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ORIGINAL ARTICLE

Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA

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ABSTRACT

Aim Mammalian carnivores are considered particularly sensitive indicators of environmental change. Information on the distribution of carnivores from the early 1900s provides a unique opportunity to evaluate changes in their distributions over a 75-year period during which the influence of human uses of forest resources in California greatly increased. We present information on the distributions of forest carnivores in the context of two of the most significant changes in the Sierra Nevada during this period: the expansion of human settlement and the reduction in mature forests by timber harvest.

Methods We compare the historical and contemporary distributions of 10 taxa of mesocarnivores in the conifer forests of the Sierra Nevada and southern Cascade Range by contrasting the distribution of museum and fur harvest records from the early 1900s with the distribution of detections from baited track-plate and camera surveys conducted from 1996 to 2002. A total of 344 sample units (6 track plates and 1 camera each) were distributed systematically across *c.* 3,000,000 ha area over a 7-year period.

Results Two species, the wolverine (*Gulo gulo*) and the red fox (*Vulpes vulpes*), present in the historical record for our survey area, were not detected during the contemporary surveys. The distributions of 3 species (fisher [*Martes pennanti*], American marten [*M. americana*], and Virginia opossum [*Didelphis virginiana*]) were substantially changed since the early 1900s. The distributions of fishers and martens, mature-forest specialists, appeared to have decreased in the northern Sierra Nevada and southern Cascade region. A reputed gap in the current distribution of fishers was confirmed. We report for the first time evidence that the distribution of martens has become fragmented in the southern Cascades and northern Sierra Nevada. The opossum, an introduced marsupial, expanded its distribution in the Sierra Nevada significantly since it was introduced to the southcentral coast region of California in the 1930s. There did not appear to be any changes in the distributions of the species that were considered habitat specialists: gray fox (*Urocyon cinereoargenteus*), striped skunk (*Mephitis mephitis*), western spotted skunk (*Spilogale gracilis*), or black bear (*Ursus americanus*). Detections of raccoons (*Procyon lotor*) and badgers (*Taxidea taxus*) were too rare to evaluate. Contemporary surveys indicated that weasels (*M. frenata* and *M. erminea*) were distributed throughout the study area, but historical data were not available for comparison.

Main conclusions Two species, the wolverine and Sierra Nevada red fox, were not detected in contemporary surveys and may be extirpated or in extremely low densities in the regions sampled. The distributions of the mature forest specialists (marten and fisher) appear to have changed more than the distributions of the forest generalists. This is most likely due to a combination of loss of mature forest

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habitat, residential development and the latent effects of commercial trapping. Biological characteristics of individual species, in combination with the effect of human activities, appear to have combined to affect the current distributions of carnivores in the Sierra Nevada. Periodic resampling of the distributions of carnivores in California, via remote detection methods, is an efficient means for monitoring the status of their populations.

Keywords

American marten, California, conservation, distributions, fisher, forest carnivores, geographic range, mammalian carnivores.

INTRODUCTION

Mammalian carnivores are important members of ecological communities and potential indicators of ecosystem conditions (Weaver *et al.*, 1996; Lambeck, 1997). Carnivores contribute key functions to ecosystems, including energy transfer, scavenging, fruit dispersal, and the regulation of populations of prey species, and are selective agents on the evolution of prey (Buskirk, 1999; Minta *et al.*, 1999; Terborgh *et al.*, 2001; Buskirk & Zielinski, 2003). Carnivores can have important direct and indirect effects on vertebrate community structure (Crooks & Soulé, 1999; Crooks, 2002) and the absence of predators can cause major changes to communities and ecosystems (Terborgh *et al.*, 2001). Because of their important ecological roles, and their vulnerability to extinction (Newmark, 1995; Wennergren *et al.*, 1995; Woodruffe & Ginsberg, 1998), it is important to understand changes in populations of mammalian carnivores.

An important way to assess the status of wildlife populations is to compare contemporary and historical distributions of populations and habitats. If the points of comparison span a period over which humans have had significant influences on habitat or populations, then such a comparison can contribute to understanding the effects of anthropogenic change on populations (Laliberte & Ripple, 2004). Unfortunately, we usually have little information about the distribution, much less the abundance, of wildlife species prior to significant human impacts on their habitats. Often, a few opportunistically collected specimens make it into museum collections and their locations are then mapped. Even this cursory information, however, is usually unavailable for a period of more than a few decades prior to its need. Thus, we usually have little understanding of historical baselines of population distributions and suffer 'shifting baseline syndrome': the phenomenon whereby each new generation redefines what is natural in terms of personal experience and is unaware of earlier declines in populations or conditions (Pauly, 1995).

Fortunately there is a comprehensive summary of the distribution of 'fur-bearing mammals' in California representing an *c.* 20-year period from *c.* 1910–1930 (Grinnell *et al.*, 1937). This information is complemented by the results of historical survey transects conducted along elevational gradients in the Sierra Nevada and Cascade Range in California during the same period (Grinnell & Storer, 1924; Grinnell *et al.*, 1930). Joseph Grinnell and his colleagues travelled throughout California collecting specimens, interviewing commercial and recreational trappers and inspecting their catches. This work resulted in coarse-scale distribution maps for 21 species and subspecies within the Carnivora. These historical data, compared with the results of contemporary surveys throughout the forests of much the same region, provide an opportunity to evaluate changes in the status of these species over a 75-year period.

Many of the data collected by Grinnell and his colleagues were provided by trappers. Trapping, however, is no longer a significant recreational or commercial enterprise in California. Furthermore, many of the species that were legally trapped in the early twentieth century have been protected from trapping for many decades [e.g. fisher (*Martes pennanti*), American marten (*M. americana*), ringtail (*Bassariscus astutus*), wolverine (*Gulo gulo*)]. Other species have been protected either by state law or by controls on the types of traps that are now legal to use [e.g. bobcats (*Lynx rufus*)]. Thus, trappers are no longer a source of reliable information on the distribution of many carnivores of interest to conservationists in California. Fortunately, several methods of detection have been developed that do not require the physical capture of animals. These include track plates (Barrett, 1983; Zielinski, 1995), remotely triggered cameras (Kucera *et al.*, 1995a; Moruzzi *et al.*, 2002), snowtracking (Halfpenny *et al.*, 1995; Beauvais & Buskirk, 1999) and non-invasive genetic sampling (Foran *et al.*, 1997; Mills *et al.*, 2000; Riddle *et al.*, 2003). We used sooted track-plates and remotely triggered cameras to estimate the distributions of small and mid-sized mammalian carnivores in the forests of the southern Cascade Range and Sierra Nevada of California during the period 1996–2002. Here we consider all species of mammalian carnivores that weigh < 20 kg (mesocarnivores *sensu* Buskirk & Zielinski, 2003) and occur in the forested regions of the Sierra Nevada and Cascade Range. They include the ermine (*Mustela erminea*), long-tailed weasel (*M. frenata*), western spotted skunk (*Spilogale gracilis*), striped skunk (*Mephitis mephitis*), ringtail, American marten, fisher, raccoon (*Procyon lotor*), badger (*Taxidea taxus*), gray fox (*Urocyon cinereoargenteus*), Sierra Nevada red fox (*Vulpes vulpes necator*), bobcat (*Lynx rufus*), coyote (*Canis latrans*),

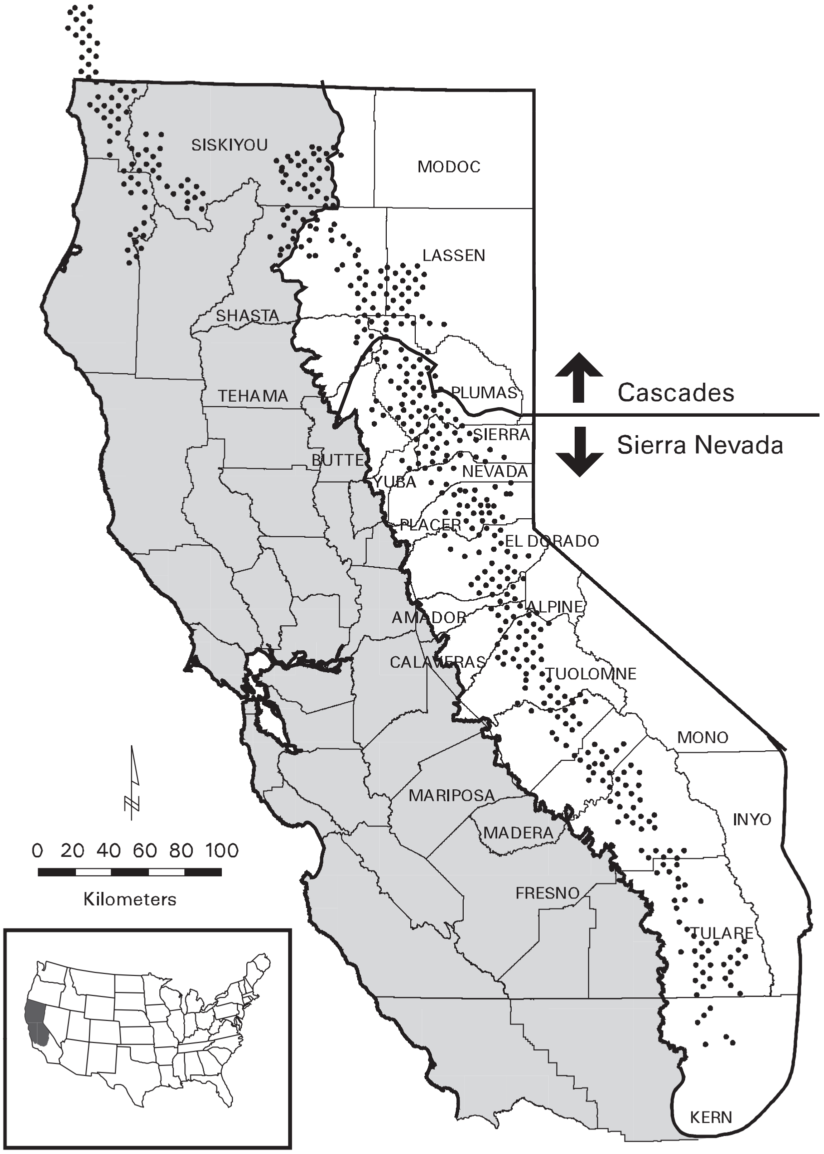

Figure 1 Sierra Nevada Ecosystem Project area (white) with counties and survey locations (dots) identified. The portion of the study area north of the bold line is the Cascades and south of the line is the Sierra Nevada.

and the wolverine. For the purposes of this analysis, we also include the black bear (*Ursus americanus*) and the marsupial opossum (*Didelphis virginiana*), because these species were regularly detected at baited track plate and camera stations.

Changes in carnivore populations have been linked to changes in human influence on their habitats (Cardillo *et al.*, 2004; Laliberte & Ripple, 2004) and the human population of few US states has increased as dramatically as that of California during the twentieth century. For more than a century, Californians of European descent have relied on the Sierra Nevada ecosystems for water, recreation, wilderness values, forage for livestock, and timber. One of the most dramatic changes in the Sierra Nevada culminated with the 'gold rush' of the mid-1800s, in which burgeoning human settlement was accompanied by increases in mining, timber harvest and fur trapping (Grinnell *et al.*, 1937; McKelvey & Johnson, 1992; Beesley, 1996). The human population of California has grown from 3.4 million in 1920 to a projected 63 million in 2040 (California Department of Finance, 1993), with corresponding increases in demand for forest resources and recreational opportunities from its forests. For example, the southern Sierra national parks and national forests receive one of the highest levels of recreational activity in the world and the central Sierran foothill region is one of the fastest growing regions in California (Duane, 1996). Moreover, a century of fire suppression has changed forest structure (increased tree densities) and increased the risk of stand-replacing wildfires [Sierra Nevada Ecosystem Project (SNEP), 1996; US Department of Agriculture (USDA), 2001]. Consequently, forest carnivores in California have experienced for centuries, and will continue to experience, significant threats to their habitats. However, human effects alone do not explain the risk of extinction; individual species possess biological traits that, when combined with increasing human disturbance, magnify their probabilities of extinction (Cardillo *et al.*, 2004). Our goals are to explore the changes in

Table 1 Species of mammalian Carnivorans (and one marsupial) that are considered to be detectable at the primary detection device, track plates, in the Cascades and Sierra Nevada mountains of California

Mustelids	
Marten	*Martes americana*
Fisher	*Martes pennanti*
Wolverine	*Gulo gulo*
Striped skunk	*Mephitis mephitis*
Western Spotted skunk	*Spilogale gracilis*
Ermine	*Mustela erminea*
Long-tailed weasel	*Mustela frenata*
Badger	*Taxidea taxus*
Procyonids	
Raccoon	*Procyon lotor*
Ringtail	*Bassariscus astutus*
Felids	
Bobcat	*Lynx rufus*
House cat	*Felis catus*
Canids	
Gray fox	*Urocyon cinereoargenteus*
Sierra Nevada red fox	*Vulpes vulpes necator*
Domestic dog	*Canis familiaris*
Others	
Black bear	*Ursus americanus*
Virginia opossum	*Didelphis virginiana*

carnivore species distributions in the conifer forests of the Sierra Nevada over a 75-year period, to relate these changes to several major anthropogenic changes that occurred during the same period, and to compare the ecological traits of species whose distributions have changed with those that have remained the same.

METHODS

Study area

The study was conducted in northern and eastern California, centred in a region that includes the Sierra Nevada and the southernmost extension of the Cascade Range (Fig. 1). This is the same area that was identified for study by the congressionally mandated SNEP (1996). Most (60%) of the area is public land, including 11 national forests and three national parks. The area is contained within the Sierran Forest – Alpine Meadows Province and includes the Sierra Nevada, Sierra Nevada Foothills, Southern Cascades, and Modoc Plateau Ecological Sections (Bailey, 1994).

Historical survey information

Historical information is represented largely by museum and trapper's records that were included in the distribution maps constructed by Grinnell *et al.* (1937). Other surveys from the same era (Grinnell *et al.*, 1930) were included if they provided significant additional data. We have redrawn the original maps to facilitate comparing them with our contemporary survey information. The duration over which data were collected varied among species but usually centred on the period from 1919 to 1925. For most species, individual records in Grinnell *et al.* (1937) were represented by a single map symbol, but for the American

Table 2 Frequencies of detection of selected species at 344 sample units (SUs) in the southern Cascades and Sierra Nevada of California, 1996–2002

		Track plates		Cameras*	
	Number (%) of SUs w/detections	Number (%) of SUs w/detections	Total number of detections	Number (%) of SUs w/detections	Number (%) of SUs w/detections by camera only
Didelphis virginiana	22 (6.4)	19 (5.5)	92	4 (1.2)	3 (0.9)
Canis sp.†	5 (1.5)	5 (1.5)	24	1 (0.3)	0 (0.0)
Urocyon cinereoargenteus	91 (26.5)	88 (25.6)	748	24 (7.0)	3 (0.9)
Vulpes vulpes	0 (0.0)	0 (0.0)	0	0 (0.0)	0 (0.0)
Ursus americanus	192 (55.8)	153 (44.5)	549	126 (36.6)	39 (11.3)
Bassariscus astutus	37 (10.8)	36 (10.5)	208	7 (2.0)	1 (0.3)
Procyon lotor	4 (1.2)	4 (1.2)	5	1 (0.3)	0 (0.0)
Martes americana	36 (10.5)	34 (9.9)	252	18 (5.2)	2 (0.6)
M. pennanti	30 (8.7)	29 (8.4)	159	10 (2.9)	1 (0.3)
Mustela sp.‡	28 (8.1)	28 (8.1)	60	0 (0.0)	0 (0.0)
Gulo gulo	0 (0.0)	0 (0.0)	0	0 (0.0)	0 (0.0)
Taxidea taxus	2 (0.6)	2 (0.6)	2	0 (0.0)	0 (0.0)
Spilogale gracilis	101 (29.4)	96 (27.9)	730	30 (8.7)	5 (1.5)
Mephitis mephitis	57 (16.6)	57 (16.6)	218	0 (0.0)	0 (0.0)
Felis sp.§	15 (4.4)	14 (4.1)	22	2 (0.6)	1 (0.3)

*Only one camera per sample unit is represented.

†Indistinguishable to species: includes *C. familiaris* and unknown canids.

‡Indistinguishable to species: includes *M. erminea*, *M. frenata*, *M. vision*, and unknown mustelids.

§Indistinguishable to species: includes *F. catus*, *F. rufus*, *F. concolor*, and unknown felids.

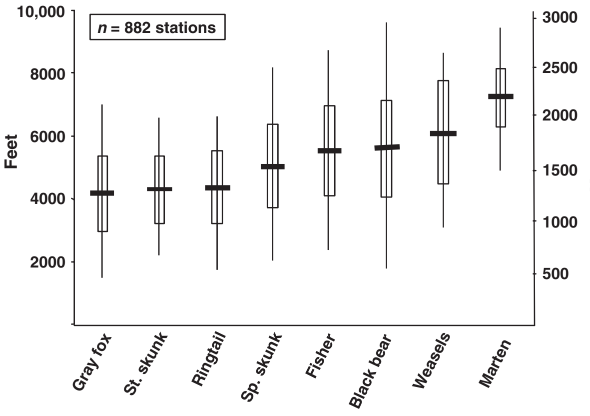

Figure 2 Distribution of elevations of detections of eight species where they were detected at stations at sample units in the Cascades and Sierra Nevada mountains, 1996–2002. Bold horizontal bars represent the mean elevation, the open boxes represent± 1 SD, and the lines represent the extent of the range of elevations.

marten the number of records at a locality was represented using a variety of symbols that corresponded to increasing numbers of records at that location (i.e. up to 5, 5–10, 11–20).

Contemporary surveys

Sampling design

Contemporary surveys were based on a grid of sampling points that encompassed a region of *c.* 3,000,000 ha enclosed by the larger SNEP study area (Fig. 1). The sample area was roughly coincident with the boundaries of conifer forests in the region and also includes areas and elevations that receive the majority of human impacts. We used a pre-existing national systematic sampling grid [the National Forest Inventory, based on the Forest Inventory and Analysis (FIA) system; Frayer & Furnival, 1999; Roesch & Reams, 1999] as the basis for selecting sample locations. Sampling was based on the region of conifer and mixed conifer-hardwood forests that constituted the historical range of the fisher (Grinnell *et al.*, 1937), a species for which there is considerable conservation interest. This large region encompassed much of the historical ranges of the other species of carnivores (Grinnell *et al.*, 1937), but excluded the highest elevation locations in the southern Sierra Nevada. All points in the FIA grid that fell within or near the historical range of the fisher were identified and the grid points were assigned a row and column number, from which a random point was selected.

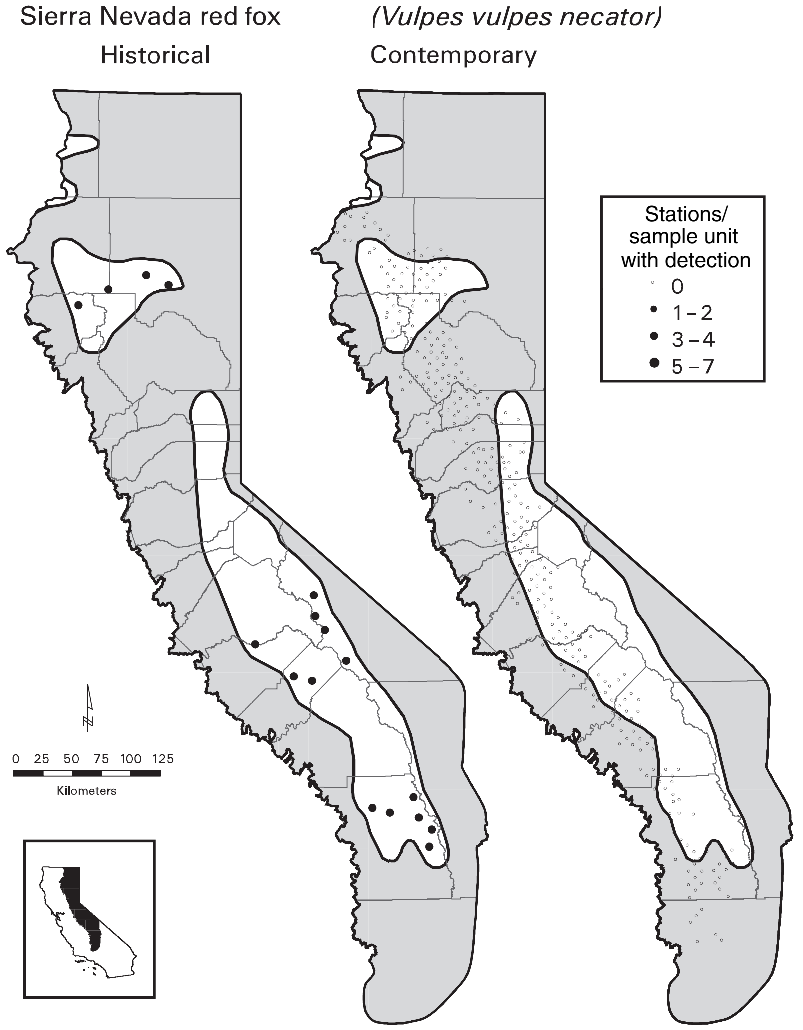

Figure 3 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the Sierra Nevada red fox. Bold lines represent the boundaries of the historical distribution as represented in Grinnell *et al.* (1937) and shading identifies portions of the study area that were outside the historical range. Black dots in the historical map represent a single record, open circles in the contemporary map represent sample units with no detections.

From this start point, alternating points in each row were selected for sampling. The same grid density [*c.* 6.8 mi (10.9 km) between points on the east/west and north/south axes; 4.8 mi (7.7 km) on diagonal axes] was maintained for all subsequent rows, but each row was offset by one FIA point to create a grid with the same spatial properties as the original but with approximately half the number of points.

Because we focused on mid-to-high elevation conifer-dominated forests, we eliminated points from our selected set that were below 800 m and above 3200 m in the southern Sierra Nevada, below 800 m and above 2700 m in the central Sierra Nevada, and below 600 m and above 2900 m in the southern Cascades.

Detection methods

At each selected grid point we established a sample unit composed of six sooted and baited track-plate stations (Zielinski, 1995). A track-plate station was placed as close as possible to the selected FIA point, and the remaining five track plates were positioned at 72° intervals *c.* 500 m from the centre station. We began by enclosing the track plates in plywood boxes but in 1998, we enclosed the plates in plastic canopies (L. Chow, pers. comm.; Zielinski, 1995) after determining that detections did not differ at the wood and plastic enclosures (W. Zielinski, unpubl. data). All sample units also included at least one remotely triggered 35-mm camera (Trailmaster 1500; Goodson and Associates, Inc., Lenexa, KS, USA) randomly paired with one of the six track plate stations and placed *c.* 100 m from the central station at a random azimuth. The exceptions were 97 of the sample units in the central Sierra Nevada where two cameras were deployed in conjunction with two of the track plates stations. Thus, sample units comprised either seven or, in the central Sierra Nevada, eight stations: six track plates and one or two cameras. All cameras were directed toward bait that was placed *c.* 2 m above the ground on the bole of a tree. Most FIA points were located using GPS (81%); the rest were located using map and compass and the centre station was placed within 100 m.

Field crews returned to all detection devices at 2-day intervals during a 16-day sampling period, for a total of eight visits. All stations were baited with raw chicken and at most sample units ($n = 284$) we applied a commercial scent lure (Gusto; Minnesota Trapline Products, Pennock, MN, USA) on

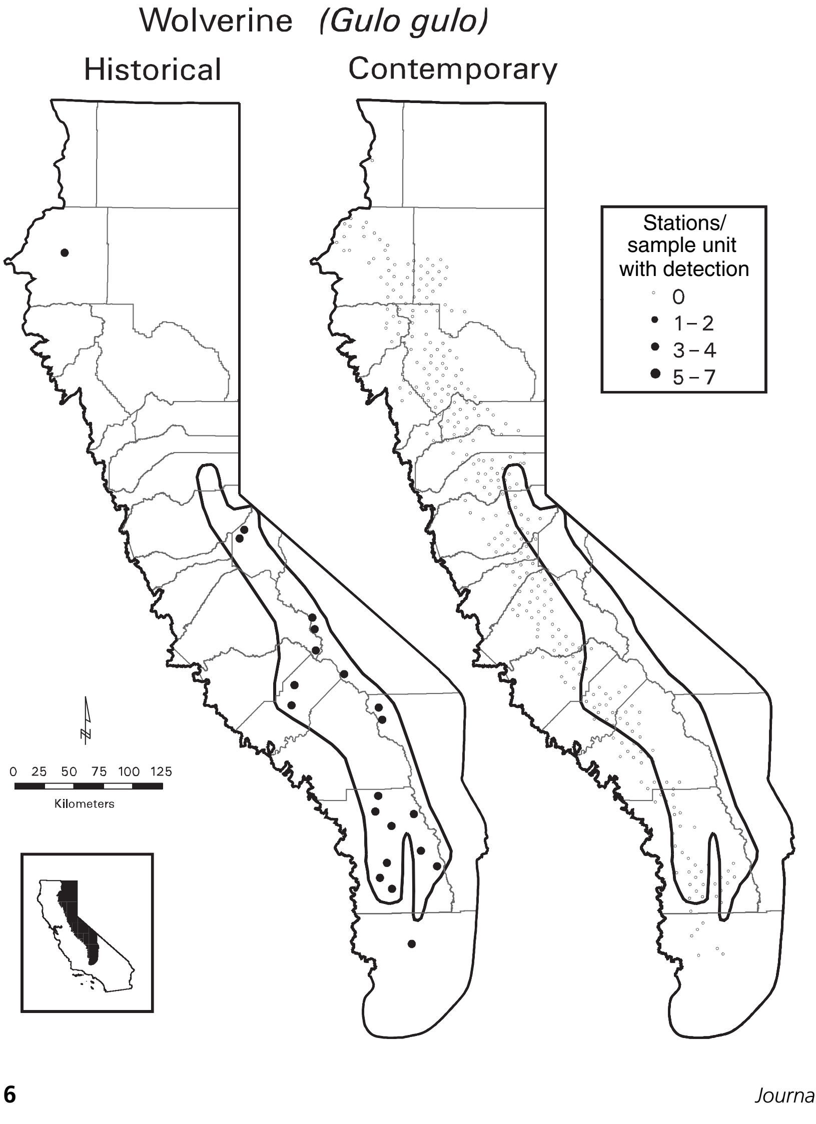

Figure 4 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the wolverine. Black dots in the historical map represent a single record, open circles in the contemporary map represent sample units with no detections. Bold lines represent the boundaries of the historical distribution as represented in Grinnell *et al.* (1937).

the first and the fifth visits to each station. In the southern Sierra ($n = 50$ units), we applied the lure on the fifth visit only if a fisher had not been detected previously at at least one of the stations. All sampling was conducted from 1 June to 1 November each year.

The number of stations within a sample unit where a species is detected has no known relationship to the number of individuals that occur there. However, we have assumed that this metric serves as an index of the importance of a sample location to a species. For example, Carroll *et al.* (1999) reported that the number of detections of fishers at a sample unit was positively related to the predicted probability of fisher occurrence. We assumed that this might be a useful index for other species and represented the results of our contemporary surveys using four categories for most sample units (detections at either 0, 1, 2–3, or 4–8 of the stations in a sample unit). Although we checked each station eight times, a single detection at any one check resulted in the classification of a detection for the station, and for the sample unit.

The species of mammals that previous work (Zielinski *et al.*, 1997) suggests are potentially detectable using the track-plate methods are listed in Table 1. Most were distinguished by species-specific characteristics of their tracks (Taylor & Raphael, 1988; Zielinski & Truex, 1995) and the use of a voucher collection of reference tracks. However, as we do not yet have a quantitative basis for discriminating bobcat from domestic cat (*F. catus*) or coyote from domestic dog (*C. familiaris*), cat tracks are referred to as '*Felis* sp.' [mountain lions (*F. concolor*) are rarely detected at track plate stations] and coyote and dog tracks as '*Canis* sp.'. Similarly, the tracks of weasels (*M. frenata* and *M. erminea*) are collectively referred to as '*Mustela* sp.'.

Measures of anthropogenic change

One of our goals is to explore the changes in carnivore species distributions in relationship to the major changes in the Sierra Nevada that have been created by humans over the same time period. Carnivores of Sierra Nevada forests are probably affected most by direct interactions with humans and by the loss of mature forest habitat, so we included in our assessment measures of change of human density and change of mature forest cover. Spatial information about human population density was represented by maps of housing density summarized for 1930 and 1990 using US Census data (Population of

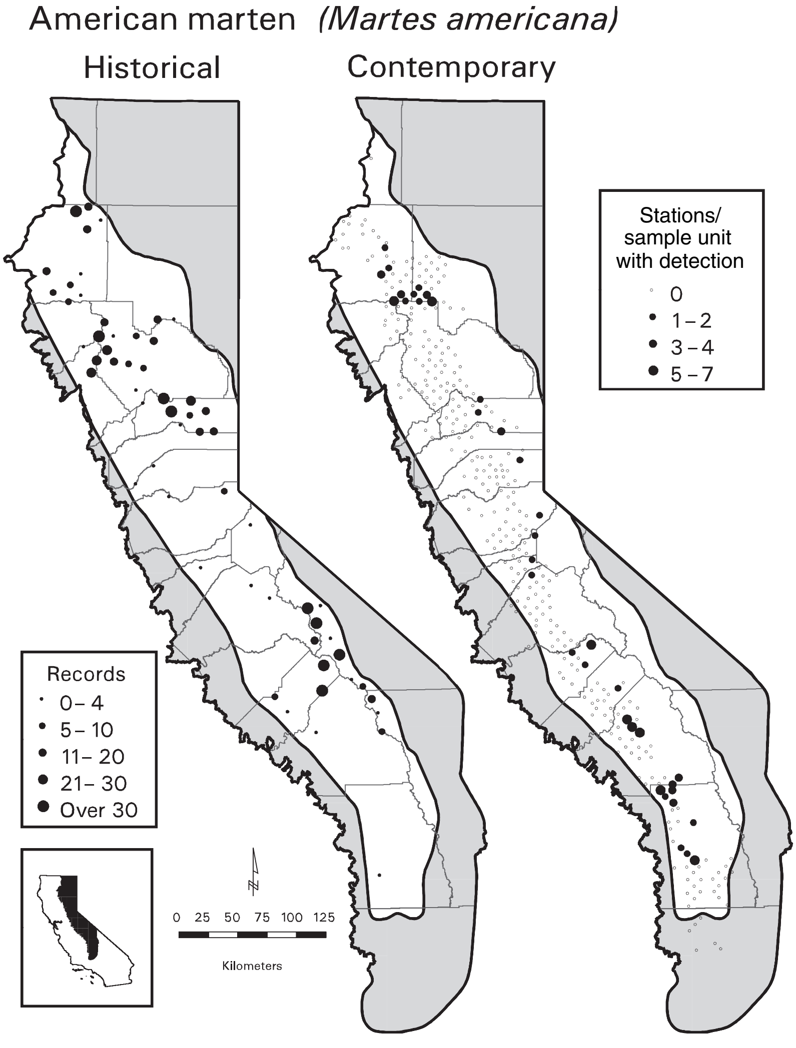

Figure 5 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the American marten. Bold lines represent the boundaries of the historical distribution as represented in Grinnell *et al.* (1937) and shading identifies portions of the study area that were outside the historical range. Black dots in the historical map represent one or more records (depending on size). Black dots in the contemporary map represent one or more stations per sample unit (depending on size) where a marten was detected (1996–2002); open circles represent sample units with no detections.

States and Counties of the United States, Forstall, 1996; Census of Population and Housing, Duane, 1996). The base map for historical vegetation is from the Vegetation Type Map Survey, conducted between 1929 and 1934 by the US Forest and Range Experiment Station, Berkeley, CA, USA and updated in 1945. This map is referred to as the Weislander map after A.E. Weislander, the Survey's director and senior map author. The original Weislander maps were *c.* 1 : 64,000 scale and were digitized into a Geographic Information System. Polygons of *c.* 200 ha (500 acre) minimum units were assigned values based on their old-growth attributes (Weislander & Jensen, 1946). Five classes were identified: 'old growth' (> 50% of conifer canopy consists of mature trees), 'young growth/old growth' (from 20 to 50% of the conifer canopy consists of mature trees), 'young growth' (< 20% of conifer canopy consists of mature trees), 'poorly stocked' (open conditions with very low density of trees) and 'non-commercial'. Contemporary vegetation data were represented by an analysis conducted by Franklin & Fites-Kaufmann (1996) for SNEP. This regionwide assessment of the distribution of late-successional vegetation has its critics (e.g. Langley, 1996) but it is the only seamless coverage that applies to roughly the same region as the Weislander and Jensen data that was also temporally coincident with the contemporary survey data. Polygons of *c.* 200 ha minimum size were assigned one of five late-successional/old-growth (LS/OG) rankings, ranging from rank 0 (no contribution to late-successional forest function) to rank 5 (very high contribution to late-successional forest function) (Franklin & Fites-Kaufman, 1996).

RESULTS

Contemporary carnivore detections

Thirteen target taxa were detected at 344 sample units from 1996 to 2002 (Table 2). Black bears were the most frequently detected species (55.8% of sample units). In decreasing order, the next most frequently detected species were: western spotted skunk, gray fox, striped skunk, ringtail, marten, fisher, and 'weasels', all occurring at from 8–30% of the sample units (Table 2). The least frequently detected species (between 1 and 6.5% of sample units) were the opossum, '*Felis* sp.', '*Canis* sp.',

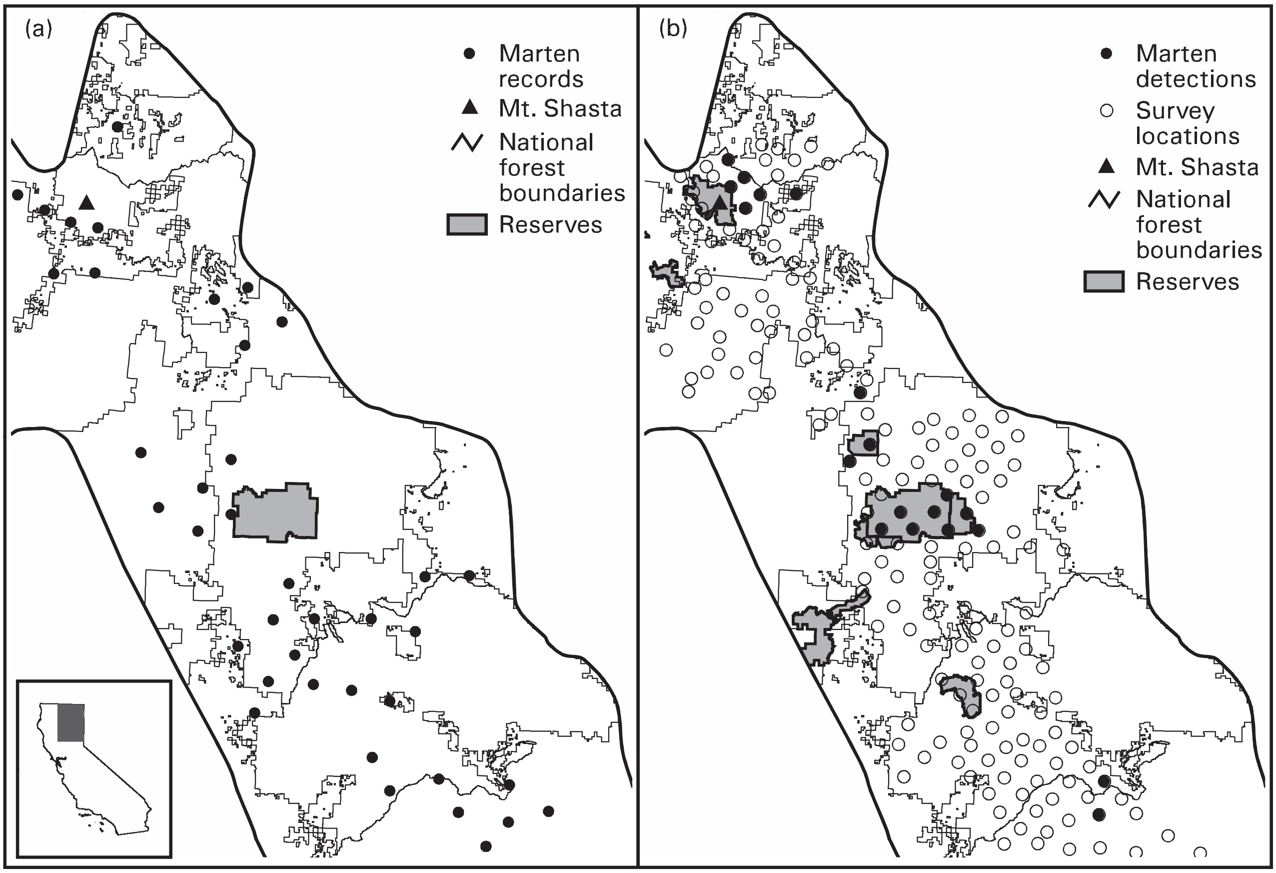

Figure 6 Northern portion of the study area depicting (a) the historical distribution of marten records (Grinnell *et al.*, 1937), national forest boundaries (thin lines) and the reserves as of 1937 (i.e. national parks), and (b): the contemporary survey data with black dots representing sample units with at least one marten detection, open circles representing sample units with no detections, and shaded polygons representing reserves (i.e. national parks, wildernesses). The closed triangle is Mt Shasta and the bold lines indicate the boundaries of the historical distribution of martens (Grinnell *et al.*, 1937).

raccoon, and badger. There were no detections of either wolverine or red fox.

Spotted skunks and black bears were the most widespread species, occurring in all counties and at all elevations sampled. Weasels were also detected throughout the region, but far less frequently than spotted skunks and bears. Martens were detected at the highest elevations on average (Fig. 2), which occurred at the eastern margin of the area surveyed, and striped skunks, ringtails and gray foxes were detected at the lowest mean elevations near the western margin. Gray foxes, opossums and striped skunks appeared to be common throughout the region but were detected less frequently in the southern than in the northern part of the study area.

With the exception of martens, all taxa were detected most frequently at only one of the seven stations (six track plate and one camera) available to them at each sample unit (Table 2). It was rare for a species to be detected at > 6 stations at the same sample unit, but this happened at 17 (16.8%), 6 (16.7%), and 5 (16.7%) of the sample units where spotted skunks, martens and fishers were detected, respectively. Black bears were the only species detected at a camera station only, at more than 2% of the sample units (Table 2). The high frequency of occasions where black bears were detected only by camera (11.3% of sample units) was due to the fact that the evidence of a bear having visited a track plate would often be a flattened box, which was not recorded as a bear detection. Had these been included, the percentage of sample units with detections at cameras only would have been considerably less.

Comparing historical and contemporary distributions

Species that were not detected

By the early 1900s, the distributions of wolverines and Sierra Nevada red foxes had already apparently declined, due primarily to trapping and grazing, respectively, and each occurred only in a portion of the Sierra Nevada (Figs 3 and 4). The red fox occurred across the high elevations of the Sierra

Figure 7 Northern portion of the study area depicting (a) the historical distribution of forest seral stages (Weislander & Jensen, 1946) with marten records as black dots (Grinnell *et al.*, 1937), national forest boundaries (thin lines) and the reserves as of 1937 (i.e. national parks) enclosed by bold lines, and (b) the contemporary distribution of late-seral stage attributes (Franklin & Fites-Kaufmann, 1996) with black dots representing sample units with at least one marten detection, open circles representing sample units with no detections, and bold lines enclosing reserves (i.e. national parks, wildernesses). Bold lines indicate the boundaries of the historical distribution of martens (Grinnell *et al.*, 1937).

Nevada, with a significant gap at the Cascade–Sierra transition, and the wolverine remained primarily in the southern Sierra Nevada. Neither species, however, was detected during contemporary surveys. Although we did not survey all of the historical range for these species we did not detect either red foxes or wolverines at any of the *c.* 60 and 150 sample units, respectively, that occurred within their ranges.

Species with substantial changes in distributions

Marten. Historically, the marten was reported to occur throughout the higher elevations of the study area (Fig. 5), but current survey results indicate that populations in the southern Cascades and northern Sierra Nevada now appear discontinuous. This is clearly evident by comparing the historical and contemporary locations centred on Plumas County (Figs. 5 and 6). There are large gaps between contemporary detections that were not present historically. There is also a large gap in contemporary detections in Tuolomne County (Fig. 5) but, unlike the situation in Plumas County, this does not correspond to a region where martens were reported historically. In addition, there are a number of detections of martens in Tulare County that were not represented by historical records in this county.

Contemporary marten detections are clustered in the vicinity of Lassen National Park (LNP) and adjacent protected wilderness areas just northwest of LNP, and the area just east of Mt Shasta (Fig. 6). These regions include areas that have some level of protection from timber harvest. Most of the areas in this region where martens occurred in the early 1900s, but were not detected in the late 1900s, are national forests that have received more impacts from humans, including timber harvest, road building, and – until the mid-1950s – trapping.

The areas within the southern Cascades region and northern Sierra Nevada where marten populations occur today also are regions where there also appears to have been the least change in the late-seral and old-growth status of the forests (Fig. 7). The areas of Plumas and Lassen county where martens were not detected, and which have been managed for timber harvest, have relatively little forests with late seral/old growth attributes (Fig. 7). Locations where marten detections occur today coincide with protected areas (national parks and wilderness) and also appear to have been affected by the distribution of LS/OG attributes.

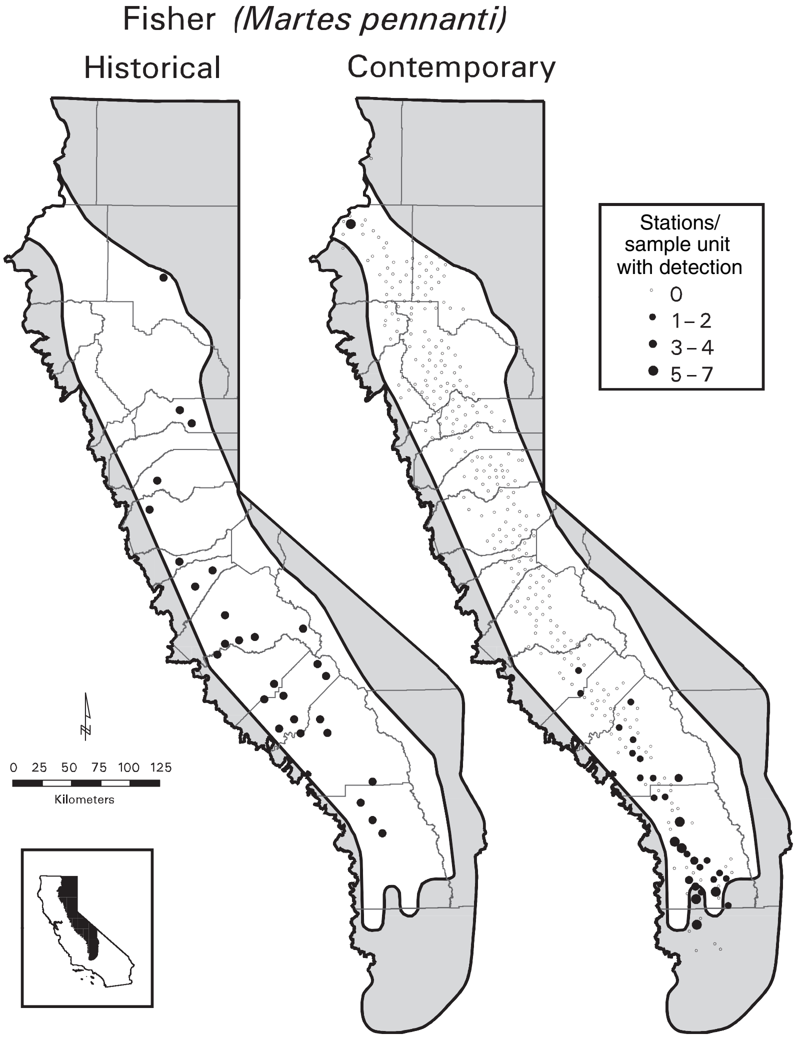

Figure 8 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the fisher. Bold lines represent the boundaries of the historical distribution as represented in Grinnell *et al.* (1937) and shading identifies portions of the study area that were outside the historical range. Black dots in the historical map represent one record. Black dots in the contemporary map represent one or more stations/sample unit (depending on size) where a fisher was detected (1996–2002); open circles represent sample units with no detections.

Fisher. The distribution of the fisher appears to have changed more than any of the species that we detected (Fig. 8). Whereas it once occurred throughout most of the Sierra Nevada, fishers were not detected across a *c.* 430 km region from the southern Cascades (eastern Shasta County) to the central Sierra Nevada (Mariposa County) (Fig. 8). Detections were most common in the extreme southern Sierra, especially in Tulare County where 26 of the 30 sample units with fisher detections occurred. The historical data are most sparse in the northern portion of the study area. For example, the only record in Plumas County is reported by Grinnell *et al.* (1930), a record that inexplicably was not included in the subsequent account of Grinnell *et al.* (1937). Compared with other species, fishers appear to be unevenly distributed in the Sierra Nevada during the historical period, referenced herein.

Opossum. The opossum is an introduced species and by 1930 (the end of the 'historical' period considered here) the opossum had not yet spread eastward into the survey area. However, our contemporary surveys detected opossums at 22 sample units. Most detections occurred in the central Sierra Nevada (Fig. 9), which is not surprising given the site of introductions and easterly direction of spread that had already been identified in the early 1900s (Dixon, 1924). However, opossum detections were also distributed sparsely across the entire study area.

Species with no substantial change in distribution

Gray fox. Historically, the gray fox was well-distributed along the western slope of the Sierra and across the Cascades in the north (Fig. 10). This pattern was largely duplicated in contemporary surveys, with the possible exception of the northern portion of the study area where none of *c.* 30 contiguous sample units located in the junction of Lassen, Shasta and Plumas counties detected a gray fox (Fig. 10). However, a cluster of detections occurred in the region of central Plumas County which was not represented by historical records.

Ringtail. Ringtails are a species of the mid-to-lower elevations and, as a result, only the western edge of their distribution

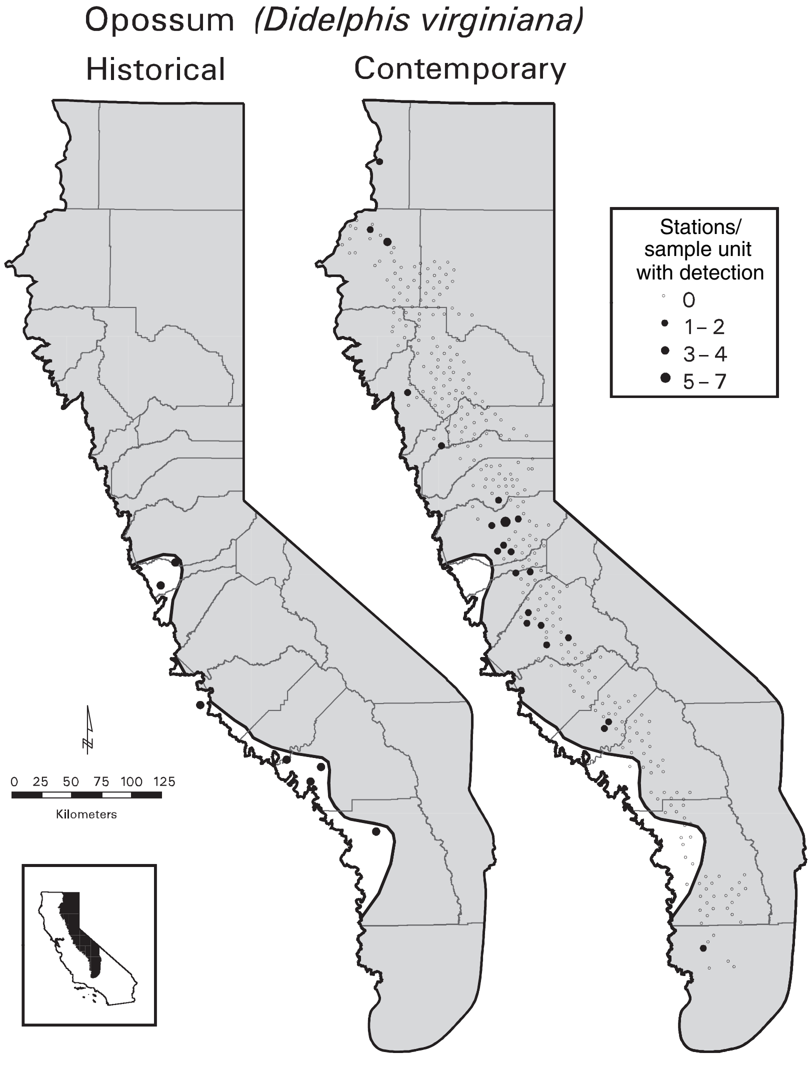

Figure 9 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the opossum. Bold lines represent the boundaries of the historical distribution as represented in Grinnell *et al.* (1937) and shading identifies portions of the study area that were outside the historical range. Black dots in the historical map represent one record. Black dots in the contemporary map represent one or more stations per sample unit (depending on size) where an opossum was detected (1996–2002); open circles represent sample units with no detections.

lies within our survey area (Fig. 11). Much of our sample area in the Cascades was east of the distribution described for this species. Although no ringtails were detected within a block of *c.* 35 sample units within the north-eastern portion of their range (Fig. 11), our surveys describe a distribution in the southern Sierra that is similar to that described by Grinnell *et al.* (1937).

Striped skunk. Striped skunks are the mustelid that occurs at the lowest elevations in the survey area (Fig. 2). The contemporary detections reflect a distribution similar to that described from the historical data (Fig. 12). The largest area without detections occurred near the junction of Lassen, Shasta, Tehama and Plumas counties in the vicinity of the high elevations associated with LNP.

Western spotted skunk. The contemporary and historical ranges of the spotted skunk are similar, indicating a population that is distributed throughout the southern Cascades and the Sierra Nevada. Like many of the other habitat generalists (i.e. ringtail, striped skunk, gray fox), it is distributed from north to south. Unlike them, the spotted skunk was detected from the eastern to the western borders of the study area (Fig. 13), across a great range of elevations.

Black bear. We detected black bears in all survey areas (Fig. 14). Their distribution was perhaps the most contiguous of any species we detected, and was consistent with the even distribution of records in the historical data base. Like the spotted skunk, the black bear was also detected from the eastern to western portions of the study area, across the full range of elevations sampled.

Weasels. Grinnell *et al.* (1937) did not provide a range map nor any substantive discussion of the distribution of either *M. erminea* or *M. frenata*. Contemporary surveys revealed a wide, but sparse, pattern of detections from north to south and across the elevational gradient from west to east (Fig. 15). An apparent concentration of detections occurred in the extreme southern Sierra Nevada.

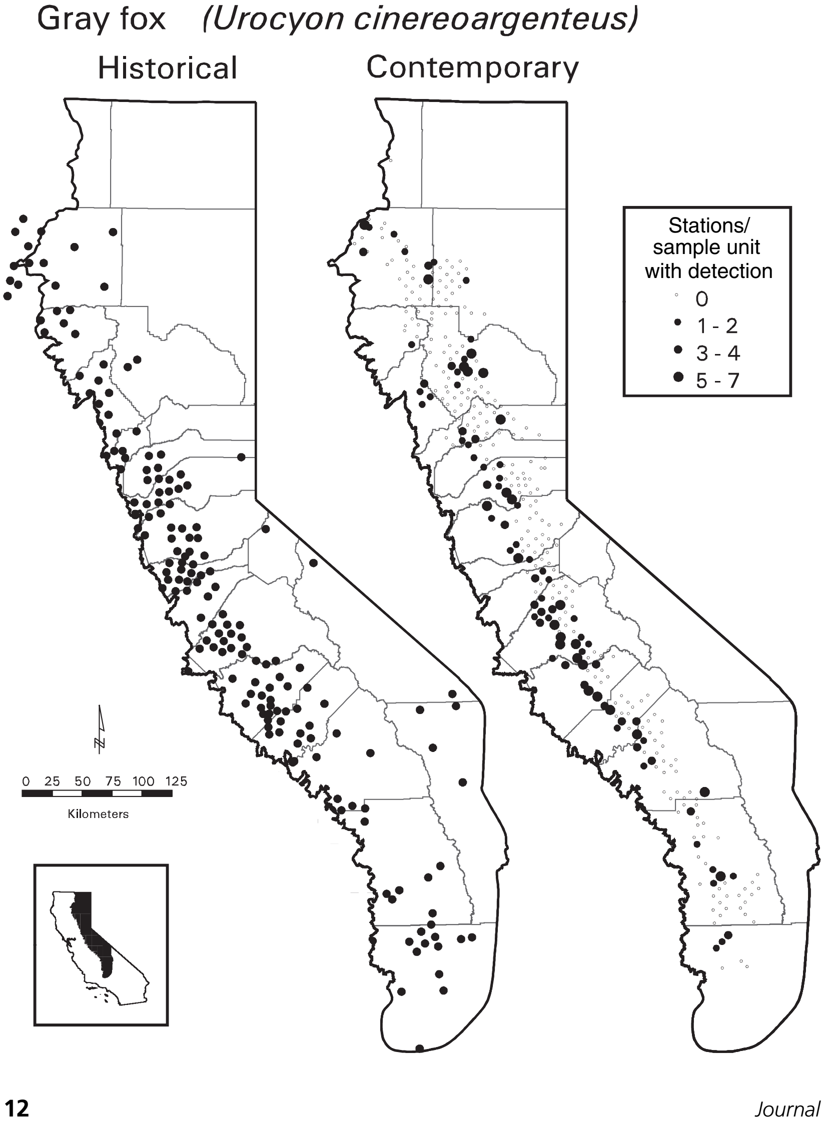

Figure 10 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the gray fox. The entire study area was considered within the historical distribution. Black dots in the historical map represent one record. Black dots in the contemporary map represent one or more stations/sample unit (depending on size) where a gray fox was detected (1996–2002); open circles represent sample units with no detections.

Species detected infrequently, or for which there was an inadequate basis for identification

The raccoon and badger have distinctive tracks but were detected too infrequently (at four and two sample units, respectively) to evaluate changes in their distributions. An algorithm does not exist that can quantitatively distinguish the tracks of bobcat from domestic cat or coyote from domestic dog. And, bobcats and coyotes were very infrequently detected at camera stations (two and one occasion, respectively), where their identity could be confirmed. These species, therefore, could not be evaluated for changes in their distributions.

Anthropogenic changes

Mature forest conditions

Comparing the Weislander map and the SNEP map reveals some important changes that occurred over the 50-year period (Fig. 16). The proportional area of polygons identified as old growth in 1945 was 50% and the combination of old growth and young growth/old growth totalled 76% (Table 3). In 1996, the proportion of area that was characterized by the greatest number of late-successional attributes (LS/OG Rank 5) was 3%, the total of the top two LS/OG ranks (4 and 5) was 12%, and the top three ranks (3, 4, and 5) was 38%. Changes were most evident in the northern Sierra Nevada (north of Yosemite National Park). Despite the difference between the methods used to classify mature forest conditions, it is evident that the southern Sierra Nevada contained a greater proportion of old growth than the northern Sierra Nevada in 1945, and that this difference has become even more pronounced in the period from 1945 to 1995. A difference in transition probabilities (Table 4) indicates that much of this change is manifest as a shift of forest from Weislander types 1 and 2 (old growth and young growth/old growth mixed) to LS/OG rank 2 (i.e. 'low contribution to LSOG forest function'). LS/OG rank 2 includes: (1) forests whose low ranking is because of harsh site conditions leading to lower canopy closure; and (2) mid-elevation productive forests whose low ranking results from anthropogenic causes (e.g. logging). Most of the LS/OG rank 2 polygons lie along the western boundary of national forest lands (primarily in the southern Cascades

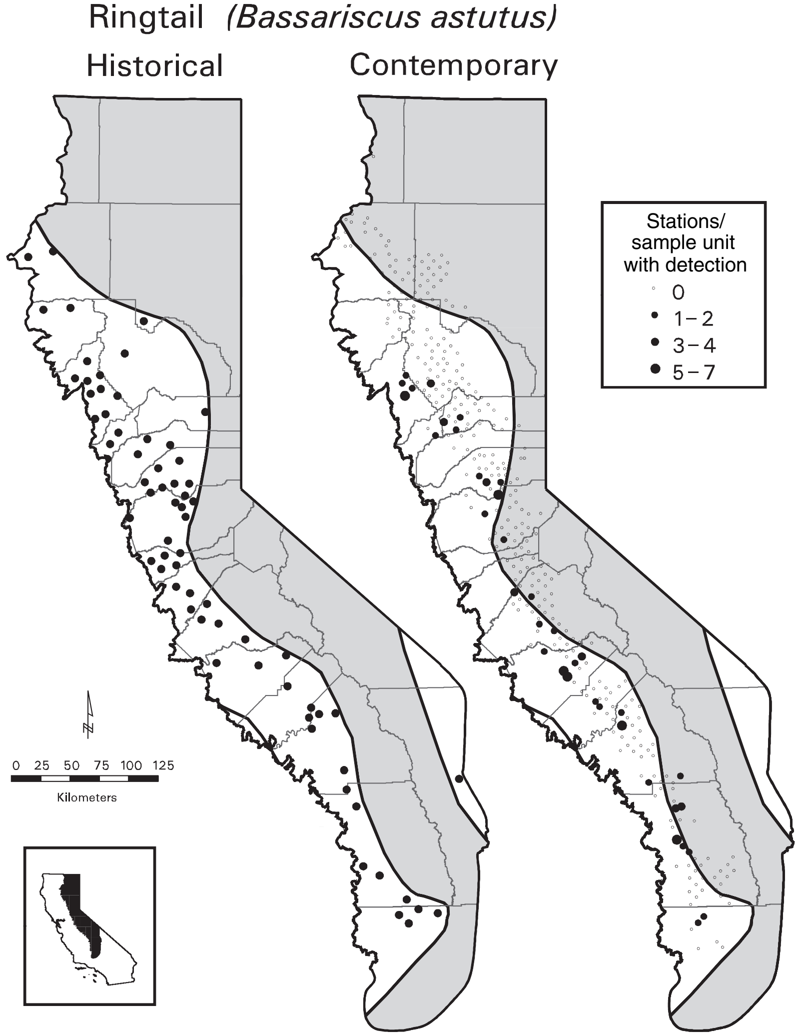

Figure 11 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the ringtail. Bold lines represent the boundaries of the historical distribution as represented in Grinnell *et al.* (1937) and shading identifies portions of the study area that were outside the historical range. Black dots in the historical map represent one record. Black dots in the contemporary map represent one or more stations per sample unit (depending on size) where a ringtail was detected (1996–2002); open circles represent sample units with no detections.

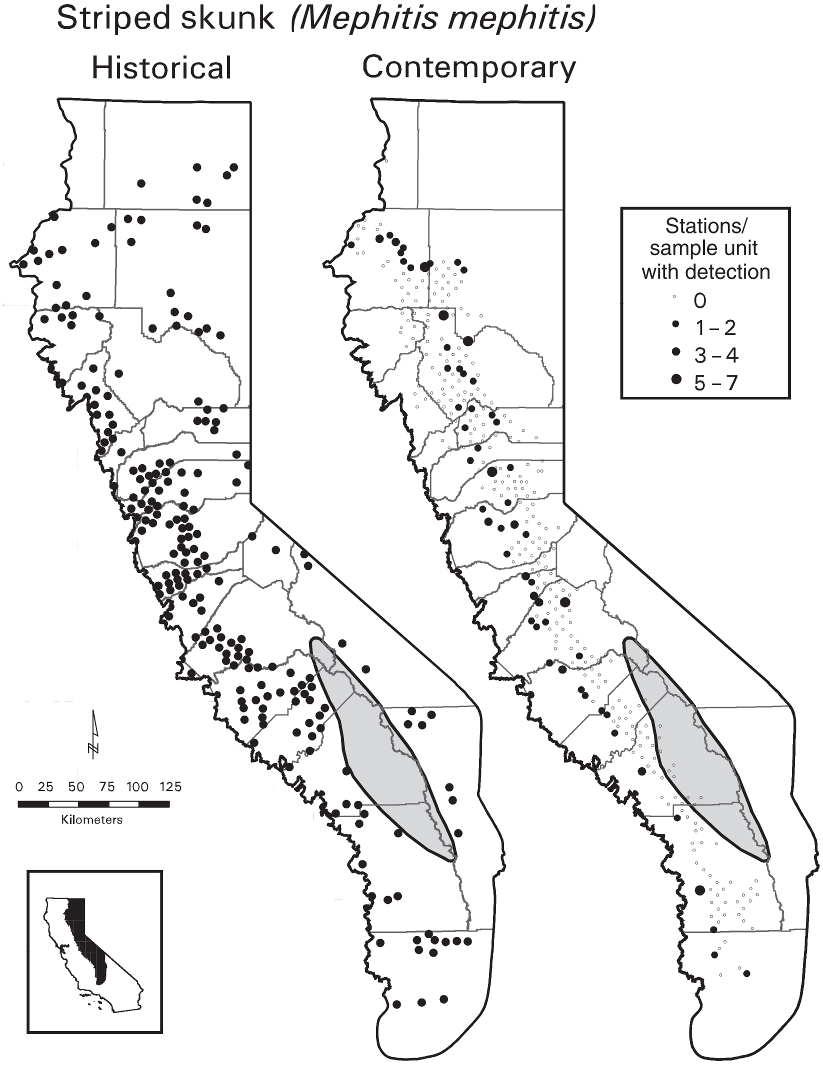

Figure 12 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the striped skunk. Shading identifies portions of the study area that were outside the historical range. Black dots in the historical map represent one record. Black dots in the contemporary map represent one or more stations per sample unit (depending on size) where a striped skunk was detected (1996–2002); open circles represent sample units with no detections.

and northern Sierra Nevada) where it appears that the loss of mature and old-growth forest conditions has been greatest.

Human populations

Measures of housing density indicate a pattern of increased growth in human settlement of the Sierra Nevada over the period from 1930 to 1990 (Fig. 17). The most dramatic increase in settlement has occurred in the central portion of the study area, in Nevada, Placer, El Dorado and Amador counties. Substantial increases have also occurred in Calaveras and Tuolumne counties. Projections for 1990–2040 (not illustrated) suggest a range of 106–579 mi^2 (at 640 units mi^{-2}) of additional land converted to human use (Duane, 1996).

DISCUSSION

The ideal data set for comparing historical and contemporary distributions of animals would be an identical set of survey locations sampled with identical methods and equal effort at time points that bound an era of significant human impacts. Unfortunately, these data rarely exist because either the tools for describing the occurrence of carnivores have changed or improved (e.g. trapping vs. detections at track or camera stations) or because our scientific predecessors could not anticipate that comprehensive, scientific surveys would be necessary. Fortunately, Joseph Grinnell and his colleagues left a legacy of empirical information about the distribution of carnivores in California. Using these data to evaluate changes in distributions requires caution in interpretation, but the opportunities that they provide are unique.

Although exposure to threats is the ultimate cause of extinction, a species' biology can predict how well it will survive the threats to which it is exposed (Cardillo *et al.*, 2004). Life history characteristics, biological traits, and environmental conditions all affect the extinction risk of carnivores (Ferguson & Lariviere, 2002; Fisher *et al.*, 2003; Jones *et al.*, 2003). Habitat generalists are at lower risk than habitat specialists, and our data confirm this pattern. The ranges of the gray fox, spotted skunk, black bear, ringtail and striped skunk have not

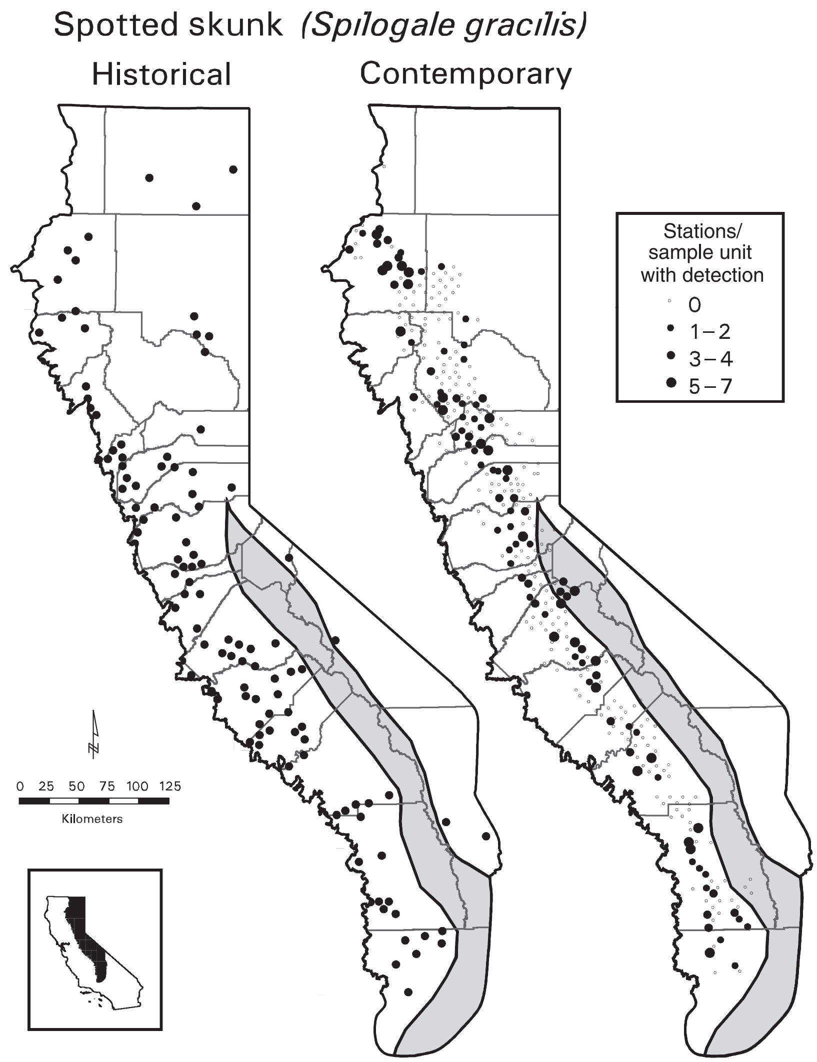

Figure 13 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the spotted skunk. Shading identifies portions of the study area that were outside the historical range. Black dots in the historical map represent one record. Black dots in the contemporary map represent one or more stations per sample unit (depending on size) where a spotted skunk was detected (1996–2002); open circles represent sample units with no detections.

changed and, with the possible exception of the ringtail, these species are all habitat generalists (Orloff, 1988; Campbell, 2003; Cypher, 2003; Gehrt, 2003; Pelton, 2003; Rosatte & Lariviére, 2003). Each also occurs at the low- and mid-elevation environments that have received the greatest use by humans. These elevations are characterized by productive and less-seasonal environments, characteristics associated with low extinction risk (Ferguson & Lariviere, 2002).

The gray fox and black bear are still trapped or hunted in California and, although our surveys do not purport to index abundance, it appears that the populations have not changed substantially as a result of harvest. The ringtail has been protected from trapping since the mid-1900s and its habitat in rocky, riparian areas in oak and mixed-conifer vegetation types does not appear to have been affected by the human activities that occur there. None of the distributions of the habitat generalists listed above appear to have been grossly affected by the pattern of residential development or the change in distribution of late-seral vegetation that occurred during the assessment period.

Conspicuous is the absence of detections of many of the generalist carnivore species in a *c.* 2000 km^2 region joining Lassen, Plumas, Shasta, Tehama counties. This region is characterized by high elevations, most of which exceed the highest elevations where these species have been reported in California (Grinnell *et al.*, 1937). Snow is deep and persistent in this region, and few of the generalist carnivores in California possess adaptations to permit life on or under snow for prolonged periods. The black bear detections represent an exception to the pattern, occurring throughout this high elevation region, presumably because they persist during the harsh winter period in a state of dormancy (Nelson *et al.*, 1973; Pelton, 2003).

Wolverines and Sierra Nevada red foxes were not detected during our contemporary surveys. Although these surveys terminated at elevations below most of their historical ranges, the absence of detections is consistent with prior knowledge and trends. By the early 1900s there was already concern about the status of these species (Dixon, 1925; Grinnell *et al.*, 1937). A summary of sightings during the 1960s and 1970s

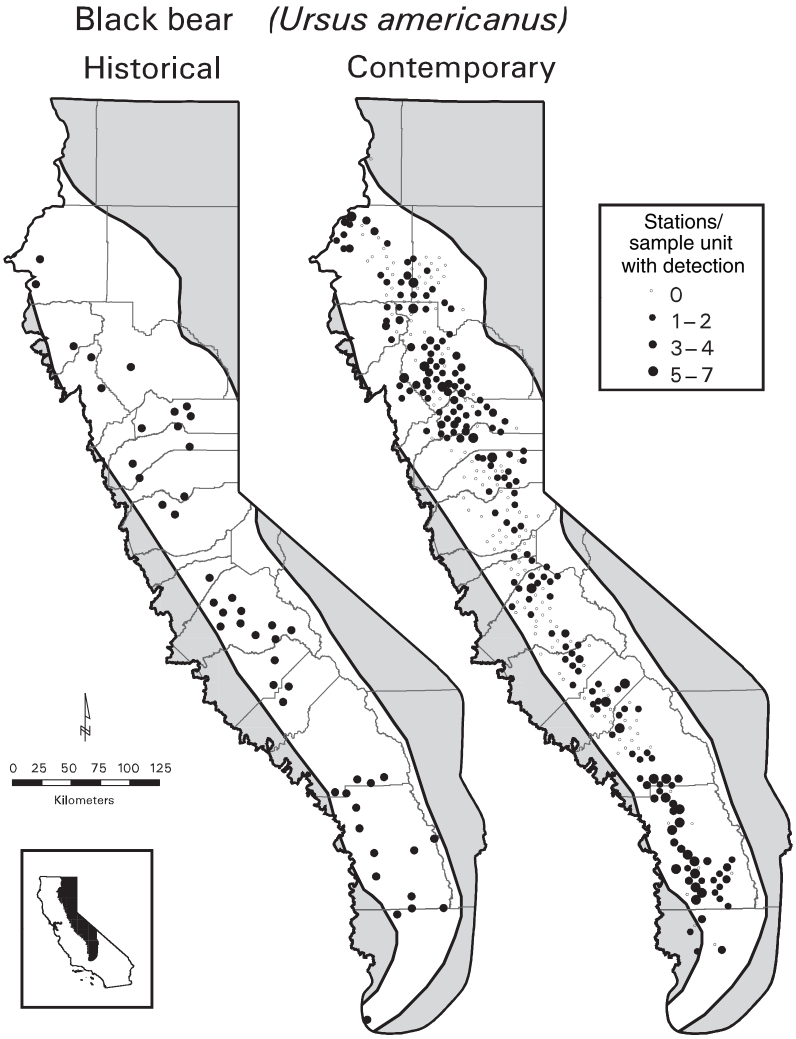

Figure 14 Distribution of historical records (Grinnell *et al.*, 1937) and contemporary survey data for the black bear. Bold lines define the boundary of the historical range (Grinnell *et al.*, 1937) and shading identifies portions of the study area that were outside the historical range. Black dots in the historical map represent one record. Black dots in the contemporary map represent one or more stations per sample unit (depending on size) where a black bear was detected (1996–2002); open circles represent sample units with no detections.

(Schempf & White, 1977) indicated that wolverine sightings were greater in the southern than the northern Sierra Nevada, but the sightings data did not suggest a downward trend. Red fox sightings, however, suggested either no change or a decline (Schempf & White, 1977). In the last 20 years, surveys for wolverines, using remote cameras at high elevation locations, have failed to detect them (Kucera & Barrett, 1993; L. Chow, unpubl. data; R. Green, unpubl. data). No specimen of wolverine or Sierra Nevada red fox has been verified to occur in California in over 50 years. Both taxa are reputed to be sensitive to the presence of humans (Grinnell *et al.*, 1937; Hornocker & Hash, 1981; Magoun & Copeland, 1998) thus changes in the abundance and distributions of humans, and their resource management activities, have probably contributed to the decrease or loss of these species from the study area. Life in high-elevation environments, which are very seasonal and unproductive, also predispose these species toward greater risk of extinction (Ferguson & Lariviere, 2002).

Although red foxes were not detected during our survey, a small population occurs in the vicinity of LNP (Kucera, 1995; J. Perrine, pers. comm.). Seven foxes have been captured over a 5-year period (J. Perrine, pers. comm., T. Kucera, pers. comm.) but their origin is currently unknown. There are historical records of Sierra Nevada red foxes from this region, but the introduced lowland red fox (*Vulpes vulpes vulpes*) has also spread throughout the area in the last century (Grinnell *et al.*, 1937; Schempf & White, 1977; Lewis *et al.*, 1995). This exotic subspecies has established itself in the foothills of the Cascades and Sierra Nevada by spreading from the Central Valley and from individuals that escaped from fur farms in the mid-1900s, some of which were located in the vicinity of LNP.

The few detections of badgers was not surprising because badgers do not typically occur in forested regions (Grinnell *et al.*, 1937), however, we were surprised that raccoons were detected so rarely. Raccoons are frequently attracted to sources of human food and are conspicuous in urban and suburban environments in California, so we expected that if they were in the vicinity of our baits that they would be detected. However, very little is known about the habits of raccoons that live in natural environments. If our sampling had focused on riparian areas, which raccoons appear to favour in natural environments (Gehrt, 2003), we may have detected them more often.

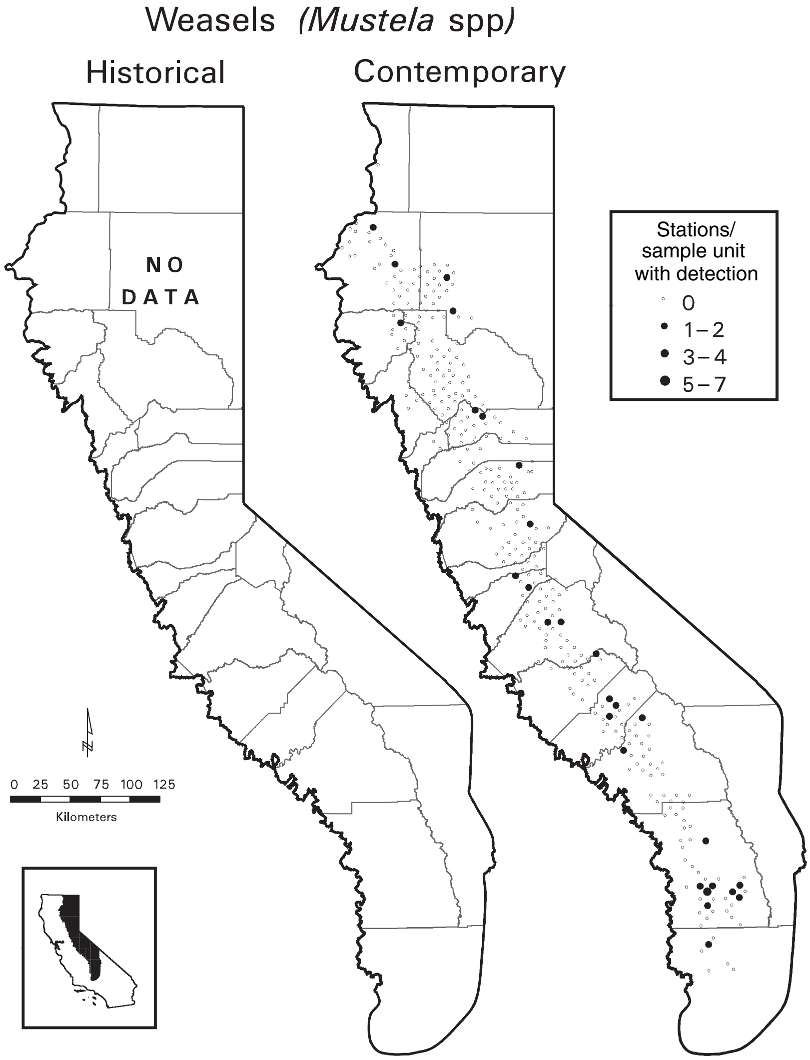

Figure 15 Distribution of the contemporary survey data for weasels. Grinnell *et al.* (1937) did not include a summary of historical records for weasels. Black dots in the contemporary map represent one or more stations per sample unit (depending on size) where a weasel was detected (1996–2002); open circles represent sample units with no detections.

The fisher, marten and opossum are the three species we detected that demonstrated the most significant changes in their distributions over the *c.* 75 years between the historical and contemporary assessments. The opossum is an introduced species with general dietary and habitat needs (Gardner & Sunquist, 2003). It has spread from its point of origin in California (the south-central coastal region; Grinnell *et al.*, 1937) relatively quickly throughout the lower and mid-elevations of the study area. This spread may be associated with the increase in residential development in the Sierra foothills (Fig. 17), and the foraging opportunities it has provided. Martens and fishers, by contrast, are among the most habitat-specialized species of mammals in North America (Buskirk & Powell, 1994). Reductions in their distributions are probably more closely linked to the influence of timber harvest and forest management during the historical and the contemporary periods.

Martens and fishers live in low productivity and highly seasonal environments, have relatively short gestations, long periods of lactation, long inter-birth intervals and large home range sizes (Ferguson & Lariviere, 2002). This suite of life history characteristics led them to be characterized as ‘bet-hedgers’ (along with wolverines), a group that is particularly vulnerable to habitat disturbance and adult mortality (Ferguson & Lariviere, 2002). The ranges of both species have contracted in North America, presumably because they are also among the most sensitive to the effects of human influence on their populations (Laliberte & Ripple, 2004). Thus, even among carnivores, which are particularly vulnerable to extinction among mammals, martens and fishers are especially vulnerable to local extirpation and our data support this conclusion. Studies conducted in Maine, Utah, and Quebec are in agreement that martens are associated with landscapes containing > 70–75% mature forest (Bissonette *et al.*, 1997; Potvin *et al.*, 2000). Loss and fragmentation of mature forest are thought to constrain marten movements (Bissonette *et al.*, 1989; Chapin *et al.*, 1998; Hargis *et al.*, 1999) and to influence demography (Fredrickson, 1990; Hargis *et al.*, 1999).

Marten responses to landscape-scale changes in forest area have not been studied in the Sierra Nevada, or in the Pacific States. However, the pattern of change in marten distribution in the Cascades and northern Sierra Nevada (Figs 6 and 7)

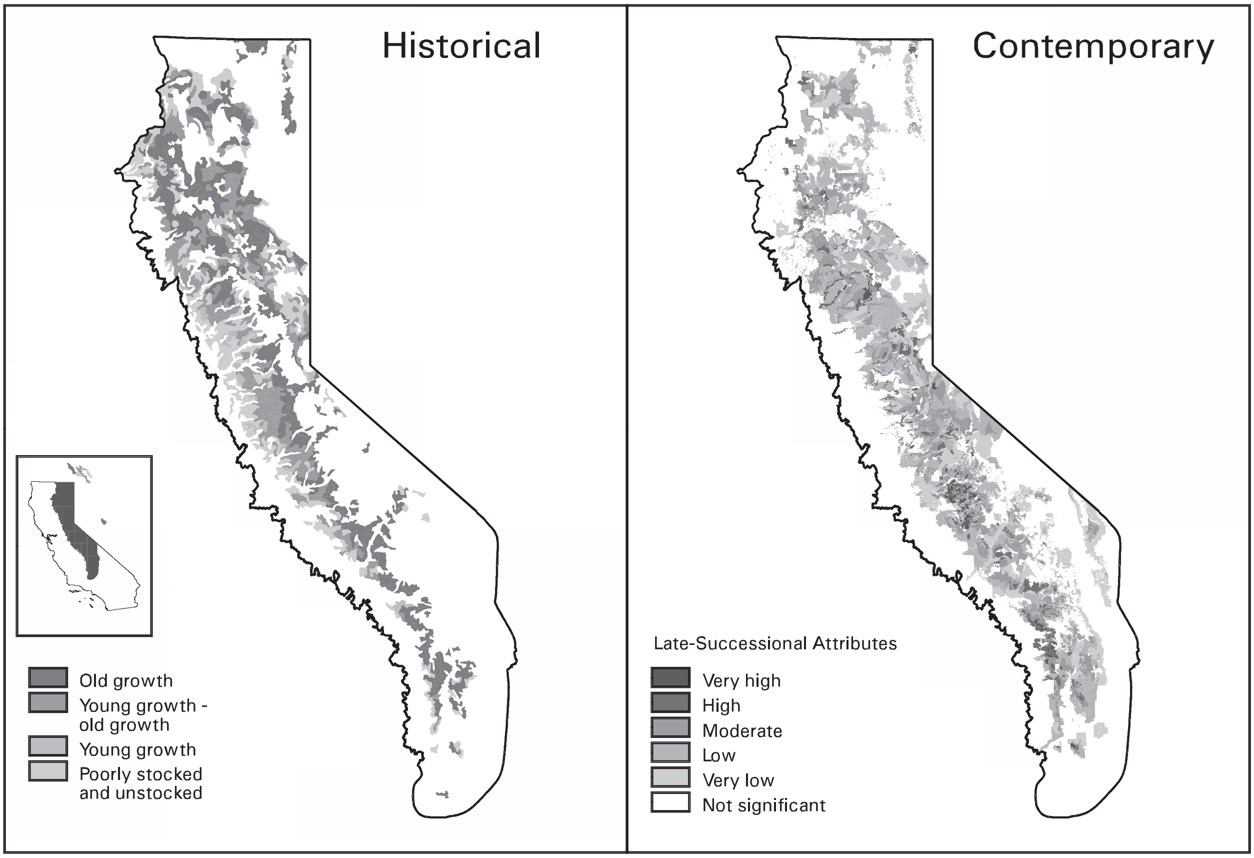

Figure 16 Maps of historical (Weislander & Jensen, 1946) and contemporary (Franklin & Fites-Kaufmann, 1996) vegetation in the Sierra Nevada Project area. The Weislander classes were defined as follows: old growth (> 50% of canopy comprised of mature trees), young growth/old growth (20–50% of conifer canopy comprised of mature trees), young growth (< 20% of conifer canopy consists of mature trees), poorly stocked (open conditions with very low density of trees), and non-commercial. The SNEP LS/OG ranks range from 0 (no contribution to late-successional forest function) to 5 (very high contribution to late-successional forest function) (Franklin & Fites-Kaufmann, 1996).

suggests that they may also respond to thresholds in the abundance and distribution of suitable habitat. Our surveys in the northern portion of the study area included almost all the elevations where marten are expected to occur. The rarity of marten detections in this region agrees with the results of previous surveys (Kucera *et al.*, 1995b; Zielinski *et al.*, 1997). The observed association of martens with areas protected from timber harvest (i.e. National Parks, Wilderness), and in areas that appear to have more residual late-seral forests, is consistent with their sensitivity to loss and fragmentation of forests. This conclusion, however, should be verified by specific studies that examine changes in vegetation more carefully and that consider other factors that may affect habitat distribution (e.g. fire, climate change).

Our survey data for martens largely support other recent descriptions of the distribution of martens in the Sierra Nevada (Schempf & White, 1977; Kucera *et al.*, 1995b). Although the earlier data do not include the same controls on sampling as the systematic surveys described here, they are valuable because they summarize marten records in the central and southern Sierra Nevada at elevations *above* where our systematic surveys terminated (usually *c.* 2100 m). Thus, although our survey data from the central and southern Sierra Nevada do not demonstrate a continuous distribution of marten detections, when interpreted with the results of previous surveys at slightly higher elevations (Kucera *et al.*, 1995b) it appears that the distribution of martens is continuous across high-elevation forests from Placer County south through the southern end of the study area.

Comparison of historical and contemporary records for fishers supports a previous description of a contemporary gap in the distribution in the Sierra Nevada (Zielinski *et al.*, 1995, 1997). The systematically collected data reported here, using a more rigorous set of data, confirm the presence of a *c.* 430 km gap in the distribution. This is of concern primarily because the gap is more than four times the known maximum dispersal distance for fishers (100 km; York, 1996). Thus, the isolation of the fisher population in the southern Sierra Nevada puts them at greater risk to extinction than if it were connected to other populations.

The fisher also occurs at a relatively low elevation which puts it in closer proximity to human activities than the congeneric

Table 3 Total and percent of area occupied by each vegetation type for assessments in 1945 (Weislander) and 1996 [Sierra Nevada Ecosystem Project (SNEP)]

	North		South		Total	
	Ha	%	Ha	%	Ha	%
Weislander & Jensen (1946)						
Rank						
1 (Old growth)	755432	43	476228	67	1231660	50
2 (Young/old growth)	568202	32	85501	12	653703	26
3 (Young)	42197	2	18328	3	60525	2
4 (Poorly Stocked)	285916	16	127662	18	413578	17
Non-commercial	124738	7	3997	1	128735	5
Total	1776485		711716		2488201	
Sierra Nevada Ecosystem Project (1996)						
LS/OG Rank						
5	17292	1	53824	8	71116	3
4	133344	8	89724	13	223068	9
3	426542	24	214231	30	640773	26
2	714471	40	199589	28	914060	36
1	270158	15	101177	14	371335	15
0	214678	12	53171	7	267849	11
Total	1776485		711716		2488201	

The Weislander classes were defined as follows: old growth (> 50% of canopy comprised of mature trees), young growth/old growth (20–50% of conifer canopy comprised of mature trees), young growth (< 20% of conifer canopy consists of mature trees), poorly stocked (open conditions with very low density of trees), and non-commercial. The SNEP LS/OG ranks range from 5 (very high contribution to late-successional forest function) to 0 (no contribution to late-successional forest function) (Franklin & Fites-Kaufmann, 1996). The dividing line between 'north' and 'south' is approximately the centre of Tuolumne county (see Fig. 1).

Table 4 Probability matrices for transitions of vegetation type classifications between 1945 (Weislander rank) and 1996 [Sierra Nevada Ecosystem Project (SNEP), late seral/old growth rank (LS/OG)]

	SNEP LS/OG rank					
	5	4	3	2	1	0
Northern Sierra						
Weislander Rank						
1 (Old growth)	0.01	0.09	0.29	0.42	0.10	0.09
2 (Young/old growth)	0.003	0.06	0.21	0.44	0.17	0.12
3 (Young growth)	0.007	0.07	0.22	0.34	0.20	0.16
4 (Poorly stocked)	0.01	0.06	0.15	0.31	0.29	0.18
0 (Non-commercial)	0	0.11	0.26	0.37	0.07	0.20
Southern Sierra						
Weislander Rank						
1 (Old growth)	0.11	0.16	0.34	0.23	0.11	0.05
2 (Young/old growth)	0.02	0.07	0.31	0.29	0.22	0.09
3 (Young growth)	0.02	0.002	0.13	0.50	0.11	0.14
4 (Poorly stocked)	0.006	0.06	0.17	0.42	0.24	0.10
0 (Non-commercial)	0.02	0.01	0.04	0.89	0	0.05

The Weislander classes were defined as follows: old growth (> 50% of canopy comprised of mature trees), young growth/old growth (20–50% of conifer canopy comprised of mature trees), young growth (< 20% of conifer canopy consists of mature trees), poorly stocked (open conditions with very low density of trees), and non-commercial. The SNEP LS/OG ranks range from 5 (very high contribution to late-successional forest function) to 0 (no contribution to late-successional forest function) (Franklin & Fites-Kaufmann, 1996). The dividing line between 'north' and 'south' is approximately the centre of Tuolumne county (see Fig. 1).

marten. Interestingly, the gap in the fisher historical distribution aligns well with the area of greatest increase in human influence (Fig. 17). In these areas homes are built in fisher habitat, roads are more common, the forests around the built environment developments are managed to reduce forest density, and there is long history of private land management for timber (compared with public land managed for multiple uses). These factors probably conspire to render home range areas less suitable, leading to the contraction of range in this area. Thus, the fisher may be especially vulnerable to extinction because it is handicapped by 'unfavourable biology' *and* by the unfortunate circumstance of occurring in a region of rapid human influence; two factors that combine to increase the risk of carnivore extinction (Cardillo *et al.*, 2004). Furthermore, the fisher populations in the Sierra Nevada are genetically less diverse than fishers elsewhere in western North America (Drew *et al.*, 2003), probably because of a combination of the 'one dimensional' shape of the geographic range in the Pacific States and the legacy of habitat fragmentation (Wisely *et al.*, 2004).

It is of interest to note how few historical records of fishers exist in the northern Sierra Nevada and the southern Cascades (Fig. 8). That this is the same region where we did not detect fishers during contemporary surveys suggests that the dearth of historical records may not simply be an artefact of sampling bias. The paucity of fisher records in the southern Cascades and northern Sierra Nevada may be because fishers, coveted by trappers, had already been trapped out by the time their status was first assessed. This region includes the primary gold-bearing region exploited during the 'gold rush' of the mid-1800s. This rapid human population expansion was accompanied by the advent of railroad logging and it is likely that considerable habitat for fishers was eliminated, and the high price for their pelts made fisher the target species for many trappers (Grinnell *et al.*, 1937). This possibility illustrates that our 'historical' distributions may not be synonymous with distributions that predate European settlement. The fisher population was likely already reduced by the time that Grinnell and colleagues assessed the distribution (Grinnell *et al.*, 1937). Despite the lack of historical records from this region, Grinnell *et al.* (1937, p. 215) described the original range of the fisher as including the region: '…south from Mount Shasta and Lassen Peak throughout the main Sierra Nevada…'. We find no reason to suspect that fishers did not once occupy forests in suitable elevations throughout the Sierra Nevada.

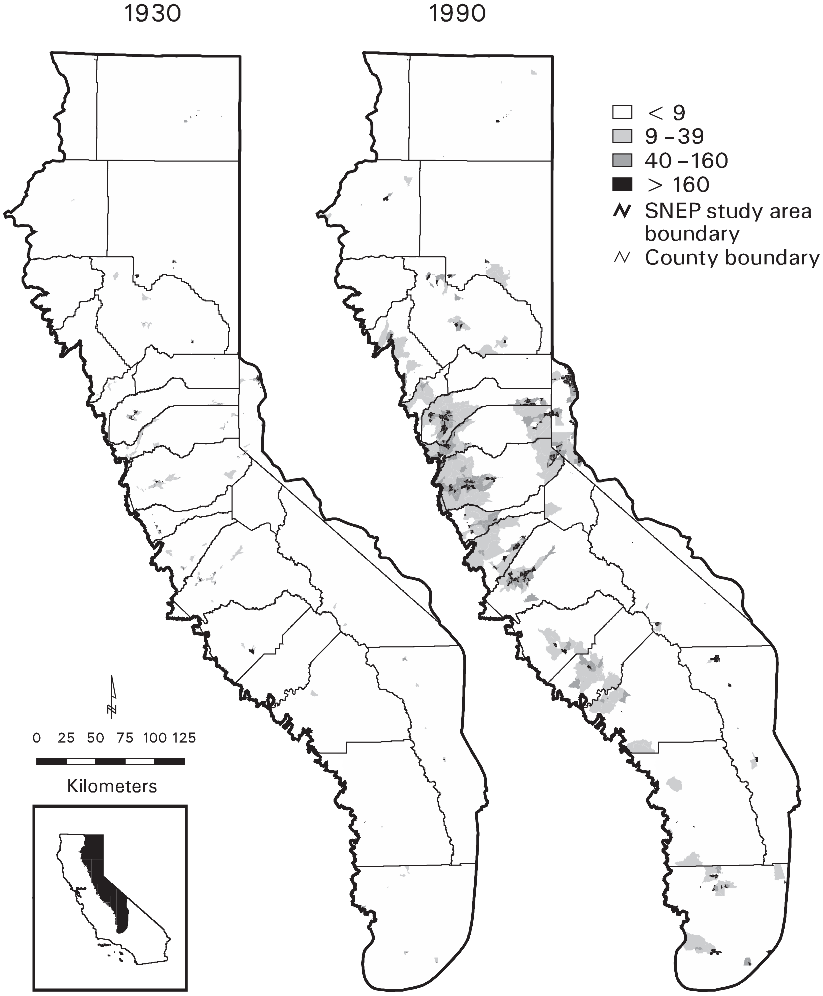

Figure 17 Housing densities (per square mile) in 1930 and 1990 for the Sierra Nevada Ecosystem Project study area. Data were compiled from Forstall (1996) and the 1990 Census of Population and Housing (Duane, 1996).

Notwithstanding the unique value of comparing historical records of trapping locations and contemporary detections, the use of these data sets to evaluate change in distributions is not without problems. Sample units of the contemporary surveys were coarsely distributed over vast areas and, as such, are best designed to detect populations rather than individuals. We are aware, for example, of individual detections of martens at camera stations and of reports of individual fisher sightings in regions where our sample units did not detect them. A survey of this nature cannot simultaneously maximize grain and extent. However, our surveys regularly detect species at locations where we have specific information from other sources (e.g. previous studies of marked individuals) about the location and relative abundances [i.e. studies of fishers (Zielinski *et al.*, 2004) and martens (Zielinski, 1981)]. Although we are confident that our survey accurately reflects the geographic distributions of each species, we know that we have not detected every individual at every location. We argue, however, that achieving the larger goal of describing the distribution of detections is the best first step toward determining the current status of each species and identifying populations at risk. It appears that the biological characteristics (generalists vs. specialists) of individual species, in combination with the effect of human activities, have combined to affect the current distributions of carnivores in the Sierra Nevada. A continued program of periodic resampling of the distributions of carnivores, via the survey methods used here, will be a useful means of assessing the effect of humans and environmental change on the forest habitats of carnivores in California.

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