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Distribution of the North American Porcupine (*Erethizon dorsatum*) in Northern California

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***Abstract.*—The North American Porcupine (*Erethizon dorsatum*) is one of the most widely distributed mammals in North America, but recent reports have suggested declines in parts of its range in the West. In California, little is known about the historical or current status of the porcupine, and maps of its distribution conflict considerably. Nevertheless, the species is of interest to natural resource managers. For much of the 1900s, foresters and others primarily treated porcupines as pests because of the undesirable damage they inflict feeding on trees and gnawing on manmade items in search of salt. More recently, porcupines have been recognized for their role in promoting forest structure and diversity, and as potential prey for the Fisher (*Pekania pennanti*). We collected records of porcupine occurrence in the northern part of California since the beginning of the 20th Century, relying on government and private databases, reports from the public, and other sources. These records confirm that porcupines may occur in most major regions and habitat types across northern California, in contrast to many published range maps. The contemporary distribution of porcupines in the state most closely resembles the California Wildlife Habitat Relationships System (CWHR) range map, which is based on projections of suitable habitat. We are unable to offer deeper insight into trends of abundance and possible changes in distribution because these records are likely spatiotemporally correlated with observer effort. This work is a first step and we recommend that a broader statewide effort be conducted to better understand the distribution, abundance, and ecology of North American Porcupines in California.**

Key Words.—citizen science; generalist; herbivore; historical; mammals; observations; range map

Introduction

The North American Porcupine (*Erethizon dorsatum*; hereafter porcupine; Fig. 1) is a wide-ranging herbivore occurring throughout much of North America, from Alaska to northern Mexico and from California to Maine (Woods 1973; Roze 2009). Porcupines are often considered diet generalists, consuming a wide range of plant species and materials including leaves, bark, needles, forbs, grasses, and mast (Woods 1973; Roze 2009). However, recent work suggests that the species instead be classified as a facultative specialist due to its seasonal dependence on cambium and conifer needles (Coltrane 2012). This seasonal specialization distinguishes it from other herbivores (Rasmussen et al. 1975) and allows it to survive and persist where many other species cannot. The wide distribution of porcupines is often attributed to their impressive physiological tolerance for heat and cold as well as their broad diet (Roze 2009). Nonetheless, little is known about what limits porcupine distribution. In Wisconsin, severe winters and predation were found to act synergistically to reduce adult porcupine survival (Pokallus and Pauli 2015), but limiting factors in other parts of its range are not well understood.

Current data suggest that California appears to be the southwestern range limit of the porcupine. However, there is little agreement about its historical distribution in the state, with published range maps varying widely (Fig. 2). To our knowledge, there have been no concerted efforts to determine the distribution of porcupines across California, and very little research of any kind has been published on porcupines in this part of their range. In an effort to describe changes in their distribution, Yocom (1971) collected reports of porcupine occurrence in coastal northern California beginning in the early 1900s and concluded that their populations appeared to spike in the region during the 1950s and 1960s. He attributed these changes to timber harvesting, which promoted forest succession and the replacement of mature conifer forests by hardwood stands, increasing the availability of saplings and other forage used by porcupines. Based on these observations, Yocom (1971) suggested that porcupines were not indigenous to coastal northern California but rather had moved from inland areas after periods of extensive forest clearing. The California Department of Fish and Wildlife (CDFW) has since suggested that wooded areas throughout the state may be suitable habitat (Timossi et al. 1995; Johnson and Harris 2012), as porcupines have been reported from the eastern San Joaquin Valley (Laurendine et al. 1996) and Santa Barbara and Los Angeles counties (Santa Barbara Museum of Natural History. 1929. SBMNH Vertebrate Zoology, Available from http://www.gbif.org/occurrence/735662294. [Accessed 29 June 2016]; Natural History Museum of Los Angeles County. 1947. LACM Vertebrate Collection, Available from http://www.gbif.

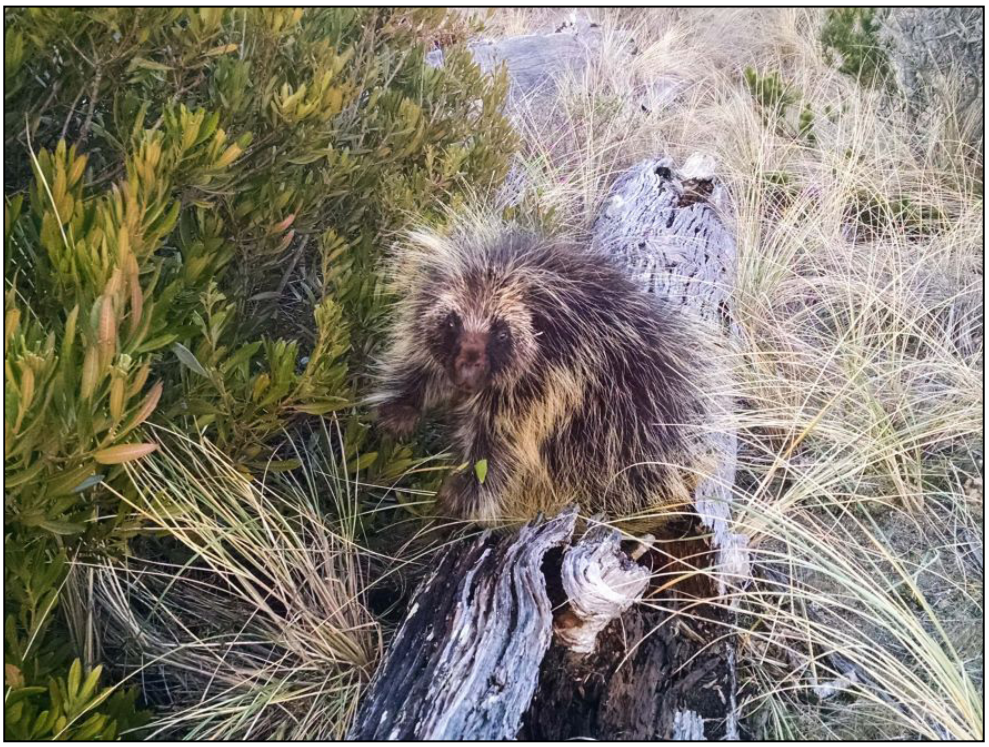

Figure 1. Adult male North American Porcupine (*Erethizon dorsatum*) in Tolowa Dunes State Park, Del Norte County, California (January 2016). (Photographed by Cara Appel).

org/occurrence/1065379749. [Accessed 29 June 2016]). The California Wildlife Habitat Relationships (CWHR) model, which predicts species occurrence based on habitat components, suggests a broad distribution for porcupines due to the widespread availability of suitable habitats (CDFW 2012; Fig. 2E), but there have been no statewide surveys to confirm this prediction.

Wildlife managers and researchers have become increasingly interested in the status of porcupines in light of their suspected decline in California (Central Sierra Environmental Resource Center [CSERC] 2011; Allen and Casady 2012) and across western North America (List et al. 1999; Mally 2008; Brown and Babb 2009). In California, the porcupine has been designated as a Species of Greatest Conservation Need (CDFW 2015). Although the feeding habits of porcupines promote ecosystem structure and diversity by contributing to a mosaic of tree stand ages and other characteristics (Snyder and Linhart 1997; Roze 2009), they are often perceived as destructive pests by foresters, timber companies, government agencies, and other landowners, leading to their eradication (Borrecco and Black 1990). Porcupines are important members of their communities, both for the effect their foraging has on maintaining diverse tree stands and as potential prey for carnivores including the Fisher (*Pekania pennanti*; Powell 1993) and the Mountain Lion (*Puma concolor*; Sweitzer et al. 1997). The dual role of the porcupine as a promoter of ecosystem stability and an agricultural pest presents challenges for managers and policy makers, who may be lobbied to both increase and decrease porcupine numbers. Information on the porcupine in California, including its current distribution and limiting factors, is therefore needed to better manage and conserve the species. As an important first step, we have described its distribution across the northern part of the state by collecting occurrence records from multiple government, research, citizen science, and other sources spanning the past century. We present them here as baseline data on the contemporary distribution of porcupines in northern California, offer interpretation of information from historical sources, and suggest directions for future research.

Methods

Study site.—We restricted our search to records of porcupine occurrence within California north of U.S. Interstate 80, which extends northeast from the San Francisco Bay Area toward Reno, Nevada (Fig. 2F). This boundary was chosen to avoid duplicating efforts by other researchers to document porcupine occurrence in the central and southern Sierra Nevada range (CSERC 2011; Rick Sweitzer, unpubl. data). Our search for records included an area represented by parts of 29 counties within the geomorphic provinces of the northern Sierra Nevada, southern Cascades, Modoc Plateau, Basin and Range, Sacramento Valley, Klamath Mountains, and the Coast Range.

We used historical and contemporary range maps and observation records of porcupines to develop a baseline description of their distribution in northern California.

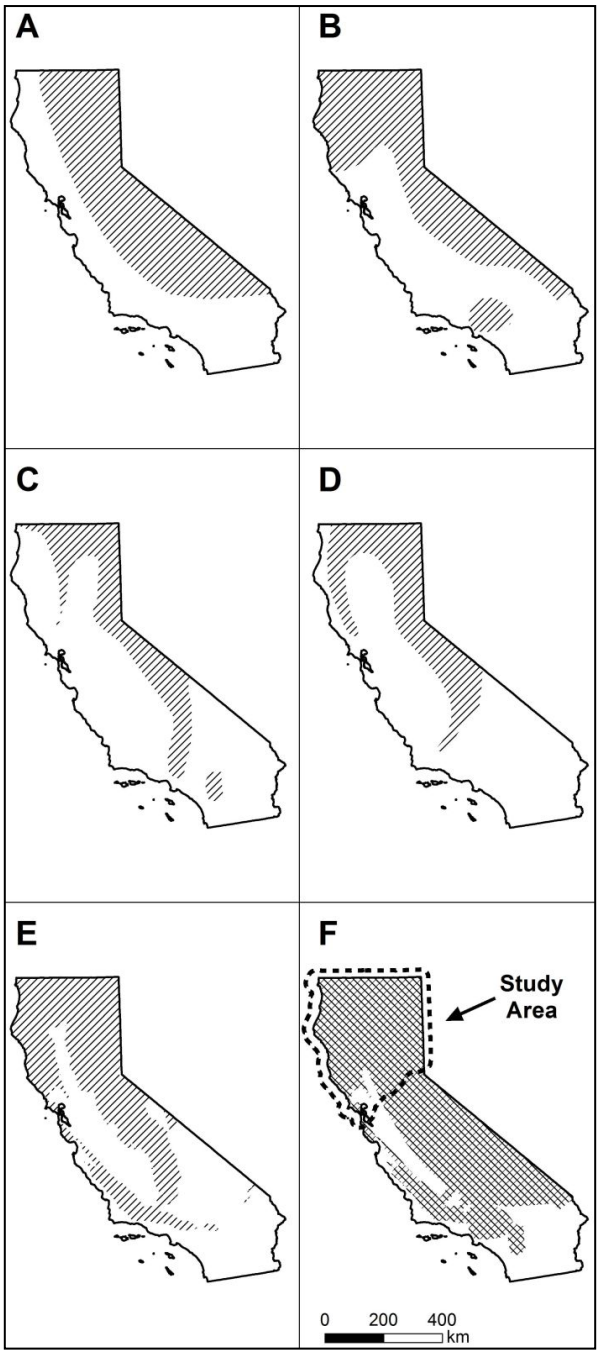

Figure 2. Digitized representations of five published range maps for the North American Porcupine in California: A) Caras 1967; B) Hall 1981; C) Roze and Ilse 2003; D) Jameson and Peeters 2004; and E) California Wildlife Habitat Relationships System (CWHR; CDFW 2012); along with F) the extent of occurrence, created as the union of maps A–E.

We used range maps from a variety of sources, including field guides and the scientific literature, and manually digitized their outlines within California. We selected a representative sample of five range maps for comparison here, prioritizing peer-reviewed sources and excluding those with very similar range depictions to highlight discrepancies in the published literature. To display the most general extent of proposed porcupine distribution in the state, we created an extent-of-occurrence boundary by merging the five maps together. All geospatial work was performed using ArcMap 10.3.1 (Esri, Redlands, California, USA).

Data sources.—We also compiled records of observations of porcupines (alive and dead) and their sign (tree damage, quills, scat, or tracks). Specifically, we used records collected through a website called Porcufinder (www.porcufinder.com), as well as previously published observational records (Yocom 1971), a database of porcupine observations in northern California maintained by CDFW employees (Richard Callas, unpubl. data), records of non-target species detected during carnivore monitoring surveys (Zielinski et al. 2005), and animal remains identified as part of a diet study of Fishers (Richard Golightly et al., unpubl. report). Additionally, we searched eight online databases for records of porcupine occurrences (Table 1). Finally, we conducted a very limited number of *ad hoc* surveys of veterinarians for instances of quilled domestic animals. These sources represent a wide range of collection methods, as, to our knowledge, there is no specific survey protocol for documenting porcupine occupancy. These records, then, are all essentially opportunistic.

One of us (WTB) established Porcufinder in 2013 to collect reports of porcupines in Mendocino, Humboldt, and Del Norte counties. Flyers requesting submission of reports were distributed in public places (e.g., trailheads) and a website address was published by local media outlets. On the online submission form, observers were asked to report the type of sighting (live porcupine, dead porcupine, tree damage, tracks, scat, or other), their confidence in the identification, time and location, and to submit photographs if available. We downloaded data from the Global Biodiversity Information Facility (GBIF) on 16 June 2016, but recent submissions to partner websites such as iNaturalist may not be included here due to indexing delays in the GBIF database (see Table 1). We restricted our download to georeferenced points, which was necessary for accurate map plotting but may have excluded some historical records. The CROS collects observations from biologists and members of the public who come across identifiable road-killed wildlife. The USDA Forest Service application NRIS is a spatial and tabular database designed for wildlife biologists and other resource specialists who use wildlife data for project analysis, assessments, planning, and monitoring. The application houses Forest Service terrestrial wildlife corporate data and uses an ArcMap interface with an Oracle database. The CNDDB and Species Explorer are databases of species lists and occurrences maintained by CDFW. The Cam-WON is a citizen science website that documents wildlife camera records. Finally, we attempted to locate records of porcupine control efforts in California by searching published literature and government archives.

Analyses.—In June 2016, we searched Flickr.com for Porcupine AND California, and iNaturalist.com for *Erethizon dorsatum* using the map feature. Several records were duplicates between Flickr and iNaturalist or between iNaturalist and GBIF, because research-grade observations with Creative Commons licenses are indexed in the GBIF database. We contacted owners of Flickr photographs to request use of their observations or suggest submission of details to Porcufinder. We also requested permission from iNaturalist users to include observations that were not indexed in GBIF due to copyright settings. Only observations for which permission was obtained are included here. We digitized all records included in the publication by Yocom (1971), which consist of personal observations and written and oral accounts from Del Norte, Humboldt, Trinity, and Mendocino counties between 1908 and 1966, after which they became too numerous to report. Because these records were not georeferenced, we placed points according to a digitized version of the printed map and the corresponding descriptions.

We recognize the value of using only independently verifiable observations to assess the status of rare species (McKelvey et al. 2008), but we excluded only a few records that were questionable, all from the Porcufinder source. These were primarily ambiguous descriptions of visual sightings or observations of sign that were submitted by observers who we could not confirm had the experience necessary to identify scat or signs of feeding. Records submitted to iNaturalist were only included if they were classified as research-grade, which requires a photograph and corroborated identification by at least one other user. We did not exclude potentially erroneous observations from the other data sources, largely because necessary details regarding the observations were rarely available to us. We accept this shortcoming because: (1) records of sign (e.g., scat or feeding) are infrequently submitted compared to observations of the animal itself, which is very recognizable; (2) the urgent need for an updated distribution of porcupines called for including all likely records; and (3) observations were spatially clustered such that if a few errors in identification occurred in each cluster, it would have little effect on the overall distribution map.

After removing duplicates (records submitted to multiple databases), we plotted the locations of all records of porcupine occurrence by decade and by source to map their spatiotemporal distribution. We then overlaid occurrences with corresponding vegetation types using a raster representation (Fire and Resource Assessment Program [FRAP] 2015) of the CWHR classification scheme (Mayer and Laudenslayer 1988) to describe basic habitat associations for northern California. We report only use of these habitat types without inferring selection because of probable bias due to the opportunistic nature of the records, and because of potential inconsistencies between historical and current vegetation due to fire, succession, and development. Further, habitats used

Table 1. Sources searched for records of porcupine occurrence in northern California, along with search terms, results, web addresses, and dates accessed. Search results include the total number of records returned prior to filtering by location or other criteria, as described in Methods.

Source Name	Affiliation	Search Term and Results	Web Address	Date Accessed
Global Biodiversity Information Facility (GBIF)	Global Biodiversity Information Facility	Genus Erethizon, 5,367 records	www.gbif.org	16 June 2016
California Roadkill Observation System (CROS)	University of California, Davis	Common porcupine, 24 records	www.wildlifecrossing.net/california	30 Oct. 2014
Natural Resources Information System (NRIS) Wildlife Module	USDA Forest Service	*Erethizon dorsatum*, 63 records	www.fs.fed.us/nrm/index.shtml	21 Oct. 2014
California Natural Diversity Database (CNDDB)	California Department of Fish and Wildlife, Biogeographic Data Branch	*Erethizon dorsatum*, 0 records	www.wildlife.ca.gov/Data/CNDDB	5 Dec. 2014
Species Explorer Data Portal	California Department of Fish and Wildlife	*Erethizon dorsatum*, 0 records	https://nrm.dfg.ca.gov/taxaquery	5 Dec. 2014
Wildlife Observer Network (CamWON)	University of California, Davis, Road Ecology Center	Porcupine, 0 records	http://wildlifeobserver.net	7 Nov. 2014
iNaturalist	California Academy of Sciences	*Erethizon dorsatum* in California, 21 records	www.inaturalist.org	16 June 2016
Flickr	Yahoo Inc.	Porcupine AND California, 1,497 records	www.flickr.com	16 June 2016

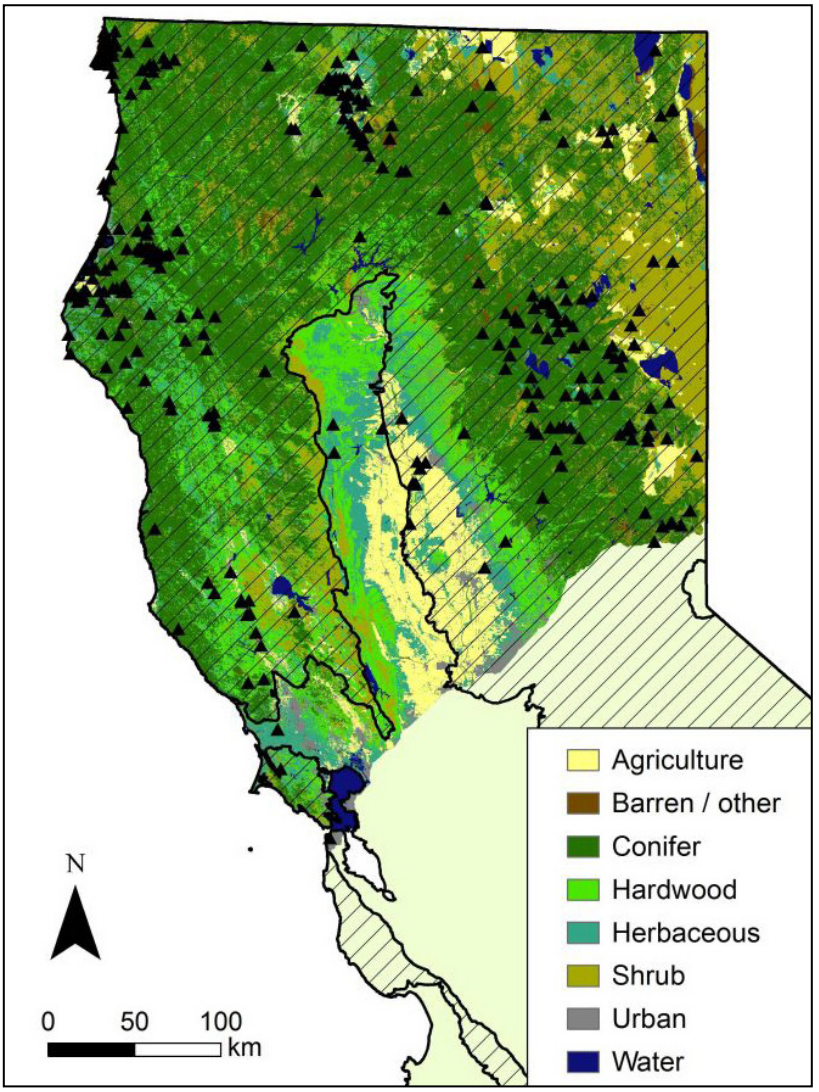

Figure 3. Porcupine occurrence records for northern California between 1908–2016 shown with California Wildlife Habitat Relationships (CWHR) vegetation life form categories and the CWHR range map (CDFW 2012), hatched.

by porcupines after periods of population decline or range contraction may not represent the full suite of habitats potentially occupied by porcupines under other circumstances. We have deposited the collated database of porcupine occurrence records online for access in Humboldt Digital Scholar (http://digitalcommons.humboldt.edu/data/1).

Results

We found 15 different published range maps for the porcupine and selected five for comparison (Fig. 2). All 15 were published between 1959 and 2012, but they were not identified explicitly as either historical or current to their time of publication. Most range maps also did not identify their conceptual bases, such as whether they represented realized or potential ranges and extent of occurrence or actual area of occupancy, which can hinder comparison (Gaston 2003). Nevertheless, we believe these five range maps are representative of the literature and illustrate the discrepancy over where porcupines are believed to occur or have occurred in California.

We also collected 363 unique records of porcupine occurrence from 19 counties in northern California between the years 1908 and 2016 (Fig. 3). We categorized records into eight types: live sightings; roadkill; museum specimens; tracks and sign (e.g., scat or tree damage); carcasses; killed (e.g., shot or trapped); detected by remote camera; and encounters with domestic dogs (Table 2). Some records from Yocom (1971) were not accompanied by descriptions and therefore we described these as unknown and included them as an additional category.

We obtained porcupine occurrence records from eight of the 11 sources we searched (Table 2). We deemed 80% (n = 70) of records submitted to Porcufinder that fell within our study area credible and included them here. We contacted seven veterinarians in Humboldt and

Del Norte counties to request information on instances of domestic animal encounters with porcupines. Of the three who responded, none could provide detailed information about such encounters, although they reported that there were no instances within their recent memory. One additional veterinarian submitted a Porcufinder report of quill removal from a dog in 2014. Generally, however, veterinarians were reticent or unable to provide records of quilled animals. This appears to be a poor source of information because patient records are often not computerized, hard-copy files are periodically destroyed, and clinics can be protective of the privacy of their patients.

We also used three track plate detections of porcupines obtained during a previous carnivore monitoring study (Zielinski et al. 2005). No porcupines were detected on cameras deployed for that study within our area of interest. Results from a diet survey of Fishers yielded no porcupine remains in any of the 388 Fisher scats examined from the Klamath and North Coast Bioregion, indicating very low or no consumption (Richard Golightly et al., unpubl. report). Sources searched that did not yield any porcupine records were CNDDB (which lists special status species only and therefore does not currently document porcupine observations), CDFW Species Explorer, and Cam-WON.

Porcupines were reported in 36 out of the 59 CWHR vegetation types present in northern California (Fig. 4) and all of the eight life form classes, which are broader categories based on Landsat imagery (Fig. 3). We found documented porcupine occurrences in all of the major geomorphic provinces, in contrast to several published range maps (Fig. 2). We also found early (pre-1940s) occurrences of porcupines in every major region of northern California except the Sacramento Valley and the Coast Range south of Humboldt County: in fact, very few occurrences were recorded in these areas until the 1980s (Fig. 5). During the past 20 years, porcupines have been observed in all major regions with the exception of the Modoc Plateau (Fig. 5).

Lastly, we found general accounts of porcupine control practices during the 20th Century on a national and regional scale, as discussed subsequently (Nelson 1925, 1926; Redington 1933; U.S. Fish and Wildlife Service [USFWS] 1948; Anthony et al. 1986; Borrecco and Black 1990). However, we were unable to obtain detailed records of the extent and locations of these efforts in California. These sources, if they exist, would add valuable information on the historical distribution and abundance of porcupines and may offer insight into subsequent population trends.

Discussion

We found documented occurrences of porcupines throughout northern California since the early 20th Century. These results suggest a distribution that differs from several published range maps and provide baseline data for further research on porcupines in the state. The distribution presented here is a product of actual occurrence records for porcupines, whereas many published range maps are based on projections of suitable habitat, expert opinion, or a combination of these methods and occurrence records. Based on the coarse-scale habitat associations and agreement with the occurrence records we collected, of the five range maps included for comparison, the CWHR range map appears to best explain porcupine distribution in northern California. We did not collect records from central and southern California, but published range maps are clearly inconsistent throughout the state. In our study area, most maps agree on porcupine distribution throughout the Sierra Nevada and the northeastern part of the state, but the Coast Range, Klamath Mountains, and Sacramento Valley regions seem to be common areas of uncertainty. Although the CWHR model was most coincident

Table 2. Porcupine occurrence records in northern California from 1908–2016, summarized by type and source. Sources include an internal database of porcupine records from California Department of Fish and Wildlife (CDFW), previously published records (Yocom), Porcufinder.com (PF), the Global Biodiversity Information Facility (GBIF), USDA Forest Service Natural Resource Inventory System (NRIS), UC Davis California Roadkill Observation System (CROS), and miscellaneous sources (Misc.), including track plate detections, iNaturalist.com, and Flickr.com. (See Methods for source descriptions.)

Type of Record	CDFW	Yocom	PF	GBIF	NRIS	CROS	Misc.	Total
Live Sighting	31	30	48	4	27	0	4	144
Roadkill	53	12	12	0	0	14	1	92
Museum Specimen	0	0	0	51	0	0	0	51
Track or Sign	7	0	1	3	6	0	3	20
Carcass	3	3	2	0	7	0	0	15
Killed	1	13	0	0	0	0	0	14
Unknown	0	12	0	0	0	0	0	12
Remote Camera	7	0	2	0	0	0	0	9
Dog Encounter	0	0	5	0	0	0	1	6
Total	102	70	70	58	40	14	9	363

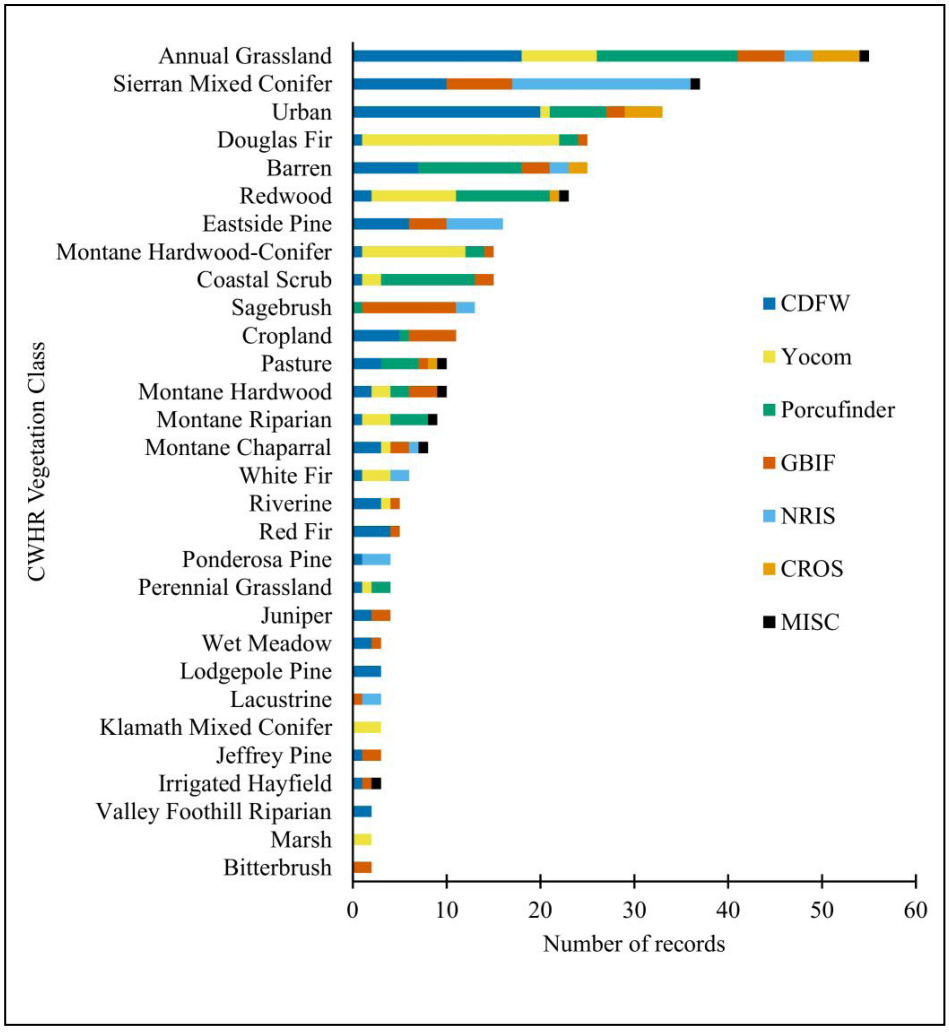

Figure 4. Porcupine occurrence records in northern California from 1908–2016 by vegetation type, according to California Wildlife Habitat Relationships (CWHR) classification. Sources include an internal database of porcupine records from California Department of Fish and Wildlife (CDFW), previously published records (Yocom), Porcufinder.com (PF), the Global Biodiversity Information Facility (GBIF), USDA Forest Service Natural Resource Inventory System (NRIS), UC Davis California Roadkill Observation System (CROS), and miscellaneous sources, including track plate detections, iNaturalist.com, and Flickr.com. (See Methods for source descriptions.) Vegetation classes with only one record (not shown): Blue Oak-Foothill Pine, Closed-Cone Pine Cypress, Deciduous Orchard, Low Sage, Mixed Chaparral, and Vineyard. Vegetation classes for which there were no records: Alpine-Dwarf Shrub, Alkali Desert Scrub, Aspen, Blue Oak Woodland, Undetermined Shrub, Undetermined Conifer, Coastal Oak Woodland, Chamise-Redshank Chaparral, Dryland Grain Crops, Desert Riparian, Desert Scrub, Evergreen Orchard, Estuarine, Eucalyptus, Fresh Emergent Wetland, Undetermined Hardwood, Irrigated Grain Crops, Irrigated Row and Field Crops, Rice, Subalpine Conifer, Saline Emergent Wetland, Valley Oak Woodland, Water.

with our data, it is largely based on porcupine habitat associations reported in the literature from studies outside of California. There is very little known about porcupine habitat use and ecology in California or coastal regions in general. In addition, the CWHR model may predict broad-scale distribution, but field studies and surveys of porcupines are needed to understand regional habitat associations at a finer scale.

Some spatiotemporal patterns are apparent in the occurrence points we collected, but they are likely due to observer effort and may not represent true changes in porcupine distribution across northern California. For example, the frequency of records in Humboldt and Del Norte counties since 2010 reflects our efforts to collect reports through Porcufinder, with the vast majority of these reports coming from a highly visible population near Crescent City, California. In contrast, numerous anecdotal reports suggest a decline in porcupine numbers on the North Coast since at least the 1990s. While this trend is supported only circumstantially, it is clear that porcupines are not as common as they were when Yocom (1971) published reporting that porcupines were seen "in Arcata, on the Humboldt State College campus, Eureka and even on the sandy beaches". Today porcupines have not been reported from any of these locations despite the high number of potential observers. Spatial bias in the location of records can arise from a number of sources. Some records represent opportunistic sightings

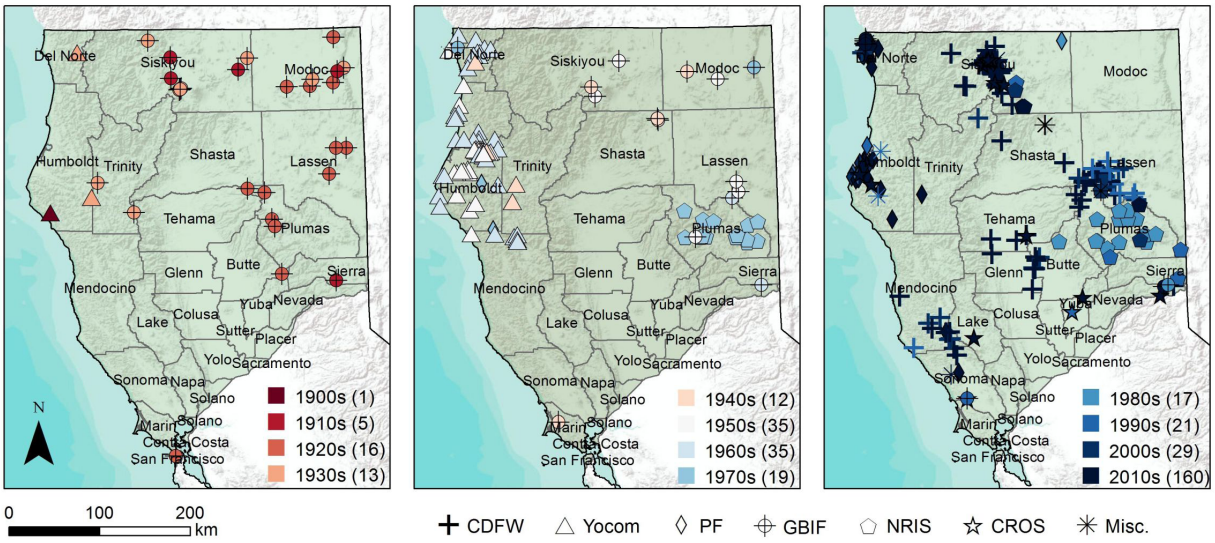

Figure 5. Porcupine occurrences in northern California between 1908–2016 by source and decade from the 1900s through 2010s, with sample sizes in parentheses. The high number of occurrences since 2010 is reflective of efforts to collect porcupine records and should not be taken to represent population trends. Sources include an internal database of porcupine records from California Department of Fish and Wildlife (CDFW), previously published records (Yocom), Porcufinder.com (PF), the Global Biodiversity Information Facility (GBIF), USDA Forest Service Natural Resource Inventory System (NRIS), UC Davis California Roadkill Observation System (CROS), and miscellaneous sources, including track plate detections, iNaturalist.com, and Flickr.com. (See Methods for source descriptions.)

from field workers, landowners, or others who make frequent, nonrandom visits to specific places. Similarly, observations are very likely biased toward linear travel features such as roads or popular hiking trails.

Overall, historical data are scarce and it is important to acknowledge that our records do not consider time periods prior to European settlement of California. Fossil records from Shasta County confirm the presence of porcupines in this area during the late Pleistocene (Feranec et al. 2007), and many native people consider the porcupine a culturally important species and use its quills for regalia or basketry. Several tribes, from the Maidu in the Sierra Nevada to the Hupa and Yurok near the coast, have a word for porcupine in their languages (Merriam 1979). Inclusion of fossil records and traditional knowledge would make for a more complete account of the occurrence of porcupines regionally, similar to recent historical range reconstructions for the North American Beaver (*Castor canadensis*) and the Gray Wolf (*Canis lupus*) in California (Lanman et al. 2013; Newland and Stoyka 2013).

Because records from Yocom (1971) are the only historical source we found for Humboldt and Del Norte counties, it is difficult to evaluate his claim that porcupines were not indigenous to the North Coast region. His records include one occurrence from 1908 in Humboldt County, one each in Humboldt and Del Norte counties from the 1930s, and two in Humboldt County and one in Del Norte County from the 1940s (Yocom 1971). These all occurred prior to the logging peak to which he attributed increased porcupine occurrence, so it is apparent that porcupines were present in this region historically, even if at lower densities than during the mid-20th Century. Yocom (1971) described an irruption of porcupines on the North Coast during the 1950s and 1960s, and similar increases in porcupine numbers were noted in Arizona (Taylor 1935; Brown and Babb 2009), western Oregon (Hooven 1971; Evans 1987), and western Washington (Dodge and Barnes 1975; Evans 1987) between the 1920s and 1970s. These trends were also attributed to land use changes (Dodge and Barnes 1975) as well as a reduction in predators of porcupines (Stone 1952; Brown and Babb 2009). Porcupine populations have since declined in Arizona (Brown and Babb 2009), but to our knowledge no recent surveys have been conducted in the other states. Importantly, Yocom (1971) did not address the potential for predator control efforts to affect porcupine populations, attributing their increase solely to timber harvest practices. Yet, during the time documented by Yocom, 1908–1971, the reduction in predator numbers due to fur trapping and government control practices could also have contributed to an increase in porcupine populations.

Further insight into historical porcupine occurrence in California may be found in the field notes of Joseph Grinnell. In the early 1900s, he noted that porcupines were common throughout the Lake Tahoe area (Grinnell 1926) and in Siskiyou County from Yreka eastward, although they were becoming more common to the west as well (Grinnell 1918). In later journals, Grinnell (1932) reported seeing porcupine feeding sign and scat, as well as hearing multiple oral reports of observations

from residents, near the Humboldt-Trinity county line in the vicinity of Hyampom and South Fork Mountain. In the Mad River area, he noted that porcupines were not rare at a local ranch, where dogs would sometimes get quilled (Grinnell 1932). Finally, nearer the coast in the Bald Hills of Humboldt County, he interviewed a longtime resident of the area who, in 1933, reported that porcupines had only recently come in (Grinnell 1933).

Grinnell (1923) offered no interpretation of his porcupine records but did attribute distributional shifts in other wildlife species to land use changes, in particular, common inland species that were seemingly moving west in response to forest clearing, or becoming common where they were once rare. Although it is certainly believable that the faunal changes observed by Grinnell and Yocom during their lifetimes were the proximate result of rapid forest clearing and development, it is important to consider the long-term history of these landscapes. Indigenous peoples had long maintained open spaces through burning and even cultivated willow stands in riparian areas, affecting available habitat for many species (Anderson 2013). Further, porcupine populations appear to fluctuate based on climatic conditions, drought regimes, and community structure (Sweitzer et al. 1997; Klvana et al. 2004; Pokallus and Pauli 2015). The dynamic nature of these processes illustrates the difficulty of trying to understand the historical range of a species.

Despite the absence of a credible map of the historical distribution of porcupines, various authors have speculated that its populations are declining across California (CSERC 2011; Allen and Casady 2012; Weiser 2012) and in other parts of the West (List et al. 1999; Mally 2008; Brown and Babb 2009). Our data are ambiguous in this regard due to their spatiotemporal inconsistency and opportunistic nature. No single reason for the putative decline has consistently been posited, but in the North Coast region, if a decline has occurred, it may be because forests have regenerated to the point that they are too mature to provide food resources, as predicted by Yocom (1971). Additionally, porcupine populations may have been abnormally high during the early- and mid-20th Century due to reduced numbers of Mountain Lions and Fishers, with the recent decline corresponding to recovering predator populations. Simultaneous efforts to control porcupines through poisoning and other methods have likely had enduring effects on their populations as well. Annual reports from the Bureau of Biological Survey and the U.S. Fish and Wildlife Service indicate that national efforts to control porcupines began in 1925, when porcupine damage was of considerable concern due to apparent population increases in some areas (Nelson 1925, 1926). Control efforts intensified over subsequent decades in the Northeast and many western states, including California (Redington 1933; USFWS 1948). These practices continued on National Forest lands in California into the 1980s (Hoffer 1967; Anthony et al. 1986), at least into the 1990s in Oregon (Borrecco and Black 1990), and perhaps later on private lands. Other hypothesized causes of recent porcupine decline include rodenticide poisoning from marijuana cultivation sites (e.g., Gabriel et al. 2012) and disease outbreaks. Finally, road mortalities contribute a substantial cause of death for porcupines across their range, perhaps disproportionately to other species due to their body size, diet, salt drive, and relatively slow gait (Roze 2009; Barthelmess and Brooks 2010). In any case, because porcupines are long-lived, produce only one offspring per year, and often occur at low densities (Roze 2009), their low fecundity may delay population recovery after any significant decline, in contrast to many other animals, particularly other rodents.

Additional work is necessary to understand the distribution, abundance, and ecology of porcupines across California. The records we collected are an important first step, but they are primarily opportunistic and are insufficient for estimating abundance or density. The lack of unbiased systematic survey data has hindered the ability of resource agencies to manage and conserve the species and its habitat, necessitating further research. Many possible field methods exist for addressing these questions, including trained detection dogs, remote camera traps, and feeding sign surveys. Informally, researchers have also used small blocks of wood soaked in a sodium solution to bait porcupines and identify their incisor scrapings on the wood (Roze 2009). This method has shown promise in some parts of the state (Richard Callas, pers. obs) but should be tested more intensively across California. Additionally, although we restricted our search to northern California, porcupines occur in other areas of the state and, in particular, are thought to have declined significantly in the central and southern Sierra Nevada (CSERC 2011). We encourage a similar review of existing records in central and southern California along with the establishment of a centralized clearinghouse for the collection of occurrence records. Ultimately, an unbiased view of the current distribution of porcupines in California will only be achieved by developing and implementing appropriate survey design and data collection protocols.

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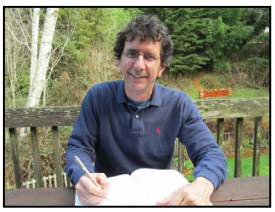

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