skamania County, WA</td>
<td>Lewis and Clark party</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1805</td>
<td>Fall</td>
<td>Lewis et al. 2002 (weather report in Voorhis No. 4, 28 October 28 1805; weather report in Codex I, 29 October 1805; Clark’s journal, 30 October 1805)</td>
</tr>
<tr>
<td>2</td>
<td>Cape Disappointment, WA</td>
<td>Lewis and Clark party</td>
<td>K(^{x})</td>
<td>H</td>
<td>1</td>
<td>1805</td>
<td>Fall</td>
<td>Lewis et al. 2002 (Clark’s journal, 18 November 1805)</td>
</tr>
<tr>
<td>3</td>
<td>Beach near Fort Clatsop, OR</td>
<td>Lewis and Clark party</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1805</td>
<td>Fall</td>
<td>Lewis et al. 2002 (Clark’s journal, 29 November 1805)</td>
</tr>
<tr>
<td>4</td>
<td>Near Fort Clatsop, OR</td>
<td>Lewis and Clark party</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1806</td>
<td>Winter</td>
<td>Lewis et al. 2002 (Lewis’s journal, 3 January 1806)</td>
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<tr>
<td>5</td>
<td>Youngs River, Clatsop County, OR</td>
<td>Lewis and Clark party</td>
<td>L/K</td>
<td>M</td>
<td>1</td>
<td>1806</td>
<td>Winter</td>
<td>Lewis et al. 2002 (Lewis’s journal, 16 February 1806; Clark’s journal, 16 February 1806)</td>
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<td>6</td>
<td>Near Fort Clatsop, OR</td>
<td>Lewis and Clark party</td>
<td>K (x2)</td>
<td>M</td>
<td>1</td>
<td>1806</td>
<td>Spring</td>
<td>Lewis et al. 2002 (Gass’s journal, 16 March 1806)</td>
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<tr>
<td>Record number</td>
<td>Location</td>
<td>Observer/ collector</td>
<td>Obs. type(^a)</td>
<td>Positional accuracy(^b)</td>
<td>Reliability score(^c)</td>
<td>Year</td>
<td>Season(^d)</td>
<td>References</td>
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<tr>
<td>7</td>
<td>North end of Deer Island, Columbia County, OR</td>
<td>Lewis and Clark party</td>
<td>O</td>
<td>H</td>
<td>4</td>
<td>1806</td>
<td>Spring</td>
<td>Lewis et al. 2002 (Lewis’s journal, 28 March 1806; Clark’s journal, 28 March 1806)</td>
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<tr>
<td>8</td>
<td>Near Rooster Rock State Park, OR</td>
<td>Lewis and Clark party</td>
<td>K</td>
<td>H</td>
<td>1</td>
<td>1806</td>
<td>Spring</td>
<td>Lewis et al. 2002 (Clark’s journal, 6 April 1806)</td>
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<td>9</td>
<td>Lower end of Hamilton Island, WA</td>
<td>Alexander Henry and David Thompson</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1814</td>
<td>Winter</td>
<td>Coues 1897:808</td>
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<tr>
<td>10</td>
<td>Above Willamette Falls, near Pudding River, OR</td>
<td>Alexander Henry and David Thompson</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1814</td>
<td>Winter</td>
<td>Coues 1897:817</td>
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<tr>
<td>11</td>
<td>Idaho/Oregon border</td>
<td>Donald McKenzie</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1818</td>
<td>Fall</td>
<td>Ross 1855:203</td>
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<tr>
<td>12</td>
<td>Near the confluence of the Cowlitz and Columbia Rivers, WA</td>
<td>John Scouler</td>
<td>K(^i)</td>
<td>L</td>
<td>1</td>
<td>1825</td>
<td>Fall</td>
<td>Scouler 1905:280; National Museum of Natural History, Leiden, The Netherlands, specimen 162189</td>
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<td>13</td>
<td>Near Fort Vancouver, WA</td>
<td>David Douglas</td>
<td>K(^i)</td>
<td>L</td>
<td>1</td>
<td>1826</td>
<td>Winter</td>
<td>Douglas 1914:154–55; Hall 1934:5; Institute Royal des Sciences Naturelles de Belgique (Brussels) or Museum National d'Histoire Naturelle (Paris)</td>
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<th>Record number</th>
<th>Location</th>
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<th>Type(^a)</th>
<th>Positional accuracy(^b)</th>
<th>Reliability score(^c)</th>
<th>Year</th>
<th>Season(^d)</th>
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<td>Between the Umpqua River and Willamette Valley, OR</td>
<td>David Douglas</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1826</td>
<td>Fall</td>
<td>Douglas 1914:67</td>
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<td>15</td>
<td>Umpqua River and south, OR</td>
<td>David Douglas and Norman McLeod</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1826</td>
<td>Fall</td>
<td>Douglas 1914:216, 241</td>
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<tr>
<td>16</td>
<td>East of the Cascades, near the US-Canada border, WA</td>
<td>David Douglas</td>
<td>O</td>
<td>L</td>
<td>5</td>
<td>1826–1827</td>
<td>—</td>
<td>Douglas 1829:329</td>
</tr>
<tr>
<td>17</td>
<td>Near Fort Vancouver, WA</td>
<td>David Douglas</td>
<td>K(^f)</td>
<td>H</td>
<td>1</td>
<td>1827</td>
<td>Winter</td>
<td>Barnston 1860:208; Douglas 1914:241; Fleming 1924:111–12; Institute Royal des Sciences Naturelles de Belgique (Brussels) or Museum National d’Histoire Naturelle (Paris)</td>
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<td>18</td>
<td>Klamath River area near the present-day Humboldt-Del Norte county line, CA</td>
<td>Jedediah Smith</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1828</td>
<td>Spring</td>
<td>Sullivan 1934:92</td>
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Table 2.2. (Continued)

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<th>Record number</th>
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<th>Obs. type&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Positional accuracy&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Reliability score&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Year</th>
<th>Season&lt;sup&gt;d&lt;/sup&gt;</th>
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<tbody>
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<td>19</td>
<td>Cowlitz River near its confluence with the Columbia River, WA</td>
<td>William Fraser Tolmie</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1833</td>
<td>Spring</td>
<td>Tolmie 1963:185</td>
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<tr>
<td>20</td>
<td>Cowlitz River, WA</td>
<td>William Fraser Tolmie</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1833</td>
<td>Spring</td>
<td>Tolmie 1963:186</td>
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<tr>
<td>22</td>
<td>Willamette Falls, OR</td>
<td>John Kirk Townsend</td>
<td>K&lt;sup&gt;1&lt;/sup&gt;</td>
<td>H</td>
<td>1</td>
<td>1835</td>
<td>Spring</td>
<td>J. Townsend 1848:265–67; US National Museum specimen 78005</td>
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<tr>
<td>23</td>
<td>Northern California [exact location uncertain—see Appendix 1 for details]</td>
<td>Ivan Gavrilovich Voznesenskii</td>
<td>K (x2)&lt;sup&gt;1&lt;/sup&gt;; K (x2)&lt;sup&gt;x&lt;/sup&gt;</td>
<td>L</td>
<td>1</td>
<td>1840–1841</td>
<td>—</td>
<td>Blomkvist 1972:100–170; Bates 1983:36-41; Alekseev 1987; Zoological Institute, Academy of Sciences, Saint Petersburg, Russia, specimens 1583 and 1584; Museum National d'Histoire Naturelle (Paris)</td>
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<tr>
<td>24</td>
<td>Plains of the Willamette Valley, OR</td>
<td>Titian Ramsay Peale</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1841</td>
<td>Fall</td>
<td>Peale 1848:58</td>
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<th>Reliability score&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Year</th>
<th>Season&lt;sup&gt;d&lt;/sup&gt;</th>
<th>References</th>
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<tr>
<td>25</td>
<td>Near Youngs River (creek) in the Umpqua Mountains, OR</td>
<td>Titian Ramsay Peale</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1841</td>
<td>Fall</td>
<td>Poesch 1961:191</td>
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<td>26</td>
<td>North of Redding, along the Sacramento River, CA</td>
<td>Titian Ramsay Peale</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1841</td>
<td>Fall</td>
<td>Poesch 1961:194</td>
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<tr>
<td>27</td>
<td>Sacramento Valley between Redding and Sacramento, CA</td>
<td>Titian Ramsay Peale</td>
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<td>2</td>
<td>1841</td>
<td>Fall</td>
<td>Poesch 1961:195</td>
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<tr>
<td>28</td>
<td>Valley of Napa Creek, CA</td>
<td>James Clyman</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1845</td>
<td>Summer</td>
<td>Clyman 1926:137</td>
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<tr>
<td>29</td>
<td>Napa County, CA</td>
<td>James Clyman</td>
<td>K</td>
<td>L</td>
<td>1</td>
<td>1845</td>
<td>Fall</td>
<td>Clyman 1926:138</td>
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<td>30</td>
<td>Between Sutter’s Fort and Suisun Bay, CA</td>
<td>Heinrich Lienhard</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1846</td>
<td>—</td>
<td>Wilbur 1941:42</td>
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<tr>
<td>31</td>
<td>Near Fort Ross, CA</td>
<td>William Benitz</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1846–1847</td>
<td>—</td>
<td>E. Finley 1937:406</td>
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<tr>
<td>32</td>
<td>Mountains of Marin County, CA</td>
<td>Andrew Jackson Grayson</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1847</td>
<td>Summer</td>
<td>Bryant 1891:52–53</td>
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<th>Year</th>
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<tr>
<td>33</td>
<td>Mouth of Feather River, CA</td>
<td>Jacob D. B. Stillman and Mark Hopkins</td>
<td>K</td>
<td>M</td>
<td>1</td>
<td>1849</td>
<td>Fall</td>
<td>Stillman 1967:27</td>
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<td>34</td>
<td>Yuba River Canyon, CA</td>
<td>Elisha Douglass Perkins</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1849</td>
<td>Fall</td>
<td>T. Clark 1967:135</td>
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<td>35</td>
<td>Sierra foothills, Plumas County, CA</td>
<td>Joseph Goldsborough Bruff party</td>
<td>K</td>
<td>L</td>
<td>1</td>
<td>1849</td>
<td>Fall</td>
<td>Reed and Gaines 1949:204</td>
</tr>
<tr>
<td>36</td>
<td>Mill Creek area, Tehama County, CA</td>
<td>Joseph Goldsborough Bruff party</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1849</td>
<td>Fall</td>
<td>Reed and Gaines 1949:240, 245</td>
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<tr>
<td>38</td>
<td>Mill Creek area, Tehama County, CA</td>
<td>Joseph Goldsborough Bruff party</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1850</td>
<td>Winter</td>
<td>Reed and Gaines 1949:301, 306–8</td>
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<td>39</td>
<td>Mill Creek area, Tehama County, CA</td>
<td>Joseph Goldsborough Bruff party</td>
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<td>L</td>
<td>2</td>
<td>1850</td>
<td>Spring</td>
<td>Reed and Gaines 1949:311, 325</td>
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<td>Reliability score&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Year</td>
<td>Season&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>40</td>
<td>West Branch, North Fork of the Feather River, CA</td>
<td>Samuel Seabough</td>
<td>K</td>
<td>M</td>
<td>1</td>
<td>1850–1880</td>
<td>—</td>
<td>Seabough 1880; Cummins 1893:87</td>
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<tr>
<td>41</td>
<td>Coast Range, Mendocino County, CA</td>
<td>A. K. Benton</td>
<td>K&lt;sup&gt;x&lt;/sup&gt;</td>
<td>L</td>
<td>3</td>
<td>1854–1856</td>
<td>—</td>
<td>Daily Union (Sacramento) 1 April 1856</td>
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<tr>
<td>42</td>
<td>Near Chico, CA</td>
<td>Unknown</td>
<td>K&lt;sup&gt;x&lt;/sup&gt;</td>
<td>L</td>
<td>3</td>
<td>1854</td>
<td>—</td>
<td>Daily Union (Sacramento) 21 June 1854</td>
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<tr>
<td>43</td>
<td>Near Fort Vancouver, WA</td>
<td>James Graham Cooper</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1854</td>
<td>Winter</td>
<td>Cooper and Suckley 1859:141; Belding 1890:24–27</td>
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<td>44</td>
<td>American River, El Dorado County (near the store of Woods &amp; Kenyon), CA</td>
<td>Unknown</td>
<td>K</td>
<td>M</td>
<td>3</td>
<td>1854</td>
<td>Spring</td>
<td>Daily Union (Sacramento) 11 March 1854</td>
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<tr>
<td>45</td>
<td>South Fork of American River (between North and South Canyon), CA</td>
<td>Alonzo Winship and Jesse Millikan</td>
<td>L</td>
<td>M</td>
<td>1</td>
<td>1854</td>
<td>Fall</td>
<td>Millikan 1900:12–13</td>
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<td>Positional accuracy(^b)</td>
<td>Reliability score(^c)</td>
<td>Year</td>
<td>Season(^d)</td>
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<td>46</td>
<td>Vicinity of the redwoods of Contra Costa, CA</td>
<td>Joseph P. Lamson</td>
<td>K (x4)</td>
<td>M</td>
<td>1</td>
<td>1854</td>
<td>Winter</td>
<td>Lamson 1852–1861:283, 284, 286, 287, 292; Lamson 1878:152–54</td>
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<td>47</td>
<td>Vicinity of the redwoods of Contra Costa, CA</td>
<td>Alexander S. Taylor</td>
<td>K(^i)</td>
<td>M</td>
<td>1</td>
<td>1855</td>
<td>—</td>
<td>California Academy of Natural Sciences 1863, 1:71</td>
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<td>48</td>
<td>Sacramento Valley, CA</td>
<td>John Strong Newberry</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1855</td>
<td>Summer</td>
<td>Newberry 1857:73</td>
</tr>
<tr>
<td>49</td>
<td>Siskiyou Mountains, Klamath Basin, CA</td>
<td>John Strong Newberry</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1855</td>
<td>Summer</td>
<td>Newberry 1857:73</td>
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<tr>
<td>50</td>
<td>Mendocino County, CA</td>
<td>Lyman Belding</td>
<td>O</td>
<td>L</td>
<td>2</td>
<td>1856–1878</td>
<td>—</td>
<td>Belding 1878, in litt.; Fisher 1920</td>
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<tr>
<td>51</td>
<td>Near Marysville, Yuba County, CA</td>
<td>Lyman Belding</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1856–1879</td>
<td>Winter</td>
<td>Belding 1879:437; Fisher 1920</td>
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<tr>
<td>52</td>
<td>Near Sacramento (caught on Mrs. Harrold’s ranch), CA</td>
<td>Unknown</td>
<td>L</td>
<td>M</td>
<td>1</td>
<td>1857</td>
<td>Fall</td>
<td>Daily Union (Sacramento) 24 September 1857</td>
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<tr>
<td>53</td>
<td>Lower Napa Valley, CA</td>
<td>Frank A. Leach</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1857–1860</td>
<td>—</td>
<td>Leach 1929:23</td>
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<th>Reliability score(^c)</th>
<th>Year</th>
<th>Season(^d)</th>
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<tr>
<td>54</td>
<td>Pope Valley, near Saint Helena, Napa Valley, CA</td>
<td>J. B. Wright</td>
<td>K</td>
<td>M</td>
<td>3</td>
<td>1858</td>
<td>Winter</td>
<td><em>Daily Alta California</em> (San Francisco) 4 February 1858</td>
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<tr>
<td>55</td>
<td>Mouth of Fraser River, BC</td>
<td>John Keast Lord</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1858–1866</td>
<td>—</td>
<td>Lord 1866:291</td>
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<td>56</td>
<td>Russian River area of the Coast Range, CA</td>
<td>L. L. Davis</td>
<td>K(^{lx})</td>
<td>L</td>
<td>3</td>
<td>1861</td>
<td>—</td>
<td><em>Daily Union</em> (Sacramento) 18 June 1861</td>
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<td>57</td>
<td>Plumas County, CA</td>
<td>S. Stevens</td>
<td>K(^{lx})</td>
<td>L</td>
<td>3</td>
<td>1865</td>
<td>—</td>
<td><em>Daily Union</em> (Sacramento) 25 November 1865</td>
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<td>58</td>
<td>Near Marin County paper mills, CA</td>
<td>Unknown</td>
<td>K(^{lx})</td>
<td>H</td>
<td>3</td>
<td>1868</td>
<td>Summer</td>
<td><em>Bulletin</em> (San Francisco) 19 August 1868</td>
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<td>59</td>
<td>Winnemucca, NV</td>
<td>Unknown</td>
<td>O</td>
<td>H</td>
<td>5</td>
<td>1871</td>
<td>Summer</td>
<td><em>Daily Union</em> (Sacramento) 26 August 1871</td>
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<td>60</td>
<td>Mendocino County, CA</td>
<td>Unknown</td>
<td>K</td>
<td>L</td>
<td>3</td>
<td>1872</td>
<td>Winter</td>
<td><em>Tribune</em> (Chicago) 24 February 1872</td>
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<tr>
<td>61</td>
<td>Salmon Creek, Marin County, CA</td>
<td>Julius Poirsons</td>
<td>K(^{lx})</td>
<td>M</td>
<td>3</td>
<td>1873</td>
<td>Winter</td>
<td><em>Daily Evening Bulletin</em> (San Francisco) 19 February 1873 [see Appendix 1 for additional citations]</td>
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<th>Year</th>
<th>Season&lt;sup&gt;d&lt;/sup&gt;</th>
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<tr>
<td>62</td>
<td>Near the peak of Mount Shasta, CA</td>
<td>Benjamin P. Avery</td>
<td>O</td>
<td>H</td>
<td>2</td>
<td>1873</td>
<td>Fall</td>
<td>Avery 1874:476</td>
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<td>63</td>
<td>Near the hot springs above Boise City, ID</td>
<td>General T. E. Wilcox</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1879</td>
<td>Fall</td>
<td>Lyon 1918:25</td>
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<tr>
<td>64</td>
<td>Foothills southwest of Mount Lassen, CA</td>
<td>Unknown</td>
<td>O</td>
<td>L</td>
<td>4</td>
<td>1879–1884</td>
<td>―</td>
<td>C. Townsend 1887:201</td>
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<tr>
<td>65</td>
<td>South Eel River, Humboldt County, CA</td>
<td>Mr. Adams</td>
<td>K</td>
<td>M</td>
<td>3</td>
<td>1880</td>
<td>Spring</td>
<td>Bulletin (San Francisco) 5 April 1880</td>
</tr>
<tr>
<td>66</td>
<td>Reeds Creek Canyon, Tehama County, CA</td>
<td>John Bogard</td>
<td>K</td>
<td>H</td>
<td>3</td>
<td>1880</td>
<td>Spring</td>
<td>Daily Evening Bulletin (San Francisco) 7 May 1880</td>
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<tr>
<td>67</td>
<td>Burrard Inlet, BC</td>
<td>John Fannin</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1880</td>
<td>Fall</td>
<td>Fannin 1891:22</td>
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<td>68</td>
<td>Mountains south of Mount Lassen, CA</td>
<td>Unknown</td>
<td>K</td>
<td>L</td>
<td>3</td>
<td>1881–1882</td>
<td>―</td>
<td>C. Townsend 1887:201</td>
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<td>69</td>
<td>Vicinity of San Rafael, CA</td>
<td>Unknown</td>
<td>L</td>
<td>L</td>
<td>2</td>
<td>1882 or prior</td>
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<td>Gassaway 1882:89</td>
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<td>Year</td>
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<td>70</td>
<td>Chico, Butte County, CA</td>
<td>William Proud</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1880s</td>
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<tr>
<td>71</td>
<td>Lulu Island (Fraser River delta), BC</td>
<td>W. London</td>
<td>O</td>
<td>H</td>
<td>4</td>
<td>1888–1889</td>
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<td>72</td>
<td>Kneeland Prairie, Humboldt County, CA</td>
<td>Unknown</td>
<td>K(^i)</td>
<td>H</td>
<td>1</td>
<td>1889–1890</td>
<td>Fall</td>
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<td>73</td>
<td>Yager Creek, Humboldt County, CA</td>
<td>F. H. Ottmer</td>
<td>K(^i)</td>
<td>H</td>
<td>1</td>
<td>1892</td>
<td>Fall</td>
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<td>74</td>
<td>A few miles east of Coulee City, WA</td>
<td>Clinton Hart Merriam</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1897</td>
<td>Fall</td>
<td></td>
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<td>75</td>
<td>Southern coast, OR</td>
<td>Henry Peck</td>
<td>K</td>
<td>L</td>
<td>3</td>
<td>Late 1800s</td>
<td></td>
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<td>76</td>
<td>Curry County, OR</td>
<td>Unknown</td>
<td>O</td>
<td>L</td>
<td>4</td>
<td>Prior to 1900</td>
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<td>77</td>
<td>Mountains north of San Francisco, Marin County, CA</td>
<td>Unknown</td>
<td>K(^i)</td>
<td>L</td>
<td>1</td>
<td>1900–1905</td>
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<th>Reliability score(c)</th>
<th>Year</th>
<th>Season(d)</th>
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<tbody>
<tr>
<td>78</td>
<td>Near Drain, OR</td>
<td>George D. Peck and Henry Peck</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1903</td>
<td>Summer</td>
<td>W. Finley 1908b:10; Peck 1904:55; Gabrielson and Jewett 1970:180–81</td>
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<td>79</td>
<td>Near Drain, OR</td>
<td>Henry Peck</td>
<td>O</td>
<td>M</td>
<td>2</td>
<td>1904</td>
<td>Spring</td>
<td>W. Finley 1908b:10; Gabrielson and Jewett 1970:180–81</td>
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<tr>
<td>80</td>
<td>Kibesillah, near Fort Bragg, Mendocino County, CA</td>
<td>Cecile Clarke</td>
<td>O</td>
<td>H</td>
<td>4</td>
<td>1912</td>
<td>Fall</td>
<td>Clarke, in litt. 1971</td>
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</tbody>
</table>

\(a\) K = killed, O = observation only, L = live-captured

\(b\) H = High (< 10 km), M = Moderate (10–50 km), L = Low (> 50 km)

\(c\) 1 = physical evidence (museum specimen) or firsthand identification based on a bird-in-hand

2 = firsthand observation with no physical evidence and no bird-in-hand, but with sufficient details to rule out other raptors

3 = secondhand identification based on a bird-in-hand

4 = secondhand observation with no bird-in-hand, but with sufficient details to rule out other raptors; proximal in time (within 10 years) and space (within approximately 100 km of physical evidence or reliable firsthand accounts)

5 = firsthand or secondhand observation with no physical evidence and no bird-in-hand, but with sufficient details to rule out other raptors; not proximal in time (within 10 years) or space (within 100 km of physical evidence or reliable firsthand accounts)

\(d\) Spring = March–May; Summer = June–August; Fall = September–November; Winter = December–February

\(\dagger\) Specimen preserved (all or part) and currently in collections (see Appendix 1 for details)

\(\dagger\times\) Specimen preserved but subsequently lost or destroyed (see Appendix 1 for details)
Table 2.3. Average body mass, wing span, wing area, and wing loading of vultures.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass (kg)</th>
<th>Wing span (m)</th>
<th>Wing area (m$^2$)</th>
<th>Wing loading (Newton/m$^2$)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lesser Yellow-headed Vulture</td>
<td>0.96</td>
<td>1.58</td>
<td>0.36</td>
<td>26.0</td>
<td>Houston (1988)</td>
</tr>
<tr>
<td>(Cathartes burrovianus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turkey Vulture</td>
<td>1.78</td>
<td>1.71</td>
<td>0.43</td>
<td>40.6</td>
<td>Houston (1988)</td>
</tr>
<tr>
<td>(Cathartes aura)</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Black Vulture</td>
<td>1.82</td>
<td>1.37</td>
<td>0.31</td>
<td>57.6</td>
<td>Houston (1988)</td>
</tr>
<tr>
<td>(Coragyps atratus)</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Egyptian Vulture</td>
<td>1.9</td>
<td>1.68</td>
<td>0.32</td>
<td>59</td>
<td>Pennycuick (1972)</td>
</tr>
<tr>
<td>(Neophron percnopterus)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Hooded Vulture</td>
<td>2.0</td>
<td>1.71</td>
<td>0.44</td>
<td>45</td>
<td>Pennycuick (1972)</td>
</tr>
<tr>
<td>(Necrosyrtes monachus)</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>King Vulture</td>
<td>3.34</td>
<td>1.52</td>
<td>0.45</td>
<td>72.8</td>
<td>Houston (1988)</td>
</tr>
<tr>
<td>(Sarcoramphus papa)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-headed Vulture</td>
<td>3.97</td>
<td>2.16</td>
<td>0.63</td>
<td>61.8</td>
<td>Mendelsohn et al. (1989)</td>
</tr>
<tr>
<td>(Trigonoceros occipitalis)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Bearded Vulture</td>
<td>5.40</td>
<td>2.58</td>
<td>0.74</td>
<td>71.6</td>
<td>Mendelsohn et al. (1989)</td>
</tr>
<tr>
<td>(Gypaetus barbatus)</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>African White-backed Vulture</td>
<td>5.80</td>
<td>2.18</td>
<td>0.75</td>
<td>75.8</td>
<td>Mendelsohn et al. (1989);</td>
</tr>
<tr>
<td>(Gyps africanus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pennycuick (1972)</td>
</tr>
<tr>
<td>Species</td>
<td>Mass (kg)</td>
<td>Wing span (m)</td>
<td>Wing area (m²)</td>
<td>Wing loading (Newton/m²)</td>
<td>Source</td>
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<td>------------------------------------------------</td>
</tr>
<tr>
<td>Rüppell’s Griffon Vulture</td>
<td>7.57</td>
<td>2.41</td>
<td>0.83</td>
<td>89.5</td>
<td>Pennycuick (1972)</td>
</tr>
<tr>
<td><em>(Gyps rueppellii)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Griffon Vulture (male)</td>
<td>7.65</td>
<td>2.53</td>
<td>0.89</td>
<td>84.3</td>
<td>Xirouchakis and Poulakakis (2008)</td>
</tr>
<tr>
<td><em>(Gyps fulvus)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Griffon Vulture (female)</td>
<td>7.74</td>
<td>2.54</td>
<td>0.89</td>
<td>85.3</td>
<td>Xirouchakis and Poulakakis (2008)</td>
</tr>
<tr>
<td><em>(Gyps fulvus)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Andean Condor (female)</td>
<td>8.4</td>
<td>2.77</td>
<td>0.97</td>
<td>85</td>
<td>McGahan (1973)</td>
</tr>
<tr>
<td><em>(Vultur gryphus)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>California Condor</td>
<td>8.8</td>
<td>2.74</td>
<td>0.98&lt;sup&gt;a&lt;/sup&gt;</td>
<td>80.8</td>
<td>H. Fisher (1946); Ferguson-Lees and Christie (2001); Snyder and Schmitt (2002)</td>
</tr>
<tr>
<td><em>(Gymnogyps californianus)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cape Vulture <em>(Gyps coprotheres)</em></td>
<td>9.29</td>
<td>2.57</td>
<td>0.85</td>
<td>107.2</td>
<td>Mendelsohn et al. (1989)</td>
</tr>
<tr>
<td>Andean Condor (male)</td>
<td>11.7</td>
<td>2.99</td>
<td>1.13</td>
<td>102</td>
<td>McGahan (1973)</td>
</tr>
<tr>
<td><em>(Vultur gryphus)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Calculated using H. Fisher’s (1946) measurement of the total surface area of the bird (wings, tail, and body) and subtracting the minimum tail area as given in Ferguson-Lees and Christie (2001).
Table 2.4. Evaluation of extinction hypotheses for California Condors in the Pacific Northwest.

| Hypothesis                                | Correct time frame? | Potential geographic extent and magnitude of effects | Suspected cause of other vulture species' declines? | Reject hypothesis?  
<table>
<thead>
<tr>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Secondary poisoning</td>
<td>Y</td>
<td>Regional/very high</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>Lead poisoning</td>
<td>Y</td>
<td>Regional/very high</td>
<td>Y</td>
<td>N</td>
</tr>
<tr>
<td>DDT/DDE and eggshell thinning</td>
<td>N</td>
<td>Regional/unknown</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>Collecting and shooting</td>
<td>Y</td>
<td>Regional/high</td>
<td>Y (locally)</td>
<td>N</td>
</tr>
<tr>
<td>Egg collecting</td>
<td>N</td>
<td>Local/low</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>Loss of nesting habitat</td>
<td>N</td>
<td>Local/low</td>
<td>Y (locally)</td>
<td>Y</td>
</tr>
<tr>
<td>Native American ritual killings</td>
<td>N</td>
<td>Local/low</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>Food increases in southern and central California</td>
<td>N</td>
<td>Regional/low</td>
<td>N</td>
<td>Y</td>
</tr>
<tr>
<td>Food declines</td>
<td>N</td>
<td>Regional/high</td>
<td>Y (locally)</td>
<td>Y</td>
</tr>
</tbody>
</table>

Intermediate	I rejected those hypotheses that were inconsistent with the time frame of the decline and those whose potential impacts had low magnitude or were localized. Information on whether the hypotheses have been the documented cause of other vulture species’ declines is given for reference but was not a factor in rejecting any hypotheses.
CHAPTER 3 – ANCIENT DNA IN MUSEUM SPECIMENS REVEALS HISTORICAL CALIFORNIA
CONDOR (GYMNOGYPS CALIFORNIANUS) POPULATION STRUCTURE AND LOSS OF
MITOCHONDRIAL DNA DIVERSITY

Jesse D’Elia, Susan M. Haig, Tom Mullins, Mark P. Miller

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Waco, Texas 76710
3.1 ABSTRACT

Critically endangered species that have undergone severe population bottlenecks often have little remaining genetic variation, making it difficult to reconstruct population histories for designing effective reintroduction and recovery strategies. Combining genetic evidence from the historical population through use of ancient DNA from museum specimens with information from the contemporary population following a bottleneck can provide a more complete picture of a species’ genetic variation across its historical range and through time. Applying this approach, we examined mitochondrial DNA diversity in the control region of the California Condor (*Gymnogyps californianus*), a species that experienced a severe population bottleneck, with only 22 individuals remaining at its lowest point. We used mtDNA harvested from museum samples (n = 67 individual birds that comprised the historical population; 1825-1984) and genetic founders of the captive population (n =14), in conjunction with inferred mtDNA sequences of the current population obtained by tracing the maternal pedigrees of the founders (n = 404), to evaluate how much genetic variation of the California Condor had been lost through time. We tested the null hypothesis that genetic diversity was constant through time. We also tested the hypothesis that the historical population was subdivided into genetically differentiated populations at its northern and southern range edges in the Pacific Northwest and Baja California, Mexico. Our examination of a 526 bp sequence of control region mtDNA revealed 18 haplotypes in the historical population, with only three surviving through the genetic bottleneck—a > 80% reduction in haplotype richness. This substantial loss of haplotypes is consistent with the hypothesis that condor populations were relatively abundant at the time of Euro-American contact, but declined rapidly as a result of human causes. A starlike haplotype network in the historical population, low levels of sequence divergence, and a high frequency of unique mutations indicate that California Condors likely experienced a rapid population expansion in their evolutionary history prior to the recent genetic bottleneck. We found no spatial sorting of haplotypes in the historical population, with the periphery of the range containing only haplotypes that were common throughout the historical range. This suggests that condors in the Pacific Northwest and in Baja California were not historically isolated from the population of condors in southern and central California. Thus, conservation strategies should consider restoring rangewide metapopulation connectivity when planning future reintroductions.
3.2 INTRODUCTION

The study of genetic variation in animal populations across space and through time is foundational to our understanding of population and evolutionary biology (Mayr 1963, Harrison 1989) and to establishing effective conservation strategies (Frankham et al. 2006). For critically endangered species, where populations are confined to a small portion of the species’ historical range for a long period of time, investigations of the contemporary depleted population often provide little insight into the species’ population history and structure prior to population declines (Matocq and Villablanca 2001, but see Haig and Ballou 1995). This can be a key limitation in understanding spatial and temporal changes in genetic variation and designing effective conservation and reintroduction strategies (Draheim et al. 2012).

Perhaps no other species in the world embodies this problem more clearly than the California Condor (Gymnogyps californianus; condor), the only surviving representative of the genus Gymnogyps. Fossil evidence shows that California Condors occupied a large portion of North America at the end of the Pleistocene Epoch, stretching from boreal habitats in present day New York, to Florida, Mexico, California, and the Pacific Northwest (Steadman and Miller 1987, D’Elia and Haig 2013). At the close of the Pleistocene their range contracted to the west coast of North America and condors became rarer, presumably a direct result of losing major food resources as a number of large mammals went extinct across the continent (Miller 1942, Emslie 1987). The dearth of fossil evidence from the Holocene led Miller (1942) to conclude that the condor was doomed to extinction and already had “one wing in the grave” prior to Euro-American influence in the American West.

Despite reduced fossil evidence through the Holocene, the observational record of California Condors during Euro-American colonization of western North America suggests that condors were once widespread and locally abundant from southern British Columbia to Baja California (Snyder and Snyder 2000, D’Elia and Haig 2013). Population declines and range contractions were documented shortly thereafter, with condors disappearing from the Pacific Northwest in the early 1900s (D’Elia and Haig 2013), and from Baja California, Mexico by the end of 1930s (Wilbur and Kiff 1980). By the 1940s, condors existed in a relatively small portion of their historical range in the mountains of southern California (Koford 1953), and by 1950 their population numbered only about 150 individuals in a severely contracted range (Snyder and Snyder 2000).
California Condors continued to decline into the latter half of the twentieth century and the species was rescued from the brink of extinction in the late 1980s, when all of the remaining wild birds were trapped for captive breeding (Snyder and Snyder 2000). At the species’ lowest point in 1982, there were only 22 California Condors in existence, and ultimately, only 14 individuals from potentially unique lineages were available to found the captive breeding program (USFWS 1996b).

In 1996, the U.S. Fish and Wildlife Service finalized its recovery plan for the California Condor and established minimum criteria for reclassifying the California Condor from an endangered species to a threatened species under the U.S. Endangered Species Act (USFWS 1996b). The plan did not provide criteria for fully recovering the California Condor and removing it from the list of endangered and threatened species given the small population size at the time (n = 82 individuals). Minimum reclassification criteria were to establish at least two non-captive populations and one captive population that: (1) each number at least 150 individuals, (2) each contain at least 15 breeding pairs, and (3) are reproductively self-sustaining and have a positive rate of population growth. In addition, the non-captive populations were required to (4) be spatially disjunct and non-interacting, and (5) contain individuals descended from each of the 14 genetic founders. Genetic founders were those individuals used to initiate the captive breeding program and whose relationships were unknown and potentially represented unique lineages.

Through aggressive captive breeding efforts, followed by over two decades of reintroductions beginning in 1992, population numbers have increased substantially. There are now over 200 individuals in the wild, spread among four release sites in the southern half of their historical range, and more than 200 individuals in captivity (Walters et al. 2010, Mace 2014). However, recovering population numbers belie significant remaining threats to the viability of the California Condor—primarily from continued contamination of their food supply by spent lead ammunition—and none of the non-captive populations are current self-sustaining (Finkelstein et al. 2012). Furthermore, condors are still absent from the entire northern half of their historical range (D’Elia and Haig 2013).

Studies of genetic variation in the California Condor have almost exclusively focused on the genetic founders of the captive population and their offspring. As expected, given the severe population bottleneck they experienced, these studies revealed that little genetic
diversity remains (Corbin and Nice 1988, Geyer et al. 1993, Chemick et al. 2000, Adams and Villablanca 2007, Romanov et al. 2009). Virtually nothing is known about the condor’s genetic diversity or spatial distribution of genetic lineages prior to the population bottleneck. Technological advances in our ability to extract, amplify, and analyze ancient DNA from museum specimens, now enable direct evaluation of genetic diversity through time, which can provide insights into a species’ historical population structure and demographic history (Wandeler et al. 2007, Draheim et al. 2012).

Studying variation in the historical California Condor population via genetic sampling of museum specimens was suggested as early as 1993 (Geyer et al. 1993) but was not feasible until more recently. Thus, only one unpublished genetic investigation of the historical population of California Condors has been attempted (see Clipperton 2005). Clipperton (2005) evaluated 324 bp from the mtDNA control region of 41 individuals and only sampled individuals collected within a narrow temporal window (1886-1905). Results from Clipperton (2005) indicated that California Condors had apparently lost little genetic variation through their bottleneck and that the species likely had inherent low levels of mtDNA diversity. Low mtDNA diversity was also found in the contemporary population of Andean Condors (Vultur gryphus, Hendrickson et al. 2003) which are relatively widespread across the Andes Mountains of South America, and number at least 10,000 individuals (BirdLife International 2014).

We used mtDNA control region sequence data to test the null hypothesis that genetic diversity has remained constant across three temporal population groupings—the historical population (1825-1984), genetic founders (1980s), and the contemporary population (2014). We also tested the hypothesis that the historical population was divided into genetically differentiated populations at its northern and southern range edges in the Pacific Northwest and Baja California. Our analyses provide new insights into the ancestral distribution of condor maternal lineages across space and the extent of condor mtDNA variation that has been lost over the past two centuries.

### 3.3 METHODS

#### 3.3.1 Samples

We obtained 107 California Condor tissue samples from throughout their historical range, spanning the collecting period from 1825 to the inception of the captive breeding program in
the 1980s (Figure 3.1). Of these, 93 were 0.5 – 2 cm² tissue samples from museum specimens that represented the historical population (1825-1984; see Appendix 2, Tables A2.1 and A2.2) and 14 were genomic DNA samples of the genetic founders of the captive population or the offspring of female founders, obtained from the San Diego Institute for Conservation Research (Table 3.1). These lineages were traced through the entire living population using the California Condor studbook (Mace 2014), allowing us to infer the haplotype for all 404 living individuals as of January 2014 (hereafter referred to as the contemporary population).

Our museum specimen sampling strategy emphasized sampling individuals from all geographic areas of the historical range and across the temporal span of specimen collections. Samples from the northern portion of the historical range, the southern extreme of the range in Baja California, Mexico, older specimens (pre-1890), and specimens collected in the mid-twentieth century (1920-1970), were relatively rare compared to the number of museum samples collected in southern California from 1890-1910, when the demand for condor specimens reached its apex (Wilbur 1978, 2012). Therefore, we attempted to maximize the number of these rare samples in our study. Nevertheless, the distribution of museum samples we acquired was uneven across space and through time (Figures 3.1 and 3.2), which we accounted for in our statistical analyses (see below).

We divided historical samples geographically into three groups: Baja California, Mexico (n = 3), southern and central California (n = 59), and the Pacific Northwest (north of San Francisco Bay) (n = 5). For statistical analyses we pooled individuals from Baja California and southern and central California due to the limited number of samples from Baja California (n = 3); however, we retained the Baja California group when mapping and describing haplotype frequencies to evaluate whether there were any unique haplotypes at the southern periphery of the historical range. We used San Francisco Bay, a potential barrier or filter to California Condor movement, as the north-south dividing line between southern and central California and Pacific Northwest samples. Although this potential barrier seemed unlikely to substantially impede condor gene flow, breaks in mountain chains have been shown to limit population connectivity in Andean Condors (Hendrickson et al. 2003) and short overwater crossings can present an obstacle to large soaring raptors that rely on thermal updrafts or slope lift for movement (Bildstein et al. 2009). Furthermore, condors released in southern and central California have not yet ventured north of this area. Other break-points for potential population groups were
not evaluated as reintroduced condors have been documented moving between southern and central California (Kelly et al. 2014).

3.3.2 Laboratory Analyses
Our analysis of genetic variation focused on the mtDNA control region (CR), the major noncoding region of animal mtDNA that plays a role in replication and transcription of mtDNA molecules (Clayton 1992). The rapid rate of sequence evolution, maternal mode of inheritance, and lack of recombination, makes mtDNA particularly useful in studies of intraspecific population structure (Wilson et al. 1985). Its haploid copy number and maternal transmission make mtDNA less susceptible than nuclear markers to the confounding influence of interpopulation gene flow and a useful marker for detecting population bottlenecks (Wan et al. 2004).

Ancient DNA studies can be extremely susceptible to external contamination (Wandeler et al. 2007); therefore we used appropriate negative controls for the extraction and amplification process throughout the procedure, following appropriate ancient DNA techniques in a dedicated clean laboratory using a UV irradiated flow hood (see Draheim et al. 2012). Before extraction, we surface sterilized museum tissues with sterile dH2O and 80% ethanol washes, incubated them in a -80°C acetone bath and then crushed them using a sterile mortar and pestle. We used a modified Qiagen DNeasy Kit (Qiagen Inc., Valencia, California) protocol for extractions, incorporating an additional 24 hour 55°C Protenase K digestion step. We amplified genomic DNA of the genetic founders using the primer pair alt1 (Clipperton 2005) and CACO-R2 (Table 3.2) producing a 930 base pair (bp) fragment containing domain I and II of the control region. Primer CACO-R2 was designed from an Andean Condor reference sequence (Genbank accession AY129646.1) (Hendrickson et al. 2003).

The degraded condition of some museum tissue samples required the use of multiple shorter PCR amplifications to generate control region sequence. A combination of control region primers from Clipperton (2005) and CACO primers designed from reference sequence generated from the genetic founders was used to produce four fragments ranging in size from 200 bp to 319 bp (alt1/piel; Indel+/CACO-R3; CACO-F5/TDKD; CACO-F3/CACO-R4) (Table 3.2).

We performed PCR amplifications in 25 ul reactions containing 2.0 mM MgCl2, 1 µM of primers, 100 µM of each dNTP, 1X PCR buffer and 1U AmpliTaq Gold DNA polymerase (Perkin
Elmer, Waltham, Massachusetts). PCR reaction conditions were: 5 minute denaturation at 94 °C followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at the indicated temperature (Table 3.2) for 30 s, and extension at 72 °C for 30 s, followed by a 10 minute 72 °C extension. All PCR products were bi-directionally sequenced with BigDye version 3.1 dye terminator sequencing chemistry and resolved on an ABI 3730 automated DNA sequencer (University of Kentucky, Advanced Genetic Technologies Center). Resulting sequence chromatograms were aligned, edited, and trimmed using the program BioEdit Sequence Alignment Editor (Hall 1999). All sequences were archived in GenBank (http://www.ncbi.nlm.nih.gov/genbank).

3.3.3 Statistical Analyses

We created input files for data analysis using program FABOX (Villesen 2007), which was also used to identify unique haplotypes and quantify haplotype richness and the number of variable sites. Differentiation due to genetic structure between the northern and southern groups was evaluated by calculating $F_{ST}$ values (Wright 1969) in ARLEQUIN 3.5 (Excoffier et al. 2005). We also used ARLEQUIN to calculate haplotype ($h$) and nucleotide diversity ($\pi$) (Nei and Tajima 1981) for spatial and temporal groups.

We constructed a median-joining network (Bandelt et al. 1999) using the program NETWORK (http://www.fluxus-engineering.com/sharenet.htm) to help visualize relationships among haplotypes. Tajima’s $D$ (1989a, 1989b) and Fu’s $F_{S}$ (1997) were calculated in DnaSP version 5 (Librado and Rozas 2009) and used to infer population history of the California Condor. We used coalescent simulations in DnaSP—which simulate retrospective lineages until they converge at a common ancestor (Emerson et al. 2001)—to establish 95% confidence limits for the null model of a demographically stable population experiencing no selection. Simulations were contingent on observed values of $\theta$ from each data set, and confidence limits were obtained from 10,000 simulations. Observed values of $D$ or $F_{S}$ that fell outside of the 95% confidence limits of the null model simulations were assumed to be significant at the $\alpha = 0.05$ level. Negative $D$ and $F_{S}$ values indicate an excess of recent mutations indicative of past population expansion, while positive $D$ and $F_{S}$ values indicate a lack of recent mutations, indicative of population bottlenecks.

We used a simple graphical approach to illustrate the loss of genetic diversity in California Condors over time. We assigned each sample to the year it was collected. If the exact
year of collection was unknown the sample was assigned to the latest possible year of collection based on Wilbur (2012). We then calculated the minimum number of haplotypes remaining in the population for each year, assuming all detected haplotypes were present at the beginning of our sampling frame. Because we sampled an unknown, but likely small, percentage of the historical population the actual number of haplotypes remaining in the population was likely higher than our minimum estimate through time. We also simulated an expected distribution of rarified haplotypes (corrected for differences in sample sizes) remaining over time and compared those expectations with the observed number of rarified haplotypes remaining through time. To get expected values we simulated 100,000 populations and randomized the identity of each specimen with respect to rarified haplotype using HP-Rare (Kalinowski 2005). We then compared this expected distribution with our observed rarified values of the minimum number of haplotypes remaining through time.

3.4 RESULTS
We successfully amplified 526 bp of mtDNA control region sequence from 67 museum samples (72% of museum specimens sampled; Appendix 2, Tables A2.1-A2.2) and 14 DNA samples from the genetic founders (100% of genetic founders sampled), and documented 18 unique haplotypes. Haplotypes of 404 extant individuals were inferred by tracing their maternal pedigree, assuming that no new mutations emerged in the relatively short time-span since the genetic bottleneck.

3.4.1 mtDNA Variation and Historical Population Structure
We found no significant spatial sorting of haplotypes in the historical population and no unique haplotypes in the northern or southern peripheries of the historical range (Figure 3.2). $F_{ST}$ values showed no significant population differentiation due to genetic structure between northern and southern groups ($F_{ST} = -0.051, P = 0.720$). Only two haplotypes, H1 and H7, were detected throughout the historical range (Appendix 2, Table A2.1). These haplotypes were the most commonly found in the core of the historical range in southern and central California where condors persisted in the wild into the late twentieth century. They are also the haplotypes that survived the genetic bottleneck and are still represented in the contemporary population.
3.4.2 mtDNA Variation Through Time

The historical population contained a minimum of 18 haplotypes with 19 variable sites, while the genetic founders to the captive population and contemporary population contained a subset of only three haplotypes with four variable sites (Table 3.3). All substitutions were transitions (Adenine↔Guanine or Cytosine↔Thymine). We observed a minimum of an 80% decline in haplotype richness from the historical population through the genetic bottleneck. The loss of most of these haplotypes appears to have occurred after about 1890 (Figure 3.3), although the exact timing of the decline is not determinable with our dataset due to the non-uniform distribution of museum samples through time (Figure 3.1). Haplotype diversity \( (h) \) declined by 24%, from 0.851 in the historical population to 0.653 in the genetic founders. Nucleotide diversity \( (\pi) \) declined by 22%, from 0.0036 to 0.0028 (Table 3.3). The contemporary population continued to lose haplotype diversity even as the population increased, with a 32% decline from historical values (Table 3.3). Nucleotide diversity in the contemporary population (0.0025) also continued to decline from the values observed for the genetic founders and was 31% lower than nucleotide diversity in the historical population (Table 3.3).

The haplotype joining network was starlike (Figure 3.4) with low levels of sequence divergence and a high frequency of unique mutations. Neutrality tests for the historical population were consistent with population expansion at some point in the California Condor’s recent evolutionary history \( (D = -1.491, F_S = -9.575) \), while neutrality tests for the genetic founders and contemporary population were consistent with a recent population bottleneck \( (D = 0.850, F_S = 1.931 \text{ and } D = 2.22, F_S = 6.05, \text{ respectively}) \) (Table 3.3). Of these tests, only the Tajima’s \( D \) for the contemporary population and the Fu’s \( F_S \) for the historical population were outside the 95% confidence intervals of null values derived from simulations (Table 3.3).

3.5 DISCUSSION

3.5.1 mtDNA Variation and Historical Population Structure

We did not detect population structure in our sample of the historical California Condor population, although we caution that sample sizes at the extremes of the historical range were limited and mtDNA only represents a single locus. This apparent lack of spatial structure in the historical population is consistent with our understanding of condor longevity, physiology, movement ecology, and the geography of their historical range. Condors are long-lived and
known to move long distances expending minimal energy due to their large wingspan and soaring mode of flight (Meretsky and Snyder 1992, Rivers et al. 2014). Mountainous areas are preferred by condors for soaring and looking for food because these areas provide upward-moving air currents that help large soaring birds stay aloft (Rivers et al. 2014). Thus, the large north-south mountain chains of the Coast Range and Sierra and Cascade Ranges likely provided effective movement corridors for condors, facilitating genetic connectivity among local groups. Although there are some small breaks in these mountain chains (e.g., San Francisco Bay), they do not appear to have separated condors into discrete evolutionary units. Nevertheless, future investigations coupling mtDNA and nuclear DNA from museum samples with next generation genomic sequencing (Bi 2013) could provide additional insights into the extent and directions of historical gene flow.

3.5.2 mtDNA Variation Through Time

Our examination of mtDNA haplotypes revealed that California Condors have lost more than 80% of their maternal lineages since Euro-American expansion into western North America. As expected by theory (Allendorf 1986), unique haplotypes were lost when California Condors experienced a severe range contraction and reduction in population size over the last two centuries. The primary causes of this decline have been attributed to secondary poisoning from predator poisoning campaigns, indiscriminate shooting, shooting for museum collections, and lead poisoning from ingesting lead bullet fragments left in large mammal carcasses (Snyder and Snyder 2000, D’Elia and Haig 2013).

Loss of genetic diversity through population bottlenecks can increase the probability of mating among related individuals potentially resulting in inbreeding depression, and can leave populations with reduced evolutionary potential (Fisher 1930) making them less resilient to future environmental changes or less fit to succeed in a variety of habitats (Keller and Waller 2002). Evidence from many studies has revealed that inbreeding can have severe consequences for a species’ fitness and extinction risk (Ralls et al. 1979, 1988; Brook 2002; Keller and Waller 2002). Inbreeding in other bottlenecked bird species has been linked to decreased fitness through increased hatching failure (Briskie and Mackintosh 2004, Heber and Briskie 2010), decreased offspring survival (Richardson et al. 2004, Brekke et al. 2010), decreased longevity (Grant et al. 2001, Hemmings et al. 2012), decreased brood size (Brown and Brown 1998), and
decreased fertility (Westemeier et al. 1998). In addition, inbred individuals have also been shown to be more sensitive to environmental stress than outbred individuals (Fox and Reed 2011). Birds that are bred in captivity for reintroduction efforts can be particularly susceptible to inbreeding given that the number of founders used to initiate reintroduction efforts is typically small (Jamieson 2010). Given the population bottleneck and severe loss of genetic diversity in California Condors, it is not surprising that inbreeding and decreased fitness have surfaced in the captive breeding program for this species (Ralls and Ballou 2004).

In California Condors, chondrodystrophy, a lethal form of dwarfism, has been detected in the post-bottleneck condor population (Ralls et al. 2000) with an estimated 18 percent of individuals carrying the putative recessive allele for that disease (Ralls and Ballou 2004). To address this issue managers carefully evaluate every potential pairing to minimize mean kinship (and inbreeding), spread the founders’ alleles among the reintroduction sites, attempt to conserve unique alleles, and consider the behavioral compatibility and reproductive performance of potential mates (Haig and Ballou 2002, Ralls and Ballou 2004, Ballou et al. 2010). These strategies are already being used for California Condors, but with little genetic diversity to begin with, the species has been genetically handicapped from the inception of the captive breeding program (Ralls and Ballou 2004). Compared with values reported for control region variability in other bird species California Condors have low nucleotide diversity (see Hendrickson et al. 2003), even when compared with other birds that have gone through severe population bottlenecks, such as the Whooping Crane (Grus americana) (see Glen et al. 1999).

Conservation breeding programs must begin prior to severe population bottlenecks to maximize retention of genetic resources. Although species can recover some loss of genetic diversity through careful captive breeding (Haig et al. 1990), this usually requires large population sizes and long periods of time. For example, the King Penguin (Aptenodytes patagonicus) on Macquarie Island, Australia, was shown to recover levels of pre-bottleneck genetic diversity over approximately 80 years, but their bottleneck was much less severe (low of about 3,400 birds) and their contemporary population numbers are several orders of magnitude larger (currently 400,000-500,000) than the current population of California Condors (Heupink et al. 2012). While recovering historical levels of genetic diversity in condors is unrealistic in the short term, continuing to increase the total population size and careful genetic management will
maximize the chances of retaining the remaining genetic diversity (Ralls and Ballou 2004, Ballou et al. 2010).

Contrary to the number of genetic founders and contemporary population size, several factors suggest that the historical population may have undergone a rapid population expansion prior to our sampling period (i.e., prior to Euro-American contact). Fu’s $F_S$, the neutrality test statistic with the most power to detect historical population expansions in non-recombining regions of DNA when sample sizes are relatively large (Ramos-Onsins and Rozas 2002, Ramirez-Sorino et al. 2008), was negative and significant. In addition, the starlike haplotype joining network (Figure 3.4), low levels of sequence divergence, and high frequency of unique mutations in the historical population are all indicative of a historical population expansion or that selection has caused a rapid spread of diverse mitochondrial lineages carrying beneficial mutations. The pattern of historical range expansion has been reported for a number of birds in North America and has been attributed to glacial retreat at the end of the Pleistocene (e.g., Milá et al. 2000, Colbeck et al. 2008, de Volo et al. 2013) or major climatic shifts following the mid-Holocene Hypsothermal dry period (e.g., Hull and Girman 2004) – a drought that lasted several thousand years in Western North America (Steig 1999).

Estimates of California Condor mutation rates are needed to gain a more nuanced understanding of the ancient demographic history of the California Condor population. If additional sequence data were unearthed from ancient DNA extracted from condor bones recovered from archeological or paleontological sites (Simons 1983, Emslie 1987, Steadman and Miller 1987, D’Elia and Haig 2013) coalescent theory could be used to provide a more detailed picture of population change through time (Emerson et al. 2001, Ho and Shapiro 2011). Examples of other species where such techniques have provided insight into their ancient demography include: Adélie Penguins (*Pygoscelis adeliae*) (Ritchie et al. 2004); Beringian Steppe Bison (*Bison priscus*) (Drummond et al. 2005); brown bears (*Ursus arctos*) and cave bears (*Ursus spelaeus*) (Stiller et al. 2010); wild and domestic horses (*Equus* spp.) (Orlando et al. 2013); and, killer whales (*Orcinus orca*) (Moura et al. 2014).

The relatively large amounts of genetic diversity revealed in the historical California Condor population contrast with studies of Andean Condors that showed low amounts of mtDNA diversity in the contemporary population (Hendrickson et al. 2003). This is unexpected as Andean Condors are still relatively widespread and numerous (Birdlife International 2014).
compared to California Condors. Reasons for this difference are not clear. It has been suggested that body size, metabolic rate, and generation time can influence rates of mtDNA evolution (Martin and Palumbi 1993), but those factors are similar for the two condors. Future investigations into mtDNA and nuclear DNA diversity in California and Andean Condors might provide additional insights into why Andean Condor mtDNA diversity is apparently much lower than in the historical population of California Condors.

3.5.3 Conservation Genetics and Reintroductions

Genetic factors are important to consider when developing species reintroduction plans to ensure that the individuals being reintroduced are genetically similar to the lineages that once existed in, and were adapted to a given area. Species that have been absent from a large portion of their historical range for an extended period of time present a challenge to those seeking to design effective reintroduction strategies. In these situations, integration of historical information from museum specimens regarding the species’ genetic variation across space and through time can provide critical context for reintroduction and recovery efforts (Murata et al. 2004).

Fortunately for the California Condor, the mtDNA lineages of museum specimens collected in in the Pacific Northwest are still represented in the post-bottlenecked population and captive breeding program. In addition, condors from the captive breeding program have proven to be quite adaptable and occupy a variety of breeding habitats including old growth redwood forests, coastal and inland mountain ranges, and the arid deserts of the Grand Canyon (Walters et al. 2010). The ability of reintroduced condors to move long distances and the apparent lack of local adaptations to particular geographic areas further supporting the use of captive bred birds to repopulate the historical range of the species. Finally, reintroduction efforts in other regions have already established that the sociality and longevity of condors can be used to foster mentor relationships in captivity that can be continued in the wild to ease the transition of captive condors to new situations (Snyder and Snyder 2000).

The amount of genetic diversity that has been lost in California Condors is substantial, but not surprising given the severe bottleneck they experienced. When evaluating reintroduction strategies it will continue to be important to consider the genetic contribution of each individual in the captive and wild populations (Haig and Ballou 2002, Ralls and Ballou
Although genetic factors are not currently the limiting factor in achieving self-sustaining populations, even if demographic limitations are relaxed, integrated genetic management of the captive and wild populations will still be needed for some time to reduce inbreeding and maximize the effective size of the captive and wild populations (Ralls and Ballou 2004). Without such management, Ralls and Ballou (2004) estimated that wild condors would become 3% more inbred per generation at population sizes close to the contemporary population. At this rate condors would be related at the level of full siblings in six generations, which is likely to reduce fitness even in the absence of current genetic abnormalities (Ralls and Ballou 2004).

Our analyses are based on sampling only a small proportion of the mitochondrial genome, and there may be important diversity at unscreened but functional sites in the mitochondrial and nuclear genomes. Although neutral markers can provide an efficient measure of genetic diversity for the purposes of translocation efforts in bottlenecked species (e.g., Wright et al. 2014), future analyses should apply genomic approaches to more directly evaluate the remaining genetic diversity at neutral and functional sites in the mitochondrial and nuclear genomes to help optimize conservation of genetic resources (Romanov et al. 2009, Angeloni et al. 2012).

Currently, condors exist as a small number of disconnected and heavily managed populations and are absent from ecosystems in the northern half of their historical range. Future recovery efforts should consider strategic placement of new reintroduction sites to facilitate range expansion, demographic connectivity, and gene flow between release sites (e.g., Alvarez et al. 2011) – as historically populations appear to have been interconnected. Expanding recovery efforts to unoccupied portions of the historical range offers the opportunity to increase the total population size of the species, which could aid in the retention of remaining genetic resources and move the California Condor one step closer to a self-sustaining, genetically viable metapopulation.

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d'Histoire Naturelle, Paris; Santa Barbara Museum of Natural History; San Diego Natural History
Museum; University of Michigan Museum of Zoology; U.S. National Museum of Natural History,
Smithsonian Institution; Clarke Historical Museum, Eureka, California; Virginia Polytechnic
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3.7 Literature cited

Adams, M.S. and F.X. Villablanca. 2007. Consequences of a genetic bottleneck in California
Condors: a mitochondrial DNA perspective. Pages 35–55 in A. Mee and L. S. Hall (eds), California
Ornithologists’ Union: Cambridge, Massachusetts, and Washington, DC.

Allendorf, F.W. 1986. Genetic drift and the loss of alleles versus heterozygosity. Zoo Biology
5:181–190.

2011. “Vulturnet” connectivity of the European populations of Cinereous Vulture: a programme
to reintroduce the species into Catalonia. Pages 356–361 in I. Zuberogoitia and J. E. Martínez
(eds), Ecology and Conservation of European Forest-Dwelling Raptors. Departamento de
Agricultura de la Diputación Foral de Bizkaia: Bilbao, Spain.

conservation biologists. Evolutionary Applications 5:130–143.


Demographic and genetic management of captive populations. Pages 219–246 in D. Kleiman,
G., K. V. Thompson, and C. K. Baer (eds), Wild Mammals in Captivity: Principles & Techniques for


Figure 3.1. Number of California Condor mtDNA samples used in the analysis, by decade.
Figure 3.2. Collection location of California Condor museum samples (gray points) and the proportion of haplotypes across the historical range (pie charts). Points are grouped by county in the U.S. and state in Mexico and do not indicate the precise location of the sample. The two most common haplotypes among museum samples, H1 and H7, are shown in the pie-charts as black and white, respectively. The 16 less common haplotypes are shown in the pie charts as gray.
Figure 3.3. The minimum number of California Condor mtDNA haplotypes surviving through time (top), and the minimum rarified number of California Condor mtDNA haplotypes ($A_r$) surviving through time (bottom). The grey area represents 95% confidence intervals around the expected rarified number of haplotypes.
Figure 3.4. Median-joining network of California Condor mtDNA control region sequences. The proportion of individuals from the museum samples and the genetic founders are shown in black and grey, respectively. Pie-chart diameter is proportional to the number of individuals with each haplotype.
Table 3.1. California Condor genetic founders and their offspring sequenced for analysis of mtDNA.

<table>
<thead>
<tr>
<th>Studbook #</th>
<th>Condor Name</th>
<th>Sex</th>
<th>Sire</th>
<th>Dam</th>
<th>Haplotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Topa-Topa</td>
<td>M</td>
<td>WILD</td>
<td>WILD</td>
<td>H1(^a)</td>
</tr>
<tr>
<td>4</td>
<td>AC-7</td>
<td>M</td>
<td>WILD</td>
<td>WILD</td>
<td>H1</td>
</tr>
<tr>
<td>6</td>
<td>AC-2</td>
<td>M</td>
<td>WILD</td>
<td>WILD</td>
<td>H1</td>
</tr>
<tr>
<td>11</td>
<td>Tama</td>
<td>F</td>
<td>WILD</td>
<td>WILD</td>
<td>H1</td>
</tr>
<tr>
<td>12</td>
<td>AC-8</td>
<td>F</td>
<td>WILD</td>
<td>WILD</td>
<td>H1</td>
</tr>
<tr>
<td>23</td>
<td>Paxa</td>
<td>M</td>
<td>4</td>
<td>8</td>
<td>H1(^b)</td>
</tr>
<tr>
<td>5</td>
<td>AC-6</td>
<td>M</td>
<td>WILD</td>
<td>WILD</td>
<td>H4</td>
</tr>
<tr>
<td>7</td>
<td>AC-5</td>
<td>M</td>
<td>WILD</td>
<td>WILD</td>
<td>H4</td>
</tr>
<tr>
<td>13</td>
<td>UNI</td>
<td>F</td>
<td>WILD</td>
<td>WILD</td>
<td>H4</td>
</tr>
<tr>
<td>18</td>
<td>BFE</td>
<td>M</td>
<td>WILD</td>
<td>WILD</td>
<td>H4</td>
</tr>
<tr>
<td>19</td>
<td>AC-1</td>
<td>M</td>
<td>WILD</td>
<td>WILD</td>
<td>H4</td>
</tr>
<tr>
<td>10</td>
<td>AC-3</td>
<td>F</td>
<td>WILD</td>
<td>WILD</td>
<td>H7</td>
</tr>
<tr>
<td>20</td>
<td>AC-4</td>
<td>M</td>
<td>WILD</td>
<td>WILD</td>
<td>H7</td>
</tr>
<tr>
<td>33</td>
<td>Sequoia</td>
<td>M</td>
<td>7</td>
<td>9</td>
<td>H7(^c)</td>
</tr>
</tbody>
</table>

\(^a\) Hereoplasmic individual with somatic mutation at Base 321 detected.

\(^b\) Progeny used to identify haplotype of female genetic founder CVF (Studbook #8)

\(^c\) Progeny used to identify haplotype of female genetic founder PPF (Studbook #9)
Table 3.2. Mitochondrial primer sequencers and PCR annealing temperatures ($T_A$) used in California Condor analyses.

<table>
<thead>
<tr>
<th>Primer Names</th>
<th>Primer Sequences</th>
<th>$T_A$</th>
</tr>
</thead>
<tbody>
<tr>
<td>CACO-R2</td>
<td>5'- CAC AAC ATC AGC ACT GAA ATT AC -3'</td>
<td>54 °C</td>
</tr>
<tr>
<td>CACO-R3</td>
<td>5'- AAT GGT CCT GAA GCT GGT -3'</td>
<td>54 °C</td>
</tr>
<tr>
<td>CACO-R4</td>
<td>5'- GGG AAC CAA AAG TGC TAA G -3'</td>
<td>54 °C</td>
</tr>
<tr>
<td>CACO-F3</td>
<td>5'- ACC AGC TTC AGG ACC ATT C -3'</td>
<td>54 °C</td>
</tr>
<tr>
<td>CACO-F5</td>
<td>5'- AAT GGT CTC AGG ACA TAA CAT G -3'</td>
<td>54 °C</td>
</tr>
</tbody>
</table>
Table 3.3. California Condor mtDNA diversity in the historical population, genetic founders, and contemporary population. Values in parentheses represent 95% confidence limits around null values.

<table>
<thead>
<tr>
<th></th>
<th>Historical</th>
<th>Founders</th>
<th>Contemporary</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>67</td>
<td>14</td>
<td>404</td>
</tr>
<tr>
<td># of Haplotypes</td>
<td>18</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td># Polymorphic Sites</td>
<td>19</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Π</td>
<td>0.0036</td>
<td>0.0028</td>
<td>0.0025</td>
</tr>
<tr>
<td>H</td>
<td>0.851</td>
<td>0.643</td>
<td>0.581</td>
</tr>
<tr>
<td>D</td>
<td>-1.491 (-1.655, 2.014)</td>
<td>0.850 (-1.729, 1.860)</td>
<td>2.224* (-1.552, 2.089)</td>
</tr>
<tr>
<td>F_s</td>
<td>-9.575* (-4.885, 5.723)</td>
<td>1.931 (-2.549, 3.843)</td>
<td>6.053 (-8.519, 7.890)</td>
</tr>
</tbody>
</table>

* value outside of 95% confidence limits around the null value.
CHAPTER 4 - ECOLOGICAL NICHE MODELS FOR CALIFORNIA CONDOR (GYMNOGYPS CALIFORNIANUS) REINTRODUCTION PLANNING

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4.1 ABSTRACT

Ecological niche models can be a useful tool to identify candidate reintroduction sites for endangered species but have been infrequently used for this purpose. In this paper, we (1) develop activity-specific ecological niche models (nesting, roosting, and feeding) for the critically endangered California Condor (Gymnogyps californianus) to aid in reintroduction planning in California, Oregon, and Washington, USA, (2) test the accuracy of these models using empirical data withheld from model development, and (3) integrate model results with information on condor movement ecology and biology to produce predictive maps of reintroduction site suitability. Ecological niche models conformed to our understanding of California Condor ecology, had good predictive performance when tested with data withheld from model development, and aided in the identification of several candidate reintroduction areas outside of the current distribution of the species. Our results suggest there are large unoccupied regions of the California Condor’s historical range that have retained ecological features similar to currently occupied habitats, and therefore warrant consideration for future reintroduction efforts. However, overlaying threat factors that could not be directly incorporated into empirical ENMs and ground reconnaissance will be necessary to ultimately select a successful reintroduction site. Our approach, which disentangles niche models into activity-specific components, has applications for other species where it is routinely assumed (often incorrectly) that individuals fulfill all requirements for life within a single environmental space.

4.2 INTRODUCTION

The saga of saving the California Condor (Gymnogyps californianus) from the brink of extinction by combining vigorous field efforts with aggressive captive breeding and releases is legendary in the field of conservation biology (reviewed by Snyder and Snyder 2000). Yet, California Condors are still one of the most critically endangered birds in the world, are completely absent from the northern half of their historical range, and there is no overall strategy for planning future reintroductions to recover a viable metapopulation (Walters et al. 2010; D’Elia and Haig 2013). Nonetheless, the recovery program has gathered extensive data on condor nest biology (Snyder et al. 1986), movement ecology (Meretsky and Snyder 1992, Hunt et al. 2007) and primary mortality factors (Rideout et al. 2012) via a scientific program of inquiry into population
declines, captive breeding, and the subsequent release of California Condors into a variety of environments, from the deserts of Arizona to the coast of California. These efforts have increased the number of captive condors available for release, and vastly improved our understanding of condor ecology and the primary threats to their survival and recovery. Thus, there is new hope and a need for a long-range vision of condor recovery—a vision that embraces a more complete assessment of available habitat over a wider area of the condor’s historical range and identifies opportunities for additional recovery areas and potential reintroduction sites (Walters et al. 2010).

Ecological niche models (ENMs) are a potentially powerful tool for helping to identify additional recovery areas and reintroduction sites (Martínez-Meyer et al. 2006, Osborne and Seddon 2012) as they provide a quantitative and spatially-explicit framework for describing the relationship between biological and physical properties of the landscape and a species’ ecological and geographic distribution (Guisan and Zimmermann 2000). ENMs have a wide range of applied uses in ecology including: understanding the ecological requirements or biogeography of species, finding new species or populations, identifying and prioritizing reintroduction sites, conservation planning and reserve design, predicting species invasions, predicting the effects of climate change or habitat loss, and for integrating information on movement ecology and demography to predict metapopulation dynamics in a spatially-explicit framework (reviewed by Peterson 2006, Franklin 2009, Peterson et al. 2011).

Despite their widespread use in ecology relatively few studies have used ENMs to identify species reintroduction sites (reviewed by Peterson et al. 2011, Osborne and Seddon 2012). Martínez-Meyer et al. (2006) introduced the idea of using ENMs to identify and prioritize reintroduction sites for California Condors, but presented their results as conceptual because they did not categorize occurrence data by activity type and did not include environmental covariates in their model that were likely to be important to condor habitat selection.

In this paper we build on the conceptual approach presented in Martínez-Meyer et al. (2006) and develop functional models for identifying candidate reintroduction areas for California Condors through: (1) producing and testing the accuracy of activity-specific (i.e., nesting, roosting, and feeding) ENMs using environmental covariates that are linked to condor
biological; (2) projecting ENMs throughout most of the recent historical range of the species to identify areas that are ecologically suitable but unoccupied; and, (3) integrating activity-specific models with information from movement ecology studies and condor biology to identify areas that are predicted to be ecologically suitable but unoccupied. Model results can help focus field surveys to further evaluate release site suitability and may identify potential recovery areas for the California Condor in unoccupied areas of its historical range that have not yet been sufficiently considered.

4.3 METHODS

4.3.1 Study Area

Our study area included California, Oregon, and Washington, USA (Figure 4.1). Within the study area the current range of the California Condor is limited to southern and central California where three captive release programs are in operation. Condors were extirpated from the northern half of their historical range, which once extended to British Columbia, Canada, early in the twentieth century (D’Elia and Haig 2013).

4.3.2 Ecological Niche Model Development

Many algorithms are available for constructing ENMs (Guisan and Zimmerman 2000, Elith and Graham 2009, Elith and Leathwick 2009). We used MAXENT, a maximum entropy–based machine learning computer program that estimates the probability distribution of a species’ occurrence based on a given set of environmental constraints (Phillips et al. 2006). We selected MAXENT because it does not require absence data, it allows for categorical and continuous environmental data, and because it is in a class of models known as generative models that outperform discriminative methods when modeling with presence-only data (Elith et al. 2006, Phillips and Dudík 2008, Elith et al. 2011). MAXENT models can be conservatively interpreted as a relative index of environmental suitability or relative density, where higher index values depict better conditions for the species (Phillips et al. 2006).

Despite their relatively good performance and ease of use, critics of presence-only ENMs warn against numerous pitfalls, including: use of questionable occurrence data (Lozier et al., 2009); overfitting models by failing to implement species-specific tuning (Anderson and
Gonzalez 2011, Warren and Seifert 2011); ignoring spatial dependency in model evaluation (Veloz, 2009); misinterpreting outputs as occurrence probability, failure to consider sampling bias or detection probabilities in data acquisition, and misinterpretation of model evaluation statistics (Yackulic et al. 2013). We attempted to navigate these pitfalls through (1) screening of occurrence data, (2) using model selection procedures, (3) evaluating the impact of spatial dependency on model performance, (4) interpreting outputs as a relative measure of suitable habitat rather than occurrence probabilities, (5) adjusting for sampling bias in model development, and (6) using and interpreting multiple model evaluation statistics.

**Condor Occurrence Data**

Presence-only niche models require species’ occurrence locations. Because condors use different habitats for nesting, roosting, and feeding (Koford 1953), we partitioned condor occurrence data into these three activities and generated separate occurrence datasets for each activity (Figure 4.1). Activity-specific occurrence data spanning the time period from 1960-2011 were obtained from a variety of reliable sources (see Appendix 3). All occurrence data were filtered to remove duplicate records and occurrence locations with a positional precision of < 1 km.

**Environmental Covariates**

To develop ENMs, we considered 13 predictor variables (i.e., covariates) related to soaring conditions and climate, terrain, landscape productivity, vegetation characteristics, and human disturbance (Table 4.1; see Appendix 4). We selected covariates based on published information on species-habitat associations (Koford 1953, Snyder et al. 1986, Meretsky and Snyder 1992), species-habitat models developed for other vultures (e.g., Donázar et al. 1993, Poirazidis et al. 2004, García-Ripollés et al. 2005, Gavashelishvili and McGrady 2006, Mateo-Tomás and Olea 2010a, Rivers et al. 2014), and the availability of GIS data at the appropriate spatial scale spanning the entire study area (i.e., California, Oregon, and Washington).
Background Data

MAXENT requires that the user specify the background (i.e., area available for the species to select), against which covariates at the occurrence points will be compared (Phillips et al. 2006, Phillips 2007, Elith et al. 2011). Ten-thousand random points within 180 km of California Condor nests (farthest documented movement by a nesting condor away from a nest (Meretsky and Snyder 1992)) were generated to serve as background data. Islands off the coast of California were excluded from the background sample as condors are not known to travel across the ocean to these areas.

We assumed no bias in survey effort for nests or roosts as researchers have conducted extensive searches for these activity locations since the 1960s (Sibley 1969, Snyder et al. 1986). Bias in survey effort for feeding locations led us to develop a separate set of background points for the feeding ENM using a stratified random sample that approximated the frequency distribution of distance of feeding locations to roads (74.6 percent of points were within 1 km of a road, 19.7 percent were within 1-2 km, 5.2 percent were within 2-3 km, and 0.5 percent were > 3 km from a road). Matching the sampling bias in our occurrence data and background data provides a better measure of the difference between the distribution of occurrences and that of the background and should therefore provide better predictive performance (Phillips et al. 2009).

Correlated Environmental Covariates

We assessed multi-collinearity among covariates by calculating univariate pair-wise Spearman correlation coefficients ($r_s$) based on values of each variable at condor occurrence points. If two covariates had $r_s > 0.70$, we retained only one of the pair to aid in interpretation of model results. Thermal height and thermal updraft velocity were the only pair of covariates that exceeded this $r_s$ value. We removed thermal height from further consideration and retained thermal updraft velocity.

Spatial Scale
Condors select habitats at a variety of spatial scales, from coarse-grained selection of mountain ranges to fine-grained selection of a particular nest cliff or cave (Stoms et al. 1993). The accuracy of the available occurrence data and resolution of some of the environmental predictor variables led us to focus our analysis at mid- (1 km²) and coarse-scale (10 km²) evaluations (see Table 4.1). These spatial scales matched the intent of our research, which was to identify candidate release areas to include in follow-up ground surveys where finer-scale habitat features could be assessed.

Model Settings and Model Selection
MAXENT (version 3.3.3a) was run with a convergence threshold of $10^{-5}$ and a maximum of 5000 iterations. We implemented bootstrap resampling with 20 replicates, holding out 25 percent of the samples for testing in each run of the model. MAXENT is in a school of models known as algorithmic models which treat the true model as an unknown, potentially complex, reality that is difficult or impossible to truly estimate (Warren and Seifert 2011). As such, MAXENT models may be vulnerable to overfitting and may not perform well without implementing appropriate measures to limit their complexity (Phillips et al. 2006, Dudík et al. 2007). To limit model complexity and avoid overfitting, we used an information theoretic approach (Akaike 1974, Burnham and Anderson 2002) to select the best of a series of models with different levels of complexity (i.e., varying levels of MAXENT’s regularization parameter ($\beta = 1, 5, 10,$ and 15) and the types of environmental features using ENMTools (Warren et al. 2010, Warren and Seifert 2011). Regularization acts as a penalty function in MAXENT whereby increasing values of $\beta$ reduce the number of parameters entered into the model (Phillips et al. 2006). In addition to varying the regularization parameter, we varied the complexity of the models by using two different sets of environmental features: (1) autofeatures, which allows models to fit up to five continuous environmental features (linear, quadratic, product, threshold, and hinge) and categorical features, with the more complex features only available when sample sizes are large enough (Phillips and Dudík 2008); and, (2) manually limiting the model to categorical, linear, and quadratic features, which constrained MAXENT to simpler models at larger sample sizes (Phillips et al. 2006). A total of eight models (each with 20 replicates) of varying levels of complexity were run for each activity type. The ENM for each activity type with the lowest median AIC$_c$ was
selected as the most parsimonious model that best fit the data (see Appendix C). We used AICc in an attempt to balance the need to predict specific model fit to the training data against the generality that enables reliable prediction outside of areas where the model was trained (Elith and Leathwick 2009, Merow et al. 2014).

4.3.3 Projecting Models
A model trained on occurrence data and environmental covariates in one geographic location can be projected across geographic space by applying it to those same environmental covariates in another area or over a broader geographic distribution (Phillips and Dudik 2008). Because we sought to project the models outside of the area used to train the model we implemented ‘clamping’, a method in MAXENT that ensures the response curves do not get extrapolated beyond the values observed at presence locations (i.e., the response curves are clamped, or fixed, at the maximum or minimum observed values (Elith et al. 2010)). We also implemented a multivariate environmental similarity surface analysis to evaluate where novel environmental conditions existed in the projection layer (Elith et al. 2011). Novel conditions were defined as those with at least one covariate beyond the range of values encountered in the occurrence or background data (see Elith et al. 2011). Implementing clamping and excluding novel environments from projections allowed us to transfer the model in geographic space while not extrapolating beyond the environmental space where the species has been observed (see Peterson et al. 2011).

4.3.4 Niche Similarity
The degree of similarity among the activity-specific ENMs was calculated using Warren et al.’s (2010) similarity statistic (I) in ENMTools, where a value of 0 indicates no overlap in suitability and 1 indicates complete overlap in suitability. We then tested the hypothesis that activity-specific niches were identical to one another using pairwise niche identity tests in ENMTools (see Warren et al. 2010). Pairwise identity tests pool occurrence data for each pair of activity-specific niches, randomize the identity of the occurrence data, and extract two new samples of equal size to the original samples for each model replicate. These new samples are then used to generate a pair of ENMs in MAXENT for each replicate model, and ENMTools uses predicted
suitability scores from these ENMs to obtain a distribution of overlap scores between activity-specific niches drawn from a shared distribution (Warren et al. 2010). Twenty-five replicates were run for each pair of activities and z-scores were calculated to test whether activity-specific niches were statistically significantly different from one another (P ≤ 0.05). We also generated maps of niche similarity and calculated pairwise percentages of niche intersection. Percent niche intersection was calculated as: \( \frac{x}{(\text{area of niche}_1 + \text{area of niche}_2) - x} \), where \( x \) is the area of niche intersection.

4.3.5 Model Evaluation

ENM performance can be evaluated with a number of statistics and it is often instructive to assess model performance using more than a single metric because each quantifies a different aspect of predictive performance (Elith and Graham 2009, Elith and Leathwick 2009). Accordingly, we assessed model performance using several different metrics: gain (Phillips 2005), overall accuracy, sensitivity, specificity, kappa (K), and area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997).

AUC and gain are threshold independent measures of model performance calculated in MAXENT on 25 percent of the data withheld for testing in each of the 20 replicate runs. Gain is a measure calculated in MAXENT that is closely related to deviance, a measure of goodness of fit used in generalized additive and generalized linear models (Elith et al. 2011). It is defined as the average log probability of the presence samples, minus a constant that makes gain of a uniform distribution equal to zero. Gain of zero indicates no model discrimination between background points and occurrence data, whereas higher values of gain indicate better discrimination ability. Gain essentially indicates how closely the model is concentrated around the presence samples and can be used to approximate an odds ratio of how much more likely the presence samples are than that of random background pixels by calculating \( \exp(gain) \) (Phillips 2005).

Overall accuracy, sensitivity, specificity and kappa (K) are all threshold-dependent measures of model fit based on a confusion matrix (Fielding and Bell 1997). This required that we decide on a threshold for continuous model output to make it binary. It also required known absences, which we represented by generating pseudo-absences (random points within the area available for selection that were > 5 km from any occurrence locations). The number of pseudo-
absences produced for each niche model was set equal to the number of presence points for that niche model. We selected a model threshold which maximized kappa (Freeman and Moisen 2008), balancing omission and commission error. Values from final ENMs for each activity-type were extracted to presence and pseudo-absence points, confusion matrices were generated based on correct and incorrect classification of the ENM outputs at these points, and threshold-dependent accuracy measures were calculated using formulas from Fielding and Bell (1997).

In addition to evaluators based on presences and pseudoabsences, we calculated the continuous Boyce index $B_{\text{cont}(0.1)}$, an evaluator based only on the presence data, and plotted predicted/expected curves for each ENM using the procedures developed by Boyce (2001) and refined by Hirzel (2006). We used a moving window increment of 0.25 for calculating $B_{\text{cont}(0.1)}$ for each replicate, and a moving window increment of 0.01 for plotting P/E curves (see Hirzel 2006). We chose a larger increment for calculating the continuous Boyce index because we found that using a moving window increment of less than 0.25 resulted in a large proportion of zero values due to low sample sizes. Both Boyce index calculations and P/E curves were truncated at a MAXENT logistic value of 0.85 due to the lack of sufficient test samples at higher logistic values.

Examination for plausibility of model results is especially important when extrapolating in geographic or environmental space (Elith et al. 2010). Therefore, in addition to measures of model performance, we examined other outputs produced by MAXENT, including jackknife plots, variable importance, response curves, and suitability maps to ensure they were producing results that were plausible given our understanding of condor habitat selection (Rivers et al. 2014) and the recent historical distribution of the species.

4.3.6. Spatial Autocorrelation
The evaluation statistics we calculated assume spatial independence of samples (Fielding and Bell 1997). When occurrence data are spatially dependent, randomly partitioning the data into test and training data may result in an overly optimistic assessment of model accuracy because of the proximity of training sites to test sites and spatial autocorrelation in the environment (Veloz 2009). To examine spatial autocorrelation in model results, we calculated Moran’s Index (I) coefficients for model residuals at multiple lag distances (10 km - 200 km at 10 km intervals).
for each activity-specific niche model, developed correlograms, and tested for significance \((P \leq 0.05)\) (Legendre and Fortin 1989; see Appendix 5). Calculations were performed in ArcMap 10.0 using the Incremental Spatial Autocorrelation Tool. Occurrence data were then thinned by removing all points within 5 km of one another and the analyses were rerun to examine the change in model evaluation statistics. We chose 5 km for data thinning because this approximated the maximum distance we could thin the data to produce models where the number of parameters did not exceed the number of occurrence points. We did not attempt to incorporate spatial dependency into final model predictions, as doing so is not recommended when making predictions outside the area used to train the model (Dormann et al. 2007); rather, thinned models were used only to evaluate the effect of spatial dependency on model performance.

4.3.7 Identifying Candidate Reintroduction Areas

We assumed that condor reintroductions would be more successful in areas predicted to have the highest suitability of nesting, roosting, and foraging habitats that were proximal to one another and were relatively expansive. To determine these areas we calculated a measure of relative suitability for establishing a reintroduction site using the following procedure:

1. Nesting, roosting, and feeding ENMs were transformed into binary rasters using a threshold value that maximized \(K\).

2. Using these three binary maps we calculated the sum of the logistic raster values within a 50 km radius of each ENM using focal statistics in ArcGIS. We used 50 km as this was the distance to which condors typically restrict their movements from nests (Meretsky and Snyder 1992).

3. Outputs from three rasters were then added together using the raster calculator and the output grid was scaled from 0 to 1 using the following calculation:

\[
\text{Grid value} = \frac{(x - \min x)}{(\max x - \min x)}
\]

where \(x\) is the sum of nesting, roosting, and feeding logistic values within 50 km of the cell, and \(\min x\) and \(\max x\) represent minimum and maximum values of \(x\) within those areas predicted as either nesting, roosting, or feeding habitat in the study area.
4.4 RESULTS
For each of the three condor activities, we developed models that had excellent accuracy at predicting test data and were good at discriminating between used and available sites (Table 4.2). Models were well calibrated, with the predicted-to-expected ratio of evaluation points increasing as habitat suitability scores increased (Figures 4.3 and 4.4). Test gain (a measure of model performance on data withheld for testing) was similar to training gain (a measure of model performance on data used to train the model) in all three models (Table 4.2), suggesting that the models were not overfit to the training data. According to our models, approximately 11%, 14%, and 23% of the currently-occupied range of the condor in southern California (approximated by the background area) is comprised of suitable nesting, roosting, and feeding habitat, respectively. Models predicted nesting, roosting, and feeding habitat in 8%, 7%, and 14% of the study area, respectively. Of the total area modeled by each activity-specific niche, the currently occupied range contained only 27% of the modeled nesting habitat, 36% of modeled roosting habitat, and 34% of modeled feeding habitat within the study area.

Activity-specific ENM residuals had significant spatial autocorrelation (Figure 4.5). Thinning data by removing points within 5 km of one another reduced spatial autocorrelation (Figure 4.5). Thinned models retained high predictive performance, despite severe reduction in sample size (Table 4.2). $B_{cont(0.1)}$ was sensitive to reductions in sample size (Table 4.2) due to the lack of sufficient data to adequately evaluate a large number of categories, but P/E curves retained relatively good form in thinned models (Figure 4.4).

All activity-specific niche models (Figure 4.6) were statistically different from one another. Nest and roost ENM predictions had the highest similarity of the ENMs ($I = 0.85, z = -3.73, P < 0.001$). Roost and feeding ENMs had similarity statistic $I = 0.70 (z = 8.48, P < 0.001)$, whereas the nest and feeding ENMs were the least similar of the models ($I = 0.54, z = -23.04, P < 0.001$). Pairwise percent overlap of the ENMs showed 46% overlap for nest and roost ENMs, 20% overlap for roost and feeding ENMs, and 16% overlap for nest and feeding ENMs (Figure 4.7).

The importance of environmental covariates differed among condor activities (Figure 4.8; Table 4.3). The importance of each covariate is calculated by MAXENT during model training by tracking improvement in model fit (i.e., gain) with incremental changes in coefficient
values during model optimization (Phillips 2005). These incremental improvements (increases in gain) are summed and normalized to calculate the percent contribution of each environmental covariate for each model run. Terrain features contributed most among covariates in predicting condor nesting and roosting habitat, while landscape productivity and vegetation characteristics had the largest contribution to the feeding model (Figure 4.8, Table 4.3).

Our reintroduction model predicted that northwestern California and southern Oregon and the Hell’s Canyon region had the most expansive areas of modeled nesting, roosting, and feeding habitat that were proximal (Figure 4.9). Suitable reintroduction sites may also be located in the North Cascades, but there is significant uncertainty in our predictions there due to the presence of conditions outside of those encountered during model training.

4.5 DISCUSSION
Selection of appropriate release sites is a key element of reintroduction science (Seddon et al. 2007) and is fundamental to a successful reintroduction project (Griffith et al. 1989), especially with species such as the California Condor that have slow reproductive cycles and expensive breeding and rearing costs. For these species, decisions on release sites have substantial and lasting ecological, financial, and regulatory implications (Snyder et al. 1996). Our results suggest that ENMs can be useful in reintroduction planning as > 70% of predicted nesting habitat for the California Condor and > 60% of predicted roosting and feeding habitat is outside of the species’ current range within the study area (Figure 4.9).

Our ENMs for the California Condor make sense ecologically. Condors are known to nest in cliffs in remote areas (Koford 1953, Snyder et al. 1986, Meretsky and Snyder 1992) and our nest models predicted suitable habitat in areas containing cliffs and low road density. Condor typically roost in trees in mountainous areas and our roost ENM predicted suitable roosting habitat in areas with steep slopes and trees. Feeding condors are typically found in mountain foothills or at coastal sites where steep mountains meet the ocean, where primary productivity is high, and ungulates or marine mammals are concentrated (Snyder and Snyder 2000). Similarly, our feeding ENM predicted suitable habitat in areas with moderate to steep slopes in areas that had high primary productivity.
To date, most distribution and habitat models for vultures have not disentangled specific activities at occurrence points (e.g., Donázar et al. 1993, Hirzel and Arlettaz 2003, Martínez-Meyer et al. 2006, Rivers et al. 2014); or, they have examined only a single activity type (e.g., nest sites; see Poirazidis et al. 2004, García-Ripollés et al. 2005, Gavashelishvili and McGrady 2006, Mateo-Tomas and Olea 2010a), despite recognition that separating activity types can be useful for highly mobile species that use distinct environments for specific activities (Guisan and Thuiller 2005, Martínez-Meyer et al. 2006). We found that separating niche models for the California Condor into activity types was informative, as condors use different habitats for nesting, roosting and feeding (Figures 4.7 and 4.8; Table 4.2). Therefore, our activity-specific models offer a more precise depiction of the condor’s use of ecological niche space than models with pooled occurrence data and provided a more refined view of the interspersion and juxtaposition of various condor habitats in geographic space. This information is essential when selecting a reintroduction site for a species that requires different (but proximal) ecosystems to survive and reproduce.

In addition to being useful in identifying potential release areas, this increased model precision will be useful in: (1) identifying activity-specific threats and areas to prioritize threat reduction measures, (e.g., identifying areas where exposure to toxins, such as lead (Finkelstein et al. 2012) and anticoagulant rodenticides (Thomas et al. 2011), may be high; targeting non-lead ammunition education programs; or identifying areas to dispose of uncontaminated carcasses where they might provide an additional food resource (see Mateo-Tomás and Olea 2010b); (2) identifying areas to survey for historical nest sites (Snyder and Snyder 2000); and, (3) developing models of habitat connectivity and metapopulation persistence over time. Future niche modeling efforts for other highly vagile species should consider activities separately, especially when those activities occur in different environments. Activity-specific niche modeling also may be useful for less mobile species if a species is using different environments for discrete activities that are essential for the species’ survival and reproduction, and occurrence data and environmental data relevant to that species are available at a spatial resolution sufficient to associate these discrete activities with particular environments.

As with all biological models, we recommend caution in interpreting our results, as variability in natural systems, errors in data used to develop the model, and uncertainty in
model structure and scale can increase the uncertainty of model results (Pauly and Christensen 2006). Our modeling effort has taken steps to reduce this uncertainty by testing our models against data withheld from model development, averaging multiple model runs, incorporating multiple spatial scales based on the species’ biology, and using model selection to find the most parsimonious model that best fit the data. The relatively good predictive performance of our models—even when models were significantly thinned to reduce spatial dependency of the training and test data—and their alignment with our knowledge of condor ecology and historical distribution suggests that, despite the uncertainties inherent in predictive modeling, they should be useful for prioritizing ground reconnaissance surveys for California Condor reintroduction sites.

Our models could not directly incorporate the primary threat to California Condor survival and recovery – lead poisoning from spent ammunition (Finkelstein et al. 2012). Thus, we must caution that identification of new reintroduction sites must consider whether voluntary or regulatory measures to remove or reduce this threat are sufficient if future reintroduction efforts are to substantively contribute to recovery of a viable condor metapopulation.

### 4.5.1 Areas for Further Research

A key assumption of ENMs is that the species is at equilibrium with their environment (Elith and Leithwick 2009). This assumption was violated by our condor dataset which spanned a period of population collapse and then expansion through reintroductions. The issue with projecting ENMs of species out of equilibrium with their environment is that in novel geographic areas (i.e., areas unavailable for condors to select) it is possible that a different suite of environmental factors may limit distributions (Dormann 2007). Whether or not our models will retain strong predictive performance across geographic space is an open question. It is encouraging that predictions generally align with our understanding of condor habitat selection and their historical distribution (D’Elia and Haig 2013). Tests of presence-only ENMs for other recovering species that have not reached equilibrium have shown that ENMs can produce useful results despite the violation in this assumption (e.g., Cianfrani et al. 2010). Similar analyses could be undertaken to evaluate California Condor model transferability in geographic space with
populations outside of our study area (e.g., in Arizona and Utah), which could inform how robust our models are to violating the assumption of equilibrium.

Traditional niche models based on all occurrences throughout the annual cycle cannot reflect the dramatic seasonal shifts in space use sometimes observed in wildlife populations (e.g., Peterson et al. 2005). Our activity-specific habitat models did not consider temporal variation in habitat use that some have suggested occurs in California Condors (Meretsky and Snyder 1992, Johnson et al. 2010). Developing seasonal habitat models (e.g., Edrén et al. 2010, Rivers et al. 2014) may be useful to delineate areas used intermittently or more intensely during certain times of the year. Projecting season-specific models to new regions might also help identify areas with seasonal opportunities or limitations that are not apparent in time-invariant niche models.

Rivers et al. (2014) found that, along the central California coast, coastal habitats were especially important, probably as a result of the availability of marine mammal carcasses and the availability of consistent onshore winds that facilitate soaring flight. We contemplated developing a separate activity-specific niche model for coastal feeding given obvious differences in inland versus coastal feeding environments. However, we chose not to given the limited area within which coastal foraging currently occurs (< 30 km stretch of coastline). As condors expand their range and additional coastal feeding occurrence data become available, separating coastal foraging occurrences from inland foraging occurrences could improve the predictive performance of our feeding model. Those planning reintroduction efforts should consider that coastal feeding sites are underrepresented in our feeding model and that coastal covariates were not included, meaning that there may be areas of coastline that are suitable for condor feeding, but which are not modeled as suitable.

Overlaying threat factors or factors that associate positively with condor habitat use that could not be directly incorporated into empirical ENMs is likely to provide information critical to selecting a successful reintroduction site. For example, overlaying areas of wind turbine development (Figure 4.10) shows areas that one may seek to avoid when establishing a reintroduction site, but which we could not incorporate into empirical models due to a mismatch in the presence of wind turbines and the time period when the occurrence data were collected. Other factors that should be considered prior to selecting release sites include: (1)
logistical considerations, (2) land ownership patterns and land conservation status, (3) low-flying aircraft flight routes, (4) distribution of large trees that could provide additional nesting habitat, (5) distribution and density of food, (6) the degree to which threats have been eliminated or abated (e.g., lead ammunition), (7) heterospecific competition and density of nest predators. Failure to consider these factors could result in selecting suboptimal or even unsuitable release sites. We recommend future analyses consider combining our ENM models with the factors above, and explicitly account for relative suitability (see Figures 4.3 and 4.4), relative importance of each ENM, and uncertainty in model predictions using a spatially explicit conservation prioritization framework such as Marxan (Ball et al. 2009) or Zonation (Moilanen et al. 2005) or using a Bayesian network approach (e.g., Laws and Kesler, 2012).

4.6 CONCLUSIONS

Our modeling results suggest that California Condors currently occupy < 30% of modeled nesting habitat, and < 40% of modeled roosting and feeding habitat within the study area, implying that there may be significant opportunities for further reintroductions (Figure 4.9). Reintroduction projects typically assume that the last place a species was observed is the best place for a reintroduction, but this is not always true (e.g., White et al. 2012). Our results suggest that at least three geographic regions the unoccupied northern portion of the historical range of the condor have retained environmental conditions that, in the absence of additional threats not included in our models, appear to be conducive to condor nesting, roosting, and feeding.

Modeling species with ranges that are in flux, including species being considered for reintroduction, is a delicate art (Elith et al. 2010). Our analyses suggest that ENMs can be useful for reintroduction planning as long as care is taken to incorporate important aspects of a species’ ecology. Outputs from our models can be integrated with movement data (see Nathan et al. 2008) to configure future individual-based models, to analyze metapopulation viability and population connectivity, and to identify areas of potential conflict between development and habitat conservation. Our approach, which separately models specific activities, has applications for other species and reintroduction programs where it is routinely assumed (often incorrectly) that individuals fulfill all their needs for survival and reproduction within a single environmental space.
ENMs developed for reintroduction planning are subject to change based on the availability of new information. As new reintroduction sites for condors are established, models can be rigorously tested and updated with new data gained from these release efforts (e.g., Cianfrani et al. 2010, Cook et al. 2010, Rinnhofer et al. 2012). Ultimately, accumulation of new data across a number of release sites will increase our ability to identify remaining areas of unoccupied but suitable habitat and develop area-specific models to tease apart differences in the use of environmental space across geographic regions (Bamford et al. 2009). Such an approach will facilitate a more complete picture of California Condor space use and will help ensure that the limited resources available for condor conservation are used wisely.

4.7 ACKNOWLEDGMENTS
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4.8 LITERATURE CITED


Figure 4.1. Study area (left) and California Condor nest (black crosses), roost (red circles) and feeding (blue triangles) occurrence data used in model development and evaluation. The gray zone is the area from which background data were selected for ecological niche model development, and which encompasses the current range of the species in southern California.
Figure 4.2. AICc, and the number of parameters for California Condor (a) nesting, (b) roosting, and (c) feeding niche models for linear, quadratic, and categorical (LQ) feature selection and autofeature selection at varying levels of regularization (β). Error bars represent the range of values encountered during 20 model runs using MAXENT’s bootstrap procedure with 25 percent of the data held out for testing.
Figure 4.3. Predicted/expected frequency of test data withheld from model development over a range of MAXENT logistic output scores for full California Condor models; (a) nesting, (b) roosting, and (c) feeding. Gray bars represent 95% confidence intervals.
Figure 4.4. Predicted/expected frequency of test data withheld from model development over a range of MAXENT logistic output scores for thinned California Condor models; (a) nesting, (b) roosting, and (c) feeding. Gray bars represent 95% confidence intervals.
Figure 4.5. Moran’s I spatial correlograms for California Condor (a) nesting, (b) roosting, and (c) feeding model showing the degree of spatial autocorrelation of model residuals at various distance bands for thinned (open circles) and unthinned models (solid circles).
Figure 4.6. California Condor (a) nesting, (b) roosting, and (c) feeding ecological niche models. Warmer colors represent areas identified by the models as having higher relative suitability. Black areas represent areas with environmental conditions not encountered during model training.
Figure 4.7. Intersection of California Condor ecological niche models: (a) nesting and roosting, (b) nesting and feeding, and (c) roosting and feeding. Black areas represent areas with environmental conditions not encountered during model training.
Figure 4.8. Average percent contribution of covariate categories for California Condor nesting, roosting, and feeding models.
Figure 4.9. California Condor reintroduction suitability map. Warmer colors indicate areas of higher relative suitability for establishing a reintroduction site. Cooler colors represent areas predicted to be either nesting or feeding habitat but with low relative suitability for establishing a reintroduction site. Gray areas are outside of predicted nesting or feeding habitat. Black represents areas outside of the environmental space encountered during model training. White boxes represent current release sites. Black boxes signify areas that have the highest potential to be suitable for reintroduction based on our models.
Figure 4.10. California Condor reintroduction suitability map overlaid with existing and permitted wind turbines (purple crosses).
Table 4.1. Covariates used to develop California Condor nesting, roosting, and feeding ecological niche models.

<table>
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<tr>
<th>Covariate</th>
<th>Description</th>
<th>Data Source</th>
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<tr>
<td><strong>Soaring Conditions and Climate</strong></td>
<td></td>
<td></td>
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<tr>
<td>Thermal Updraft Velocity*</td>
<td>Annual mean velocity of rising air (m/s)</td>
<td>Regional Atmospheric Soaring Prediction Maps (<a href="http://www.drjack.info/RASP/index.html">http://www.drjack.info/RASP/index.html</a>)</td>
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<tr>
<td>Thermal Height*</td>
<td>Annual mean thermal height (m)</td>
<td>Regional Atmospheric Soaring Prediction Maps (<a href="http://www.drjack.info/RASP/index.html">http://www.drjack.info/RASP/index.html</a>)</td>
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<td>Horizontal wind power class at 50m Wind above the ground (category)</td>
<td>National Renewable Energy Lab High Resolution Resource Data (<a href="http://www.nrel.gov/rredc/wind_resource.html">http://www.nrel.gov/rredc/wind_resource.html</a>)</td>
</tr>
<tr>
<td>Winter Severity</td>
<td>Mean minimum winter temperature (°C x 100)</td>
<td>PRISM Climate Data (<a href="http://www.prism.oregonstate.edu">http://www.prism.oregonstate.edu</a>)</td>
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<td><strong>Terrain</strong></td>
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<tr>
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<td>Maximum slope within a 1 km$^2$ neighborhood (degrees)</td>
<td>National Atlas (<a href="http://nationalatlas.gov">http://nationalatlas.gov</a>)</td>
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<tr>
<td><strong>Landscape Productivity</strong></td>
<td></td>
<td></td>
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<td>Euclidean distance to the nearest stream, river, lake, or reservoir (m)</td>
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Table 4.1. (Continued)

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<td>Median canopy cover (%)</td>
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</tr>
<tr>
<td>Land Cover Type</td>
<td>Majority land cover type (category)</td>
<td>National Land Cover Database 2006 (<a href="http://www.mrlc.gov/index.php">http://www.mrlc.gov/index.php</a>)</td>
</tr>
<tr>
<td><strong>Human Disturbance</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Road Density*</td>
<td>km of road/ km²</td>
<td>Data Basin (<a href="http://databasin.org/datasets">http://databasin.org/datasets</a>)</td>
</tr>
<tr>
<td>Human Population Density*</td>
<td>humans/km²</td>
<td>2010 Census Data (<a href="http://www.census.gov/geo/maps-data">http://www.census.gov/geo/maps-data</a>)</td>
</tr>
</tbody>
</table>

* Environmental covariate entered into models using focal statistics to get mean values within a 10 km² radius. All other covariates modeled at 1km resolution.
Table 4.2. Model characteristics and measures of predictive accuracy for California Condor ecological niche models.

<table>
<thead>
<tr>
<th>Measures</th>
<th>Models with All Data</th>
<th>Spatially-thinned Models</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nesting</td>
<td>Roosting</td>
</tr>
<tr>
<td><strong>Model Characteristics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Training Data (n)</td>
<td>75</td>
<td>107</td>
</tr>
<tr>
<td>Test Data (n)</td>
<td>24</td>
<td>35</td>
</tr>
<tr>
<td>Logistic Threshold</td>
<td>0.04</td>
<td>0.13</td>
</tr>
<tr>
<td><strong>Accuracy Measures</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall Accuracy</td>
<td>0.93</td>
<td>0.94</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Specificity</td>
<td>0.88</td>
<td>0.91</td>
</tr>
<tr>
<td>Cohen’s Kappa (K)</td>
<td>0.86</td>
<td>0.88</td>
</tr>
<tr>
<td>Boyce Index_{cont[0,1]}</td>
<td>0.88</td>
<td>0.92</td>
</tr>
<tr>
<td>Test AUC</td>
<td>0.98</td>
<td>0.95</td>
</tr>
<tr>
<td>Training Gain</td>
<td>2.84</td>
<td>2.02</td>
</tr>
<tr>
<td>Test Gain</td>
<td>2.87</td>
<td>1.98</td>
</tr>
</tbody>
</table>
Table 4.3. Average percent contribution of covariates for California Condor ecological niche models.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Nesting</th>
<th>Roosting</th>
<th>Feeding</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Soaring Conditions and Climate</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thermal Updraft Velocity</td>
<td>1</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Wind Speed</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Winter Severity</td>
<td>13</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td><strong>Terrain</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cliffs</td>
<td>52</td>
<td>37</td>
<td>18</td>
</tr>
<tr>
<td>Terrain Ruggedness</td>
<td>2</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td><strong>Landscape Productivity</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Landscape Productivity (max NDVI)</td>
<td>5</td>
<td>7</td>
<td>28</td>
</tr>
<tr>
<td>Distance to Water</td>
<td>7</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td><strong>Vegetation Characteristics</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy Cover</td>
<td>4</td>
<td>20</td>
<td>3</td>
</tr>
<tr>
<td>Canopy Height</td>
<td>4</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Land Cover Type</td>
<td>3</td>
<td>5</td>
<td>23</td>
</tr>
<tr>
<td><strong>Human Disturbance</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Road Density</td>
<td>8</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td>Human Population Density</td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>
CHAPTER 5 - CONCLUSION

The long absence of the California Condor from the Pacific Northwest and the crisis situation of condor conservation in the late twentieth century have, until recently, resulted in a lack of focus on recovery efforts in the Pacific Northwest. It is my hope that by articulating the history of the California Condor in the region, assessing the condor’s historical genetic diversity and population structure, and identifying potential reintroduction suitability through ecological niche modeling, we might inform future dialogue over the role of the Pacific Northwest in condor conservation.

From the historical review in Chapter 2 it is clear that the California Condor was (and still is) culturally important to many Native American tribes in the region and was regularly observed and collected by early explorers and settlers. The species’ historical occurrence in the region is verified by prehistoric and historic physical evidence and numerous firsthand accounts. The number and extent of occurrence records demonstrate that human observations and interactions with condors in the Pacific Northwest were far more prevalent than previously reported.

Evidence now strongly suggests that condors were a resident species in the region. The long breeding and rearing period of the California Condor make long-distance seasonal migration extremely unlikely. Furthermore, two juvenile birds were shot in the Pacific Northwest and preserved in museums. Because young condors often stay in close proximity to their nest site for the first year or two of life, it is quite possible that these birds were hatched in the region and that at least a portion of the condor population was resident.

From a reconstruction of the (admittedly fragmented) historical record, the most plausible hypothesis for the population decline and range collapse of the California Condor is increased mortality from secondary poisoning from laced carcasses and possibly from collecting and indiscriminant shooting. Although direct evidence of condors being poisoned in the Pacific Northwest is limited, the feeding habits of condors make them particularly vulnerable to this threat. Moreover, contemporary studies show that predator poisoning is a major factor in population declines for many vulture species around the world. Collecting and shooting resulted in some direct loss to the condor population, and although the number of reports of condors killed, captured, or removed from the population in the Pacific Northwest is relatively small,
there may have been significant losses that went unreported. Lead poisoning is the leading hypothesis for the lack of a current self-sustaining wild condor population (Walters et al. 2010; Finkelstein et al. 2012; Rideout et al. 2012), and it may also have played a role in the condor’s range contraction. However, there is some uncertainty regarding the bioavailability of lead to condors during this time period due to differences in firearms and ballistics—which may have resulted in less lead fragmentation—prior to the turn of the century. Loss of food resources, loss of nesting habitat, egg collecting, and Native American ritual sacrifice were not likely causes of the condor’s disappearance from the region.

Molecular analyses in Chapter 3 show that California Condors have lost > 80% of their mitochondrial DNA haplotype richness since Euro-American expansion into the West. This substantial loss of haplotypes is consistent with the hypothesis that condor populations were relatively abundant at the time of Euro-American contact, but declined rapidly as a result of human causes. We found no spatial sorting of haplotypes in the historical population, with the periphery of the range containing haplotypes that are common across their range. Our results suggest that condors in the Pacific Northwest and in Baja California were not historically isolated from the population of condors in southern and central California; meaning that establishing an interconnected network of condor populations would be consistent with our understanding of historical population connectivity.

Proper reintroduction planning requires a systematic approach for identifying candidate reintroduction sites. Ecological niche models in Chapter 4 suggest that there are vast areas in the Pacific Northwest that have similar ecological properties to those areas currently occupied by California Condors. These models, when overlaid with data on known threats, provide preliminary identification of areas likely to be suitable for a reintroduction and will help focus ground surveys to evaluate specific reintroduction sites. Our approach, which separately models specific activities and combines them with information on movement ecology has applications for other species where it is routinely assumed (often incorrectly) that individuals fulfill all requirements for life within a single niche.

Taken together these chapters provide foundational information for conservation decision makers to weigh some of the risks and benefits of a condor reintroduction to the Pacific Northwest and to identify areas where the potential for reintroduction success is high.
However, there are remaining questions that, if answered, would enhance our ability to weigh risks and benefits of a reintroduction, would expand our scientific knowledge of California Condors in the Pacific Northwest, or would do both.

5.1 Areas of Further Research

Historical Distribution and Movement Patterns

The ability to rapidly search through millions of pages of historical information via the internet made discovery of many of the historical condor locations possible. As additional historical content is scanned and made accessible, and as search engine technology improves, it is likely that more archival information will be revealed that can be added to our California Condor occurrence records in the Pacific Northwest. However, historical accounts without associated physical evidence need to be treated with some skepticism as it is often difficult to separate lore from reality, especially for species that are identified at a distance by people that may not have the experience in discerning condors from other large raptors.

Additional studies of museum specimens could help resolve questions around historical condor movements through evaluation of stable isotopes. Naturally occurring stable isotopes (variants of chemical elements that differ in the number of neutrons they contain, and which have a stable mass due to lack of substantive decay) vary across the landscape as a result of variation in biogeochemical processes and water transport (Rubenstein and Hobson 2004, Hobson et al. 2010). These isotopes move through the food web and are incorporated into growing tissues of plants and animals. Once animal tissue is done growing, the isotopic signature is preserved in that tissue (Hobson 2005). Thus, museum specimens can be analyzed to determine isotope ratios, which can offer insights into past diet, movements, location, and contaminant exposure (Vo et al. 2011).

Studies of isotopic signatures in feathers and bones of museum specimens have been used to study changes in the diet of California Condors and other large avian scavengers over time, from the late-Pleistocene to the present (Chamberlain et al. 2005, Fox-Dobbs et al. 2006). Because of their long molting period, condor feathers in museums could also be used to investigate changes in isotope ratios throughout the annual-cycle to better understand historical movement patterns and population connectivity.
Hydrogen isotope ratios (δD) have shown promise for investigating latitudinal raptor movements in North America (Lott and Smith 2006). However, because of the topographic relief in the western U.S., additional work to calibrate hydrogen isotope values in feathers with isotopic values in precipitation, or to develop additional isotopic markers, may be necessary before we are able to reliably evaluate historical movement patterns of raptors on the Pacific coast based on hydrogen isotopes (Lott and Smith 2006).

**Molecular Ecology**

The field of molecular genetics continues to evolve at a rapid pace as new techniques and analytical tools are developed (Tautz et al. 2010, Ekblom and Galindo 2011). Areas of potential inquiry that may provide further insights into the California Condor’s demographic history and evolution include:

1. Analysis of ancient nuclear DNA (Greenwood et al. 1999) to provide additional markers for evaluating historical population connectivity;
2. Extraction of mtDNA and nuclear DNA from Pleistocene and early Holocene condor bones (Rohland and Hofreiter 2007, Ginolhac et al. 2012) to evaluate *Gymnogyps* phylogenetics and phylogeography, especially the relationship between *Gymnogyps amplus* and *G. californianus*; and,
3. Calibration of the California Condor’s molecular clock (see van Tuinen and Hedges 2001) which would allow one to apply coalescent theory to estimate population change through time (Emerson et al. 2001, Ho and Shapiro 2011).

**Identification of Potential Release Sites**

The ecological niche models presented in Chapter 4 are critical components to begin identifying potential release sites in the Pacific Northwest. Additional work that would help refine my evaluation of those areas most suitable for siting a potential release site include:

1. Developing a separate ecological niche model to identify areas likely to support coastal feeding. This model should include covariates likely to be most important to
coastal foraging and feeding such as terrain ruggedness, accessibility by humans, and marine mammal stranding and haul-out data;

2. Testing the transferability of ecological niche models in geographic space. Testing the models with data from releases in northern Arizona could provide additional insights into model performance;

3. Conducting ground surveys of the sites with the highest reintroduction potential to gather site specific information, and identify logistical considerations that could not be captured in spatial modeling (e.g., access and availability of electricity and water);

4. Combining ENMs with other potentially important factors (including information gleaned from ground surveys) that could not be directly integrated with ENMs in a spatially-explicit conservation prioritization framework such as Marxan (Ball et al. 2009) or Zonation (Moilanen et al. 2005). Bayesian Networks should also be explored as a potentially useful decision aid that can be used to calculate the probability of reintroduction success at various sites (e.g., Laws and Kesler 2012); and,

5. Combining ENMs with an individual-based population simulation modeling framework such as VORTEX (Lacy 1993, 2000) or HexSim (Marcot et al. 2013, Schumaker 2014). Population simulations could be useful for evaluating the probability of success of various reintroduction scenarios (e.g., Bustamante 1998, Huber et al. 2014), modeling source-sink dynamics (Schumaker et al. 2014) and for setting reasonable population targets or recovery goals (e.g., Carroll et al. 2006). Such simulations might also provide insights into how long it might take to reach recovery goals (Bustamante 1998).

5.2 REINTRODUCTIONS: CHALLENGES AND OPPORTUNITIES

The number of species reintroduction projects has skyrocketed in recent decades (Seddon et al. 2007). This is not surprising, as these projects attract considerable public attention and many zoos have shifted toward a more conservation-oriented mission that lends itself to breeding animals for reintroduction (Seddon et al. 2007). Condor reintroductions are no exception, with a high level of media interest for every egg hatched and public gatherings to witness condor
releases to the wild. Although the captive breeding program has secured the near-term survival of the condor, the species’ long-term prospects remain uncertain. The primary contemporary threat to the condor’s survival and recovery—ingestion of lead from ammunition in carcasses—continues to plague the conservation program at all release sites, despite regulatory and voluntary measures to reduce this threat (Walters et al. 2010; Finkelstein et al. 2012; Rideout et al. 2012; Kelly et al. 2014). In addition, there are novel threats that have emerged since the range collapse, including (1) collision hazards with overhead wires (Meretsky et al. 2000) and wind turbines (Barrios and Rodríguez 2004),44 (2) ingestion of microtrash (Mee et al. 2007), and (3) marine contaminants and associated eggshell abnormalities (Burnett et al. 2013). There has also been significant land development and changes in agricultural practices throughout the condor’s historical range, but especially in southern California, raising questions about the future prospects of condor recovery in what has traditionally been considered the species’ stronghold.

Deciding whether and when to initiate reintroduction efforts involve trade-offs among multiple objectives (Converse et al. 2012). In addition to population establishment and aiding in species recovery, other objectives that must be considered are the risks and costs associated with reintroduction, social acceptability, and scientific objectives that may be achieved through a reintroduction (Converse et al. 2012, Laws and Kesler 2012, IUCN/SSC 2013).

Could the Pacific Northwest offer a safe environment for the California Condor and aid in the species’ overall recovery? Perhaps, but some caution is warranted. First, the landscape in the Pacific Northwest has undergone some dramatic changes in the last century, most notably through human population expansion and associated residential, commercial, and agricultural development. Energy development, in the form of wind farms and overhead transmission lines, has also expanded rapidly over the last few decades. A major international airport now sits near historical foraging grounds for condors. Food resources have shifted due to changes in livestock economies, changes in marine mammal densities and distribution, and changes in riverine

44 Although no California Condors have yet been killed by wind turbines, significant mortality of several other vulture species has been documented (e.g., de Lucas et al. 2012), and large soaring raptors may be particularly vulnerable to this threat given the overlap in areas that generate the most wind power and areas that are regularly patrolled by large raptors due to their favorable soaring conditions and open habitats.
systems, with the associated reductions in salmon populations ascending waterfalls (where they may have once provided a significant predictable food resource for condors). Species assemblages have changed, with regional apex predator extinctions (e.g., gray wolves and grizzly bears)\textsuperscript{45} and changes in the numbers and distribution of avian predators and scavengers. By-products of industry have entered the food chain and, in some cases, bioaccumulated in potential food items. Finally, fire regimes and forest structure have changed over time, and forests have invaded many historically open mountaintop balds—potentially rendering some historical foraging areas too densely packed with trees for condors to effectively exploit. On the other hand, provided lead-free ammunition is used, hunters and ranchers have the potential to provide a tremendous condor food source in the form of carcasses and gut piles (Mateo-Tomás and Olea 2010b). In addition, vulture restaurants—where carcasses from road kills or other clean food sources are provided in concentrated and safe feeding areas—have been used in conservation efforts for other avian scavengers (e.g., Gilbert et al. 2009) and could be applied to condor recovery efforts; however, such efforts must take into account the existing availability of food resources, evaluate the need for a network of feeding sites, and consider the potential impacts on vulture space-use and impacts on non-target species (Margalida et al. 2010, Kane et al. 2014).

Our ecological niche models in Chapter 4 provide a foundation for prioritizing ground surveys. Other threat factors that could not be incorporated directly into the models should be overlaid on aggregated ecological niche models to help eliminate sites that are likely to be unsuitable for a reintroduction effort and to help prioritize those sites that appear potentially suitable for a reintroduction effort. Information on the distribution of public attitudes toward a reintroduction would also be helpful to understand potential social barriers to a successful reintroduction and to design an effective education strategy (e.g., Pate et al. 1996, Morzillo et al. 2009, Balčiauskas and Kazlauskas 2014).

Conservation programs that involve captive breeding and reintroductions are expensive, time consuming, and usually unsuccessful (Snyder et al. 1996). Nonetheless, the California

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\textsuperscript{45} Recovery efforts are underway in the Pacific Northwest for both species. Grizzly bears remain rare in the coterminous United States outside of the Greater Yellowstone Ecosystem, but wolves have rapidly expanded into Oregon and Washington in the last few years.
Condor captive breeding program has been extraordinarily effective, and there are so many captive birds that zoos and release sites will soon reach their capacity (John McCamman, U.S. Fish and Wildlife Service Condor Coordinator, pers. comm., 2012), meaning there are enough birds to initiate another release site. However, existing release sites continue to have significant operating costs, management challenges, and unsustainable mortality rates due to poisoning from lead ammunition (Walters et al. 2010). Adding yet another release site in the Pacific Northwest without first removing the current primary threat to the species (i.e., lead ammunition in their food) is unlikely to substantively improve the species’ status without considerable management intervention (e.g., annually chelating birds that are exposed to lead, monitoring nests, supplemental feeding with clean carcasses, and tracking all birds with radiotelemetry or GPS). Conversely, a wait-and-see approach will mean more habitat degradation and expansion of the human footprint throughout the region without consideration of condor recovery needs. Developing a vision of condor recovery that actively considers the full recent historical range of the condor and outlines necessary steps to recover the species would be a logical next step in identifying those areas in the region that are essential to conserving the species. Whatever path is taken, removing the threats that continue to cause unsustainable mortality will be necessary to achieve species recovery. In addition, without effective protection of those areas that are essential to the long-term viability of a self-sustaining California Condor metapopulation, conservation options will continue to be narrowed.

Establishing appropriate spatial and numerical recovery goals for threatened and endangered species that have been extirpated from much of their former range presents challenges to decision makers, as the question of how much is enough in setting conservation objectives is not a simple matter (Tear et al. 1996; Carroll et al. 2010). However, information on the historical distribution of a species can be helpful in establishing a baseline to facilitate the development of recovery actions that fully consider the effects of anthropogenic changes in the last several hundred years rather than shifting the baseline to the current crisis situation (sensu Pauly 1995).

Initially, condor recovery strategies were focused on the immediate crisis of impending extinction and did not consider the condor’s historical range. Despite the successes of the
recovery program to date, lack of detailed information on the history of California Condors in the Pacific Northwest, genetic structure of the historical population, and maps of potentially suitable habitat have limited exploration into the role this region could play in their recovery. My hope is that this dissertation fills some of these important information gaps and invigorates a discussion of when and where Condors might be restored to the region.

Extinction still hangs over the California Condor like the sword of Damocles, held fast only by a thin thread of dedicated professionals and volunteers. Nearly skewered by the blade of extinction in the 1980s, the condor is now on the path to recovery. However, populations are still small and continue to persist only because of intensive management intervention. Much has been done, but more is needed. If remaining threats can be controlled or eliminated, restoration of California Condors to the Pacific Northwest could not only restore an important piece of the region’s natural heritage but could also establish another hedge against extinction for one of the rarest and most iconic birds in the world.

5.3 LITERATURE CITED


BIBLIOGRAPHY


Barnes, E. P. 1925. Elk in Del Norte County. California Fish and Game 11:90.


Bulletin (San Francisco newspaper). 1856. The California Condor. 16 May.


Bulletin (San Francisco newspaper). 1880. State news in brief. 5 April.


Clarke, C., in litt. 1971. March 1971 letter from Cecile Clarke to Sanford Wilbur regarding a possible condor sighting in Mendocino County, CA.


Cooper, J. G., and G. Suckley. 1859. The Natural History of Washington Territory, with Much Relating to Minnesota, Nebraska, Kansas, Oregon, and California, Between the Thirty-Sixth and Forty-Ninth Parallels of Latitude, Being Those Parts of the Final Reports on the Survey of the Northern Pacific Railroad Route, Containing the Climate and Physical Geography, with Full Catalogues and Descriptions of the Plants and Animals Collected from 1853 to 1857. Bailliére Brothers: New York.


Cronise, T. F. 1868. The Natural Wealth of California: Comprising Early History; Geography, Topography, and Scenery; Climate; Agriculture and Commercial Products; Geology, Zoology, and Botany; Mineralogy, Mines, and Mining Processes; Manufactures; Steamship Lines, Railroads, and Commerce; Immigration, Population and Society; Educational Institutions and Literature; Together with a Detailed Description of Each County; Its Topography, Scenery, Cities and Towns, Agricultural Advantages, Mineral Resources, and Varied Productions. H. H. Bancroft & Company: San Francisco.


Feranec, R. S. 2009. Implications of radiocarbon dates from Potter Creek Cave, Shasta County, California, USA. Radiocarbon 51:931–936.


Johnson, M., J. Kern, and S. M. Haig. 2010. Analysis of California Condor (Gymnogyps californianus) use of six management units using location data from global positioning system


Oregon Fish and Game Commissioner’s Board. 1901. Annual Reports of the Department of Fisheries of the State of Oregon to the Legislative Assembly, Twenty-first Regular Season. W. H. Leeds: Salem, Oregon.


Rowe, S. P., and T. Gallion. 1996. Fall migration of Turkey Vultures and raptors through the southern Sierra Nevada, California. Western Birds 27:48–53.


Sage, R. B. 1846. Scenes in the Rocky Mountains, and in Oregon, California, New Mexico, Texas, and the Great Prairies; or Notes by the Way, During an Excursion of Three Years, with a Description of the Countries Passed Through, Including Their Geography, Geology, Resources, Present Condition, and the Different Nations Inhabiting Them. By a New Englander. Cary & Hart: Philadelphia.


Soulé, M. E. 1983. What do we really know about extinction? Pages 111–124 in C. M. Schowenwald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas (eds), Genetics and


Swan, J. G. 1870. The Indians of Cape Flattery, at the Entrance to the Strait of Fuca, Washington Territory. Smithsonian Contributions to Knowledge 220. Smithsonian Institution: Washington, DC.


The Nature Conservancy, in litt. 2007. A proposal to explore the establishment of a California Condor (re)introduction program in the Lassen Foothills Project Area, California. Letter from Simon Avery (Dye Creek Preserve Manager) to Mark Weitzel (Hopper Mountain National Wildlife Refuge Project Leader). March 1, 2007.


Townsend, J. K. 1839. Narrative of a Journey Across the Rocky Mountains, to the Columbia River, and a Visit to the Sandwich Islands, Chili, &c, with a Scientific Appendix. Henry Perkins: Philadelphia.


Tribune (Chicago newspaper). 1872. A Vulture Eagle, measuring upward of nine feet from tip to tip, has been killed in Mendocino County, Cal. February 24.


Wetmore, A. 1931b. The Avifauna of the Pleistocene in Florida. Smithsonian Miscellaneous Collections 85(2). Smithsonian Institution: Washington, DC.


Willamette Farmer (Salem, Oregon). 1872. Highland Farmers’ Club. 6 July.

Willamette Farmer (Salem, Oregon). 1887. State and territorial news. 25 March.


APPENDICES
APPENDIX 1. ANNOTATED HISTORICAL RECORDS OF CALIFORNIA CONDOR OBSERVATIONS IN
THE PACIFIC NORTHWEST

Record Number\(^46\): 1
Location: Near the confluence of the Wind River and Columbia River, Skamania County, WA
Observer(s): Lewis and Clark party [October 1805 weather reports in Voorhis 4 and Codex I,
Clark’s journal (Oct. 30)]
Date: 28–30 October 1805
Observation Type: Observation
Reference(s): Lewis et al. 2002 (30 October 1805)\(^47\)
Quotation(s):
\[\text{October 28 (weather report in Voorhis No. 4): } \text{“first Vulture of the Columbia Seen to day”}\]
\[\text{October 29 (weather report in Codex I): } \text{“rained moderately all day. Saw the first large Buzzard or Voultur of the Columbia.”}\]
\[\text{October 30 (Clark): “Scattered about in the river, this day we Saw Some fiew of the large Buzzard[.] Capt. Lewis Shot at one, those Buzzards are much larger than any other of ther Spece or the largest Eagle white under part of their wings &c.”}\]

Record Number: 2
Location: Cape Disappointment, WA
Observer(s): Lewis and Clark party [Clark’s journal]
Date: 18 November 1805
Observation Type: Killed; specimen preserved but lost
Reference(s): Lewis et al. 2002 (18 November 1805)

\(^46\) Record numbers correspond to the numbers in Figure 2.11.
\(^47\) In addition to Lewis and Clark’s journals, several members of the expedition kept journals, some entries of which are similar or the same for a given day. Apparently, copying journal entries from each other was not uncommon. Our records include all instances where California Condors were mentioned by the expedition, although journal entries that provided no additional details to those of Lewis or Clark were left out. Readers wishing to see all of the journal entries are directed to Lewis et al. (2002).
\(^48\) In Voorhis No. 4 for October 29 Clark writes, “I shot at a vulture.” (Lewis et al. 2002).
\(^49\) Lewis makes no mention of this observation in his journal for that day.
Quotation(s): Clark’s journal, 18 November: “Rubin Fields Killed a Buzzard of the large Kind near
the meat of the whale we Saw: W. 25 lb. measured from the tips of the wings across 9½ feet,
from the point of the Bill to the end of the tail 3 feet 10¼ inches, middle toe 5½ inches, toe nale
1 inch & 3½ lines, wing feather 2½ feet long & 1 inch 5 lines diamiter tale feathers 14½ inches,
and the head is 6½ inches including the beak.” 50

Gass’s journal, 20 November: “Wednesday [November] 20th.—We had a fine clear morning . . . .
At four o’clock in the afternoon, Capt. Clarke and his party returned to camp, and had killed a
deer and some brants. They had been about 10 miles north of the cape [Cape Disappointment],
and found the country along the seashore level with spruce-pine timber, and some prairies and
ponds of water. They killed a remarkably large buzzard, of a species different from any I had
seen. It was 9 feet across the wings, and 3 feet 10 inches from the bill to the tail.”

Record Number: 3
Location: Near Astoria, OR
Observer(s): Lewis and Clark party [Clark’s journal]
Date: 29–30 November 1805
Observation Type: Observation
Reference(s): Lewis et al. 2002 (29–30 November 1805)
Quotation(s): November 29: “The Shore below the point at our Camp is formed of butifull
pebble of various colours. I observe but fiew birds of the Small kind, great numbers of wild fowls
of Various kinds, the large Buzzard with white wings, grey and bald eagle’s.”

November 30: “Some rain and hail with intervales of fair weather for 1 and 2 hours dureing the
night and until 9 oClock this morning at which time it Cleared up fair and the Sun Shown, I Send
5 men in a Canoe in the Deep bend above the Peninsulear to hunt fowles, & 2 men in the thick
woods to hunt Elk[,] had all our wet articles dried & the men all employed dressing their Skins, I
observe but few birds in this Countrey of the Small kinds—great numbers of wild fowl, The large

50 Nicholas Biddle (first editor of the Lewis and Clark journals) noted that the head of this specimen was
in Peale’s Museum (Lewis et al. 2002). Charles Willson Peale, a noted painter, was the proprietor of
Peale’s Museum in Philadelphia, the only natural history museum in the country at that time. The
museum was originally housed in present-day Independence Hall, but was later moved to Baltimore,
Maryland. The currently location of the specimen is unknown.
Buzzard with white under their wings Grey & Bald eagle large red tailed hawk, ravins, Crows, & a small brown bird which is found about logs &c. but few small hawks or other smaller birds to be seen at this time.”

**Record Number: 4**

Location: Near Fort Clatsop, OR

Observer(s): Lewis and Clark party [Lewis’s journal]

Date: 3 January 1806

Observation Type: Observation

Reference(s): Lewis et al. 2002 (3 January 1806)

Quotation(s): “the bald Eagle and the beatifull Buzzard of the columbia still continue with us.”

**Record Number: 5**

Location: Youngs River, Clatsop County, OR

Observer(s): Lewis and Clark party [Clark’s journal]

Date: 16 February 1806

Observation Type: Live-captured, then killed

Reference(s): Lewis et al. 2002 (16–17 February 1806)

Quotation(s): “Shannon and Labiesh brought in to us to day a Buzzard or *Vulture* of the Columbia which they had wounded and taken alive. I believe this to be the largest Bird of North America . . . we have Seen it feeding on the remains of the whale and other fish which have been thrown up by the waves on the Sea Coast. these I believe constitute their principal food, but I have no doubt but that they also feed on flesh. we did not meet with this bird un[t]ille we had decended the Columbia below the great falls [Celilo Falls]; and have found them more abundant below tide water than above. this is the Same Species of Bird which R. Field killed on the 18th of Novr. last and which is noticed on that day tho’ not fully discribed then I thought this

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51 Lewis’s journal for this day indicates he saw “a great abundance of fowls” but does not specifically list the California Condor.

52 Note: Lewis’s journal includes a similar entry on 17 February 1806, along with a drawing of the head of the California Condor (Figure 2.12).
of the Buzzard Specis. I now believe that this bird is rather of the Vulture genus than any other, tho’ it wants some of their characteristics particularly the hair on the neck, and the feathers on the legs. This is a handsome bird at a little distance. It’s neck is proportionally longer than those of the Hawks or Eagle. . . . Shannon and Labiesh informed us that when he approached this Vulture after wounding it, that it made a loud noise very much like the barking of a Dog.”

**Record Number: 6**

Location: Near Fort Clatsop, OR  
Observer(s): Lewis and Clark party [Gass’s journal]  
Date: 15 March 1806  
Observation Type: Killed (x2)  
Reference(s): Lewis et al. 2002 (16 March 1806)  
Quotation(s): “Yesterday [15 March 1806] while I was absent getting our meat home, one of the hunters killed two vultures, the largest fowls I had ever seen. I never saw any such as these except on the Columbia river and the seacoast.”

**Record Number: 7**

Location: North end of Deer Island, Columbia County, OR  
Observer(s): Lewis and Clark party [Clark’s journal, Lewis’s journal]  
Date: 28 March 1806  
Observation Type: Observation  
Reference(s): Lewis et al. 2002 (28 March 1806)  
Quotation(s): *Clark’s journal:* “The men who had been Sent after the deer returned with four only, the other 4 haveing been eaten entirely by the Voulturs except the Skin.”  
*Lewis’s journal:* “The men who had been sent after the deer returned and brought in the remnent which the Vultures and Eagles had left us; these birds had devoured 4 deer in the

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53 There is no mention of this incident in either Lewis’s or Clark’s journal; perhaps not surprising given that they had already described the species in detail and they had long entries for other species around this time.  
54 Lewis and Clark’s party did not see Turkey Vultures west of the Rocky Mountains until 9 April 1806.
course of a few hours. the party killed and brought in three other deer a goose some ducks and an Eagle. Drewyer also killed a tiger cat. Joseph Fields informed me that the Vultures had draged a large buck which he had killed about 30 yards, had skined it and broken the back bone.”

Record Number: 8
Location: Near Rooster Rock State Park, OR
Observer(s): Lewis and Clark party [Lewis’s journal, Clark’s journal]
Date: 5–6 April 1806
Observation Type: Killed
Reference(s): Lewis et al. 2002 (5–6 April 1806)
Quotation(s): Lewis’s journal, 5 April 1806: “we saw the martin, small gees, the small speckled woodpecker with a white back, the Blue crested Corvus, ravens, crows, eagles Vultures and hawks.”
Clark’s journal, 6 April 1806: “Jos: Field killed a vulture of that Speces already described.”

Record Number: 9
Location: Lower end of Hamilton Island, WA
Observer(s): Alexander Henry and David Thompson
Date: 19 January 1814
Observation Type: Observation
Reference(s): Coues 1897:808
Quotation(s): “Some extraordinarily large vultures [editorial note by Coues: Pseudogryphus californianus] were hovering over camp.”

Record Number: 10
Location: Above Willamette Falls, near Pudding River, OR
Observer(s): Alexander Henry and David Thompson
Date: January 1814

55 The only vulture species that the party had described in their journals to this point was the California Condor. Lewis and Clark’s party did not see Turkey Vultures west of the Rocky Mountains until 9 April 1806.
Observation Type: Observation
Reference(s): Coues 1897:817
Quotation(s): “I sent for the eight deer killed yesterday. The men brought in seven of them, one having been devoured by the vultures [editorial note by Coues: *Pseudogryphus californianus*]. These birds are uncommonly large and very troublesome to my hunters by destroying the meat, which, though well covered with pine branches, they contrive to uncover and devour.”

**Record Number: 11**
Location: Idaho/Oregon border
Observer(s): Donald McKenzie
Date: Fall 1818
Observation Type: Observation
Reference(s): Ross 1855:203
Quotation(s): “Eagles and vultures, of uncommon size, flew about the rivers.”

**Record Number: 12**
Location: Near the confluence of the Cowlitz and Columbia Rivers, WA
Observer(s): John Scouler
Date: September 1825
Observation Type: Killed; specimen 162189 in the National Museum of Natural History, Leiden, The Netherlands.
Reference(s): Scouler 1905: 280
Quotation(s): p. 280, 22 September 1825: “This morning we breakfasted at the Kowlitch [Cowlitz] village & we were treated with much civility, although they were in a very unsettled state & were preparing for war in consequence of the circumstances formerly alluded to. On arriving on board the ship much of my time was employed procuring & preserving birds. The incessant rains we experienced at the advanced period of the year rendered the

56 Exact location unclear. Somewhere in the mountainous terrain southeast of Walla Walla, Washington, probably near the Idaho border.
accumulation of plants hopeless. The river at this season was beginning to abound in birds. I obtained specimens of *Pelecanus onocrotalus*, *Falco*—& a species of *Vultur*, which I think is nondescript. My birds were princip[a]ly obtained from the Indians, who would go through any fatigue for a bit of tobac[c]o."

**Record Number: 13**

Location: Near Fort Vancouver, WA  
Observer(s): David Douglas  
Date: Winter 1826  
Observation Type: Killed\(^{57}\)  
Reference(s): Douglas 1914:154–55; Hall 1934:5  
Quotation(s): *Douglas 1914, 154–55*: “On the Columbia there is a species of Buzzard, the largest of all birds here, the Swan excepted. I killed one of this very interesting bird, with buckshot, one of which passed through the head, which rendered it unfit for preserving; I regret it exceedingly, for I am confident it is not yet described. I have fired at them with every size of small shots at respectable distances without effect; seldom more than one or two are together. When they find a dead carcase or putrid animal matter, so gluttonous are they that they will eat until they can hardly walk and have been killed with a stick. They are of the same colour as the common small buzzard found in Canada, one of which was sent home last October. Beak and legs bright yellow. The feathers of the wing are highly prized by the Canadian voyageurs for making tobacco pipe-stems. I am shortly to try to take them in a baited steel-trap.”  
*Hall 1934, 5*: “When opportunity favoured I collected woods, and gathered Musci, &c., and from this time to March 20th I formed a tolerable collection of preserved animals and birds . . . [including] *Sacroramphos californica* [California Condor].”

**Record Number: 14**

Location: Between the Umpqua River and Willamette Valley, OR

\(^{57}\) This bird was preserved and eventually ended up in either the Institute Royal des Sciences Naturelles de Belgique (Brussels) or the Museum National d’Histoire Naturelle (Paris); the location of this specimen and the other specimen Douglas collected and preserved (record 17) cannot be assigned with certainty.
Quotation(s): “This morning [10 or 11 October 1826] we passed a hill of similar elevation and appearance to that we passed yesterday. Several species of Clethra were gathered—one in particular, *C. grandis* [sic], was very fine—and many birds of *Saccomphos californica* [California Condor] and *Ortyx californica*, and two other species of great beauty were collected. This part of the time was rainy, ill-adapted for hunting. The last two days’ march we descended the banks of Red Deer River, which empties itself into the River Arguilar or Umpqua, forty-three miles from the sea.”

**Record Number: 15**
Location: Umpqua River and south, OR
Observer(s): David Douglas and Norman McLeod
Date: October 1826
Observation Type: Observation
Reference(s): Douglas 1914:216, 241
Quotation(s): *Douglas 1914*, 216: “The Large Buzzard, so common on the shores of the Columbia, is also plentiful here [Umpqua River region]; saw nine in one flock.”
*Douglas 1914*, 241: “I think they [California Condors] migrate to the south, as great numbers were seen by myself on the Umpqua River, and south of it by Mr. McLeod, whom I accompanied.”

**Record Number: 16**
Location: East of the Cascade Range, near the US-Canada border, WA
Observer(s): David Douglas
Date: 1826–1827
Observation Type: Observation
Reference(s): Douglas 1829:329
Quotation(s): “I have met with them [Vultur californianus] as far to the north as 49° N. Lat. [the Canadian border] in the summer and autumn months, but no where so abundantly as in the Columbian valley between the Grand Rapids [Celilo Falls] and the sea.”

Record Number: 17
Location: Near Fort Vancouver, WA
Observer(s): David Douglas
Date: 3 February 1827
Observation Type: Killed
Reference(s): Barnston 1860:208; Fleming 1924:111–12; Douglas 1914:241
Quotation(s): Barnston 1860, 208; Fleming 1924, 111–12: “The Spring of 1827 was severe, and much snow had fallen. The consequence was that many horses died at Fort Vancouver, and we were visited by the various species of beasts and birds of prey that abound in that country. Most conspicuous among these were the California vulture. This magnate of the air was ever hovering around, wheeling in successive circles for a time, then changing the wing as if wishing to describe the figure 8; the ends of the pinions, when near enough to be seen, having a bend waving upwards, all his movements, whether of soaring or floating ascending or descending, were lines of beauty. In flight he is the most majestic bird I have seen. One morning a large specimen was brought into our square. . . . It has been frequently a matter of surprise how quickly these birds collect when a large animal dies. None may be seen in any direction, but in a few minutes after a horse or other large animal gives up the ghost they may be descried like specks in the æther, nearing by circles to their prey.”
Douglas 1914, 241: “Killed a very large vulture, sex unknown . . . During the summer [they] are seen in great numbers on the woody part of the Columbia, from the ocean to the mountains of

58 Although Douglas reports here that condors occurred north to the Canadian border (during his travels to the east of the Cascade Range), he makes no specific mention of these sightings in his journals, which is odd given the details he provides for the condors he observed and collected west of the Cascades.
59 This bird was preserved and eventually ended up in either the Institute Royal des Sciences Naturelles de Belgique (Brussels) or the Museum National d’Histoire Naturelle (Paris); the location of this specimen and the other specimen Douglas collected and preserved (record 13) cannot be assigned with certainty.
60 Although Barnston writes “Spring,” in the next paragraph he begins with “March of 1827 arrived,” consistent with the February date given by Douglas.
Lewis and Clarke’s River [Columbia River], four hundred miles in the interior. In winter they are less abundant. . . . Feeds on all putrid animal matter and are so ravenous that they will eat until they are unable to fly. Are very shy: can rarely get near enough to kill them with buck-shot; readily taken with a steel trap.”

Record Number: 18
Location: Klamath River area near present-day Humboldt-Del Norte county line, CA
Observer(s): Jedediah Smith
Date: 22 May 1828
Observation Type: Observation
Reference(s): Sullivan 1934:92
Quotation(s): “Among the animals I observed in the country [were] . . . Large & small Buzards, Crows, Ducks, Ravens, several kinds of hawks, Eagles and a few small birds.”

Record Number: 19
Location: Cowlitz River, near its confluence with the Columbia River, WA
Observer(s): William Fraser Tolmie
Date: 21 May 1833
Observation Type: Observation
Reference(s): Tolmie 1963:185
Quotation(s): “At 11½ passed our yesterday’s encampment & scared some large vultures & crows from their feast.”

Record Number: 20

61 The fact that Jedediah Smith differentiates between large and small buzzards, hawks, and eagles, along with the location and time period, makes this a credible sighting. Many other observers subsequently found condors to be numerous in northern California in the mid-1800s.
62 The fact that Tolmie describes “large” vultures, along with the known occurrence of condors along the lower Columbia River during this time period, makes this a credible sighting.
Location: Cowlitz River, WA
Observer(s): William Fraser Tolmie
Date: 22 May 1833
Observation Type: Observation
Reference(s): Tolmie 1963:186
Quotation(s): “Arrived about 11 at a deserted Indian village & startled some large vultures, who hovering above at length perched on the neighbouring trees, awaiting our departure . . . fired twice at vultures.”

**Record Number: 21**

Location: Near Fort Vancouver, WA
Observer(s): John Kirk Townsend
Date: 1834–1836
Observation Type: Observation
Reference(s): Audubon 1840:13
Quotation(s): “I once saw two [California Condors] near Fort Vancouver feeding on the carcass of a pig that had died.”

**Record Number: 22**

Location: Willamette Falls, OR
Observer(s): John Kirk Townsend
Date: April 1835
Observation Type: Killed; US National Museum specimen 78005 (juvenile)
Reference(s): J. Townsend 1848:265–67
Quotation(s): “As I gazed upon them [Turkey Vultures], interested in their graceful and easy motions, I heard a loud rustling sound over my head, which induced me to look upward; and there, to my inexpressible joy, soared the great Californian, seemingly intent upon watching the motions of his puny relatives below. Suddenly, while I watched, I saw him wheel, and down like

63 The fact that Tolmie describes “large” vultures, along with the known occurrence of condors along the lower Columbia River during this time period, makes this a credible sighting.
an arrow he plunged, alighting upon an unfortunate Salmon which had just been cast, exhausted with his attempts to leap the falls, on the shore within a short distance. At that moment I fired, and the poor Vulture fell wounded, beside his still palpitating quarry.”

Record Number: 23
Location: Sacramento Valley or Sonoma County, CA
Observer(s): Ivan Gavrilovich Voznesenskii
Date: 1840–1841
Observation Type: Killed (x4); specimens preserved and shipped to the Russian Academy of Sciences, but two were subsequently lost. The other two are now at the Saint Petersburg Zoological Museum, Russia (specimens 1583 and 1584).
Reference(s): Blomkvist 1972:100–170; Bates 1983:36–41; Alekseev 1987
Quotation(s): None

Record Number: 24
Location: Plains of the Willamette Valley, OR
Observer(s): Titian Ramsay Peale
Date: September 1841
Observation Type: Observation
Reference(s): Peale 1848:58

64 The story continues with Townsend swimming (naked) across the river and his ensuing fight with the condor that including throwing rocks and kicking sand in its eyes. He ultimately killed the bird when he “hit him fairly on the head with a large stone” then pounced on him and dispatched him by severing the spine with a knife.

65 In addition to four condor specimens, Voznesenskii also obtained an entire condor skin used by the Central Miwok Indians as a dance costume, and a condor cape. The dance costume and condor cape are now housed in the Peter the Great Museum of Anthropology and Ethnography, Saint Petersburg, Russia. The precise location where Voznesenskii collected his specimens is unclear. However, we know that from 11 April 1841 to 5 September 1841 he was in the vicinity of Fort Ross, Sonoma County, California, where he and A. G. Rotchev collected many birds. In May and June 1841, he traveled the entire length of the Russian River, and on 16 June 1841 made the first ascent of Mount Saint Helena, Sonoma County, California.]
Quotation(s): “This cannot be considered a common bird in Oregon; we first saw them on the plains of the Willamette River, but subsequently observed that they were much more numerous in California, from the fact that the carcasses of large animals are more abundant, which they certainly prefer to the dead fish on which they are obliged to feed in Oregon, and all the countries north of the Spanish settlements in California.”

Record Number: 25  
Location: Near Youngs River (creek) in the Umpqua Mountains, OR  
Observer(s): Titian Ramsay Peale  
Date: 24 September 1841  
Observation Type: Observation  
Reference(s): Poesch 1961:191  
Quotation(s): “we saw today Goldenwing woodpeckers (red var.), Ravens, Crows, Stellers & Florida Jays, Californian Vultures, and a few Larks.”

Record Number: 26  
Location: North of Redding (along the Sacramento River), CA  
Observer(s): Titian Ramsay Peale  
Date: 5 October 1841  
Observation Type: Observation  
Reference(s): Poesch 1961:194  
Quotation(s): “I saw two species of marmots, and several birds not seen before. Sev California Vultures, etc.”

Record Number: 27  
Location: Sacramento Valley (between Redding and Sacramento), CA  
Observer(s): Titian Ramsay Peale  
Date: 18 October 1841  
Observation Type: Observation  
Reference(s): Poesch 1961:195
Quotation(s): “Numbers of Californian Vultures, Turkey buzzards, and Ravens were assembled this morning to enjoy the feast we have prepared for them.”

**Record Number: 28**
Location: Valley of Napa Creek, CA
Observer(s): James Clyman
Date: August 1845
Observation Type: Observation
Reference(s): Clyman 1926:137
Quotation(s): “Beside the raven and turk[e]y Buzzard of the states you see here the royal vulture [California Condor] in greate abundance frequently measureing Fourteen feet from the extremity of one wing to the ext[r]emity of the other.”

**Record Number: 29**
Location: Napa County, CA
Observer(s): James Clyman
Date: 8 September 1845
Observation Type: Killed
Reference(s): Clyman 1926:138
Quotation(s): “Killed 5 Deer one large grissled Bear one wild cat and a Royal vulture [California Condor] this is the largest fowl I have yet seen measuring when full grown full 14 feet from the ext[r]emity of one wing to the ext[r]emity of the other. Like all the vulture tribe this fowl feeds on dead carcases but like the Bald Eagle prefers his meat fresh and unputrefied[,] they seem [to] hover over these mountains in greate numbers are never at the least fault for their prey but move directly and rapidly to the carcase cutting the wind with their wings and creating a Buzzing sound which may [be] heard at a miles distance and making one or two curves they immediately alight and commence glutting[.]”

**Record Number: 30**
Location: Between Sutter’s Fort and Suisun Bay, CA
Observer(s): Heinrich Lienhard  
Date: 1846  
Observation Type: Observation  
Reference(s): M. Wilbur 1941:42  
Quotation(s): “I had seen large numbers of vultures, turkey buzzards, ravens, crows, and magpies perched on a sycamore tree nearby, and knew there must be a carcass somewhere in the vicinity.”66

**Record Number: 31**  
Location: Near Fort Ross, CA  
Observer(s): William Benitz  
Date: 1846–1847  
Observation Type: Observation  
Reference(s): E. Finley 1937:406  
Quotation(s): “Shortly after William Benitz acquired the Fort Ross property he took his rifle and set up the mountain-side to try to kill one of several ‘vultures or California condors’ perched on the dead limb of a pine tree, in order to obtain feathers, which he knew would be highly prized by his Indian retainers.”67

**Record Number: 32**  
Location: Mountains of Marin County, CA  
Observer(s): Andrew Jackson Grayson  
Date: July 1847  
Observation Type: Observation  
Reference(s): Bryant 1891:52–53

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66 Lienhard’s distinction between vultures and turkey buzzards, along with his location and the time period, makes this a credible sighting.
67 It is unclear whether Benitz ever killed a condor—the Fort Ross Interpretive Association (2001) reports that he did, but documentation is lacking.
Quotation(s): “In the early days of California history it [the California Vulture] was more frequently met with than now, being of a cautious and shy disposition the rapid settlement of the country has partially driven it off to more secluded localities. I remember the time when this vulture was much disliked by the hunter for its ravages upon any large game he may have killed and left exposed for only a short length of time. So powerful is its sight that it will discover a dead deer from an incredible distance while soaring in the air. A case of this kind happened with myself whilst living in the mountains of Marin County, California, in the year 1847. At that time my main dependence for meat wherewith to feed my little family was my rifle. . . . One fine morning I had shot a large and exceedingly fat buck of four points, on the hills above my little cabin. Taking a survey of the sky in every direction I could not discover a single vulture, and, as my cabin was but a short distance from the spot, I concluded not to cover my game as I could return with my horse to pack it home before the vultures would be likely to trouble it. But for this lack of caution I was doomed, as in many other events in my life, to disappointment. I was gone about two hours, when, on returning, I found my game surrounded and covered by a flock of at least a dozen vultures, and others still coming. Some so far up in the heavens as to appear like a small black speck upon the clear blue sky.”

**Record Number: 33**

Location: Mouth of Feather River, CA  
Observer(s): Mark Hopkins  
Date: 19 September 1849  
Observation Type: Killed  
Reference(s): Stillman 1967:27  
Quotation(s): “Just before night, Mark shot a large bird in the top of a tree, which we thought was a wild turkey. It was directly over our heads, and fell into the water alongside the boat. It measured nine feet from tip to tip of wings, and its head and neck were bare of feathers and of yellow color. It was of the vulture family.”

**Record Number: 34**

Location: Yuba River Canyon, CA
Observer(s): Elisha Douglass Perkins
Date: 20 September 1849
Observation Type: Observation
Reference(s): T. Clark 1967:135
Quotation(s): [Descending through the Yuba River Canyon toward the Sacramento Valley] “Our road was improving rapidly, hills becoming less lofty & steep, country more rolling. Pines & their kind are disappearing & in their place we have scrub oaks. Saw in my mornings march several large vultures, such as I never before met with, perched on a dead tree. Their heads & necks entirely bare of feathers & red—body black, & immense claws & beak. A buzzard by the side of one looked like a black bird, & as one sailed close over my head I judged his spread of wing to be seven foot. I should take them to be a species of condor from the recollections I have of the bird.”

Record Number: 35
Location: Sierra foothills, Plumas County, CA
Observer(s): J. G. Bruff party
Date: 20 October 1849
Observation Type: Killed
Reference(s): Reed and Gaines 1949:204
Quotation(s): “6 dead and 1 abandoned ox on road . . . Saw on the road side a small black & yellow fox, dead, also a dead deer, and numerous remains of them. Shot a large very dark brown Vulture, measuring 9 feet from tip to tip.”

Record Number: 36
Location: Mill Creek area, Tehama County, CA
Observer(s): J. G. Bruff party
Date: 15–19 November 1849
Observation Type: Observation
Reference(s): Reed and Gaines 1949:240, 245
Quotation(s): Reed and Gaines 1949, 240 (15 November 1849): “Poyle and his comrades returned late, unsuccessful. Shot nothing, nor obtained the deer left hanging to a tree; the eagles & vultures had left nothing but the skeleton & skin; an officious and disagreeable interferance with our rights.”

Reed and Gaines 1949, 245 (19 November 1849): “Seymours young man assisted, to skin & cut up the meat [of an ox they had killed]. Poyle, bro’t a sack full of meat up from the ravine ½ mile down, and we had liver & coffee for dinner—After dinner P. returned for balance of the meat, and reached the spot just in time to save it, as the eagles & vultures were gathering apace, and commenced operations.”

Record Number: 37
Location: Yoncalla, Douglas County, OR
Observer(s): Roselle Putnam
Date: 1849–1852
Observation Type: Killed
Reference(s): Putnam 1928:262
Quotation(s): “The largest wild bird in the country is the vulture which is only an overgrown buzzard—it only preys on the dead carcase—I saw one measured which I think was between ten & eleven feet from the point of one wing to the point of the other.”

Record Number: 38
Location: Mill Creek area, Tehama County, CA
Observer(s): J. G. Bruff party
Date: 6–24 February 1850
Observation Type: Observation

68 The Bruff party had shot a condor earlier in the vicinity (see record 35). This, combined with the fact that Turkey Vultures have generally migrated south by mid-November in northern California, makes these likely condor observations.

69 Roselle Putnam was Jesse Applegate’s eldest daughter. Applegate is one of the best known of Oregon’s pioneers. He took part in the early government of Oregon and helped establish the Applegate Trail (a safer alternative to boating the Columbia River rapids). The Applegate River (a tributary to the Rogue River) and Applegate Valley of southern Oregon are named in his honor.

70 The bird was measured, but the account does not mention whether it was dead or alive.

Quotation(s): Reed and Gaines 1949, p. 301 (6 February 1850): “3 large vultures passed over.”

p. 306 (19 February 1850): “About 4 p.m. I noticed 12 vultures, soaring very high, in circles, overhead, and moving toward the S.W.”

p. 307 (20 February 1850): “Numerous vultures & eagles flying about.”

p. 308 (24 February 1850): “Many eagles & vultures soaring over head.—No doubt attracted by the ox carcasses.”

Record Number: 39
Location: Mill Creek area, Tehama County, CA
Observer(s): J. G. Bruff party
Date: 4–29 March 1850
Observation Type: Observation
Reference(s): Reed and Gaines 1949:311, 325.

Quotation(s): p. 311 (4 March 1850): “Parties returned at Sun-Set, and soon after. They bro’t in a deer. Yesterday they shot one, and eat half, hanging the other half in a tree: Today they found but one ham of it, the eagles & vultures had feasted upon it.”

p. 325 (29 March 1850): “Saw a bald eagle and several vultures soaring over head.”

Record Number: 40
Location: West Branch, North Fork of the Feather River, CA
Observer(s): Samuel Seabough
Date: 1850–1880

71 The Bruff party had shot a condor earlier in the vicinity (see record 35). This, combined with description of the vultures as “large” and the fact that Turkey Vultures are generally absent in northern California in February, makes these likely condor observations.

72 The Bruff party had shot a condor earlier in the vicinity (see record 35).

73 Seabough arrived in California in 1850 (Cummins 1893), so this individual must have been collected between 1850 and the publication of this article in 1880. No further details are available to narrow the timing of this incident.
Observation Type: Killed
Reference(s): Seabough (1880)

Quotation(s): “The forests of the Sierra Nevada are not remarkable for a great variety of animal life. There is the black-tailed deer, the large gray wolf . . . now and then a vulture almost as large as the Andean condor—I have seen a specimen shot on the West Branch, North Fork of Feather river, that measured 11 feet 6 inches from tip to tip of its outstretched wings.”

Record Number: 41
Location: Coast Range, Mendocino County, CA
Observer(s): A. K. Benton
Date: 1854–1856
Observation Type: Killed
Reference(s): Daily Union (Sacramento) 1 April 1856

Quotation(s): “Mr. Benton has exhibited to us several of the warlike implements of the various tribes—among them an oval-shaped, sharp-edged flint, which is used as an eating knife in peace, and scalpel in war; also the brace bone of an elk’s leg, smoothly rounded, and as sharp as a needle at the point. This weapon our informant seized from a refractory Indian. . . . Last, but not least, of this cabinet of curiosities, is a plume of raven blackness, plucked from a vulture killed in the coast range of mountains. This feather is over two feet long, and the quill barrel measured an inch in circumference. The bird from which it was taken yielded itself reluctantly to his captor, although pierced to the heart by the unerring bullet of the sportsman.”

Record Number: 42
Location: Near Chico, CA
Observer(s): Unknown
Date: 1854
Observation Type: Killed

74 The dates given for this record are when A. K. Benton was at the Nomen Lackee (Round Valley) Indian Reservation. From the quotation in the newspaper it sounds like Benton was the sportsman who shot the condor, but it is not entirely clear.
Reference(s): Daily Union (Sacramento) 21 June 1854
Quotation(s): “A CALIFORNIA VULTURE.—The Editor of the Marysville Herald may well ‘plume himself’, on receipt of a vulture’s quill measuring twenty-five inches in length. The bird measured nine feet four inches from tip to tip of the wings. It was shot near Chico.”

Record Number: 43
Location: Near Fort Vancouver, WA
Observer(s): J. G. Cooper
Date: January 1854
Observation Type: Observation
Reference(s): Cooper and Suckley 1859:141; Belding 1890:25
Quotation(s): Cooper and Suckley 1859, p. 141: “In January, 1854, I saw, during a very cold period, a bird which I took for this [the California Vulture], from its great size, peculiar flight, and long bare neck, which it stretched out as it sat on a high dead tree, so as to be scarcely mistakenable for any other bird.”
Belding 1890, p. 25: “Cooper, 1870. This confirms the observations of Dr. Suckley and myself, as we saw none [California Vultures] during a long residence and travels near the Columbia, except one which I supposed to be this, seen at Fort Vancouver in January. Like several other birds seen there by Townsend and Nuttall, they seem to have retired more to the south since 1834.”

Record Number: 44
Location: American River, El Dorado County (near the store of Woods & Kenyon), CA
Observer(s): Unknown
Date: March 1854
Observation Type: Killed
Reference(s): Daily Union (Sacramento) 11 March 1854
Quotation(s): “CALIFORNIA VULTURE.—A vulture of enormous proportions was shot on the American river, near the store of Woods & Kenyon, in El Dorado county, a few days since, which measured nine feet from tip to tip of its wings. A friend presented us yesterday with a quill,
which is a quill from one of its wings, with the remark that it was handed us as a weapon with which to defend the rights of the people. We shall endeavor to apply it to that purpose.”

**Record Number: 45**

Location: South Fork of American River (North Canyon), CA  
Observer(s): Alonzo Winship and Jesse Millikan  
Date: Fall 1854  
Observation Type: Live-captured and released  
Reference(s): Millikan 1900:12–13  
Quotation(s): “As he [Jesse Millikan] was crossing the aqueduct over North Canyon, he saw an enormous condor asleep at the base of a cliff that jutted about twenty feet above the flume. Surprised that the bird had not been awakened by his footsteps along the flume, he hesitated a moment, then decided to attempt to kill the bird. Having nothing but his shovel he threw it with all his force, striking the condor and breaking its wing.”  

**Record Number: 46**

Location: Vicinity of the redwoods of Contra Costa, CA  
Observer(s): Joseph P. Lamson  
Date: January–February 1854  
Observation Type: Killed (x4); 1 wounded and escaped; other observations  
Reference(s): Lamson 1852–1861:283, 284, 286, 287, 292; Lamson 1878:152–54  
Quotation(s): Lamson 1852–1861, 283: “Thursday 2 February [1854]. I was standing at the door of my cabin, which I heard the report of a rifle, and turning my eyes in the direction of the sound, I saw a California Vulture fall to the ground. I hastened up the cañon, and speedily purchased the bird of the owner, who did not place a very high value on it. It was not a large one, being only eight feet six inches in alar extent, and three feet ten inches long from the point of the
Bill to the end of the tail, and weighing twenty-one pounds. The longest feathers in the wings were twenty-six inches. I was desirous of preserving the skin of one of these birds, but chose to wait until I should obtain a larger specimen. So I cut off the wings, and pulled out some of the feathers from the body, which I preserved as well as some of the bones and threw the body away."

_Lamson 1878, 152–54_: “February 9, 1854. In a walk some days since through the Redwoods, I encountered an old man by the side of the road engaged in making shingles. He was a very coarse-looking fellow with a dark complexion and a black, bushy beard, that more than half covered his face, giving an additional grimness to his rough, harsh features. He was an old Kentucky rifleman, and, as I learned to-day, a first-rate marksman. He had shot a Vulture some time before, and it was lying near his cabin, half decayed. Some quills were scattered over the ground, and I picked up two or three of them, when he ordered me in the rudest manner to leave them. I then offered to buy some of them, but he would neither sell nor give them away. He wanted them for himself. . . . To-day I passed his cabin again, and he accosted me with considerable civility . . . he had shot two Vultures yesterday, though one of them, which he had only wing-tipped, and tied to a stake, had escaped. He was willing to sell me the remaining bird, and the payment of five bits made me its owner. . . . I skinned my bird, and left it with the Kentuckian, while I continued my walk. . . . I saw six or eight of them perched on trees, sitting in perfect idleness and scarcely moving. . . . On returning, I called for the skin of my bird which measured nine feet four inches from tip to tip of the wings, and three feet eleven inches in length.”76

_Record Number: 47_
Location: Vicinity of the redwoods of Contra Costa, CA
Observer(s): Alexander S. Taylor
Date: 1855
Observation Type: Killed

76 Additional details of this story are provided in Lamson’s journal (Lamson 1852-1861).
Reference(s): California Academy of Natural Sciences 1863:71
Quotation(s): “Donations to the Cabinet. From Mr. A. C. Taylor, quills taken from a California Vulture (Cathartes californianus, Shaw) killed in the vicinity of the Red Woods of Contra Costa. The bird measured 13½ feet across the wings.”

Record Number: 48
Location: Sacramento Valley, CA
Observer(s): John Strong Newberry
Date: July 1855
Observation Type: Observation
Reference(s): Newberry 1857:73
Quotation(s): “A portion of every day’s experience in our march through the Sacramento valley was a pleasure in watching the graceful evolutions of this splendid bird [the Californian Vulture]. Its colors are pleasing; the head orange, body black, with wings brown and white and black, while its flight is easy and effortless, almost beyond that of any other bird. As I sometimes recall the characteristic scenery of California, those interminable stretches of waving grain, with, here and there, between the rounded hills, orchard-like clumps of oak, a scene so solitary and yet so home-like, over these oat-covered plains and slopes, golden yellow in the sunshine, always floats the shadow of the vulture.”

Record Number: 49
Location: Siskiyou Mountains, Klamath Basin, CA
Observer(s): John Strong Newberry
Date: August 1855
Observation Type: Observation
Reference(s): Newberry 1857:73
Quotation(s): “After we left the Sacramento valley, we saw very few [Californian Vultures] in the Klamath basin, and none within the limits of Oregon. It is sometimes found there, but much more rarely than in California.”
**Record Number: 50**
Location: Mendocino County, CA
Observer(s): Lyman Belding
Date: 1856–1878
Observation Type: Observation
Reference(s): Belding 1878 in litt.; Fisher 1920
Quotation(s): “I have never shot a Cal Condor have seen a few along Feather River [probably in the vicinity of Marysville—see record 51] in former years & a few in Mendocino Co - - I will try to get you one or two - have not much confidence in my ability to do so.”

**Record Number: 51**
Location: Near Marysville, Yuba County, CA
Observer(s): Lyman Belding
Date: 1856–1879
Observation Type: Observation
Reference(s): Belding 1879:437; Fisher 1920
Quotation(s): “The California Condor appears to be very rare in this region. I have seen it on no more than two or three occasions in Yuba County in winter, and do not think I have seen it at any other place. They probably visit the vicinity of Marysville only in winter, and are never common.”

**Record Number: 52**
Location: Near Sacramento (caught on Mrs. Harrold’s ranch), CA
Observer(s): Unknown
Date: September 1857
Observation Type: Live-captured
Reference(s): Daily Union (Sacramento) 24 September 1857

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77 Fisher (1920) provides information on when Belding was in California, which helps narrow down the timing of this observation.
Quotation(s): “DECIDEDLY VORACIOUS.— Mr. Sutton, of the Western Hotel, corner of K and 10th streets, was presented a few days since with a young vulture, which he has placed in the yard of his establishment. . . . Length of wings from tip to tip, about 10 feet 6 inches; length of head and beak, 7 inches; length of claws, from 7 to 9 inches. He is fed regularly and literally on raw heads and bloody bones, and can clean a skull or bone in the most approved style. . . . The vulture was caught on Mrs. Harrold’s ranch, near this city [Sacramento].”

Record Number: 53
Location: Lower Napa Valley, CA
Observer(s): Frank A. Leach
Date: 1857–1860
Observation Type: Observation
Reference(s): Leach 1929:23
Quotation(s): “In the later [18]50’s, in the central and northern parts of the state, it was not uncommon also to see the great Condors (Gymnogyps californianus) associated with flocks of a dozen or more buzzards, feeding on the remains of a dead horse or steer. I frequently saw them between the years of 1857 and 1860 on the bare hills of lower Napa Valley. They were so much larger than the buzzards that there was no trouble in distinguishing one from the other. Generally where there was a flock of the smaller birds gathered about a carcass, there would be two or three of the big Condors. It is my impression that after 1859 or 1860 the latter were seldom seen, in the Napa section at least; and I think the extinction of the Condor in northern California took place in the decade following 1860.”

Record Number: 54
Location: Pope Valley, near Saint Helena, Napa Valley, CA
Observer(s): J. B. Wright
Date: January 1858
Observation Type: Killed
Reference(s): Daily Alta California (San Francisco) 4 February 1858
Quotation(s): “VULTURE SHOT.—Last week, while Mr. J. B. Wright, of Pope Valley, near St. Helena, Napa Valley, was out hunting, he shot a large vulture, that was flying off with a hare it had killed, weighing nine pounds. The bird measured fourteen feet from tip to tip of wings. We have one of the tail feathers in our office, that measures twenty-six inches in length.”

**Record Number: 55**

Location: Mouth of Fraser River, BC  
Observer(s): John Keast Lord  
Date: 1858–1866  
Observation Type: Observation  
Reference(s): Lord 1866:291  

**Record Number: 56**

Location: Russian River area of the Coast Range, CA  
Observer(s): L. L. Davis  
Date: 1861  
Observation Type: Killed  
Reference(s): *Daily Union* (Sacramento) 18 June 1861  
Quotation(s): “A LARGE BIRD.—The Grass Valley National has the following account of a California vulture: We write this article with a pen plucked from the pinions of a vulture killed on the coast range, which weighed thirty pounds, and measured from tip to tip of its wings, fourteen feet. The longest quill measured thirty-four inches in length. L. L. Davis who presented us with the quill informs us that the vulture is quite common on the Russian river portion of the Coast Range. They are very large, and particularly fond of pork. They will descend with a sweep upon a forty-pounder, kill him at the first blow, seize him in their talons and bear him away with scarcely any perceptible hindrance to their flight. Davis assures us that they would carry off children if any were to be found.”

**Record Number: 57**
Location: Plumas County, CA
Observer(s): S. Stevens
Date: 1865
Observation Type: Killed
Reference(s): Daily Union (Sacramento) 25 November 1865
Quotation(s): “A HUGE BIRD.—We saw recently, says the Nevada Transcript, at the shop of Z. Davis, the wing of a bird recently shot by S. Stevens in Plumas county. The feathered giant is said to be of the Condor family, and measured eleven feet from tip to tip of the wings.”

Record Number: 58
Location: Near Marin County paper mills, CA
Observer(s): Unknown
Date: 17 August 1868
Observation Type: Killed
Reference(s): Bulletin (San Francisco) 19 August 1868
Quotation(s): “PROUD BIRD OF THE MOUNTAIN.—A condor was shot on Monday near the Marin county Paper Mills, which measured nine feet from tip to tip of wings. It was brought to the city yesterday, and will be taken to a taxidermist to be stuffed and preserved as a curiosity.”

Record Number: 59
Location: Winnemucca, NV
Observer(s): Unknown
Date: August 1871
Observation Type: Observation
Reference(s): Daily Union (Sacramento) 26 August 1871
Quotation(s): “A MONSTER.—Last Tuesday evening, about 7 o’clock, says the Winnemucca ‘Register’ of August 19th, the people in the lower town were startled by the sudden appearance of a huge monster we are at a loss to know whether to call fowl or beast, notwithstanding it had wings and could fly. It was certainly the biggest creature ever seen in this country with feathers. If a bird, it belongs to a giant species unknown to American ornithology. Our attention was
attracted by hearing some one sing out ‘holy mother, see that cow with wings.’ We stepped to
the door just in time to see the monster alight with something of a crash on the roof of Mrs.
Collier’s dwelling-house, where it remained for several minutes taking a quiet survey of the land
and the astonished multitude who stood gazing at that unexpected visitor. It could not have
weighed less than 75 or 100 pounds, with a pair of ponderous wings, which, when stretched out
to the breeze, must have been fully 12 feet from tip to tip. Its color was that of a raven, with the
exception that the tips of its wings and tail were white. An ‘old salt’ who happened to get sight
of the bird thinks he must be a renegade member of the condor family. He says he has
frequently met with just such ‘critters’ on the coast of South America.”

Record Number: 60
Location: Mendocino County, CA
Observer(s): Unknown
Date: Winter 1872
Observation Type: Killed
Reference(s): Tribune (Chicago) 24 February 1872
Quotation(s): “A vulture eagle, measuring upward of nine feet from tip to tip, has been killed in
Mendocino County, Cal.”

Record Number: 61
Location: Salmon Creek, Marin County, CA
Observer(s): Julius Poirsons
Date: February 1873
Observation Type: Killed
Reference(s): Daily Evening Bulletin (San Francisco) 19 February 1873
Quotation(s): “A California condor was killed in Marin county the other day which measured
nine feet from tip to tip and weighed seventeen pounds.”

78 Several other accounts of this shooting were given in several other newspaper articles and publications
around the same time: Daily Union (Sacramento) 19 February 1873; Daily Evening Bulletin (San Francisco)
Record Number: 62
Location: Near the peak of Mount Shasta, CA
Observer(s): Benjamin P. Avery
Date: September 1873
Observation Type: Observation
Reference(s): Avery 1874:476
Quotation(s): “A few snowbirds were twittering a thousand or two thousand feet below, and nearly up to the very crest of the Main Peak [of Mount Shasta] we saw a solitary California vulture wheeling slowly around.”

Record Number: 63
Location: Near the hot springs above Boise City, ID
Observer(s): General T. E. Wilcox
Date: Fall 1879
Observation Type: Observation
Reference(s): Lyon 1918:25
Quotation(s): “In the fall of 1879 I came upon two [California Vultures] which were feeding on the carcass of a sheep. They hissed at me and ran along the ground for some distance before they were able to rise in flight. They were much larger than turkey buzzards, with which I was quite familiar, and I was very close to them so that I could not be mistaken in their identity. The cattle-men said that the California vulture or buzzard was not uncommon there before they began to poison carcasses to kill wolves. . . . Boise River mountains rise to over 7000 feet just back of where the vultures were feeding. The exact locality was near the Hot Springs above Boise City. Poison and population have now destroyed that far northern habitat.”

Record Number: 64
4 March 1873; Proceedings of the California Academy of Sciences 5:43; Bulletin (San Francisco) 22 March 1873.
Location: Foothills southwest of Mount Lassen, CA
Observer(s): Unknown
Date: 1879–1884
Observation Type: Observation
Reference(s): C. Townsend 1887:201
Quotation(s): “In 1884 a hunter at Red Bluff told me that he had killed a vulture of immense size in the southeastern part of Tehama County two or three years previous, and that he had seen others in the foothills southwest of Mount Lassen within the last four or five years. As this is all the information I could obtain with regard to this species, it has probably almost disappeared from Northern California, where it was once certainly common.”

Record Number: 65
Location: South Eel River, Humboldt County, CA
Observer(s): Mr. Adams
Date: Spring 1880
Observation Type: Killed
Reference(s): Bulletin (San Francisco) 5 April 1880
Quotation(s): “On South Eel river, Humboldt county, Mr. Adams recently poisoned a bird of the vulture species which measured nine feet across the wings, four feet from beak to tail and eight inches from crown to tip of beak.”

Record Number: 66
Location: Reeds Creek Canyon, Tehama County, CA
Observer(s): John Bogard
Date: May 1880
Observation Type: Killed
Reference(s): Daily Evening Bulletin (San Francisco) 7 May 1880
Quotation(s): “A large California vulture was killed a few days ago in Reed’s creek canyon, Tehama county, by John Bogard of Tehama. It measured 8 feet from tip to tip.”
Record Number: 67
Location: Burrard Inlet, BC
Observer(s): John Fannin
Date: September 1880
Observation Type: Observation
Reference(s): Fannin 1891:22
Quotation(s): “In September, 1880, I saw two of these birds [California Vultures] at Burrard Inlet. It is more probable they are accidental visitants here.”

Record Number: 68
Location: Mountains south of Mount Lassen, CA
Observer(s): Unknown
Date: 1881–1882
Observation Type: Killed
Reference(s): C. Townsend 1887:201
Quotation(s): “In 1884 a hunter at Red Bluff told me that he had killed a vulture of immense size in the southeastern part of Tehama County two or three years previous, and that he had seen others in the foothills southwest of Mount Lassen within the last four or five years. As this is all the information I could obtain with regard to this species, it has probably almost disappeared from Northern California, where it was once certainly common.”

Record Number: 69
Location: Vicinity of San Rafael, CA
Observer(s): Unknown
Date: 1882 or before
Observation Type: Live-captured
Reference(s): Gassaway 1882:89

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This is a compilation of columns originally published in the San Francisco Evening Post, written circa 1880–1882.
Quotation(s): “Attached to one of the many picnic ‘groves’ is a local celebrity of unique accomplishments. He is called the ‘San Rafael Octopus,’ and is so designated on account of the facility with which he hugs eight girls at a time, and renders himself generally useful to visiting organizations. A young man gifted like that ought to make a proud record for himself at an Oakland church sociable. Why the picnic ground of the period should not be considered complete without an attenuated, disreputable and anything but inodorous bear chained to a post in its midst, as well as a melancholy eagle moping in a chicken coop, it would be hard to tell. In addition to these forlorn captives, we saw at one place a huge vulture, or California condor, tied to a stake. The proprietor kindly offered to illustrate this bird’s proverbial voracity by feeding it with fish. After eagerly devouring its weight in tomcods three times over, it paused to gasp for breath with the tail of the last fish sticking out of its stuffed and swollen neck.”

Record Number: 70
Location: Chico, Butte County, CA
Observer(s): William Proud
Date: Prior to 1890, probably 1880s
Observation Type: Observation
Reference(s): Belding 1890:24
Quotation(s): Belding quotes Mr. William Proud as noting that condors are “sometimes seen” near Chico, California.

Record Number: 71
Location: Lulu Island (Fraser River delta), BC
Observer(s): Mr. W. London
Date: 1888–1889
Observation Type: Observation
Reference(s): Rhoads 1893:39

80 All of William Proud’s observations of other birds reported in Belding (1890) were from 1884–1885.
Quotation(s): “Seen on Lulu Island as late as ‘three or four years ago’ by Mr. W. London81. ‘None seen since, used to be common.’”

Record Number: 72
Location: Kneeland Prairie, Humboldt County, CA
Observer(s): Unknown
Date: 1889 or 1890
Observation Type: Killed; specimen in the Clarke Museum in Eureka, CA
Reference(s): F. Smith 1916:205
Quotation(s): “There is no doubt but that the Condor (Gymnogyps californianus) once occurred in numbers in Humboldt County, California. There are now two mounted specimens in Eureka. One, in the collection of the Public Library, was mounted by Mr. Charles Fiebig, and was secured from a dead spruce tree on the Devoy place, on Kneeland prairie, eighteen miles from Eureka, altitude 2200 feet, in the fall of 1889 or 1890.”

Record Number: 73
Location: Yager Creek, Humboldt County, CA
Observer(s): F. H. Ottmer
Date: Fall 1892
Observation Type: Killed; specimen in Eureka High School’s Hall of Ornithology, Eureka, CA
Reference(s): F. Smith 1916:205
Quotation(s): “The [California Condor specimen] is in the collection of Dr. Ottemer in Eureka and was mounted by William Rotermund. This specimen was captured near the old Olmstead place on Yager Creek, altitude 1800 feet, about sixty miles east of Eureka, in the fall of 1892. Old settlers claim that the Condor was plentiful in early days in the Humboldt region. In my opinion it is now [in 1916] extinct here.”

81 William London was one of the first white settlers on Lulu Island, arriving in 1881. He was a prominent businessman and served as a city councilor for the City of Richmond (Lulu Island) from 1883-1887 (Kidd 1927).
Record Number: 74
Location: A few miles east of Coulee City, WA
Observer(s): C. Hart Merriam
Date: September 1897
Observation Type: Observation
Reference(s): Jewett et al. 1953:160
Quotation(s): “The last record of the species [California Condor] for the state [Washington] appears to be that of Dr. C. Hart Merriam (letter of January 4, 1921). In the early morning of September 30, 1897, Dr. Merriam saw a condor on the ground in open country a few miles east of Coulee City.”

Record Number: 75
Location: Southern coast, OR
Observer(s): Henry Peck
Date: Probably late 1800s
Observation Type: Killed
Reference(s): W. Finley 1908b:10
Quotation(s): “Mr. [Henry] Peck also gives the record of a condor that was killed on the coast of southern Oregon a number of years ago.”

Record Number: 76
Location: Curry County, OR
Observer(s): Unknown
Date: Prior to 1900
Observation Type: Observation
Reference(s): Koford (1941) notes, 11 April (at the Museum of Vertebrate Zoology, Berkeley, CA)
Quotation(s): “One rancher had told him [Stanley Jewett] that after they started poisoning for varmints the vultures disappeared but the condors did not. Jewett asked him what he meant by ‘vulture’ and the man gave an excellent condor description.”  

Record Number: 77
Location: Mountains north of San Francisco, Marin County, CA
Observer(s): Unknown
Date: 1900–1905
Observation Type: Killed
Reference(s): Chicago Field Museum specimen 39613
Quotation(s): None

Record Number: 78
Location: Near Drain, OR
Observer(s): George D. Peck and Henry Peck
Date: 1 June 1903
Observation Type: Observation
Reference(s): Peck 1904:55; W. Finley 1908b:10; Gabrielson and Jewett 1970:181
Quotation(s): Peck 1904, 55: “June 1, 1903, I saw two Cal. Vultures. They were at a great height and I could not have identified them if I had not often seen them in Los Angeles County, Cal. I saw several of the great Vultures during the month of June. The birds that I saw were about thirty miles from the coast.”

W. Finley 1908b, 10: “Mr. Henry Peck informs me that on or about July 4, 1903, he and his father saw two California condors at Drain, Douglass County, Oregon. They were quite high in the air and were sailing about over the mountains. The elder Mr. Peck saw them several times after that. He states that the birds were instantly recognized by both of them.”

Gabrielson and Jewett 1970, 181: “Jewett has talked to several well-informed woodsmen who described accurately to him condors seen in southern Oregon at about the time of the Peck

82 The rancher apparently got Turkey Vultures and condors reversed at first, which Jewett clarified by asking him what he meant by “vulture.”
observation, and it seems highly probable that two or more of these big birds strayed into southern Oregon, perhaps to remain for some time.”

**Record Number: 79**
Location: Near Drain, OR
Observer(s): Henry Peck
Date: 9 March 1904
Observation Type: Observation
Reference(s): W. Finley 1908b:10; Gabrielson and Jewett 1970:181
Quotation(s): W. Finley 1908b, 10: “In March 1904, Mr. Henry Peck writes, ‘I saw four condors which were very close to me, almost within gun shot. I recognized them first by their size, and second by the white feathers under their wings. The birds were all flying very low, as there was a high wind blowing.’”
Gabrielson and Jewett 1970, 181: “[Stanley] Jewett has talked to several well-informed woodsmen who described accurately to him condors seen in southern Oregon at about the time of the Peck observation, and it seems highly probable that two or more of these big birds strayed into southern Oregon, perhaps to remain for some time.”

**Record Number: 80**
Location: Kibesillah (near Fort Bragg, Mendocino County), CA
Observer(s): Miss Cecile Clarke
Date: Fall 1912
Observation Type: Observation
Reference(s): Clarke 1971, in litt.
Quotation(s): In a March 1971 letter to Sanford Wilbur, Miss C. Clarke wrote: “In the fall of 1912, I saw one [California Condor] flying south in Kibesillah. I did not know the bird, but I was up on eagles, hawks, turkey vultures, etc. [and so] I decided to find out. I asked everyone I knew and finally a very old man told me that he had seen it. He said it was the same old condor that goes north in the spring and south in the fall.”
Record Number: 81
Location: Siskiyou County, CA
Observer(s): Henry Frazier
Date: Spring 1925
Observation Type: Observation
Quotation(s): “In the spring of 1925, on the divide west of Copco Dam in Siskiyou County, Frazier saw six birds that he thought were adult California condors. There was snow on the ground, and the six birds were feeding on a dead cow. Mr. Frazier gave a good description of condors.”
### APPENDIX 2. CALIFORNIA CONDOR SPECIMENS SAMPLED FOR MOLECULAR ANALYSES

Table A2.1. California Condor specimens collected from museums and sequenced (526 bp) for analysis of mtDNA.

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*a AMNH (American Museum of Natural History); ANSP (Academy of Natural Sciences of Philadelphia); BMNH (British Museum of Natural History); CAS (California Academy of Sciences); DMNS (Denver Museum of Nature & Science); EHS (Eureka High School, California); FMNH (Field Museum of Natural History); LACM (Natural History Museum of Los Angeles County); MNd’HN (Museum National d’Histoire Naturelle, Paris); RMNH (National Museum of Natural History Naturalis, The Netherlands); SBMNH (Santa Barbara Museum of Natural History); SDNHM (San Diego Natural History Museum); UMMZ (University of Michigan Museum of Zoology); USNM (U.S. National Museum of Natural History, Smithsonian Institution).
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<sup>a</sup> ANSP (Academy of Natural Sciences of Philadelphia); BMNH (British Museum of Natural History); CAS (California Academy of Sciences); CHM (Clarke Historical Museum, Eureka, California); FMNH (Field Museum of Natural History); LACM (Natural History Museum of Los Angeles County); MNd‘HN (Museum National d’Histoire Naturelle, Paris); SBNHM (Santa Barbara Natural History Museum); SDNHM (San Diego Natural History Museum); USNM (U.S. National Museum of Natural History, Smithsonian Institution); VT (Virginia Polytechnic Institute and State University); WFVZ (Western Foundation of Vertebrate Zoology).

<sup>b</sup> These specimens were likely those collected by David Douglas near Fort Vancouver, Washington from 1826-1827 however, their provenance is not definitive (Wilbur 2012).

<sup>c</sup> This specimen was genotyped as belonging to haplogroup H1.
APPENDIX 3. DETAILED DESCRIPTION OF CALIFORNIA CONDOR OCCURRENCE DATA

California Condor occurrence data were obtained from a variety of reliable sources. Datasets are described below and the number of occurrence points entered into Ecological Niche Models (ENMs) from each dataset is given in Table A3.1.

Nest Dataset (1960-2011)

Chris Cogan (University of California Channel Islands), with the assistance of Jan Hamber (Santa Barbara Natural History Museum), compiled information in the Condor Recovery Office files to produce a spatial layer that contained many of the known historical nests (prior to reintroduction efforts in the 1990s) from southern California. They used, among other materials, maps that had been produced by Noel Snyder (U.S. Fish and Wildlife Service, retired) and his team in the 1980s, as well as earlier maps produced by Carl Koford (University of California, Berkeley [deceased]), Fred Sibley (U.S. Fish and Wildlife Service, retired), Dean Carrier (U.S. Forest Service, retired), and Sanford Wilbur (U.S. Fish and Wildlife Service, retired). We then refined this dataset as follows:

1. removed all entries which were not condor nests (e.g., those that included a description as "not clearly a condor nest" or "not a condor nest" or "turkey vulture nest only");
2. added recent nests in Monterey and San Benito counties from data provided by Joe Burnett at the Ventana Wildlife Society and Daniel George at Pinnacles National Monument; and,
3. added nest data provided by the California Condor Recovery Office for nests observed since 1992 (i.e., the start of reintroduction efforts).

Only those nests that were in use from 1960-2011 were included in the final dataset used to build ENMs.

McBee Records (1960-1984)

Beginning in the 1960s and continuing through 1984, F. Sibley and S. Wilbur compiled a set of records on condor sightings from individuals familiar with condors (Cogan 1993). Each observation was given a reliability evaluation of positive, neutral, or negative by condor
biologists based on the detailed information in the description and the observer’s familiarity with condors (see Cogan 1993 for additional details). All of the records that were given a “positive” evaluation by F. Sibley or S. Wilbur (n = 7,341) were transferred to a condor GIS and are referred to as “McBee Records” (after the name of the type of index cards they were recorded on – McBee Cards). The McBee records included information on activity in a 5 digit code (ACTIVITY) and information on longitudinal and latitudinal accuracy (ACC_X and ACC_Y). We selected records with ACC_X and ACC_Y ≤ 0.1 (accurate within 1 km) for overnight roosts, and (non-proffered) feeding based on the following activity codes (see Cogan 1993 for full description of the activity codes): Roosting = 25000-25999 and Feeding = 32000-32999.

**Overnight Roosts (1950-1980)**

Hardcopy maps with historical roost locations were located in the Condor Recovery Program office in Ventura, California that were part of a 1973 “Roost Report” sent by S. Wilbur to the California Condor Technical Committee on October 19, 1973. J. D’Elia confirmed with S. Wilbur that these maps did represent historical roosts and converted them to GIS shapefiles though heads-up digitizing in Google Earth. J. D’Elia also sent the maps to individuals involved in condor field work from the 1960s to the 1980s (J. Hamber, S. Wilbur, and J. Grantham (U.S. Fish and Wildlife Service, retired)) to ensure that the roost dataset was complete. These individuals identified several additional overnight roosts that were regularly used by condors and those locations that could be mapped with precision of ≤ 1 km were added to the GIS dataset.

**Field Surveys and Telemetry Studies (1982-1987)**

GIS data from the intensive field and telemetry studies in the 1980s (Cogan 1993) was obtained from C. Cogan. This dataset contains 10,294 condor observations and includes activity codes and accuracy codes similar to the McBee dataset (although the accuracy codes had different meaning, with accuracy ≤ 1 meaning accurate within 1 km). We selected records with ACCX and ACCY ≤ 1 for overnight roosts, and (non-proffered) feeding based on the following activity codes (see Cogan 1993 for full description of the ACTIVITY codes): Roosting = 25000-25999 and Feeding = 32000-32999.
Monitoring Data from Captive Release Programs (1992-2011)

Since the inception of the California Condor release program, beginning in 1992, California Condors were fitted with radio telemetry transmitters. By 2005, reliable satellite-based telemetry that integrated global positioning systems (GPS) was deployed to track some condors. These tracking devices allow biologists to monitor condor movements, and when combined with field observations, provide information on location and behavior (Cogan et al. 2012).

Observations from field monitoring data associated with captive release programs was obtained from Pinnacles National Monument, Ventana Wildlife Society, and the U.S. Fish and Wildlife Service. These data are based on field observations at each of the three current release sites and were provided as separate shapefiles for overnight roosts (not including roosts near release pens) and non-proffered feeding events.

Literature Cited


Table A3.1. California Condor occurrence datasets and number of data points by activity-type.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Activity-type</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Nesting(^a)</td>
<td>Roosting</td>
<td>Feeding</td>
</tr>
<tr>
<td>Nest dataset (1960-2011)</td>
<td>99</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>McBee records (1960-1984)</td>
<td>-</td>
<td>48</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>Overnight roosts (1950-1980)</td>
<td>-</td>
<td>45</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Telemetry Studies (1982-1987)</td>
<td>-</td>
<td>43</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>Captive Releases (1992-2011)</td>
<td>-</td>
<td>6</td>
<td>210</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Nests were recorded in several of these datasets, but were already compiled into a single nest dataset. Of the 99 nest occurrences, 9 were in coast redwood (*Sequoia sempervirens*) or giant sequoia (*Sequoiadendron giganteum*) trees.
APPENDIX 4. DETAILED DESCRIPTION OF ENVIRONMENTAL PREDICTOR VARIABLES FOR CALIFORNIA CONDOR ECOLOGICAL NICHE MODELS

Soaring Conditions and Climate

*Thermal Height and Thermal Updraft Velocity*

Condors are a large soaring bird, dependent upon rising air to move around the landscape and find food (Koford 1953). Atmospheric conditions are rarely accounted for in habitat selection or niche models, but there have been recent advances in integrating atmospheric data with raptor soaring patterns (Mandel et al. 2008, Bohrer et al. 2012). Monthly thermal height (i.e., the upper limit of thermal activity) and thermal updraft velocities ($W^*$) were derived from the National Oceanic and Atmospheric Administration’s (NOAA’s) Rapid Update Cycle (RUC) Sounding Forecast (http://ruc.noaa.gov/) data from April 2007-April 2009. Thermal updraft velocities were calculated as $W^* = \left(\frac{g}{T_o}Q_sD\right)^{1/3}$, where $D$ is the boundary layer depth (or thermal depth), $Q_s$ is the surface heating, and $(g/T_o)$ is a known buoyancy constant obtained by dividing the earth’s gravitational acceleration ($g$) by the average temperature ($T_o$)). Monthly averages for thermal height and thermal updraft velocities were converted to annual averages for the analysis. The original data was available in 12 km$^2$ pixels, which we resampled to 1 km$^2$ pixels using the RESAMPLE tool and the BILINEAR technique. We then used the FOCAL STATISTICS tool to summarize MEAN values within 10 km of each cell. We used a 10 km circular radius and ignored NoData values in our FOCAL STATISTICS calculation.

*Wind Speed*

Horizontal wind speeds are a potentially negative factor for soaring birds over flat terrain because they can rip apart thermals, but potentially a positive factor for soaring birds in rugged terrain where they can provide slope lift. High resolution average annual wind resource potential at 50 m above the ground was downloaded for California and the Pacific Northwest from the National Renewable Energy Lab. Both datasets had a 2.5 km$^2$ resolution and were resampled with the RESAMPLE tool to 1 km$^2$ grids using the MAJORITY resampling technique. The California and Pacific Northwest grids were then combined into a single grid using the MOSAIC TO NEW RASTER tool. Wind resource potential (i.e., power class) is a categorical
variable and is an indicator of likely wind strength, with a higher wind power class representing higher wind resource levels (Table A4.1).

**Winter Severity**

Because of their long nesting periods (Koford 1953), we hypothesized that nesting birds might be constrained by winter severity. Average minimum temperature (a proxy for winter severity) was obtained from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) Climate Group (2004). PRISM data are spatially gridded average monthly and annual minimum temperatures for the climatological period 1971-2000. Data, which were originally 400 m² resolution, were resampled to a 1 km² grid using the RESAMPLE tool with the BILINEAR resampling technique.

**Terrain**

Condors use cliffs and mountainous terrain for nesting and roosting (Koford 1953, Snyder et al. 1986). In addition, mountainous terrain can also create rising air for soaring condors, as winds are deflected off cliffs and steep slopes (i.e., slope lift). We obtained a 100 m² resolution Digital Elevation Model (DEMs) from the National Atlas ([http://nationalatlas.gov/mld/elev100.html](http://nationalatlas.gov/mld/elev100.html)) to derive cliff and terrain ruggedness layers.

**Cliffs**

Cliffs were identified by calculating slope from the 100m² DEM using the SLOPE tool with the output set to DEGREES. We then resampled the slope layer to 1 km² pixels using the AGGREGATE tool, specifying a cell factor of 10 with an aggregation technique of MAX. This returned the maximum slope (from the 100 m resolution map) within 1 km² cells for the entire study area.

**Terrain Ruggedness**

To calculate terrain ruggedness, we first resampled the 100 m² DEM to 1 km² pixels using the AGGREGATE tool, specifying a cell factor of 10 and an aggregation technique of MEAN. We then calculated a Surface Area Raster using DEM Surface Tools (Jenness 2004) for ArcGIS 10.
Elevation units were in meters and output units were km$^2$. Flat terrain returned a value of 1, whereas more rugged terrain (i.e., high surface area) had higher values. We then used the FOCAL STATISTICS tool to summarize MEAN values within 10 km circular radius of each cell and ignored NoData values.

**Landscape Productivity**

*Maximum NDVI*

Direct measures of scavenger food availability are difficult to obtain because they are dependent upon numerous factors, including number of animals, differential mortality rates, competition from other scavengers, and rates of decomposition. Furthermore, current food availability in southern California may not be a good indicator of high quality habitat as ungulate densities, ranching practices, and livestock numbers have experienced drastic changes over the last half-century. To provide an indirect measure of terrestrial food availability we used an index of net primary productivity (maximum Normalized Difference Vegetation Index (NDVI) during the growing season). NDVI is a satellite-derived measure that can be used as an indicator of relative plant biomass or greenness and has been shown to be positively correlated with ungulate densities at landscape scales (Pettorelli et al. 2009, 2011).

We obtained Conterminous United States AVHRR Remote Sensing Phenology Metrics - Maximum Normalized Difference Vegetation Index (MaxNDVI) layers for the years 2006 through 2010 from the USGS/EROS website (http://phenology.cr.usgs.gov/). All areas classified as water (VALUE=255) were reclassified to “NoData.” In addition, the 2010 MAXN layer contained zero values, which are defined as areas “where MAXN could not be detected due to insufficient change in time-series NDVI or insufficient input data.” These areas were also reclassified to NoData. Mean cell values were calculated over the five year period using Cell Statistics in Spatial Analyst, ignoring all NoData cells. The resulting floating point grid was converted to an integer grid using standard rules for rounding. We then used the FOCAL STATISTICS tool to summarize MEAN values within 10 km of each cell. We used a 10 km circular radius and ignored NoData values in our FOCAL STATISTICS calculation.

To evaluate whether maxNDVI was correlated with ungulate densities in our study area we obtained mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) density estimates, by
game management unit, from State wildlife agencies for the same five year period for which we had maxNDVI data (2006-2010) [note: deer density estimates were not available for Washington State, so those game management units were excluded from the analysis]. Average maxNDVI values were then calculated within State game management units using ZONAL STATISTICS and we evaluated the correlation between average maxNDVI and average deer and elk densities. Maximum NDVI had a significant positive (logarithmic) relationship to deer densities ($r^2 = 0.50$, $p < 0.0001$) and elk densities ($r^2 = 0.12$, $p = 0.0003$) (Figures A4.1 and A4.2).

**Distance to Water**

Condors appear to be attracted to areas of water for bathing (Koford 1953). They may also use rivers and waterways for navigation, as they appear to follow rivers during long distance movements (Arizona Condor Review Team 2002). Therefore we included a distance to water (streams, rivers, lakes, and reservoirs) metric derived from the 1:2,000,000 scale Streams and Waterbodies of the United States data layer in the National Atlas of the United States ([http://www.nationalatlas.gov](http://www.nationalatlas.gov)). For waterbodies (polygon features), the following Feature attributes were selected: “Lake”, and “Reservoir.” For streams and rivers (linear features) the following Feature attributes were selected: “Shoreline”, “Stream”, “Left Bank” and “Right Bank.” Euclidean distances were calculated for each of these features with an output pixel size of 1 km$^2$. The grids were then merged using the MOSAIC TO NEW RASTER tool, with a Mosaic Operator of MINIMUM (the output cell value of overlapping areas is the minimum value (i.e., distance) of the overlapping cells).

**Vegetation Characteristics**

Observational data suggest that condors tend to forage in relatively open areas with limited canopy cover and low vegetation height (Snyder and Snyder 2000). Vegetation characteristics were derived from the 2006 National Land Cover Database (NLCD) ([http://www.mrlc.gov/nlcd2006.php](http://www.mrlc.gov/nlcd2006.php)) and LANDFIRE data ([http://landfire.cr.usgs.gov](http://landfire.cr.usgs.gov)). Specifically, we derived canopy cover and dominant land cover type from the NLCD and canopy height from LANDFIRE.
**Canopy Cover**
Percent canopy cover was obtained from the 2006 NLCD (http://www.mrlc.gov/nlcd2006.php) at a resolution of 30 m². We resampled this grid to 1 km² using BILINEAR resampling.

**Canopy Height**
Canopy height was derived from LANDFIRE data (http://landfire.cr.usgs.gov). The 30 m² grid was reclassified according to Table A4.2. The reclassified grid was then resampling using MAJORITY resampling to obtain a 1 km² grid.

**Landcover**
Landcover from the 2006 NLCD (http://www.mrlc.gov/nlcd2006.php) for the coterminous U.S. in 30 m² pixels was reclassified to aggregate classes that had similar vegetation structure (Table A4.3). The reclassified raster was then resampled to 1 km² pixels using MAJORITY resampling (i.e., the most common land cover type within the 1 km² pixel was assigned to the entire pixel).

**Human Disturbance**
Condors suffer from a variety of human-induced mortality factors, including lead poisoning, collisions with overhead powerlines, and ingestion of microtrash (Rideout et al. 2012). Although a spatial map of the intensity of each of these factors is not available at the temporal and spatial-scales of our analysis, surrogate measures of these stressors, via spatial layers of human population density and road density (a measure of human access), were available.

**Human Population Density**
We downloaded Tiger/Line files (shapefiles) containing the 2010 Census Population and Housing Unit Counts—Block Data for CA, OR and WA (separately) from http://www.census.gov/geo/maps-data/data/tiger-data.html. These files were combined into a single file using the MERGE tool. We calculated the area of all block polygons in km², and then calculated the population density (in people/km²) for each block. We converted the merged polygon layer to a raster using the POLYGON TO RASTER tool. We specified the “Value field” as the population density, the “Cell assignment type” as MAXIMUM_AREA, and the “Cellszie” as
100m. We resampled the raster to a resolution of 1 km² using the AGGREGATE tool, specifying the cell factor as 10 and aggregation technique as MEAN. We then used the FOCAL STATISTICS tool to summarize MEAN values within 10 km of each cell. We used a 10 km circular radius and ignored NoData values in our FOCAL STATISTICS calculation.

Road Density

We downloaded the “Road density (length in meters/sq. kilometer) for the contiguous U.S.” layer from Data Basin (http://databasin.org/datasets). This raster layer required minimal processing as it was already at a resolution of 1 km². We used the FOCAL STATISTICS tool to summarize MEAN values within 10 km of each cell. We used a 10 km circular radius and ignored NoData values in our FOCAL STATISTICS calculation.

Literature Cited


Figure A4.1. Relationship between maximum NDVI and deer density, by game management unit in California and Oregon ($r^2 = 0.50$, $p < 0.0001$).
Figure A4.2. Relationship between maximum NDVI and elk density in California, Oregon, and Washington ($r^2 = 0.12$, $p = 0.0003$).
Table A4.1. Wind power classes used to characterize the National Renewable Energy Lab’s average annual wind resource potential at 50 m above the ground for California Condor ecological niche models.

<table>
<thead>
<tr>
<th>Power Class</th>
<th>Category</th>
<th>Wind Power Density (Watt/m$^2$)</th>
<th>Wind Speed (m/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Poor</td>
<td>0-200</td>
<td>0-5.6</td>
</tr>
<tr>
<td>2</td>
<td>Marginal</td>
<td>200-300</td>
<td>5.6-6.4</td>
</tr>
<tr>
<td>3</td>
<td>Fair</td>
<td>300-400</td>
<td>6.4-7.0</td>
</tr>
<tr>
<td>4</td>
<td>Good</td>
<td>400-500</td>
<td>7.0-7.5</td>
</tr>
<tr>
<td>5</td>
<td>Excellent</td>
<td>500-600</td>
<td>7.5-8.0</td>
</tr>
<tr>
<td>6</td>
<td>Outstanding</td>
<td>600-800</td>
<td>8.0-8.8</td>
</tr>
<tr>
<td>7</td>
<td>Superb</td>
<td>&gt; 800</td>
<td>&gt; 8.8</td>
</tr>
</tbody>
</table>
Table A4.2. Reclassification table used to group LANDFIRE categories into vegetation heights for California Condor ecological niche models.

<table>
<thead>
<tr>
<th>Category Description</th>
<th>LANDFIRE Values</th>
<th>New Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare or very low vegetation (&lt; 0.5m)</td>
<td>31, 66, 67, 75, 76, 81, 100, 101, 104</td>
<td>1</td>
</tr>
<tr>
<td>Low vegetation (0.5-1m)</td>
<td>102, 105</td>
<td>2</td>
</tr>
<tr>
<td>Medium vegetation (1-5m)</td>
<td>106, 108, 103</td>
<td>3</td>
</tr>
<tr>
<td>Tall vegetation (&gt; 5m)</td>
<td>107, 109, 110, 111, 112</td>
<td>4</td>
</tr>
<tr>
<td>Other/non-habitat</td>
<td>11, 14-25, 32, 60-65, 80, 82-85, 95</td>
<td>0</td>
</tr>
</tbody>
</table>
Table A4.3. Reclassification table used to aggregate National Landcover Types for use in California Condor ecological niche models.

<table>
<thead>
<tr>
<th>Value</th>
<th>Landcover Type</th>
<th>New Value</th>
<th>Aggregated Land Cover Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>11</td>
<td>Water</td>
<td>11</td>
<td>Non-habitat</td>
</tr>
<tr>
<td>12</td>
<td>Perennial ice and snow</td>
<td>12</td>
<td>Perennial ice and snow</td>
</tr>
<tr>
<td>21</td>
<td>Low intensity residential</td>
<td>21</td>
<td>Developed</td>
</tr>
<tr>
<td>22</td>
<td>High intensity residential</td>
<td>21</td>
<td>Developed</td>
</tr>
<tr>
<td>23</td>
<td>Commercial/industrial</td>
<td>21</td>
<td>Developed</td>
</tr>
<tr>
<td>24</td>
<td>Developed high intensity</td>
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<td>Developed</td>
</tr>
<tr>
<td>31</td>
<td>Bare rock/sand/clay</td>
<td>31</td>
<td>Bare rock/sand/clay</td>
</tr>
<tr>
<td>41</td>
<td>Deciduous forest</td>
<td>41</td>
<td>Deciduous forest</td>
</tr>
<tr>
<td>42</td>
<td>Evergreen forest</td>
<td>42</td>
<td>Evergreen forest</td>
</tr>
<tr>
<td>43</td>
<td>Mixed forest</td>
<td>43</td>
<td>Mixed forest</td>
</tr>
<tr>
<td>52</td>
<td>Shrubland</td>
<td>52</td>
<td>Shrubland</td>
</tr>
<tr>
<td>71</td>
<td>Grassland/herbaceous</td>
<td>71</td>
<td>Grassland/herbaceous/pasture</td>
</tr>
<tr>
<td>81</td>
<td>Pasture/hay</td>
<td>71</td>
<td>Grassland/herbaceous/pasture</td>
</tr>
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<td>82</td>
<td>Row crops</td>
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<tr>
<td>90</td>
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</tr>
<tr>
<td>95</td>
<td>Emergent herbaceous wetlands</td>
<td>11</td>
<td>Non-habitat</td>
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