



Reproduction, abundance, and population growth for a fisher (*Pekania pennanti*) population in the Sierra National Forest, California

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In the west coast region of the United States, fishers (*Pekania pennanti*) exist in 2 remnant populations—1 in northern California and 1 in the southern Sierra Nevada, California—and 3 reintroduced populations (western Washington, southern Oregon, and northeastern California). The West Coast Distinct Population Segment of fishers encompassing all of these populations was proposed for listing as threatened by the U.S. Fish and Wildlife Service in October 2014. There are likely fewer than 500 total fishers in the southern Sierra Nevada population isolate, but empirical data on demographic rates, population size, and population growth are almost entirely lacking. Our goal was to estimate demographic parameters and current abundance of a fisher population at the north margin of the southern Sierra Nevada region. Radiocollared fishers were monitored from 2007 to 2013 to estimate survival and demographic rates, and camera traps were used to estimate population size based on detections of individual animals in a capture–mark–resight (CMR) framework. A Leslie matrix model was used to estimate a deterministic population growth rate (λ). Fisher abundance ranged from 48 animals in 2010 to 62 animals in 2012, whereas mean population density varied from 0.075 to 0.096 fishers/km². Reproductive status was determined for 89 of 93 total denning opportunities; denning and weaning rates were estimated at 84% and 70%, and litter size was 1.6 kits. We documented 8 den failures, mostly associated with predator attacks. Demographic rates in the study population were comparable to reports from elsewhere in California or Oregon, but the CMR-based population density was the lowest reported in the United States. The estimated λ for the population was 0.966 (range 0.786–1.155), which was in agreement with no indication of a positive or negative trend in population density. An encouraging result from sensitivity analyses was that minor improvements in fisher survival and fecundity, facilitated by proposed mitigation or management to reduce exposure to several agents of mortality, could improve λ to 1.06–1.09 over the longer term. We believe that the combination of a population growth rate slightly below 1.0, small population size and low density, multiple challenges to survival and reproduction, and damage to habitat from wildfires warrants concern for the viability of the fisher population in our study area, which may extend to the overall southern Sierra Nevada population if λ trends below 1.0 in other parts of the region. There is a need for continued monitoring and potential mitigation for threats to survival to assure continued presence of fishers in the southern Sierra Nevada, California.

Key words: density, fecundity, fisher, lambda, mark–resight, Martes, *Pekania pennanti*, reproduction

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Information on population size and demographic parameters is fundamental for managing wildlife populations, especially when declines in abundance or range size have occurred and the species is the focus of conservation management. The fisher (*Pekania pennanti*) is one such species, and in the western United States, these animals were in decline after the early 1900s by the combination of commercial trapping (Lewis and

Zielinski 1996) and loss of forest habitat from logging and development (Lofroth et al. 2010). Fishers are a medium-sized mammal with a pre-European distribution in North America that encompassed the boreal forest zone of Canada, the Great Lakes region and northeastern United States, a portion of the Rocky Mountains in the United States, and mountainous areas of Washington, Oregon, and California (Gibilisco 1994). They

are a mature or old forest-obligate species (Powell et al. 2003), and while the era of clear-cut logging has mostly been replaced by more sustainable practices in western United States forests (North et al. 2009), an emerging concern for fishers in this region is large-scale loss of habitat from wildfires promoted by buildup of fuels from historic suppression of fires (Noss et al. 2006; Scheller et al. 2011). Increasingly frequent wildfires are particularly problematic for dense canopy, mature forests in the western United States (Bonan 2008; Safford et al. 2012) that provide denning and resting habitat for fishers (Purcell et al. 2009; Zhao et al. 2012; Aubry et al. 2013).

Multiple different field studies recently reported that fisher populations in the western United States are challenged by exposure to infectious disease (Keller et al. 2012; Gabriel 2013), attacks by larger predators (Wengert et al. 2014), collisions with vehicles on busy highways (Chow 2009; Lewis 2014), and exposure to rodent poisons (Gabriel et al. 2012; Thompson et al. 2013). Therefore, in October 2014, the U.S. Fish and Wildlife Service proposed to list the West Coast Distinct Population Segment (DPS) of fisher as threatened under the Endangered Species Act (U.S. Department of the Interior Fish and Wildlife Service 2014). The basis for the proposed listing (U.S. Fish and Wildlife Service listing proposal) included habitat loss from wildfire and vegetation management, exposure to rodenticides and other toxicants, and the cumulative effects of these and other stressors acting on small populations (U.S. Department of the Interior Fish and Wildlife Service 2014).

Within the West Coast, DPS fishers currently exist in 3 reintroduced populations in western Washington (Lewis 2014), southern Oregon (Aubry and Lewis 2003), and northeastern California (Powell et al. 2013) and 2 remnant populations in northern California and in the southern Sierra Nevada, California (Zielinski et al. 2005). Although the recent reintroductions of fishers near Mount Lassen succeeded in establishing a third population of 30 to < 100 animals in northeastern California (A. Facka, North Carolina State University, pers. comm.), the small fisher population of < 500 total animals in the southern Sierra Nevada region remains spatially and genetically isolated from all other fishers in the West Coast DPS (Knaus et al. 2011; Spencer et al. 2011). Therefore, and long prior to October 2014, there has been heightened concern regarding the status of fishers in the southern Sierra Nevada region (Grinnell et al. 1937; Zielinski 2013).

Fishers in the southern Sierra Nevada population currently occupy approximately 4,400 km² of mid-elevation, mixed-coniferous forest between the Merced River in Yosemite National Park in the north to the Greenhorn Mountains in the Sequoia National Forest in the south (Fig. 1; Spencer et al. 2014). Our goal in this study was to provide empirical data on demographic parameters and current abundance and density of the fisher population within Fisher Core Habitat Area 5 in the southern Sierra Nevada region (Fig. 1) to support conservation and management planning by the USDA Forest Service and the National Park Service. We estimated fisher population size and density across 4 years using capture-mark-resight (CMR—McClintock and White 2009) techniques from camera

trap surveys and livetrapping, reproductive rates and fecundity from close monitoring of denning behavior during 6 spring den seasons, and population growth rates by integrating survival and demographic rates into a matrix population model. Also, information on mean population density from CMR analyses was used to estimate the number of fishers in Fisher Core Habitat Area 5.

MATERIALS AND METHODS

Study area and site description.—The overall study area was the non-wilderness region of the Bass Lake Ranger District in the Sierra National Forest, near Oakhurst, California, and covered approximately 1,125 km² (Fig. 2). The study area encompassed a mix of public and private land with elevations ranging from 758 to 2,652 m (Fig. 2). Field work was carried out between 1,000 and 2,400 m in elevation, corresponding to fisher occurrence in the region. For purposes of analyses, the study area was partitioned into 3 subregions based on geographic features or landmarks: Nelder Creek, Sugar Pine, and Miami Mountain (subregion 1); Central Camp, Whisky Ridge, Grizzly Meadow, and Jackass Rock (subregion 2); and Chowchilla Mountain, Rush Creek, and Sweetwater Mine (subregion 3; Fig. 2). Less intensive research, primarily restricted to camera trapping and monitoring of radiocollared fishers by fixed-wing airplane, was also conducted in the Yosemite South part of the overall study area (Fig. 2).

Subregion 1 encompassed a focal study region where camera surveys and livetrapping were repeated each year as part of the larger study assessing the effects of forest management (commercial thinning, brush control, control burning) on fishers and other components of the forest ecosystem (Popescu et al. 2012). A complete description of the focal study area is detailed elsewhere (Zhao et al. 2012), and of limited relevance here except to note that research effort (livetrapping and camera trapping) was typically higher in the focal study area such that camera trapping and livetrapping were unbalanced within the 3 subregions among years.

Primary tree species in approximate order of abundance for conifers and then hardwoods are incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), California black oak (*Quercus kelloggii*), mountain dogwood (*Cornus nuttallii*), white alder (*Alnus rhombifolia*), and aspen (*Populus tremuloides*). Giant sequoia (*Sequoiadendron giganteum*) was present but restricted to remnant populations in a few areas. Common shrubs and tree-like shrubs in the study area include willow (*Salix* sp.), whiteleaf manzanita (*Arctostaphylos viscidula*), greenleaf manzanita (*Arctostaphylos patula*), mountain misery (*Chamaebatia foliolosa*), elderberry (*Sambucus caerulea*), bush chinquapin (*Chrysolepis sempervirens*), mountain whitethorn (*Ceanothus cordulatus*), Sierra gooseberry (*Ribes roezlii*), and buckthorn (*Rhamnus californica*).

Trapping and radiotelemetry.—Individual fishers were live captured in steel mesh traps (Tomahawk Live Trap Company, Hazelhurst, Wisconsin) modified to include a plywood cubby

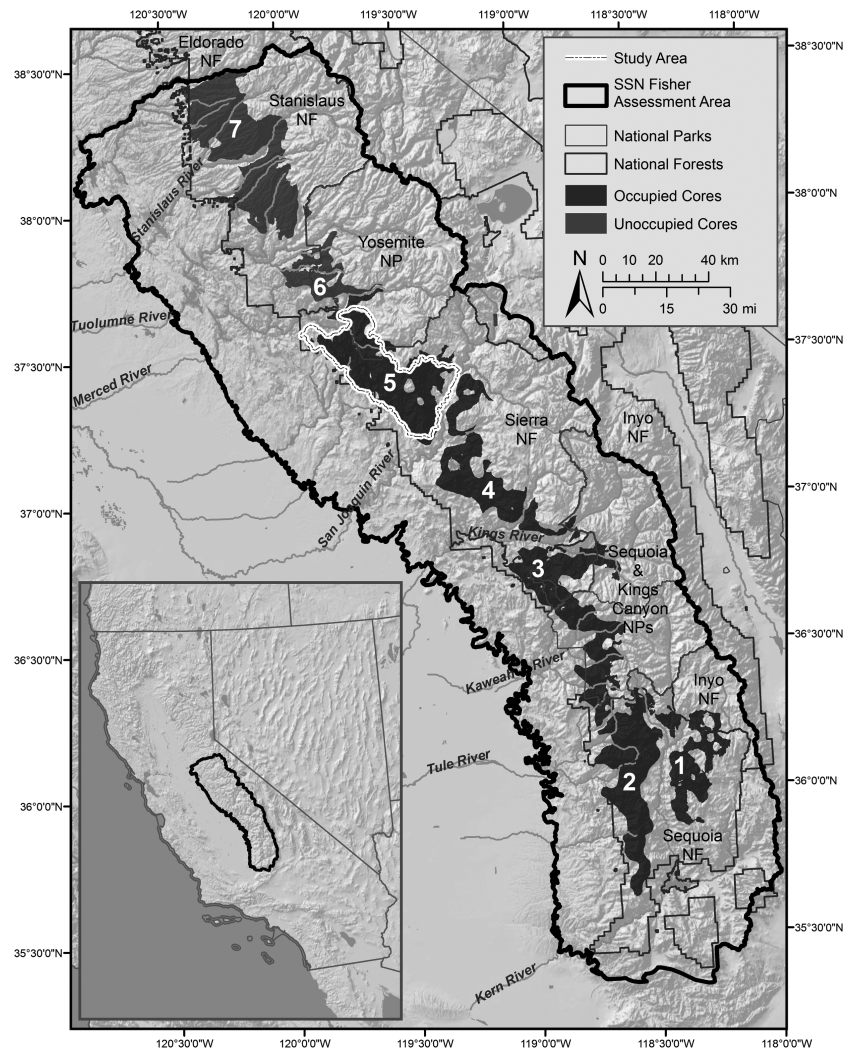


Fig. 1.—Map illustrating the distribution of 5 occupied and 2 unoccupied fisher (*Pekania pennanti*) core habitat areas in the Southern Sierra Nevada Fisher Conservation Planning and Assessment area. Habitat cores were mapped as contiguous polygons having a predicted probability of fisher occupancy exceeding 0.41 and large enough to support ≥ 5 adult female fishers (detailed by [Spencer et al. 2015](#)). This figure was originally developed by the Conservation Biology Institute (San Diego, California) and was redrawn and included in this manuscript by permission of W. Spencer.

box to provide the animals with a secure refuge where they were less likely to injure themselves ([Wilbert 1992](#)). Trapping to mark animals with radiocollars was focused during the fall and winter seasons between December 2007 and March 2012. Traps were baited with venison and checked daily by late morning. We restrained captured animals in a handling cone and sedated them using a mixture of ketamine hydrochloride and diazepam (1 mg diazepam/200 mg ketamine) injected intramuscularly. Sedated fishers were weighed, classified by age and gender based on examination of teeth and genitalia, and measured for standard morphological features. Ages assigned at capture were juvenile (< 12 months), subadult (12–23 months, 1 year old), and adult (≥ 24 months; ≥ 2 years old). Teats on females were measured for base diameter and height using digital calipers (± 1 mm), and those data were used to identify females that reproduced when they had not been monitored during the denning period ([Matthews et al. 2013a](#)). Each animal was permanently identified by subcutaneous insertion

of passive integrated transponder (PIT) tags (Biomark, Boise, Idaho) and fitted with Holohil or ATS VHF radiocollars with mortality switches (Holohil Systems Model MI-2M, Ontario, Canada; Advanced Telemetry Systems Model 1930 or 1940, Isanti, Minnesota). Radiocollars were modified by attaching small bands (0.5–1.0 cm) of infrared reflective tape along the lengths of the antennas in unique patterns, and leather break-away devices were inserted into radiocollars fitted to juvenile fishers to avoid injury and provide room for growth between recaptures. After handling, we returned animals to the cubby box and released them after recovery. Capture and handling followed American Society of Mammalogists guidelines ([Sikes et al. 2011](#)) and were approved by the Animal Care and Use Committee of the University of California, Berkeley (protocol R139).

Monitoring and home ranges.—Radiocollared fishers were monitored for survival status and to evaluate home range extent and movement behavior by relocating them 4–6 days/week

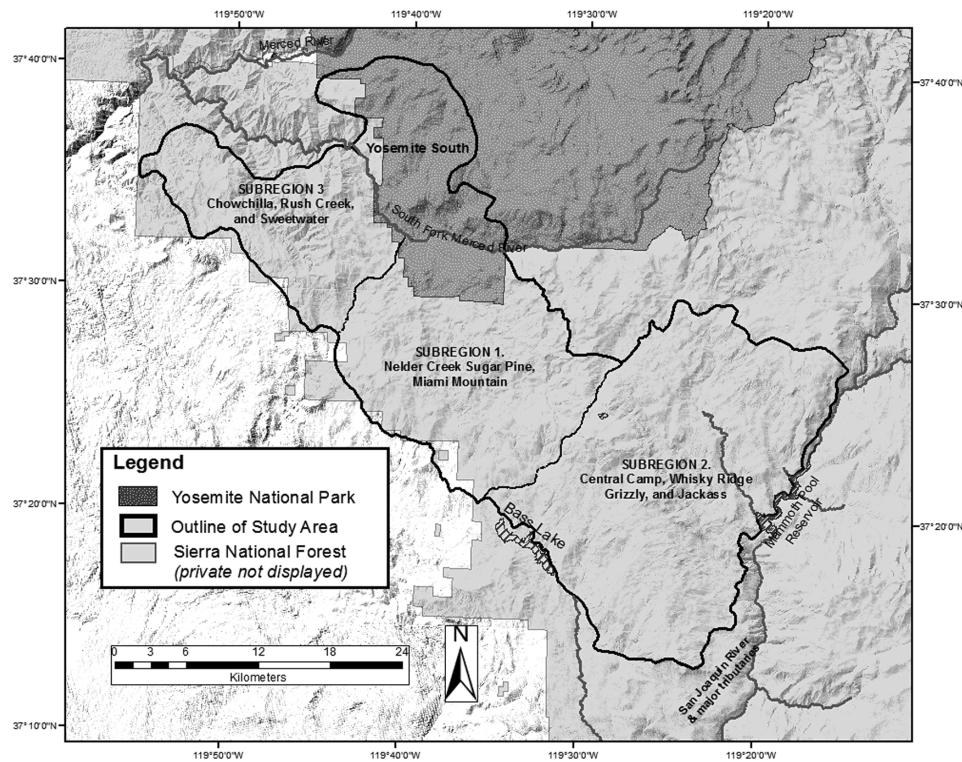


Fig. 2.—Map illustrating the overall study area and identifying the 3 subregions used for mark–resight population estimates. The study area is within the Bass Lake Ranger District, Sierra National Forest, California, and also included a relatively small portion of Yosemite National Park (Yosemite South).

throughout the year by fixed-wing airplane (Cessna 185, Cessna Aircraft Co., Wichita, Kansas). Standard methods were used to obtain aerial radiotelemetry locations (AT locations) from the airplane (Thompson et al. 2012a), and we assessed error by calculating distances between estimated locations obtained by the biologist in the airplane and locations of “test” collars at fixed positions in the study area ($n = 501$ test collars). Mean error for AT locations was 339 m (range 15–1,220 m).

Locations were used to develop home range models for individual fishers using the fixed-kernel density method in Home Range Tools for ArcGIS 9.3 (Rodgers et al. 2007). Ninety-five percent fixed-kernel home ranges were produced for individual animals for 4 periods (October–March) from 2008 to 2012 when ≥ 25 locations were available for a fisher. Home range area from fixed-kernel utilization distributions is sensitive to the choice of bandwidth as a smoothing parameter (Gitzen and Millspaugh 2003), and we used the ad hoc method to identify the most appropriate bandwidth for fisher home ranges (Kie 2013). Our purpose for determining fisher home ranges was to evaluate areas sampled by camera surveys and livetrapping and to use those data to estimate fisher population density (detailed below).

Camera surveys and livetrapping.—Motion sensing, camera traps (Silent Image Professional, Rapidfire PC85; RECONYX Inc., Holmen, Wisconsin) were systematically deployed near the center of 1×1 -km grid cells within the study area beginning at the start of each of 5 camera survey years (15 October–14 October the following year). Fine-scale spacing of cameras

ensured that radiocollared fishers had multiple chances of detection (O’Connell et al. 2010), and the 1-km² grid layer was central to other research objectives aimed at assessing responses of fishers to relatively small-scale forest management activities in the study area (Popescu et al. 2012).

We placed camera traps within 1-km² cells by navigating to the grid center with a handheld Global Positioning System unit (Garmin model 60 CSx; Garmin, Olathe, Kansas) and placing the camera trap at the nearest position including one or more habitat elements known important for fishers (e.g., presence of mature or large diameter trees, moderate to steep slopes, canopy cover $\geq 60\%$, proximity to permanent streams—Zielinski et al. 2004; Purcell et al. 2009). Cameras were focused on bait trees upon which we attached baits and applied scent lures as attractants. We used small pieces of venison (140–250 g) in a dark colored sock for a meat bait for fishers and 8–10 hard-shell pecans strung onto a length of wire and formed into a “nut ring” as bait for squirrels. Our initial purpose of the nut bait was to index squirrel abundance, but the pecans were also consumed by fishers. The scent lures we used were Hawbaker’s Fisher Scent Lure, Caven’s “Gusto” scent lure (Minnesota Trapline Products, Pennock, Minnesota), and ~4 g of peanut butter smeared on the nut ring (Popescu et al. 2014). Camera trap stations were typically visited every 8–10 days over 32–40 days to maintain cameras and to refresh scent lures and baits. However, the camera trap protocol varied across the study area. Camera traps placed outside of the focal study area within subregion 1 were removed after two or three 8- to

10-day sessions when fishers were detected prior to 32–40 days of survey duration. We removed all cameras after four 8- to 10-day sessions, unless the unit had been disturbed and the bait tree was out of view, or if the unit had been inoperative due to expended batteries or malfunction for more than 5 days during any session. In those cases, we extended the survey by one or more 8- to 10-day periods to assure adequate survey effort (Slauson et al. 2009). Camera trap surveys were done during all months of each camera survey year, but our time frame of interest for this study was mid-October to mid-March, related to assumptions for mark–resight analyses of a closed population scenario.

We also focused our livetrapping effort from mid-October to mid-March each year and did not trap between mid-March and late June to prevent disturbance to denning fishers. Livetrapping provided resightings for population estimation, allowed for examining individuals for evidence of reproduction, and facilitated replacing expended radiocollars and the capture of young-of-the-year juveniles and previously unknown fishers in the study area. Livetrapping is labor intensive, and we gained advantage from detections of noncollared fishers at camera stations by trapping in the same general areas where we detected fishers, but only after completing the camera surveys to prevent interference with those surveys. Data from camera detections were used to design linear traplines of 5–10 traps bracketing positive detection stations. Our traplines were usually successful at capturing targeted animals within 5 nights of trapping and were generally removed after targeted fishers were captured, but always after 10 nights of trapping when no fishers were captured. Fishers sometimes shed their radiocollars, or collars separated at the breakaways as designed. Dropped radiocollars were retrieved from the field, and the locations of shed radiocollars were included in the resight data set.

Resighting and mark–resight analyses.—We identified radiocollared fishers detected at camera traps by the pattern of infrared reflective tape on the antennas (Popescu et al. 2014). Detections of known ID fishers were counted once per camera trap station per calendar day. We were not able to unambiguously identify all radiocollared fishers detected at camera traps due to occasional loss of bands and breakage of collar antennas; these detections were counted as marked unidentified. Noncollared animals were counted as unmarked sightings, and all recaptured fishers were identifiable from radiocollar frequencies or by scanning for PIT tags.

We compiled data on fisher resightings for each of four 5-month survey periods from October 16 to March 15 during 4 years. We considered the population as approximating closure during October to mid-March because most mortalities in the study site occurred between mid-March and September (R. A. Sweitzer, pers. obs.), natal dispersal by juvenile-age fishers in the population was focused during March to August (R. A. Sweitzer, pers. obs.), and fisher reproduction in California begins the 3rd week in March (Matthews et al. 2013b).

The number of resightings for each collared fisher at camera stations or livetraps were counted for each 1-km² grid that was surveyed each season. Recent insight on the consistency

of different data types for estimating abundance indicates that camera detections can be used to assess animal space use similar to fixed-kernel home range models (Popescu et al. 2014). We therefore used information on positions of camera traps in relation to fisher home ranges when compiling the CMR data set. Detection histories for each collared animal were developed, and only those fishers that were available for resighting based on presence of cameras or livetraps within the boundaries of their October to March home ranges were included in the analyses. We also compiled data on the numbers of survey cameras and livetraps deployed, survey camera nights, and livetrapping nights for each 5-month survey period.

We analyzed resight data using mark–resight robust-design, log-normal Poisson models (McClintock and White 2009). The mark–resight robust design is analogous to the mark–recapture robust design of Kendall et al. (1995, 1997) in modeling resight probabilities as functions of individual covariates and allowing open population between primary sampling occasions. Along with data on marked animals, mark–resight models incorporate sightings of unmarked animals; thus, the robust design allows for estimating the number of unmarked animals in the population (U), apparent survival between primary intervals (ϕ), the intercept for mean resighting rate (α), random individual heterogeneity (σ^2), and transition probabilities between observable and unobservable states (γ'' and γ' —McClintock and White 2009). Two quantities of interest, total population size (N) and overall mean resighting rate (ψ), are derived parameters (McClintock and White 2009).

The Poisson log-normal mark–resight model takes the following form:

$$[\alpha(\cdot)\sigma(\cdot)U(\cdot)\phi(\cdot)\gamma''(\cdot)\gamma'(\cdot)]$$

in which ϕ and γ'' (and γ') were modeled using a sin link, while α , σ , and U were modeled using a log link.

The model assumptions are geographic closure, population closure within primary intervals, no unidentified loss of marks, no error in identifying marked and unmarked animals, equal resighting probability for both marked and unmarked individuals, and sampling with replacement within secondary periods (McClintock and White 2009). We used camera survey year as the primary sampling interval and the number of resights and livetrapping recaptures within each primary interval as the resighting histories (Appendix I). Along with capture histories, robust-design Poisson log-normal models require 3 other quantities: marked superpopulation, the number of marked individuals known to be in the population during primary interval j , number of times marked individuals were sighted, but individual marks could not be identified, and total unmarked individual sightings during primary interval j (Table 1).

We used a grouping variable (subregion or area) to account for spatial segregation of camera trap effort among the 3 subregions (Fig. 2) and to more efficiently estimate resighting probabilities (Magle et al. 2007). Each fisher was assigned to one of the subregions based on the centroids for their 60% October–March home range. In addition, we used area and time

Table 1.—Summary data on noncollared and collared fishers (*Pekania pennanti*) that were detected by camera traps and livetraps in four 5-month camera survey years (16 October–15 March) in the Bass Lake Ranger District, Sierra National Forest, October 2008 to March 2012.

Region/year	Unmarked seen	Marked no ID	Known marked	Known marked fishers resighted
Subregion 1. Nelder Grove, Sugar Pine, Miami Mountain				
2008–2009	37	12	22	21
2009–2010	55	73	20	20
2010–2011	157	35	14	14
2011–2012	108	42	18	18
Subregion 2. Central Camp, Whisky Ridge, Grizzly, Jackass				
2008–2009	53		7	7
2009–2010	9	2	10	9
2010–2011	18	1	13	12
2011–2012	37	1	15	15
Subregion 3. Chowchilla Mountain, Rush Creek, Sweetwater				
2008–2009	10		7	7
2009–2010	5		8	7
2010–2011	1		8	7
2011–2012	3	1	13	13

specific covariates cams (camera effort for each subregion during each primary sampling interval in hours) and live (number of days livetrapping was conducted) to account for variation in resighting probabilities and individual covariates *weight* and *sex* to account for individual and gender-based resighting probabilities, apparent survival, and abundance. In the model parameterization, state transition probabilities remained constant [$\gamma'(\cdot)$ and $\gamma''(\cdot)$], apparent survival was modeled as a function of region [$\phi(\text{area})$], and different combinations (additive and interactions) of the individual and time and region-based covariates were allowed.

We considered 19 different candidate models and used AICc (Akaike information criterion adjusted for small sample size—Burnham and Anderson 2002) to rank them. We then used model averaging for the top ranked models with a cumulative Akaike weight > 0.95 to compute parameters and unconditional variances. The area grouping parameterization allowed for estimating population size and density for each subregion separately. We conducted the analyses in program RMark v2.1.7 (Laake 2013) for R 3.0.2 (R Core Team 2013), which is an interface for program MARK (White and Burnham 1999). Lastly, the subregion and year-specific abundances were converted to densities by dividing population estimates by the area sampled by cameras and traps for each subregion and year (Jordan 2007). Areas sampled were estimated from subregion- and year-specific polygons created in ArcGIS 10.2 (Environmental Systems Research Institute 2011) that encompassed the centroids of all 1-km² grid cells with a survey camera or a livetrapping with a fisher capture during 15 October to 16 March. We then plotted the October to March home ranges with the sampling polygons, and, based on visual assessment of spatial intersection of the 95% home range isopleths, applied a 1,300-m buffer for each polygon. We defined the width of the buffer for the polygons as the radius of the mean October to March home range for subadult and adult female fishers in the population (20.8 km² ±

0.89 SE, $n = 70$), which encompassed most areas used by radio-collared fishers in each subregion and excluded areas below or above the typical elevation range of fisher camera detections in the study area (1,100–2,200 m).

Reproduction and fecundity.—Female fishers exhibiting behavior consistent with denning were monitored during late March–mid April. We recognized denning behavior by an abrupt change from a pattern of successive AT locations that were dispersed within a female's home range to a pattern where AT locations were spatially clustered (Zhao et al. 2012). When we identified clustering of AT locations, a UTM coordinate was produced and a technician navigated to the area with a handheld GPS unit to investigate. We used standard ground-based radio-telemetry homing methods with a handheld receiver (model R1000; Communication Specialists, Inc., Orange, California) to investigate suspected denning areas and to locate specific den structures being used for denning (Matthews et al. 2013b). When we had localized female fishers in possible den structures, 2–4 automatic “den cameras” were attached to nearby trees and focused on the bole of the den structure. All den cameras were cleaned and descended, and we did not place any baits or scents near den trees to avoid attracting other predators. We returned to these structures the day after initial placement of den cameras and then every 3–5 days to confirm use based on regular occupancy and images indicating up and down movements on the tree or snag. Structures that were used ≥ 3 times in succession and with evidence of up-down movements were considered denning structures (Zhao et al. 2012). We defined “denning opportunities” as the total number of individual, breeding age (≥ 2 years old) female fishers either directly monitored in mid-March to June (Matthews et al. 2013b), or measured for teat size during July to January to assess reproductive status (Matthews et al. 2013a). We considered kits weaned when denning continued until 31 May or later (Matthews et al. 2013b), unless the female was known to have died before 30 June (Facka et al. 2013).

We chronicled the activities of known-denning female fishers for the duration of each denning season by continuous monitoring. Female fishers typically transfer kits from structures in which they were born (natal dens) to 1–6 other trees or snags (preweaning dens—Lofroth et al. 2010) during April to June (Matthews et al. 2013b). Each time we had evidence that a denning fisher moved kits to a new preweaning den (images of females transporting kits away from den trees, cessation of occupancy over multiple checks), we searched for the female using ground telemetry and repositioned cameras around the next preweaning den (Zhao et al. 2012). Den cameras were removed in mid-June when females ceased localizing to den structures.

We assessed litter size for denning females using images from den cameras or, less frequently, by climbing den trees and using a video camera (Peep-A-Roo Video Probe System, Sandpiper Technologies, Manteca, California) to count kits inside den cavities (Matthews et al. 2013b). We minimized disturbance to denning females by restricting visits to den structures to service cameras to once every 3–5 days, using deployments of

den cameras for obtaining the majority of kit counts, and not approaching den trees for climbing until ground-based telemetry indicated the female was well away from the den structure (Zhao et al. 2012). We estimated maximum reproductive rate as the sum of the number of adult-age female fishers (≥ 24 months) in the radiocollared population that localized to den trees during the den season plus the number of adult females with enlarged teats that were not monitored but measured before January divided by the number of adult-age female fishers in the population during mid-March to late January. We estimated weaning rate as the number of adult-age females known to have survived and localized to den trees through 31 May, whereas annual estimates of fecundity were calculated as the total number of weaned kits/number of females with known kit counts. Although the weaning index is reliable for identifying reproduction, the procedure does not always identify females with den failures or the number of kits produced (Matthews et al. 2013a). Therefore, we did not consider data on teat size when estimating weaning rates, kit production, or litter size.

Fertility and population growth rate.—We developed an age-structured Leslie matrix model (LM model) to estimate a deterministic population growth rate (λ) for the study area during 2008–2012 using the observed reproductive rates and data on fisher survival (R. A. Sweitzer, pers. obs.). The LM model was a “pre-birth-pulse” model (Mills 2007) based on capturing, monitoring, and estimating age-specific survival for the fisher biological year from 18 March to 17 March. The fisher biological year was defined based on when fishers initiated denning behavior in 5 studies of fishers in the western United States (R. A. Sweitzer, pers. obs.). Matthews et al. (2013a) previously reported age-related variation in denning rate and kit production for fishers in northern California; denning rates and litter size were lower for 2-year-old females than ≥ 3 -year-old females, and mature females (≥ 6 years old) produced fewer kits than 3- to 5-year-old females. Therefore, we defined 3 adult female age classes for estimating and including fertility in the LM model. Fertilities (F_j) were calculated from Mills (2007) as:

$$F_j = m_j P_0 \quad (1)$$

where age-specific fecundity for young adult (2 year olds), adult (3–5 years old), and mature adult (≥ 6 years old) female fishers, m_j , was estimated as the product of the overall proportion of each age female in the population that denned $\times$ litter size $\times$ sex ratio at birth (0.5—York 1996), where denning rates and litter sizes were specific to each adult age class. Juvenile survival (P_0) was from the birth pulse (Powell 1993) in year j to immediately prior to the birth pulse in year $j + 1$ (Mills 2007). We estimated juvenile survival from the product of 2 indirect estimates of survival and 1 direct estimate of juvenile survival. Indirect survival estimate 1 was kit survival in den trees from late March to early June, based on the proportion of known-denning females that actually weaned kits. Indirect survival estimate 2 was the Kaplan–Meier estimate of survival (Pollock et al. 1989; Koen et al. 2007) from 10 June to 1 September for all denning female fishers known to have weaned kits ($n = 62$).

Here, we assumed that young fishers were dependent on mothers to provision them with prey and that they were unlikely to survive if their mothers died before 1 September (Powell 1993; Facka et al. 2013). The direct estimate of survival was the Kaplan–Meier staggered entry (KME) survival rate of all juvenile female fishers captured and monitored by radiotelemetry from 30 September to 17 March. Complete details of KME survival analyses were provided by R. A. Sweitzer (pers. obs.). The product of the 3 period-specific estimates used for P_0 was 0.572, and the 95% confidence interval (95% CI) for P_0 was calculated from the variance (VAR) of the product of the 3 estimates, where VAR was:

$$\text{VAR}(X_1 \dots X_n) = \prod_{i=1}^n (\text{var}(X_i) + (E[X_i])^2) - \prod_{i=1}^n (E[X_i])^2$$

with E being the expected proportions of monitored denning females that weaned kits, monitored denning females that survived the 10 June to 1 September summer period, and the number of juvenile females that survived from 30 September to 17 March (Table 2).

Insight from monitoring of individual radiocollared fishers in the study area, and known-ages for 9 female fishers that died during the first 3 years of the study (ages determined from cementum annuli; Mattson’s Laboratory, Milltown, Montana—Poole et al. 1994), indicated that female fishers seldom lived to ≥ 9 years of age. We, therefore, included 8 age classes in our LM (A) formulation, where the numbers of fishers in each age class n_1 to n_8 at time $t + 1 = \mathbf{A} \times \mathbf{n}$ vector at t_0 according to equation 2:

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \\ n_5(t+1) \\ n_6(t+1) \\ n_7(t+1) \\ n_8(t+1) \end{bmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 & F_8 \\ P_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & P_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & P_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & P_6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & P_7 & P_8 \end{bmatrix} \times \begin{bmatrix} n_1(t_0) \\ n_2(t_0) \\ n_3(t_0) \\ n_4(t_0) \\ n_5(t_0) \\ n_6(t_0) \\ n_7(t_0) \\ n_8(t_0) \end{bmatrix} \quad (2)$$

Age-specific fertility in the LM model was 0 for subadults (F_1), 0.311 for young adults (F_2), 0.411 for adults (F_3 – F_5), and 0.367 for mature adults (F_6 – F_8 ; Table 2). R. A. Sweitzer, in an analysis to be published elsewhere, used KME analyses to evaluate annualized survival for radiocollared fishers at this study site (R. A. Sweitzer, pers. obs.), and we used those data as estimates of subadult female survival (P_1 ; 0.724, 95% CI 0.592–0.856) and adult female survival (P_2 – P_7 ; 0.721, 95% CI 0.623–0.820). Also, although P_8 was set to 0 (death before age 9), we assumed that age 8 females reproduced before death, and F_8 was set as 0.367 (Table 2). Numbers of fishers in age classes n_1 , n_2 , and n_3 for the $\mathbf{n}$ vector at time t_0 were the number of radiocollared female fishers present in the population on 17

March 2012, just before the birth pulse in population year 6 ($n_1 = 5$, $n_2 = 3$, $n_3 = 9$). We multiplied the LM by the new vector of abundances for n_{t+1} for 20 successive years and summed the number of individuals in each age class each year to obtain a total n , and the population growth rate (λ) for year $t + 1$ was calculated as n_{t+1}/n_t . After several years, a stable age distribution was achieved and λ converged to a constant value, which was the estimate of λ for the set of demographic parameters evaluated. We calculated a lower and upper range for λ based on the 95% CIs for female survival and age-specific fertility.

LM sensitivity analyses.—We considered our LM model realistic because it was based on current knowledge of the life history of fishers, and it was parameterized with empirically

Table 2.—Information on age-specific reproductive rates and fertility used to estimate population growth rates for the fisher (*Pekania pennanti*) population in the Bass Lake Ranger District, Sierra National Forest, October 2008 to June 2013.

	Empirical estimates	Lower 95% CI value	Upper 95% CI value
Reproductive rate ^a			
Juvenile, subadult	0.000	0.000	0.000
Young adult (2 years old)	0.778	0.626	0.950
Adult (3–5 years old)	0.900	0.862	0.971
Mature adult (≥ 6 years old) ^b	0.750	0.750	0.750
Mean litter size ^c			
Juvenile, subadult	0.00	0.00	0.00
Young adult	1.40	1.02	1.50
Adult	1.62	1.28	1.90
Mature adult	1.71	1.71	1.71
Survival rates			
Kit survival in the den season ^d	0.823	0.766	0.870
Survival of adult females that weaned kits during summer ^e	0.880	0.792	0.968
Juvenile survival ^f	0.790	0.653	0.926
Juvenile (P_0) ^g	0.572	0.525	0.618
Subadult (P_1) ^h	0.724	0.592	0.856
Adult (P_{2-7}) ^h	0.721	0.623	0.820
Fertility ⁱ			
Young adult (F_2)	0.311	0.168	0.440
Adult (F_3, F_4, F_5)	0.417	0.290	0.570
Mature adult (F_6, F_7, F_8)	0.367	0.337	0.396
Leslie matrix ^j	0.966	0.786	1.155

^a Rates are the “Proportion denning from monitoring” in Table 6.

^b There were 3 years with data on reproduction for mature adults; we did not calculate a 95% CI for a mean with 3 data points.

^c Mean litter sizes reported in Table 8.

^d Estimated from the proportion of denning females weaning kits at the end of the late March to early June den season (Table 6).

^e Kaplan–Meier staggered entry (KME) survival rate from 10 June to 1 September.

^f KME survival rate for radiocollared juveniles from 30 September to 17 March (R. A. Sweitzer, pers. obs.).

^g Product of kit survival in the den season $\times$ denning female survival in summer (KME survival analyses) $\times$ juvenile survival from 30 September to 17 March (KME survival analyses).

^h KME annualized survival rate from 18 March to 17 March (R. A. Sweitzer, pers. obs.).

ⁱ Fertilities were the product of reproductive rate $\times$ mean litter size $\times 0.5 \times$ juvenile survival (P_0). Also, see text.

^j Estimated with a Leslie matrix model using the survival rates, P_0, P_1 , and P_{2-7} , and fertility rates (F_2 – F_8) in each column.

developed demographic rates (Table 2). Nevertheless, there is uncertainty for any model projection because demographic rates are variable, and emerging stressors can impact the biology of the species (U.S. Department of the Interior Fish and Wildlife Service 2014). We therefore assessed the sensitivity of λ in the LM model to 10% reductions in female survival (all age classes), juvenile female survival, adult female survival, and fecundity (all adult age classes). Different types of regulatory change and mitigation have been proposed to help reduce fisher deaths from exposure to rodent poisons at trespass marijuana grow sites and roadkill (Spencer et al. 2015), and, over the longer term, it is possible that appropriate management of forest habitats will help reduce contact rates between fishers and 2 felid carnivores that kill fishers (Wengert 2013; Wengert et al. 2014). Therefore, we also assessed how 10% increases in survival, fecundity, and both survival and fecundity for all age classes influenced λ . Fertility is linked to juvenile survival and fecundity according to equation 1 and in changes to fertility associated with 10% changes in the demographic rates were carried into the model when evaluating sensitivities.

RESULTS

Resightings, population size, and density.—We captured and radiocollared 101 individual fishers (57 females and 44 males) on 258 occasions during 9,732 trap-nights between December 2007 and March 2012. Livetraps to capture or recapture fishers were deployed in the fewest number of 1-km² grids in camera year 2010–2011 ($n = 141$) and the largest number of 1-km² grids in survey year 2011–2012 ($n = 259$; Table 3). Grid-level survey effort with cameras and livetraps was consistently high in subregion 1 and lowest in subregion 3 in all survey years (Table 3). Livetrapping provided nearly all of the resight effort

Table 3.—Summary data on camera trap and livetrapping activities within four 5-month camera survey years (16 October–15 March) in the Bass Lake Ranger District, Sierra National Forest study area, October 2008–March 2012.

Subregion, year	Camera surveys		Livetraps		Estimated area surveyed (km ²) ^a
	Grids	Nights	Grids	Nights	
Subregion 1. Nelder Grove, Sugar Pine, Miami Mountain					
2008–2009	147	4,462	121	1,027	223.2
2009–2010	160	5,817	161	875	307.2
2010–2011	132	4,995	72	411	214.3
2011–2012	141	5,245	147	1,016	224.6
Subregion 2. Central Camp, Whisky Ridge, Grizzly, Jackass					
2008–2009	48	1,289	17	158	267.6
2009–2010	12	349	56	272	248.0
2010–2011	20	1,048	47	237	244.2
2011–2012	65	2,522	80	316	305.5
Subregion 3. Chowchilla Mountain, Rush Creek, Sweetwater					
2008–2009	16	400	25	144	128.8
2009–2010	2	79	39	252	111.8
2010–2011	1	33	22	124	136.2
2011–2012	14	513	32	149	132.8

^a Based on 1,300 m buffer applied to polygons encompassing grids surveyed by cameras and grids with livetrapping captures.

in subregion 3 in survey years 2009–2010 and 2010–2011 (Table 3). Camera sightings combined with livetrapping recaptures were successful at detecting most radiocollared fishers known present in each subregion in all years (Table 3). Camera traps accounted for 86% of 1,421 total radiomarked fisher detections, with livetrapping recaptures providing 201 sightings (Appendix I).

Mark–resight analyses and AICc selection identified 3 models that explained 96% of the variation in the candidate model set (Table 4). Variable *area* best predicted the intercept for mean resighting rate (α), with high predicted resighting rates for subregion 1 (18.9 ± 0.8 sightings/individual) compared to subregion 2 (3.4 ± 0.5) or subregion 3 (3.3 ± 0.6 sightings/individual). Variable *area* was also the best predictor for the number of unmarked individuals (U) in each subregion and year ($\text{AICc}_{\text{wt}} > 0.95$). Variable *time* (season as factor) had a moderate contribution in predicting U ($\text{AICc}_{\text{wt}} = 0.54$), with a lower number of unmarked animals predicted across all subregions during year 2. Individual covariates *weight* and *sex* had no contribution to the top models, while variable *cams* (camera trapping effort) had a high contribution (cumulative $\text{AICc}_{\text{wt}} > 0.95$; Table 4) to explaining individual heterogeneity within regions and primary intervals (σ). Livetrapping effort (*live*) had a relatively low importance for explaining variation in σ ($\text{AICc}_{\text{wt}} = 0.18$).

Mean overall abundance across all subregions ranged from 48 fishers in March 2010 to 62 fishers in March 2012 (Table 5). Estimates of areas sampled were generally consistent within subregion among years (Table 3), but a larger area surveyed in subregion 1 in 2009–2010 was due to a program that extended camera surveys north into the Yosemite South region of Yosemite National Park (Fig. 2) in winter 2010. In 2011–2012, research effort was expanded in the Grizzly and Jackass portion of subregion 2 when noncollared fishers were detected in areas that had not been surveyed previously. There was no evidence for a consistent trend for increase or decrease

in fisher abundance in the study area; mean population density calculated across all 3 subregions was 0.084 fishers/km² in 2008–2009, 0.075 fishers/km² in 2009–2010, 0.085 fishers/km² in 2010–2011, and 0.096 fishers/km² in 2011–2012 (Table 5). Subregion 1 had the highest mean density at 0.098 fishers/km², and subregion 2 had the lowest mean density (0.077 fishers/km²; Table 5).

Denning activity, litter size, and weaning rates.—In 6 denning seasons from 2008 to 2013, we identified 93 adult-age female fishers that had the opportunity to reproduce. Reproductive status was determined for 89 of those denning opportunities, including 73 from monitoring by radiotelemetry and automatic cameras within the spring denning season, and 16 by teat measurements obtained after the denning season (Table 6). We were unable to determine reproductive status of 4 monitored females when their radiocollars were shed ($n = 3$) or ceased functioning ($n = 1$) before denning status could be determined.

Sixty-two (85%) of the 73 monitored fishers initiated denning behavior, whereas 13 (81%) of 16 adult females captured after the denning seasons reproduced based on size of teats. Seventy-five of 89 (84%) adult female fishers that were monitored or physically examined initiated denning and reproduced (Table 6). The average date that radiomonitoring females initiated denning behavior was 28 March (range 22 March–9 April). The average date that females ceased localizing to den trees was 9 June (range 30 May–22 June). Among the 62 monitored females that initiated denning, 51 (82%) subsequently weaned kits from den trees (Table 7). The overall weaning rate for the 73 known status female fishers was 70% (range 0.64–0.79, excluding 2008 when sample size was small; Table 7).

We obtained kit counts for 48 monitored females that denned during the study (Table 8). Forty-two kit counts were obtained using automatic cameras, 4 were from den cavity investigations with a video camera, and in 2 cases, both methods were used.

Table 4.—Poisson log-normal mark–resight models for estimating fisher (*Pekania pennanti*) abundance in the Sierra Nevada, California. AICc for top model was 1056.218; k = number of parameters, AICc = Akaike information criterion, AICc_{wt} = Akaike weight. Model averaging was performed on the top 3 models.

Model	k	ΔAICc	AICc_{wt}	Cumulative Wt	Deviance
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{cams}) U(\sim 1 + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	11	0.000	0.420	0.420	1032.526
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{cams}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	14	0.272	0.366	0.786	1025.746
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{cams} + \text{live}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	15	1.797	0.171	0.956	1024.858
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{cams} + \text{live} + \text{area}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	18	5.282	0.030	0.986	1020.910
$\alpha(\sim 1 + \text{area} + \text{time}) \sigma(\sim 1 + \text{time} + \text{cams} + \text{live}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	22	7.595	0.009	0.996	1012.834
$\alpha(\sim 1 + \text{sex} + \text{area}) \sigma(\sim 1 + \text{sex} + \text{cams} + \text{live}) U(\sim 1 + \text{sex} + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	18	10.767	0.002	0.998	1026.395
$\alpha(\sim 1 + \text{area} + \text{time}) \sigma(\sim 1 + \text{cams} + \text{live}) U(\sim 1 + \text{time}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	16	11.408	0.001	0.999	1032.023
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{cams} + \text{live} + \text{time}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	19	12.215	0.001	1.000	1025.299
$\alpha(\sim 1 + \text{area} + \text{time}) \sigma(\sim 1 + \text{cams} + \text{area}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	20	18.591	0.000	1.000	1029.095
$\alpha(\sim 1 + \text{area} + \text{time}) \sigma(\sim 1 + \text{area} + \text{time}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	22	21.109	0.000	1.000	1026.348
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1) U(\sim 1 + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	11	28.665	0.000	1.000	1061.191
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{live}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	14	29.126	0.000	1.000	1054.600
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{cams} + \text{live} + \text{weight}) U(\sim 1 + \text{time} + \text{area} + \text{weight}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	17	32.263	0.000	1.000	1050.401
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{cams} + \text{live}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	21	34.583	0.000	1.000	1042.472
$\alpha(\sim 1 + \text{sex} + \text{area} + \text{time}) \sigma(\sim 1 + \text{area} + \text{time} + \text{cams} + \text{live}) U(\sim 1 + \text{sex} + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	44	36.897	0.000	1.000	972.920
$\alpha(\sim 1 + \text{area}) \sigma(\sim 1 + \text{cams} + \text{live} + \text{sex}) U(\sim 1 + \text{time} + \text{area}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	16	38.019	0.000	1.000	1058.635
$\alpha(\sim 1 + \text{time}) \sigma(\sim 1 + \text{cams}) U(\sim 1 + \text{time}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	13	117.783	0.000	1.000	1145.637
$\alpha(\sim 1) \sigma(\sim 1) U(\sim 1) \phi(\sim 1) \gamma'(\sim 1) \gamma'()$	5	179.733	0.000	1.000	1225.581
$\alpha(\sim 1 + \text{sex}) \sigma(\sim 1 + \text{sex}) U(\sim 1 + \text{sex}) \phi(\sim 1 + \text{area}) \gamma'(\sim 1) \gamma'()$	7	319.068	0.000	1.000	1360.587

Table 5.—Mark–resight estimates of population size (n) and density (fishers/km²) of fishers (*Pekania pennanti*) for 3 subregions in each of four 5-month survey years (16 October–15 March) in the Bass Lake Ranger District, Sierra National Forest. Estimates of population size and density are for 15 March, which closely coincides with the end of the fisher population year (18 March).

Subregion, year	n	95% CI	Density ^a	Density range ^b
Subregion 1. Nelder Grove, Sugar Pine, Miami Mountain				
2008–2009	27.9	23.6–32.2	0.125	0.106–0.144
2009–2010	22.3	19.0–25.6	0.073	0.062–0.083
2010–2011	19.1	16.3–22.0	0.089	0.076–0.103
2011–2012	23.2	20.2–26.2	0.103	0.090–0.117
Subregion 2. Central Camp, Whisky Ridge, Grizzly, Jackass				
2008–2009	18.8	10.5–21.2	0.070	0.044–0.097
2009–2010	16.3	10.4–21.4	0.066	0.037–0.094
2010–2011	22.5	15.4–24.5	0.092	0.066–0.118
2011–2012	24.6	17.8–26.5	0.080	0.062–0.099
Subregion 3. Chowchilla Mountain, Rush Creek, Sweetwater				
2008–2009	7.2	5.8–8.6	0.056	0.045–0.067
2009–2010	9.7	8.7–10.6	0.086	0.078–0.095
2010–2011	10.0	8.8–11.3	0.074	0.065–0.083
2011–2012	14.0	12.8–15.3	0.106	0.096–0.115

Time period	Total abundance ^c	No. collared on 15 March ^d	Estimated percent population marked
March 2009	54	32	59.5
March 2010	48	33	68.4
March 2011	52	33	63.9
March 2012	62	44	71.2

^a Population size (n) divided by the estimated sample area for the subregion in the survey year included in Table 3.

^b Calculated based on the lower and upper values of the 95% CI divided by the estimate of the sampled area provided in Table 3.

^c Sum of the year- and subregion-specific estimates of population size from the mark–resight analyses.

^d Count of all radiocollared fishers known present in the population on 15 March of each survey year.

A total 75 kits were known produced, and the average litter size for the 48 litters was 1.6 (range 1–3; Table 8). Eight female fishers died before kits were weaned from den trees (Table 6), however, and the weaning litter size for the monitored female fishers that denned was 1.4 kits/litter (range 1.2–1.7; Table 8).

Denning attempts for 11 (17.7%) of 62 females that were being monitored failed prior to weaning kits (Table 7). Three of the denning failures were females that initiated denning but appeared to abandon the natal den 17, 35, and 41 days later, potentially related to the death of kits. Eight den failures were due to death of the denning female (7 deaths were killed by predators—Wengert et al. 2014), and one was the result of a denning female found dead on a local highway that likely died after secondary exposure to rodenticides (Gabriel et al. 2012). One of the 7 females that died from predator attack was determined infected with canine distemper virus, which may have contributed to her vulnerability (Keller et al. 2012).

Six of 8 deaths of denning females occurred when den trees were known and being monitored. In one case, den camera images included a bobcat (*Lynx rufus*) with a kit in its mouth, and the partial carcass of the denning female was recovered nearby. In a second case, the den structure was a large, unstable snag, which we did not attempt to climb to determine litter size because of safety considerations. In each of the other 4 cases, we climbed the den trees to assess litter size and recovered kits in accordance with California Department of Fish and Wildlife policy. A total 5 live kits were recovered from 2 of the den trees

(litter size was 2 and 3), 2 deceased kits were found in a den cavity of the 3rd tree, and we failed to find kits in the 4th tree. For this 4th tree, the lack of images of the denning female from den cameras suggested she had moved the litter to a different, unidentified den tree several days prior to her death.

The 5 orphan kits that were rescued were raised in captivity by a local wildlife rehabilitation organization licensed by the California Department of Fish and Wildlife and under the supervision of a zoo veterinarian. One orphan kit died in captivity by urinary tract blockage attributed to a parasitic nematode, whereas the other 4 survived captive rearing. Two kits from 1 litter were released within their mother's home range, and the 2 kits from the 2nd litter were released into an area with suitable fisher habitat abutting the south margin of the study site.

Juvenile survival and deterministic population growth.—Six of the 62 female fishers that weaned kits from den trees in early June died before 1 September, and their summer season KME survival rate was 0.880 (95% CI 0.792–0.968). Four of 32 young-of-the-year female fishers captured after 30 September perished, and the 30 September–17 March survival rate for juvenile females was 0.790 (95% CI 0.653–0.926). Therefore, our estimate of first year juvenile female survival (P_0) was 0.572 (95% CI 0.530–0.618), which contributed to age-specific fertility varying from 0.311 for young adult females to 0.417 for adult females (Table 2). Empirical estimates for survival and reproduction in our LM model produced an estimate of $\lambda = 0.966$ (range = 0.786–1.155; Table 2). The upper range

Table 6.—Basic data on adult-age female fishers (*Pekania pennanti*; ≥ 2 years old) that were monitored for reproductive activities during 6 spring den seasons (late March to mid-June) with radiotelemetry and automatic cameras and numbers of females that were captured and measured for teat size outside of the denning season on the Bass Lake Ranger District in the Sierra National Forest, California, spring 2008 to spring 2013.

Age class, den season	No. females ^a	Monitored mid-March to 31 May ^b	Limited monitoring, den status not determined ^c	Denning by monitoring ^d	Females with teats measured, number that reproduced ^e	Denning status evaluated ^f	Proportion denning from monitoring ^g	Overall proportion that denned ^h
Age (years)								
2	30	26	4	20	1, 1	27	0.77	0.78
3–5	51	37	14	34	13, 11	50	0.92	0.94
≥ 6	12	10	2	8	2, 1	12	0.80	0.75
Year								
2008	11	2	9	2	9, 7	11	1.00	0.82
2009	17	14	3	13	2, 2	17	0.93	0.88
2010	17	15	2	13	1, 1	16	0.87	0.88
2011	16	11	5	9	3, 3	14	0.82	0.86
2012	17	17		14		17	0.82	0.82
2013	15	14	1	11		14	0.79	0.79
All years	93	73	20	62	16, 13	89	0.85	0.84

^a All females ≥ 2 years of age that were known in the population during all or part of the population year. Includes females that were captured after the end of the denning season in mid-June.

^b Number of females monitored by radiotelemetry during all or part of the denning season until at least 31 May (some were monitored until mid- to late June), including those that died or had a dropped/failed collar after their denning status had been determined.

^c Number of females (≥ 2 years old) that were not directly monitored during all or part of the denning season, including those for which dropped or failed radio-collars prevented determination of denning status during the denning period.

^d Number of females determined denning by direct monitoring with radiotelemetry and automatic cameras during the denning season.

^e Number of females that were not directly monitored in the denning season, but then captured and measured for teat size during July to January. Includes the number that reproduced based on size of teats as detailed by [Matthews et al \(2013a\)](#).

^f Number of females (≥ 2 years old) for which denning status was determined from monitoring during the den season or from measurements of size of teats during July–January.

^g Number of females that denned based on direct monitoring divided by the number of adult females minus the number with limited monitoring for which denning status was not determined.

^h Number of females for which denning status was evaluated divided by the number of adult females minus the number with insufficient monitoring for which denning status was not determined.

Table 7.—Information on adult-age female fisher (*Pekania pennanti*; ≥ 2 years old) denning activities during 6 spring den seasons (late March to mid-June) on the Bass Lake Ranger District in the Sierra National Forest, California, spring 2008 to spring 2013.

Age class, den season	Monitored mid-March to 31 May ^a	Denned from monitoring ^b	Ceased denning ^c	Died while denning ^d	Denned to weaning ^e	Proportion denning females weaning kits ^f	Weaning rate ^g
Age (years)							
2	26	20	1	2	17	0.85	0.65
3–5	37	34	2	5	27	0.79	0.73
≥ 6	10	8		1	7	0.88	0.70
Year							
2008	2	2			2	1.00	1.00
2009	14	13	1	1	11	0.85	0.79
2010	15	13		3	10	0.77	0.67
2011	11	9	1	1	7	0.78	0.64
2012	17	14		3	11	0.79	0.65
2013	14	11	1		10	0.91	0.71
All years	73	62	3	8	51	0.82	0.70

^a Number of females monitored by radiotelemetry during all of part of the period before they died or had a dropped/failed collar after denning status had been determined.

^b Number of females determined to have denned based on direct monitoring with radiotelemetry and automatic cameras.

^c Number of females that exhibited denning behavior but ceased denning behavior prior to 31 May. Cause of cessation of denning behavior was not determined.

^d Number of females that were known to have died while denning.

^e Number of females exhibiting denning behavior that continued denning until 31 May.

^f Number of females that denned divided by the number that denned to weaning.

^g Number of females monitored during a denning season divided by the number that weaned kits.

Table 8.—Information on fisher (*Pekania pennanti*) kit production for 6 spring den seasons (late March to mid-June) on the Bass Lake Ranger District in the Sierra National Forest, California, spring 2008 to spring 2013.

Age class, den season	Denning females with kit counts ^a	Kits ^b	Known it deaths ^c	Kits weaned ^d	Litter size ^e	Kits weaned per litter (fecundity) ^f
Age (years)						
2	15	21	2	19	1.40	1.27
3–5	26	42	7	35	1.62	1.35
≥ 6	7	12		12	1.71	1.71
Year						
2008	2	3		3		1.50
2009	9	15		15	1.7	1.67
2010	11	20	7	13	1.8	1.18
2011	7	11		11	1.6	1.57
2012	11	16	2	14	1.5	1.27
2013	8	10		10	1.3	1.25
All years	48	75	9	66	1.6	1.4

^a Number of denning females for which kit counts were determined by images from den cameras, den cavity video, or both.

^b Total number of kits counted.

^c Kits that were known present in den trees when the mother died or those that were found dead inside den cavities. The estimate assumes that 5 orphan kits that were removed from den cavities would have perished if they had not been rescued.

^d Estimated number of kits weaned from den trees based on kit counts for females exhibiting denning behavior until May 31 or later. Includes 2 kits observed with an adult female fisher at a camera trap in July 2008; the adult female was captured and radiocollared 2 weeks later.

^e Number of denning females with kit counts divided by the number of kits counted.

^f Number of kits weaned divided by the number of denning females with kit counts.

estimate for λ extended well above 1.0, suggesting the population was not necessarily in persistent decline (Fig. 3).

The population growth rate was approximately 4 times as sensitive to reduced survival as reduced fecundity. Lambda declined by $\approx 10\%$ (0.966–0.870) when survival was reduced by 10%, compared to a $\approx 2.6\%$ decline (0.966–0.941) when fecundity was reduced by the same amount. Moreover, λ was about 2 times as sensitive to a 10% decline in adult survival (5% decline; 0.966–0.918) than juvenile survival (2.6% decline; 0.966–0.941). When we increased survival by 10%, λ increased to 1.06 (10% improvement), whereas λ improved to nearly 1.0 (0.99; 2.4% increase) when fecundity was increased by the same amount. A 10% increase for both survival and fecundity produced a 13% increase in λ (0.966–1.089).

DISCUSSION

Fisher abundance and population density.—The number of fishers estimated present in the study area was 48–62 individual animals, and the relatively narrow range in the confidence intervals (Table 5) was likely due to the combination of a relatively high probability of detection (0.4–0.8) for our camera protocol when cameras were within the home ranges of radiocollared fishers (Popescu et al. 2014), and in all years, we likely had

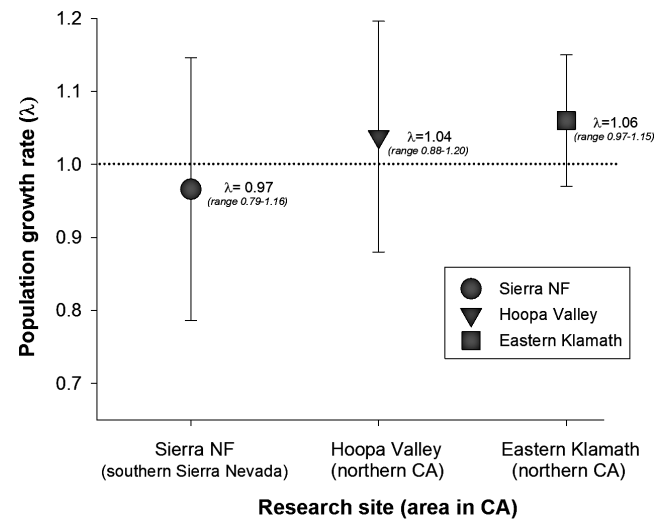


Fig. 3.—Plot to compare the estimated population growth rate (95% CI) from this study in the Sierra National Forest, California, to population growth rates estimated for 2 populations in northern California. Information on the estimated fisher (*Pekania pennanti*) population growth rate for the Hoopa Valley region in northern California was from Higley et al. (2013), whereas the population growth rate for the Eastern Klamath region of northern California was drawn from Swiers (2013).

over 60% of the fisher population in the study area marked with radiocollars (Table 5).

The estimates of mean annual population density we developed (0.072–0.096 fishers/km²; Table 5) were generally consistent with but lower than from 2 previous studies of a fisher population in Fisher Core Habitat Area 4 south of our study site. Jordan et al. (2011) used a CMR approach to estimate a density of 0.063–0.109 fishers/km² for fishers in the High Sierra District, Sierra National Forest (High Sierra SNF) during 2002–2004. Thompson et al. (2012b) used scat detector dogs and genetic detections in a spatially explicit CMR framework to estimate a fisher density of 0.065–0.28 fishers/km² in the High Sierra SNF in fall 2007 but emphasized that a modal density of 0.104 fishers/km² was the most appropriate point estimate from their research. At a research site in Hoopa Valley in northern California, Higley et al. (2013) used CMR methods to determine that density of fishers was stable and increasing at 0.12–0.29 fishers/km² over a 9-year period from 2005 to 2013. In central Massachusetts, Fuller et al. (2001) applied CMR models to camera sightings and reported fisher densities of 0.19–0.25 fishers/km². Weir and Corbould (2006) and Weir et al. (2011) used data on the minimum number known alive to estimate density of fishers at 0.009 and 0.018 fishers/km² at 2 different sites in the sub-boreal forests of northern British Columbia, Canada. Although the minimum number of alive approach will underestimate density by not accounting for non-collared fishers that were present but not captured, it is likely that fisher population density in the sub-boreal forest is much lower than in forested habitats in central Maine or in California. Considering just those studies that used CMR methods, the

densities we estimated are the lowest reported in California or elsewhere in the United States.

Conservation planning is underway for fishers in the southern Sierra Nevada, including modeling to estimate areas of suitable habitat in 7 Fisher Core Habitat areas in the Sierra Nevada (Fig. 1; Spencer et al. 2015). Fisher Habitat Core Area 5 (our study area) encompassed 1,096 km² of suitable fisher habitat (Spencer et al. 2015). We calculated the mean density and 95% CI for the 12 area- and year-specific densities developed by our CMR modeling (Table 5; 0.085 fishers/km², 95% CI 0.073–0.097). Assuming that habitats within the 595–667 km² that we surveyed each year by camera traps and livetraps (Table 3) were representative of suitable fisher habitat in Fisher Habitat Core Area 5, we estimated that there were 93 (range 80–106) fishers within Fisher Habitat Core Area 5.

Fisher demography in the southern Sierra Nevada Mountains.—The mean denning and weaning rates for fishers in our study were not particularly low in comparison to other populations of fishers in the West Coast DPS (Table 9). However, and as Matthews et al. (2013b) noted, reports of low weaning rates from some studies may be due to incorrect age assignment. In this study, we monitored most of our study animals from when they were juveniles until death, and ages for 9 female fishers that were captured early in the study were determined by cementum annuli. Kit production in our study area did trend slightly lower than in other fisher populations in the western United States and especially in comparison to northern British Columbia (Table 9).

Close monitoring of denning behavior by several studies in the West Coast DPS is providing insight on difficulties female fishers encounter while attempting to reproduce. In 5 denning seasons when we monitored denning behavior for multiple radiocollared females, we documented 8 cases when females died or were killed with dependent kits in den cavities (Table 6). Death of denning female fishers may be fairly common, based on reports from northern California ($n = 5$; Matthews et al. 2013b), northeastern California ($n = 5$; Stirling Fisher Reintroduction Project—Powell et al. 2013), in the High Sierra District, Sierra National Forest, CA ($n = 3$, Kings River Fisher Project; R. Green, USDA Forest Service, Pacific Southwest

Research Station, Fresno, California, pers. comm.), and in western Washington ($n = 2$, Olympic Fisher Reintroduction Project—Lewis et al. 2012). Evidence that a significant number of females exhibiting denning behavior often die before weaning is important because weaning rates may be biased high unless estimates are from monitoring through the full duration of the denning period (Facka et al. 2013).

Population growth and threats to survival.—Estimates of λ for fishers derived from empirical data specific to the area of inference are rare for California and absent for the southern Sierra Nevada. Our LM model analysis suggested slightly negative growth ($\lambda = 0.966$) for the period of the research (Table 2). The upper range for λ (1.155) was well above 1.0, however, suggesting stability or growth in some years. The estimated range for λ (Table 2) was consistent with the estimated population densities, which did not indicate a persistent decline during 4 years from 2008–2009 to 2011–2012 (Table 5). Higley et al. (2013) integrated data on apparent survival from CMR models and data on reproduction in a series of random effects models to evaluate λ for fishers in the Hoopa Valley in northern California. Their “Females Only” model (most similar to our LM model) produced a λ estimate of 1.038 (Fig. 3; Higley et al. 2013). Swiers (2013) used robust-design and Pradel models to estimate a population growth rate of 1.06 for a fisher population in the eastern Klamath Mountains in northern California (Fig. 3). Therefore, and for 3 recent studies reporting similar data, our fisher population at the north margin of the southern Sierra Nevada region in California was the only one with a growth rate trending below 1.0 (Fig. 3).

Indication of a population growth rate below 1.0 was in agreement with evidence that fishers are exposed to a diversity of challenges to survival and reproduction in the study area. For example, 63 (56%) of 113 individual fishers radiocollared during the study were known to have died (R. A. Sweitzer, pers. obs.). Cause of death was determined for the majority of those animals and identified causes of death included attacks by predators (Wengert et al. 2014), roadkills on local highways, infectious disease (Keller et al. 2012; Gabriel 2013), and acute toxicosis caused by exposure to rodenticides (Gabriel et al. 2012). Sensitivity analyses revealed that change in fisher

Table 9.—Comparative review of data on fisher (*Pekania pennanti*) reproductive rates (%) and kit production reported by studies in western North America. Data from the Sierra National Forest are from this study in the Bass Lake Ranger District. Blanks indicate that no data were reported for the demographic rate.

Location of research ^a	Estimated reproductive rate		Kit production		Source of data
	Reproduced	Dennded to weaning	Mean litter size	Mean kits weaned/litter	
Sierra National Forest	0.84	0.82	1.6	1.4	This study; Tables 6–8
Sequoia National Forest, CA	0.54				Truex et al. (1998)
Stirling area, Northeast CA	0.77	0.77	1.80		Powell et al. (2013)
Hoopa Valley, Northern CA	0.87	0.65		1.80	Matthews et al. 2013b
Rogue River region, OR	0.59	0.44	1.90		Aubry and Raley (2006)
British Columbia, Canada	0.83	0.67	2.60	2.60	Weir (2009)
British Columbia, Canada		0.69 ^b			Weir and Corbould (2008)

^a Locations are ordered from south to north below the Sierra National Forest (this study).

^b Reported as “whelping rate,” which was assumed to indicate dennded to weaning.

survival was more important than fecundity for deterministic population growth. This is important because if regulatory change or mitigation efforts are successful at reducing the number of individual fisher deaths caused by exposure to rodenticides (Gabriel et al. 2013) or wildlife–vehicle collisions on local highways (Chow 2009), to a degree sufficient to improve survival by just 10%, the growth trajectory for our study population could become positive ($\lambda \approx 1.06$). Further, it is possible that appropriate management of forest habitats can help reduce contact rates between fishers and several felid carnivores over the longer term (Wengert 2013; Wengert et al. 2014). Our study identified multiple deaths of denning females from attacks by predators near den trees, and images from den cameras revealed direct predation on fisher kits by a bobcat. Therefore, reduced contact rates between fishers and larger carnivores mediated by appropriate management of denning habitats could simultaneously increase both adult female survival and fecundity, which would produce an even more positive improvement in λ (≈ 1.09). Reinforcing this possibility, Tucker et al. (2014) identified genetic evidence for population subdivision among fishers in the overall southern Sierra Nevada region and, based on those data and increasing detections of fishers at long-term monitoring stations (Zielinski et al. 1995, 2005, 2013), hypothesized that both the abundance and range extent of fishers in Fisher Core Habitat Areas 4 and 5 (Fig. 1) increased significantly after the 1990s. Empirical data from this study neither confirm nor inform directly on the Tucker et al. (2014) hypothesis of contemporary range expansion, but our results do suggest that abundance of fishers in the region could begin to increase with modest improvements in female survival or appropriate management to maintain cover and secure refuge habitat near den and rest sites (Zhao et al. 2012; Aubry et al. 2013).

Management and conservation.—The combination of a λ trending slightly below 1.0, low population density, no indication of increase in density, and as few as 93 fishers within Fisher Habitat Core area 5 warrants concern for their continued viability in the region. We also know that fishers are genetically limited in our study area and in the southern Sierra Nevada region in general (Knaus et al. 2011; Tucker et al. 2014), and they are exposed to multiple sources of cause-specific mortality (Gabriel 2013). Moreover, our study spanned a period of 6 years when 3 large wildfires (Rim Fire, Aspen Fire, and Big Meadow fire; InciWeb 2014) significantly reduced availability of suitable habitat for fishers immediately to the south and north of the study site. Similar wildfires capable of damaging thousands of hectares of denning and resting habitats used by fishers in a very short time are likely to increase in frequency and intensity with climate change (Safford and Van de Water 2013). Considering that there are likely fewer than 500 individual fishers within California's southern Sierra Nevada region (Spencer et al. 2011) and that these animals are exposed to multiple known and emerging stressors, the population cannot be considered secure (Reed and McCoy 2014). We recommend that agencies maintain ongoing research, including regional-scale monitoring in the southern Sierra Nevada (Zielinski et al. 2013). Future analyses should focus on evaluating whether

the negative growth trajectory for fishers within Fisher Core Habitat Area 5 persists. Moreover, if λ is at or trends below 1.0 in any of the other habitat core areas, it will be necessary to mitigate for major threats to fisher survival and re-evaluate forest management approaches (North et al. 2009) to facilitate maintaining contiguous expanses of suitable fisher habitat that will promote improved survival and reproduction.

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APPENDIX I

Number of camera trap detections and livetrapped captures/recaptures identified for radiocollared fishers (*Pekania pennanti*) in 3 different subregions of the study area. Counts of detections were for four 5-month survey years (16 October–15 March) from October 2008 to March 2012 in the Bass Lake Ranger District, Sierra National Forest, California. Dots indicate that the animal was not radiocollared or was not available for detection during that survey year.

Subregion, ID	Survey year 2008–2009		Survey year 2009–2010		Survey year 2010–2011		Survey year 2011–2012	
	Camera detections ^a	Capture ^b	Camera detections	Capture	Camera detections	Capture	Camera detections	Capture
1. Nelder Grove, Sugar Pine, Miami Mountain								
F01	18	1	11	1	18	2	.	.
F03	26	3	12	1	.	.	6	1
F04	1	1	4	1	.	.	.	.
F05	0	0	1	0	.	.	.	.
F12	12	1	17	2	14	1	33	1
F13	0	1	0	3	.	.	0	1
F14	5	2	.	.	.	.	.	.
F15	20	0	29	2	.	.	.	.
F16	7	3	.	.	.	.	.	.
F17	11	3	13	3	8	0	25	0
F18	9	2	8	2	43	0	24	1
F19	19	2	.	.	.	.	.	.
F20	5	1	.	.	.	.	.	.
F24	2	2	.	.	.	.	.	.
F25	12	2	12	1	.	.	.	.
F26	9	3	5	0	.	.	.	.
F30	.	.	2	0	.	.	.	.
F32	.	.	39	2	.	.	.	.
F34	.	.	26	4	11	0	.	.
F43	.	.	.	.	14	1	50	1
F47	.	.	.	.	8	3	10	0
F49	.	.	.	.	.	.	25	1
F56	.	.	.	.	.	.	26	1
M02	.	.	23	1	.	.	.	.
M04	16	2	.	.	.	.	.	.
M05	21	2	.	.	.	.	.	.
M08	23	2	20	2	2	1	41	0
M10	6	0	6	2	.	.	.	.
M13	3	1	.	.	.	.	.	.
M14	25	1	.	.	.	.	.	.
M15	.	.	1	3	9	1	1	1
M20	.	.	38	8	.	.	.	.
M29	.	.	.	.	5	3	7	2
M30	.	.	.	.	4	1	17	0
M31	.	.	.	.	10	1	14	2
M32	.	.	.	.	11	2	20	2
M34	.	.	.	.	.	1	.	.
M36	.	.	.	.	.	.	44	2
M37	.	.	.	.	.	.	2	1
M42	.	.	.	.	.	.	19	1
2. Central Camp, Whisky Ridge, Grizzly, Jackass								
F07	.	.	0	0	0	1	.	.
F08	5	1	.	.	.	.	.	.
F09	3	1	.	.	.	.	.	.
F10	0	1	.	.	.	.	.	.
F11	6	0	0	1	.	.	.	.
F28	.	.	0	0	0	1	.	.
F31	.	.	1	2	.	.	.	.
F36	.	.	0	1	2	0	.	.
F37	.	.	3	1	0	0	.	.
F38	.	.	.	.	1	1	3	0
F39	.	.	.	.	1	0	1	2
F44	.	.	.	.	0	0	.	.
F45	.	.	.	.	4	1	7	0

Appendix I *Continued*

Subregion, ID	Survey year 2008–2009		Survey year 2009–2010		Survey year 2010–2011		Survey year 2011–2012	
	Camera detections ^a	Capture ^b	Camera detections	Capture	Camera detections	Capture	Camera detections	Capture
F50	.	.	.	.	.	.	0	1
F51	.	.	.	.	.	.	4	1
F54	.	.	.	.	.	.	0	2
F57	.	.	.	.	.	.	1	1
F58	.	.	.	.	.	.	0	1
F59	.	.	.	.	.	.	0	1
M12	1	1	.	.	.	.	.	.
M16	10	1	6	3	.	.	.	.
M17	6	1	.	.	1	1	20	1
M18	.	.	0	0	0	1	.	.
M19	.	.	1	1	4	1	.	.
M23	.	.	0	0	0	0	.	.
M27	.	.	.	.	1	2	8	1
M35	.	.	.	.	0	0	2	1
M38	.	.	.	.	0	0	0	2
M39	.	.	.	.	0	1	0	0
M44	.	.	.	.	.	.	0	1
3. Chowchilla Mountain, Rush Creek, Sweetwater								
F06	1	1	0	0	2	0	2	1
F21	1	1	1	1	.	.	.	.
F22	0	2	.	.	.	.	.	.
F23	4	3	0	2	.	.	.	.
F27	0	2	.	.	.	.	.	.
F29	.	.	.	.	0	1	1	1
F33	.	.	0	4	.	.	.	.
F42	.	.	.	.	0	0	.	.
F46	.	.	.	.	0	1	3	0
F48	.	.	.	.	0	1	1	0
F52	.	.	.	.	.	.	0	1
F53	.	.	.	.	.	.	0	1
F55	.	.	.	.	.	.	0	1
M11	9	2	11	3	1	1	0	0
M21	.	.	0	3	.	.	.	.
M22	.	.	7	3	.	.	.	.
M25	.	.	0	1	0	1	.	.
M26	.	.	.	.	2	1	0	1
M33	.	.	.	.	0	2	3	1
M35	.	.	.	.	.	.	2	1
M40	.	.	.	.	.	.	6	2
M41	.	.	.	.	.	.	0	1
M43	.	.	.	.	.	.	0	1

^a Count of detections by calendar day; multiple detections in a calendar day were counted as 1 detection.

^b Dropped collars retrieved from the field were included as recaptures of the animal.