

Estimating population size of fishers (*Pekania pennanti*) using camera stations and auxiliary data on home range size

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Abstract. Estimating density and population size is often more challenging than measuring indices of abundance because of uncertainty about the effective area of surveys. We combined hierarchical modeling of detection/non-detection data from camera stations with auxiliary information on home range sizes to address this issue. We used this approach to estimate the total population size of fishers (*Pekania pennanti*) throughout the largest remaining native range (Northern California and Southern Oregon [NCSO], 48,760 km²) of this species in the Pacific States of the United States. After controlling for various habitat, gender, and survey factors affecting detection probability, local abundance, and home range size, we estimated an average density of 6.6 fishers per 100 km² (95% confidence interval [CI]: 5.1–8.6) and a total of 3196 fishers (95% CI: 2507–4184). We mapped how fisher density varied throughout the range and demonstrated spatial autocorrelation in density at lag distances up to 40 km. These findings represent the first robust estimate of fisher population size for the range in NCSO. They are important for setting a baseline against which to monitor changes in population status and spatial distribution of fishers which are a species of conservation concern at federal and state levels. However, we note that our estimate of population size is very sensitive to assumptions about the effective area of camera surveys. Our methods could likely be applied to other forest carnivores and highlight the benefits of coordination between researchers to collect and share comparable survey and telemetry data.

Key words: camera station; density; fisher; home range; monitoring; *Pekania pennanti*; population size; Royle-Nichols model; spatial autocorrelation.

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INTRODUCTION

The loss of geographically isolated populations is a critical conservation issue because population losses can be a prelude to species extinction (Ceballos and Ehrlich 2002, Luck et al. 2003). As populations shrink, they may be at greater risk of local extinction due to stochastic demographic, environmental, and genetic factors (Shaffer 1981). Monitoring that provides good quantitative data on abundance and its dynamics is essential for

population viability analyses and detecting changes in the status of small and isolated populations (Beissinger and Westphal 1998, Yoccoz et al. 2001, Reed et al. 2003). For practical reasons, many large-scale monitoring programs have relied on indices of abundance that may not always accurately reflect population status (Pollock et al. 2002, Noon et al. 2003). In recent years, advances in analytical methods and non-invasive survey methods have made direct estimation of abundance more feasible (Luikart et al. 2010,

O'Connell et al. 2011, Kéry and Royle 2015). However, challenges remain to convert robust estimates of local abundance at points or along transects (e.g., capture–recapture designs and other advanced hierarchical modeling approaches) to measures of density and population size. This often requires auxiliary information on home range size and an understanding of the spatial ecology of the species being studied.

The fisher (*Pekania pennanti*) is a forest carnivore of conservation concern in the western United States because of a combination of stressors including historical trapping (Dixon 1925, Grinnell et al. 1937, Lewis and Zielinski 1996), timber harvesting (Weir and Corbould 2010, Sweitzer et al. 2016), disease (Gabriel et al. 2012a), poisoning (Linsdale 1932, Gabriel et al. 2012b), and climate change (Lawler et al. 2012). There are only two populations of native fishers remaining in the Pacific States, one in Northern California and Southern Oregon (NCSO) and the other in the Southern Sierra Nevada Mountains of California (SSN; Fig. 1). The SSN population is listed as “threatened” under the California Endangered Species Act (California Fish and Game Commission 2016). The U.S. Fish and Wildlife Service recently withdrew a proposed rule to list the Pacific States populations of fishers as threatened under the U.S. Endangered Species Act (USDI Fish and Wildlife Service 2016a).

Even though the NCSO population of fishers has not been listed under the federal and state Endangered Species Acts, connectivity of this population to nearby introduced populations and the SSN population is a conservation priority for the species throughout the Pacific States (Lofroth et al. 2010). For this reason, accurate information about the population status of fishers is needed throughout the Pacific States. Although some studies have estimated vital rates and abundance of fishers within local study areas (Jordan 2007, Thompson 2008, Matthews et al. 2011), results from systematic monitoring efforts across large geographic areas have so far been restricted to the SSN range (Zielinski et al. 2013, Sweitzer et al. 2016). Estimates of fisher density for the NCSO range are limited to a few small study areas where intensive research occurred (Buck et al. 1983, Thompson 2008, Matthews et al. 2011). There has been one attempt to calculate total population size for the NCSO range,

but it was calculated using “expert-based” extrapolation of data on density from small study areas (44–850 km²) and it did not include confidence intervals (CIs; Self et al. 2008). Without better estimates of population size, strong inferences about the status of fishers will not be possible at the scale needed to conserve the species.

Camera stations are a well-established method to study fishers and other forest carnivores (Zielinski and Kucera 1995, Karanth and Nichols 1998, Kays and Slauson 2008, Kucera and Barrett 2011). At a minimum, cameras provide detection/non-detection data (1 or 0) that can be expressed as a daily or weekly detection history for each surveyed site during a short enough time period when the population associated with each site can be assumed closed (Slauson et al. 2009, Sweitzer et al. 2016). Hierarchical models allow researchers to estimate either occupancy or abundance using these data (Royle and Nichols 2003, MacKenzie et al. 2006). Both of those modeling approaches have been applied to fisher survey data from California (Royle and Dorazio 2008, Zielinski et al. 2013).

We report here on results from a large-scale monitoring effort using baited camera stations to survey fishers and other mammals throughout much of the NCSO range. By combining this information with data from several other camera station survey projects, we modeled how fisher abundance varied throughout the entire NCSO range. We gathered auxiliary information on home range size so that we could convert our estimates of local abundance to estimates of density and total population size. We used an analysis of spatial autocorrelation to help map how fisher density varied across the NCSO range. Finally, we provide recommendations on how coordination among researchers to collect and share comparable data can lead to better integrated assessments of population size for fishers and other carnivores.

METHODS

Study area

We defined the NCSO range using the geographic information systems (GIS) layer used by the U.S. Fish and Wildlife Service in their status review of fishers under the federal Endangered Species Act (USDI Fish and Wildlife Service

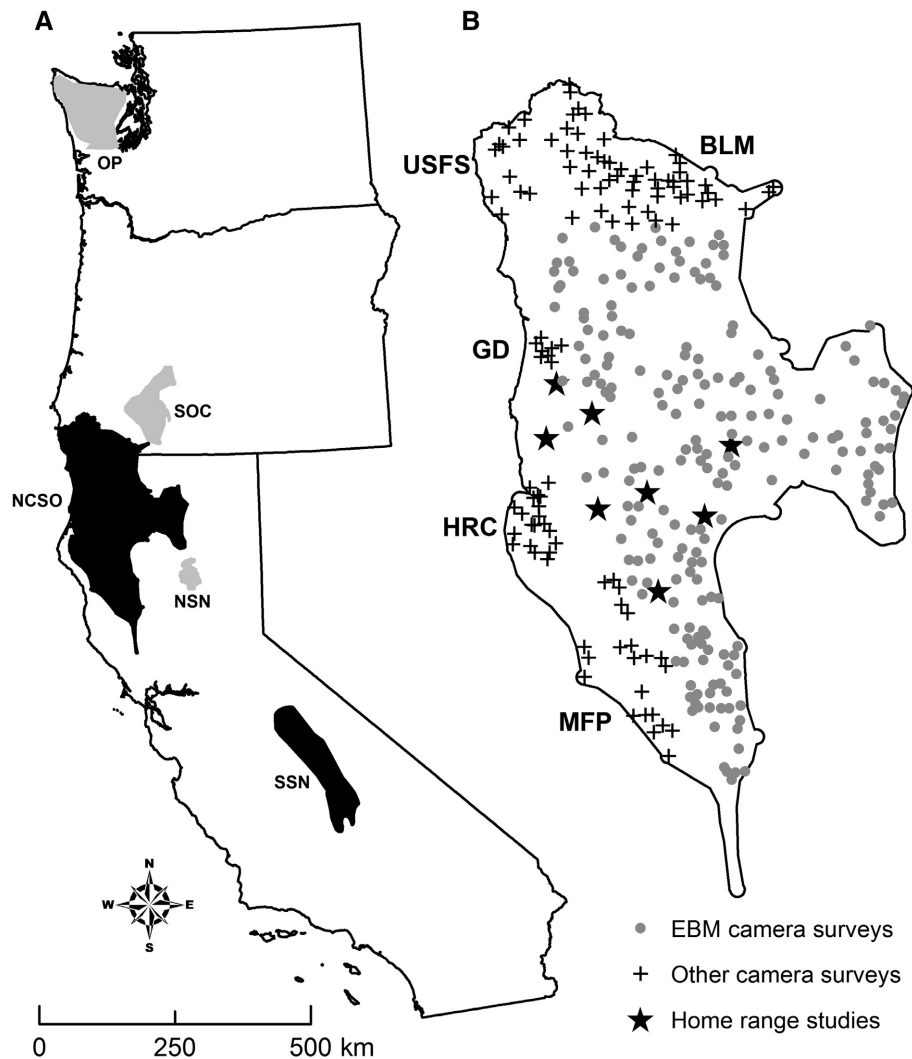


Fig. 1. Ranges of the remaining native (black) and re-introduced (gray) populations of fishers on the west coast of the United States (A) and locations of camera station sites and home range studies used to estimate the population size of the largest of these ranges (B). The native populations are in Northern California and Southern Oregon (NCSO) and the Southern Sierra Nevada mountains (SSN). The re-introduced populations are in the Olympic Peninsula (OP), the Southern Oregon Cascades Mountains (SOC), and the Northern Sierra Nevada Mountains (NSN). Camera stations in the NCSO were from Ecoregion Biodiversity Monitoring (EBM) and Mendocino Fisher Project (MFP) of the California Department of Fish and Wildlife and from Humboldt Redwoods Company (HRC), Green Diamond Resource Company (GD), U.S. Forest Service (USFS), and the Bureau of Land Management (BLM). Each survey location represents a pair of concurrently surveyed camera stations 1–3 km apart.

2016b). This range covers 48,760 km² in NCSO in the United States. It spans 39.7° N–42.7° N in latitude and from the Pacific Coast to 220 km inland. Elevations vary from 0 to 2700 m above sea level (mean, 785). Average annual precipitation varied

from 465 to 4249 mm (mean, 1595 mm). Habitats are primarily montane conifer forest dominated by coast redwood (*Sequoia sempervirens*) along the coast and either Douglas-fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), white fir

(*Abies concolor*), or a mixture of these and other species inland. Forests intergrade with oak (*Quercus* spp.)-dominated forests at lower elevations. Pockets of chaparral and annual grasslands punctuate this mosaic across generally steep slopes (Schoenherr 1992).

Camera station surveys

Data were combined from six different projects that used camera stations within the NCSO range (Fig. 1). All projects generally followed the protocol of Zielinski and Kucera (1995) in terms of spacing between stations, use of passive infrared sensor cameras, baiting to attract mustelids, and survey duration. The majority (65%) of camera surveys were from the Ecoregion Biodiversity Monitoring (EBM) project of the California Department of Fish and Wildlife (CDFW, Furnas and Callas 2015). For EBM, sampling grid hexagons were randomly sampled each year without replacement from the Forest and Inventory Analysis (FIA) sampling frame (Bechtold and Patterson 2005). The distance between adjacent hexagon centers from this grid was 5.35 km. There were two camera stations ~1.6 km apart within each selected hexagon. Surveys occurred on public agency and private industrial forestland ownerships. The primary camera station was usually located at a hexagon centroid, but private property, steep terrain, and other logistical issues often required relocating survey sites to more accessible locations within selected hexagons. Where relocation was not feasible, the selected hexagon was not sampled. We limited survey points to areas surrounded by at least 20 ha of forest in excess of 10% canopy cover. We randomized the location of secondary camera stations which also needed to meet the 20 ha and 10% canopy cover criterion; crews drove to a location approximately 1450 m from the first camera as determined by a global positioning system device, and then walked until reaching a location 1600 m from the first camera or 200 m from the road. For our analyses, we included only sites for which we were able to survey both sites within a hexagon.

For EBM, a “stealth-mode” Reconyx PC 90 or PC 900 infra-red sensor, motion-activated, digital camera (www.reconyx.com) was affixed to a tree at each station. It was placed approximately 1 m above the ground aimed at a shallow angle

(<20°) toward bait placed 3–5 m distant at the base of a tree. Cameras were set to high trigger sensitivity, three pictures per trigger, one-second trigger interval, and no delay quiet period. We baited camera stations with 400 g of chicken parts and 160 g of “fishy” cat food in a sock nailed approximately 1 m up the bait tree bole, half an apple impaled on a nail below the sock, 500 mL of oatmeal-peanut butter mixture on a plate surrounded by a ring of sliced apple at the base of the tree, and a salt lick placed next to the grain. “Gusto” scent lure (www.minntrapprod.com) was applied to the sock and low hanging branches of at least two nearby trees behind the bait tree. For the majority (95%) of survey sites, we did not return to rebait cameras weekly as recommended by Zielinski and Kucera (1995). Our survey season began in early August and continued through late November or early December. The duration of surveys was 2–5 weeks, and both stations within a hexagon were always surveyed concurrently.

The EBM surveys covered only 61% of the NCSO range and the gaps in our coverage included Oregon and locations in California along the coast. Therefore, we augmented our data with surveys from other projects that followed field methods comparable to ours (Fig. 1). The Mendocino Fisher Project (MFP) of the CDFW used the same protocol except that rebaiting occurred weekly. Protocols for the remaining projects were generally consistent with the recommendations of Zielinski and Kucera (1995) in terms of passive infra-red sensor cameras, baiting to attract mustelids, and survey duration (Table 1). As the sampling designs from these projects were variable, we selected sites from each project to approximate the EBM design; we chose pairs of concurrently surveyed stations 1–3 km apart in the same FIA hexagon. Surveys from Humboldt Redwoods and Green Diamond Resource Company in California occurred in August–December, whereas surveys from the U.S. Forest Service and the Bureau of Land Management (BLM) in Oregon occurred March–July.

All photos from surveys were reviewed to identify detections of fishers. We used this information to create a detection history for each site that indicated whether (“1”) or not (“0”) a fisher was observed for each 24-h survey day up to 28 d. If the survey duration was <28 d, or if the camera was

Table 1. Sources of camera station data used in modeling the abundance of fishers in Northern California and Southern Oregon.

Project	Sites	Years	Start date	Average duration in days (SD)	Average distance between paired sites in kilometers (SD)†	Bait	Camera
EBM	416	2010–2014	August–November	18 (7.6)	1.6 (0.21)	M S G F	R
MFP	44	2012–2013	October–November	26 (6.1)	1.6 (0.10)	M S G	R
HRC	40	2011–2014	August–November	30 (0.0)	2.3 (0.86)	M S	B
GD	16	2010	September–December	26 (5.2)	1.7 (0.40)	M S	C P
USFS	60	2015	May–July	15 (2.1)	1.0 (0.10)	M S	B
BLM	66	2011–2014	March–June	30 (0.0)	2.1 (0.51)	M S	B

Note: EBM, Ecoregion Biodiversity Monitoring; MFP, Mendocino Fisher Project; HRC, Humboldt Redwoods Company; GD, Green Diamond Resource Company; USFS, U.S. Forest Service; BLM, Bureau of Land Management; SD, standard deviation; M, meat; S, scent lure; G, grain; F, fruit; R, Reconyx PC90 or PC900; B, Bushnell Trophy; C, Cuddeback; P, Primos.

† Each pair of cameras was surveyed concurrently.

not functional some of the time, these days were treated as missing data (“x”) in a full 28-d detection history (e.g., 00000110101000xxxxxxxxxxxx for a 14-d survey).

Abundance modeling

Royle and Nichols (2003) proposed a model for estimating abundance from detection/non-detection survey data by building on the assumption that detection probability is often higher at sites with higher local abundance (Kéry et al. 2010, 2013). Under this model, the probability of detecting occupancy (P) of a species at site i is modeled as $P_i = 1 - (1 - r)^{N_i}$, where N_i is local abundance and r is the probability that a particular individual is detected. Local abundances N_i are seen as random draws from a probability distribution suitable for counts. Heterogeneity in this distribution as well as in parameter r can be modeled in terms of site- and survey-specific covariates. We modeled station-level (survey site) fisher abundance N_i as a Poisson random variable with expected value λ_i . For expected local abundance (λ_i) that varied by site (i) and individual detection probability (r_{ij}) that varied by site and survey (j): $\lambda_i = e^{B_i}$ and $r_{ij} = e^{D_{ij}} / (1 + e^{D_{ij}})$, where $B_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_K x_{iK}$, $x_{i1} \dots x_{iK}$ were site-level covariates for abundance, and $D_{ij} = \delta_0 + \delta_1 u_{ij1} + \delta_2 u_{ij2} + \dots + \delta_L u_{ijL}$ and $u_{ij1} \dots u_{ijL}$ were site- and survey-level covariates for detection. Survey-level detection probability (P_{ij}) was $P_{ij} = 1 - (1 - r_{ij})^{N_i}$. We refer to the above model structure as the “standard” Royle-Nichols (RN) model. Models were solved by maximum-likelihood estimation via R statistical software

(version 3.0.1, www.r-project.org) using the occuRN function from the unmarked package (Fiske and Chandler 2011).

We included model covariates for explaining variation in fisher detection probability and abundance based on the findings of previous studies. We expected that detection probability would vary seasonally so we created a covariate, $yday$, representing the number of days since the beginning of the year of each survey day (Slauson et al. 2012, Sweitzer et al. 2016). To address changes in detection probability after a fisher visited a station, we created a covariate representing Markov dependency (Hines et al. 2010, Slauson et al. 2012) between detection history days at each station where lag_x on survey day k was the maximum of the detection history values (0 or 1) on days $k - x$ through $k - 1$, or it was zero if these data were not available. Based on preliminary modeling, we found that a three-day dependency ($lag3$) was most predictive of detection probability and used this covariate in our modeling. To address a potential reduction in attraction of fishers to stations due to removal or degradation of bait items and the lack of rebaiting for most of the EBM surveys, we created a covariate, $bday$, representing the number of days since rebaiting or the number of days since the beginning of the survey if rebaiting did not occur. As we lacked detailed information on the dates of rebaiting events for non-EBM surveys, we assumed rebaiting occurred every seven days for those surveys. Preliminary modeling suggested that inclusion of the $bday$ covariate outperformed (e.g., lower Akaike’s information criterion [AIC])

a simple number-of-days-since-start-of-survey covariate in the detection model. We also expected that detection probability would increase as forest canopy cover increased (Sweitzer et al. 2016) and created a covariate representing average total percent canopy covered in the 250-m buffer surrounding each survey site (*evc250*) using land-use/land-cover data derived from the LANDFIRE Existing Vegetation Cover map (Toney et al. 2009). To control for differences in detection probability among the six survey projects, we created a categorical variable distinguishing data from each source (*project*).

Based on a review of the literature, we expected that fisher abundance would vary with tree canopy cover (Carroll et al. 1999, Sweitzer et al. 2016), elevation (Davis et al. 2007, Sweitzer et al. 2016), latitude (Carroll et al. 1999, Davis et al. 2007), and distance from the coast (Carroll et al. 1999). We calculated a covariate representing average total percent canopy covered in the 800-m buffer surrounding each survey site (*evc800*) using land-use/land-cover data derived from the LANDFIRE Existing Vegetation Cover map (Toney et al. 2009). Similarly, we used a 30-m resolution digital elevation model to compute average elevation (m) within the same 800-m buffers around survey sites (*elev800*) which was always included with its quadratic term (*elev800*²) to investigate a possible unimodal association. We chose larger buffers for covariates on abundance (800 m) than for those on detection probability (250 m) after reasoning that habitat conditions at larger scales affected selection of home ranges, whereas habitat conditions at smaller spatial scales governed fisher behavior in the vicinity of camera stations. We did not use buffers larger than 800 m because of the 1.6-km separation between paired stations in our sampling design. Latitude (*lat*) and distance from coast (*coastdist*) which was always included with its quadratic term (*coastdist*²) to investigate a possible unimodal association were readily computed using GIS.

To select a final model suitable for predicting how site-level abundance varied across the study area, we followed an information-theoretic approach to compare models containing all combinations of covariates (Burnham and Anderson 2002). First, we fit 32 intercept-only abundance models representing all combinations of *yday*, *bday*, *lag3*,

evc250, and *project* as detection probability covariates. We selected the model with the lowest AIC score and used those detection probability covariates in all subsequent models. Second, we fit 16 abundance models representing all combinations of *evc800*, *coastdist* + *coastdist*², *lat*, and *elev800* + *elev800*² as abundance covariates. We selected the model with the lowest AIC score as our final model of fisher abundance at camera stations.

Under the selected model, we calculated the mean of expected local abundance ($\bar{\lambda}$) across all camera sites as well as three measures of detection probability across all sites and surveys. The detection probabilities, all based on probability prior to first detection (*lag3* = 0), were the mean individual detection probability (\bar{p}) and the mean species detection probability conditional on occupancy (Royle and Nichols 2003) for a single-day survey (\bar{p}_{cond}) as well as over 28 d ($\bar{p}_{\text{cond}}^{(28)}$). Please see Appendix S1 for details on how we calculated detection probabilities conditional on occupancy.

Home range size and effective area of camera station surveys

We reviewed findings from previous studies that used telemetry and trapping data to estimate home range size of fishers at eight locations within the NCSO range (Buck et al. 1983, Seglund 1995, Dark 1997, Zielinski et al. 2004, Reno et al. 2008, Thompson 2008; Hoopa Tribal Forestry, *unpublished data*). These studies were all from 40.5° N–41.0° N in latitude and 20–120 km inland from the coast. From these studies, we compiled information on home range estimates of 107 female and 61 male fishers that used a 100% minimum convex polygon method (Mohr 1947). We restricted inclusion of home range data in our analysis to those individuals with at least 10 data points (Table 2). We were unable to set a higher inclusion threshold because many of the studies we used included home ranges calculated using less than 30 locations per individual. Fisher home range size is known to vary by gender (Powell 1993, Yaeger 2005) and is believed to increase with distance from the coast (Lofroth et al. 2010). We fit a generalized linear mixed model with a log-link function and normally distributed errors to assess how home range size varied by gender and distance to coast. The random effect in this model addressed variation

Table 2. Sources of fisher home range data used to estimate the effective area of camera station surveys.

Study area	Source of home range data				Gender		Number of locations used in home range			
	Study	Latitude (°N)	Longitude (°W)	Distance to coast (km)	F	M	Mean	SD	Min	Max
Korbel	Thompson (2008)	40.95	123.92	20	5	0	21	10	10	33
Bald Hills	Thompson (2008)	41.22	123.86	20	5	2	24	14	12	45
Hoopla	<i>Unpublished data</i>	41.08	123.62	40	74	45	128	133	10	607
Pilot Creek†	Zielinski et al. (2004)	40.61	123.58	60	3	2			20	
Cedar Gap†	Zielinski et al. (2004)	40.20	123.19	70	4	0			20	
Big Bar	Buck et al. (1983)	40.69	123.27	80	4	5	31	26	10	84
Hayfork	Reno et al. (2008)	40.57	122.89	110	6	0	33	6	25	40
Trinity Lake	Seglund (1995)	40.92	122.72	120	3	3	18	8	12	35
Trinity Lake	Dark (1997)	40.92	122.72	120	3	4	29	16	13	60

Notes: SD, standard deviation. Home ranges were calculated using a 100% minimum convex polygon method.

† Summary statistics on the number of locations used for home ranges were not available for these studies.

among the eight study locations. We fit models with all combinations of the gender and distance to coast covariates and an intercept-only model and used AIC scores to confirm the predictive value of both covariates (Burnham and Anderson 2002). Models were solved via R statistical software using the glmmPQL function (Breslow and Clayton 1993, Venables and Ripley 2002).

Our purpose in modeling home range size was to determine the effective area of local abundance estimated throughout the NCSO range using camera stations and to convert local abundance to density by dividing it by this area. Using the home range model results, we calculated predicted values of average home range size for each 1-km increment of *coastdist* between 20 and 120 km. To avoid making predictions beyond the range of values used in regression, we assigned the predicted values at 20 or 120 km to all distances either below or above these bounds. We scaled each predicted annual home range to a smaller area expected to be used in fall (1 August–31 December) when the majority of the camera station surveys we used were conducted. Unfortunately, we had access to raw telemetry data from only one study location to recalculate home ranges ourselves (Hoopla Tribal Forestry, *unpublished data*). Furthermore, to address the potential for low sample size confounding conclusions about seasonal difference in spatial ecology (Powell 1993), we limited home range calculations to individuals with at least 30 data points in both time periods (annual and fall). This restriction is why we needed to choose

a wide range of dates (1 August–31 December) to represent fall. For 35 females and 15 males, we calculated 100% MCP home range estimates throughout the year and during the fall and computed the ratio of the latter to the former. For each gender, we used the average of the individual ratios as our seasonal scaling factor for adjusting home range size and calculated its standard error (SE).

We used fall home range estimates as the effective areas associated with our predicted values of camera station-level abundance throughout the NCSO range. First, we took each 1-km increment in distance from coast (20–120 km) and gender predicted value of annual home range size from regression and multiplied it by a gender-specific scaling factor to get estimates of effective area during the fall. Second, we assumed an approximately balanced gender ratio in the population (Powell 1993, Slauson et al. 2009) and took a simple average of the female and male fall home range predictions at each distance increment. The results were predicted values of effective survey area that we could apply to all locations throughout the NCSO range.

Density and extrapolation of estimates across the study area

We did not assume the camera station sites were a random sample of fisher habitat throughout the study area. Instead, we created a GIS layer of centroids of all 2169 FIA hexagons within the NCSO range and an equal number of points 1.6 km distant in a different random

direction from each centroid to match the EBM design. We assumed these 4338 points provided a random sample of fisher habitat throughout the study area and calculated abundance covariate values of *evc800*, *elev800*, *lat*, and *coastdist* at each point. At every point, we divided the predicted value of abundance from our final RN model by effective survey area (average of predicted female and male seasonally scaled home range sizes for *coastdist* at that point) to get predicted density.

We used bootstrapping to compute average density for the NCSO range in a way that reflected its multiple sources of error (Efron 1982). We took 10,000 resamples without replacement of our data such that each resample permitted variation due to multiple sources of error simultaneously (e.g., site-level abundance, home range size, seasonal scaling of home range size). We used the mean of the means of predicted densities from each resample as our estimate of average density throughout the NCSO range. We got an estimate of total population size by multiplying this density by the study area (48,760 km²). We reported 95% CIs on our estimates of average density and population size as the 2.5th and 97.5th percentiles from the resampling distribution.

Our specific procedures for resampling were as follows. We resampled abundance at each of the 4338 random GIS points by drawing from a random normal distribution using the predicted values and their SE from our final model. For each resample of predicted abundance at all those points, we took a subsample to avoid pseudo-replication that would otherwise inflate apparent precision. We did this by taking a random sample without replacement from the resampled points equal to the number of station pairs used in abundance modeling ($n = 321$) and included those points and their pairs in the subsample ($n = 642$). For home range regression with *coastdist* and gender, we randomly selected with replacement from the set of individual home ranges we used to get a new set of equal size. For each resample, we fit a new home range regression model and calculated new predicted values of home range size for each 1-km *coastdist* increment by gender. We then resampled new seasonal scaling rates by drawing from a random normal distribution using the estimated scaling

rates and their SE. We used the resampled values from these three steps to calculate new values of predicted fisher density at the 642 points retained in the resample after sub-sampling and took the average. We used the distribution of the averages from the 10,000 resamples to get an estimate and CI for average density.

We mapped how density varied across the study area by using Kriging to smooth the values at the 4338 random points into a continuous prediction surface (Bailey and Gatrell 1995). This method allowed us to interpolate density between points and make inferences about the distances at which there was spatial autocorrelation in fisher density among locations. It also allowed us to assess whether the covariates we used in modeling adequately addressed autocorrelation. We first created a sample variogram of the predicted values at the random points and then fit a spherical model to it. The parameters in this model included the “range” (distance below which there was autocorrelation in density), “nugget” (amount of autocorrelation at the smallest distances), and “sill” (non-spatial variance among all points). Semivariance was our measure of spatial autocorrelation which we standardized so that the sill was equal to one. Lower semivariance and a small nugget represented greater autocorrelation in the data set. To evaluate the role of covariates in mitigating autocorrelation, we repeated this process on the residuals of a density model including the covariates from our final abundance model. We created the sample variogram and fit the variogram model using the variogram and fit.variogram functions from the gstat package (Pebesma 2004) in the R programming language. We used the variogram model of predicted densities and a Kriging tool in ArcGIS (version 10; Environmental Systems Research Institute, Redlands, California, USA) to create a 1-km raster grid of interpolated densities throughout the NCSO range. We compared our predicted densities to the findings of previous studies that estimated fisher density at four locations in the study area (Buck et al. 1983 [Big Bar], Thompson 2008 [Bald Hills and Korbell], Matthews et al. 2011 [Hoopa]). We did this by calculating the average predicted density from Kriging within the area of each previous study and comparing those to the results reported from each study.

Evaluation of modeling assumptions

We would have preferred to restrict our use of camera stations to only those surveyed in the fall. Unfortunately, the only camera data we had access to in Oregon were from summer when our assumption about smaller seasonal home ranges may not have been valid. For this reason, we separately estimated total population size using only data from the EBM project and compared this estimate to that using all of the data. We followed the same analytical steps described above except that we skipped the model selection procedure and used the best local abundance model as determined using all of the data. We removed the *project* covariate from the detection component of this model. We also evaluated the effect of seasonal scaling of home range sizes, by repeating modeling without any seasonal scaling.

We tested the assumptions of the RN model (1) that any covariance of paired station abundances was adequately modeled by the abundance covariates and (2) that any population estimation bias resulting from equating male and female individual detection probability was small. Since camera detection data came from pairs of concurrently surveyed stations approximately 1.6 km apart, we expected abundances at paired stations to have a positive covariance. Presumably, our standard RN model structure accounted for some of this covariance to the extent that paired stations had similar site covariate values. To account for and evaluate any remaining covariance of paired abundances, we extended the RN model structure. We modeled paired local abundances N_i and N_{i+1} (odd i only) as pairwise draws from a bivariate Poisson distribution with covariance $\gamma \times \text{invpairedist}_i$, where parameter γ is a non-negative constant and covariate invpairedist_i is the inverse of the distance between stations i and $i + 1$. The expected values of N_i and N_{i+1} were $\lambda_i + \gamma \times \text{invpairedist}_i$ and $\lambda_{i+1} + \gamma \times \text{invpairedist}_i$ respectively. We referred to this as the “station-pair” model. When parameter $\gamma = 0$, paired abundances were independent and the station-pair model was identical to our standard RN model. We fitted two station-pair models: one with no covariates other than *invpairedist* and the other with the addition of the

were fitted by maximum-likelihood estimation using R statistical software and the *nlm* function.

Since it was not possible for us to reliably determine gender from photographs of fishers, we modeled local abundance and individual detection probability the same for males and females in the standard model. To investigate possible bias of this procedure, we ran simulations of our density estimates for fishers for scenarios with large, gender-based differences in detection probability. We generated data sets with no covariates based on our previous estimates of mean local abundance (λ_0) and mean individual detection probability (r_0) at camera stations predicted by our best standard RN model, and based on mean female and male fall home range sizes (h_F , h_M) from our generalized linear mixed model of home range size. We expected that the ratio of mean local abundance for females to mean local abundance for males ($\lambda_F:\lambda_M$) should be comparable to the ratio of home range sizes ($h_F:h_M$) and therefore set $\lambda_F = \lambda_0 h_F / (h_F + h_M)$ and $\lambda_M = \lambda_0 h_M / (h_F + h_M)$ for all simulations. For gender-specific individual detection probabilities r_F and r_M , we wanted the average to be comparable to our best data-based estimate r_0 while investigating sensitivity of density estimates to the ratio $r_F:r_M$. In each simulation, we chose one of three treatments for $r_F:r_M$: 2:1, 1:2, or 1:4 prior to 1 September and 1:2 afterward. For each simulation, we generated a data set for 642 survey sites and a 28-d survey with dates corresponding to our original survey data. Site-level, gender-specific abundances N_{Fi} and N_{Mi} , $i = 1 \dots 642$, were random draws from Poisson distributions with means λ_F and λ_M , respectively. We calculated site-level gender detection probabilities $P_{Fi} = 1 - (1 - r_F)^{N_{Fi}}$ and $P_{Mi} = 1 - (1 - r_M)^{N_{Mi}}$ and with these generated gender-specific detection histories y_F and y_M and a combined detection history y_{ALL} . Using the standard model with no covariates, we estimated mean local abundance $\hat{\lambda}_0$. As before, we fitted models by maximum-likelihood estimation via R statistical software using the *occuRN* function from the *unmarked* package. The effect of interest was the $\hat{\lambda}_0/\lambda_0$ ratio representing the bias of the gender-blind estimate under gender-based heterogeneity. We calculated the mean of this ratio across 1000 simulations within each of the three

Table 3. Summary statistics on biophysical conditions at survey sites used in abundance modeling and the random locations used to extrapolate fisher population size across the range of the species in Northern California and Southern Oregon.

Covariate	Inter-quantile range (5–95%)	
	Camera stations used in abundance modeling	Random GIS points used in extrapolating population size throughout NCSO range
Tree canopy cover (<i>evc800</i>)	18.5–69.7%	6.2–70.9%
Distance to coast (<i>coastdist</i>)	15.7–191.6 km	8.9–187.4 km
Latitude (<i>lat</i>)	39.6–42.4° N	39.5–43.4° N
Elevation (<i>elev800</i>)	297–1736 m	196–1740 m

Notes: GIS, geographic information systems; NCSO, Northern California and Southern Oregon. Overlap of inter-quantile ranges suggests that extrapolation based on regression associations from the camera stations was appropriate.

treatments. We provide the R code and data used for all analyses (See Appendix S2).

RESULTS

Summary statistics

The camera station data we used were from 642 stations (321 station pairs). The average number of functional survey days per station of the data we used in modeling was 20 (standard deviation [SD] = 8). Fishers were detected at 25.4% of stations and 40.5% of station pairs. For stations at which fishers were detected, they were observed on an average of 12.0% of functional survey days. The range of biophysical conditions at camera stations largely overlapped the range

of conditions at the random GIS points we used to extrapolate population size across the study area (Table 3).

Detection probability and abundance

Our best model for explaining detection probability contained the *lag3*, *bday*, *evc250*, and *project* covariates (Table 4). However, it only outperformed the saturated model also including *yday* by 0.50 AIC points. As there was little difference in average predicted detection probability among the two top models summing to the top 1.00 of AIC weights, we chose *lag3*, *bday*, *evc250*, and *project* but not *yday* as the detection covariates to include in a final model for extrapolating abundance across the NCSO study area. Although

Table 4. Model selection results for detection probability and local abundance of fishers at camera stations from Northern California and Southern Oregon.

Model, covariates†	Par‡	AIC	ΔAIC	AICwt	Total AICwt	Model estimate§
Detection						\bar{r}
<i>lag3</i> + <i>evc250</i> + <i>project</i> + <i>bday</i>	10	2993.07	0.00	0.56	0.56	0.042
<i>lag3</i> + <i>evc250</i> + <i>project</i> + <i>yday</i> + <i>bday</i>	11	2993.57	0.50	0.44	1.00	0.041
Intercept only	2	3098.56	105.49	<0.00	1.00	0.084
Abundance						$\bar{\lambda}$
<i>evc800</i> + <i>coastdist</i> + <i>coastdist</i> ² + <i>lat</i> + <i>elev800</i> + <i>elev800</i> ²	16	2944.27	0.00	0.86	0.86	0.593
<i>evc800</i> + <i>coastdist</i> + <i>coastdist</i> ² + <i>lat</i>	14	2948.01	3.74	0.13	0.99	0.570
Intercept only	10	2993.07	48.81	<0.00	1.00	0.597

Notes: AIC, Akaike's information criterion; Model selection for detection covariates was for an intercept-only abundance model. Model selection for abundance always included covariates from top detection model. Covariate *lag3* represents whether a fisher was detected in the previous three days, *evc250* was average tree canopy cover within a 250-m buffer, *yday* was the survey day measured from 1 January, *bday* was the number of days since the beginning of the survey or since rebaiting, and *project* was a categorical variable representing the six camera station survey projects. Covariate *evc800* was average tree canopy cover within an 800-m buffer, *elev800* was average elevation within an 800-m buffer, *coastdist* was distance to coast, and *lat* was latitude.

† Models in the top 0.95 of cumulative AIC weights are shown here in addition to null (intercept-only) models.

‡ Number of parameters in models. The covariate *project* is a categorical covariate we modeled using five dichotomous variables representing the five camera trap projects other than Ecoregion Biodiversity Monitoring which we treated as the baseline.

§ Derived parameter estimates from our models. \bar{r} represents average daily detection probability of an individual fisher. $\bar{\lambda}$ represents average local abundance of fisher.

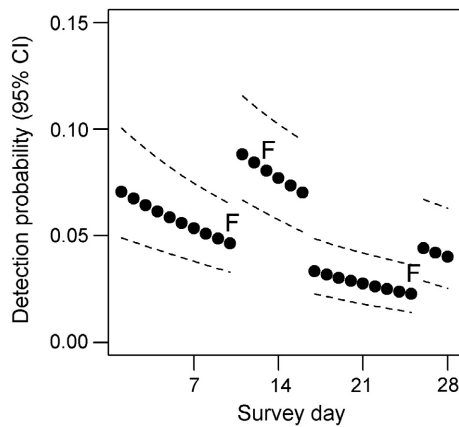


Fig. 2. Associations between daily detection probability of individual fishers at camera stations and the number of days since the beginning of the survey (*bday*) and whether a fisher was detected in the previous three days (*lag3*). In this hypothetical example, the camera station was baited at the beginning of survey day 1 only and fisher (F) was detected on days 10, 13, and 25. Latitude, elevation, canopy cover, and coast distance were at their mean values.

detectability declined gradually over the course of the survey since initial baiting or rebaiting, the observation of a fisher in the previous three days was strongly and positively associated with detection probability (Fig. 2). After controlling for the other covariates in our final model, there were no differences in detection probabilities among camera station projects with respect to EBM, except the BLM surveys in Oregon which were lower. For all projects, average detection probability of an individual fisher if present (*r*) was 0.039 per day (*SD* = 0.018). Average survey-level detectability of occupancy (\bar{P}_{cond}) was 0.052 per day (*SD* = 0.028). Average site-level detectability of occupancy ($\bar{P}_{\text{cond}}^{(28)}$) was 0.734 (*SD* = 0.163) after 28 d.

We found the best model explaining abundance was the saturated model containing the *evc800*, *coastdist* + *coastdist*², *lat*, and *elev800* + *elev800*² covariates (Tables 4, 5). It outperformed the closest model without *elev800* + *elev800*² by 3.74 AIC points. Abundance was positively associated with tree canopy cover and negatively associated with latitude. Abundance increased with elevation, but declined at the highest elevations locations where tree canopy declined in sub-alpine and alpine habitats. Average predicted abundance at camera stations was 0.593 (*SD* = 0.402) fishers per site

compared to an average of 0.477 (*SD* = 0.373) fishers at random GIS points.

Home range size

As expected, annual home range size (100% MCP) varied with gender and distance to coast. The regression model with both covariates outperformed the null model and models with just one of the covariates. For female fishers, average annual home range size varied from approximately 6 km² at 20 km from the coast to approximately 13 km² at 120 km. For males, average home range size varied from 12 km² at 20 km to approximately 27 km² at 120 km (Fig. 3). Using data from the Hoopa study location, we estimated scaling ratios of annual to fall home ranges of 0.707 (*SE* = 0.024) for females and 0.549 (*SE* = 0.048) for males. After

Table 5. Final Royle-Nichols model used to estimate fisher abundance at camera stations.

Parameter†	Estimate	SE	95% CI _{LO}	95% CI _{UP}
Model parameters for abundance				
Intercept	−0.339	0.180	−0.692	0.015
Tree canopy cover (<i>evc800</i>)	0.507	0.134	0.244	0.769
Distance to coast				
<i>coastdist</i>	0.077	0.141	−0.200	0.353
<i>coastdist</i> ²	−0.336	0.095	−0.523	−0.149
Latitude (<i>lat</i>)	−0.442	0.113	−0.663	−0.222
Elevation				
<i>elev800</i>	0.298	0.109	0.085	0.510
<i>elev800</i> ²	−0.067	0.073	−0.210	0.077
Model parameters for detection				
Intercept	−3.071	0.183	−3.429	−2.713
Markov dependency (<i>lag3</i>)	0.735	0.130	0.480	0.990
Days since baiting (<i>bday</i>)	−0.394	0.083	−0.557	−0.232
Tree canopy cover (<i>evc250</i>)	0.118	0.127	−0.131	0.368
Project‡				
MFP	0.086	0.233	−0.371	0.542
HRC	−0.349	0.373	−1.080	0.382
GD	−0.245	0.341	−0.912	0.422
USFS	−0.875	0.503	−1.862	0.111
BLM	−1.693	0.416	−2.508	−0.877

Note: BLM, Bureau of Land Management; GD, Green Diamond Resource Company; HRC, Humboldt Redwoods Company; MFP, Mendocino Fisher Project; USFS, U.S. Forest Service; SE, standard error.

† All covariates were standardized.

‡ Model parameterized with Ecoregion Biodiversity Monitoring as baseline for *project*.

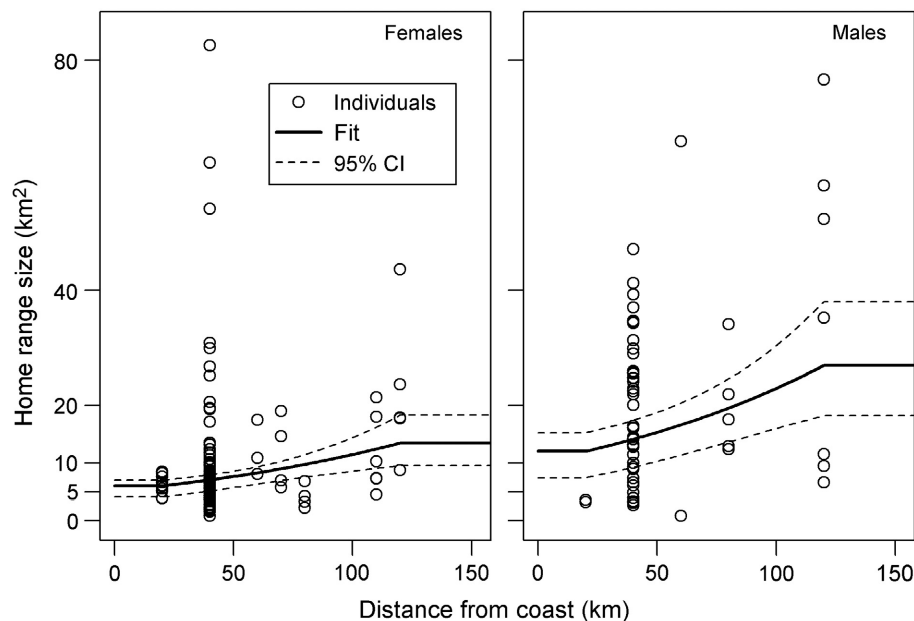


Fig. 3. Relationship between annual fisher home range size and distance to coast by gender. The points above represent 100% minimum convex polygon home range estimates for fishers from six study locations in Northern California. The lines are regression fits of these data by gender. Extrapolation was truncated to the range of distances from the fisher data (20–120 km).

applying these ratios to the annual home range sizes at our random GIS points and averaging by gender, we estimated a NCSO-average fall home range size of 8.33 km^2 ($SD = 2.55$).

Density and population size

Average fisher density across the NCSO range was $6.6 \text{ fishers}/100 \text{ km}^2$ (95% CI: 5.1–8.6). Our estimate for total population size was 3196 fishers (95% CI: 2507–4184). Average density was maximized at 67 km from the coast. Using the density predictions at random GIS points throughout the NCSO, we fit a semivariogram model with a range of 40 km and a nugget of 0.40 on a standardized scale (Fig. 4). Using a density model including the $evc800$, $coastdist + coastdist^2$, lat , and $elev800 + elev800^2$ covariates, we fit a semivariogram model with a nugget of 0.70 on a standardized scale. The difference in nugget sizes suggests that the covariates we used addressed most of the spatial autocorrelation in density. Using the semivariogram parameters from the predicted values at random points to help us map density throughout the NCSO range via Kriging, we found a core area of predicted high

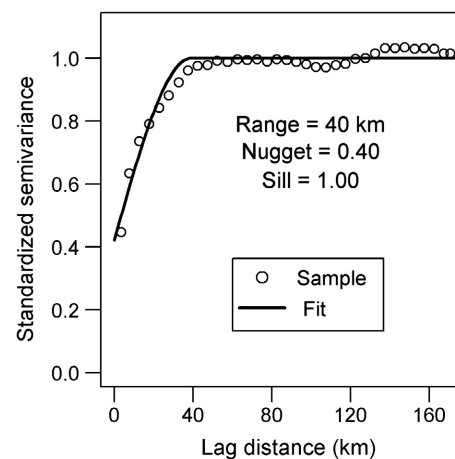


Fig. 4. Spatial autocorrelation in fisher density throughout its range in Northern California and Southern Oregon. We created an anisotropic sample variogram of our predicted densities at 4338 random geographic information systems points throughout the study area. We fit a spherical model to the sample variogram and estimated range, nugget, and sill parameters. The results suggest that spatial autocorrelation in fisher density was present at distances up to 40 km between locations.

density (>10 fishers/100 km²) extending from 39.0° N to 41.5° N in latitude and centered on distances ~40–80 km from the coast (Fig. 5). We found close agreement between the results of previous studies of density and our predicted values at the locations of these studies (Table 6). We provide a compressed Keyhole Markup Language file (KMZ) for use with Google Earth software (Google, Mountain View, California, USA) to view the map of interpolated predicted densities presented in Fig. 5 (see Appendix S2).

Evaluation of modeling assumptions

The restriction of modeling to EBM data had little effect on our overall estimate of population size throughout the NCSO range. In particular,

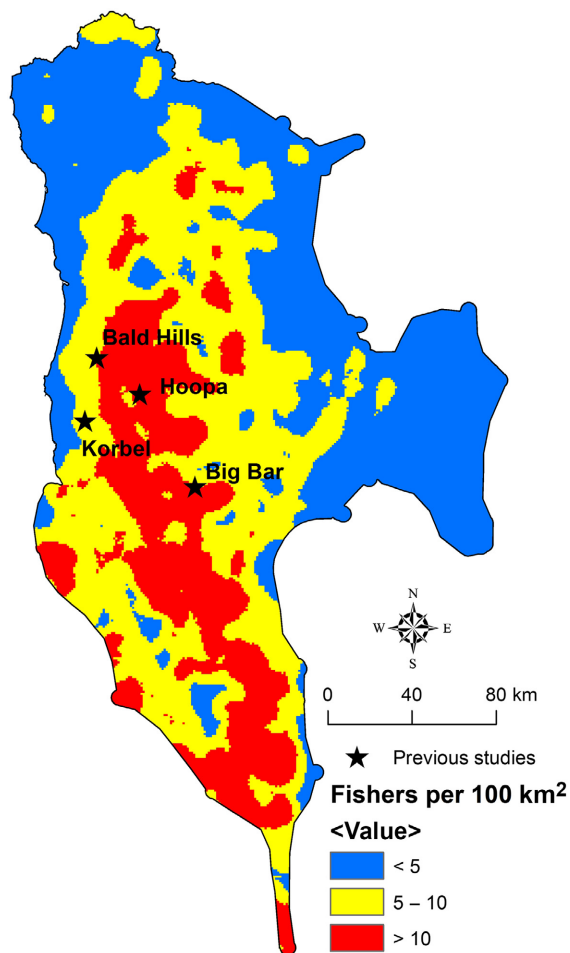


Fig. 5. Spatial variation in fisher density throughout the study area and the locations of four previous studies that estimated density.

Table 6. Comparison of our fisher density estimates with results from previous studies in Northern California.

Location†	Area (km ²)	Density (Fishers/100 km ²)	
		Our estimate‡	Previous study§
Bald Hills	100	9.6	10.0
Korb	100	7.7	8.5
Hoopa	100	13.3	14.0
Big Bar	160	11.0	8.0
Average		10.4	10.1

† See Fig. 5.

‡ Based on our abundance and home range modeling throughout the study area. We computed the average predicted density within the boundaries of each study area.

§ Published findings for study locations: Bald Hills and Korb (Thompson 2008), Hoopa (Matthews et al. 2011), and Big Bar (Buck et al. 1983).

the estimate from this approach (3300 fishers) was 3% larger than our estimate using the larger data set, but the CI (2561–4356) overlapped our estimate (3196 fishers) using the larger data set. In contrast, the removal of seasonal scaling of home range size from our analysis reduced our estimate of population size (1921 fishers; 95% CI: 1533–2516) by 40%.

The results of our supplemental modeling suggest that the standard RN model we used for population estimation was unlikely to have provided biased estimates due to violations of model assumptions. Without covariates, the station-pair model outperformed the standard model, but upon inclusion of covariates the standard model outperformed the station-pair model (Appendix S3: Table S1). For a large difference in detection probabilities among genders (100% in fall, 300% in spring/summer), our simulations suggest a small (5–8%) under estimation of density (Appendix S3: Table S2).

DISCUSSION

Our results represent the first robust estimates of density and population size of fishers for the NCSO range which is the largest native population remaining in the Pacific States of the United States. Our results, clipped to four areas where local density was independently estimated by previous studies, were remarkably similar to the results of those studies. Furthermore, the CI for our estimate of population size overlaps the only other estimate of population size for the NCSO

(4018 fishers; Self et al. 2008). The consistency of these estimates is one reason why our numbers are likely to be helpful to managers planning the conservation of this species. A credible population estimate and map of density at the scale at which conservation planning is needed can be used as a baseline against which to monitor for a population trend and changes in the spatial distribution of this species.

Monitoring population status and distribution is especially important for fishers in the Pacific States because the remaining population ranges are fragmented by anthropogenic and ecological barriers with less connectivity than before European settlement (Lofroth et al. 2010). Re-introductions are one of the primary actions being used to expand fisher populations and their range. Two re-introduced populations in the Southern Oregon Cascades Mountains and Northern Sierra Nevada Mountains (NSN) are immediately adjacent to the NCSO range (Fig. 1). Our results suggest that current fisher density is low (<5.0 fishers/100 km²) in the portions of the NCSO range nearest to these re-introduced populations. However, observations from the last five years suggest that the frequency of fisher detections at camera stations in the area adjacent to the NSN range may be increasing (Klug 2014; P. Figura, CDFW, *unpublished data*). At least one of these observations was of a re-introduced fisher from the NSN range (B. Furnas, CDFW, *unpublished data*). Furthermore, it is interesting to note that our density map predicted high density (>10.0 fishers/km²) in the extreme southern appendage of the NCSO range (Fig. 5). This area was included because of a documented occurrence in Lake County from 2013. Although this area contributed little to the total predicted population size (e.g., ~ 30 fishers), it will be important to monitor whether the recent detection in this area represents an expansion of fishers into a portion of their historical range (Allen et al. 2015).

The RN model has not been applied widely to estimate abundance, in part because it is more sensitive to parametric assumptions and performs poorly when abundance is high (Kéry and Royle 2015). Based on our literature search of the term, "RN model," we found only four published studies that used this model to estimate abundance of a wildlife species (Stanley and Royle 2005, Ariefiandy et al. 2014, Duquette

et al. 2014, Erb et al. 2015). However, Royle and Dorazio (2008) demonstrated use of the model to estimate local abundance of fishers from track plate survey data in the NCSO range. The results of our supplemental modeling suggest that any violations of the assumptions of the RN model we made were unlikely to have led to large biases in our estimates of abundance and density. We agree with the assessment of Royle and Dorazio (2008) that the RN model may often be appropriate for carnivore survey data for which local abundance is low and territoriality is well defined. Indeed, we believe our camera station data may be useful for estimating abundance of other carnivores including black bear (*Ursus americanus*), western gray fox (*Urocyon cinereoargenteus*), and coyote (*Canis latrans*).

Two alternatives to the RN model are N-mixture and non-spatial capture-recapture models (Otis et al. 1978, Royle 2004). We could not fit either of these models because we were unable to distinguish individual fishers from our camera station images. Nevertheless, these models and the RN model only provide estimates of local abundance, not density. It is necessary to apply additional information about the effective area of surveys to calculate density. We used information on home range size as others have done (Karanth 1995, Bales et al. 2005). If it were possible for us to distinguish individual fishers (e.g., by adding hair snares to collect genetic samples), we might have considered the use of a spatial capture recapture model (SCR) to directly estimate density without the need for auxiliary information on home range size (Royle et al. 2014). However, we used a sampling grid in which paired camera stations were usually separated by large distances to survey fishers over a large geographic region. For this design, we would be unlikely to get enough recaptures among >2 stations to effectively fit a SCR. For this reason, we believe the combination of local abundance estimates and complementary information on home range size may remain the most feasible option for efficiently measuring the population status of fishers or other carnivores over a large area. One variation might be to implement the intensive surveys required for fitting a SCR in a few small but representative areas throughout the range and use the findings from those studies to validate estimates based on

non-spatial modeling of camera station data over the entire range.

We attempted to put as much thought into our calculation of effective survey area as we did for abundance modeling. We did this by pooling information on home range size from within the NCSO range, modeled how it varied with gender and distance from the coast, and scaled home ranges from annual estimates of space use to those for just the fall when most of the camera station surveys we used occurred. Furthermore, we used bootstrapping to incorporate uncertainty in the auxiliary data into our CIs for density and population size. These steps were important because the estimation of density is highly sensitive to changes in effective area. For example, if we had not seasonally scaled home range sizes, our estimates of density and population size would have been 40% smaller. Our estimate of population size was also sensitive to delineation of the NCSO range. The definition of this range was based on previous range mapping (Lewis et al. 2012) and careful screening of hundreds of documented fisher occurrences since 1993 including from the EBM and MFP projects (see fig. 1 in USDI Fish and Wildlife Service 2016a).

We note that the seasonal scaling factors we used were approximately 20% smaller than those found by Popescu et al. (2014) for fishers in the SSN range. This fact highlights one shortcoming of our analysis: the unavailability of home range information throughout the study area. All of the data used in our seasonal scaling analysis were from a single study area with the largest sample size (Hoopa Tribal Forestry, *unpublished data*). If we had instead used a scaling ratio based on the findings of Popescu et al. (2014), our population estimate would have been smaller (2634 fishers; 95% CI: 1906–3717) than the estimate using a scaling ratio based on the Hoopa data (3196 fishers; 95% CI: 2507–4184), but the CIs for each estimate overlap the mean of the other. All of the telemetry studies used in other aspects of our home range analysis were from similar latitudes which prevented us from effectively including this covariate in our home range model. Home range is known to vary with latitude (Lofroth et al. 2010), but the telemetry studies we used were all situated close (average = 40.08° N, SD = 0.21) to the average latitude (41.03° N) for the NCSO range. This coincidence may have

mitigated our problem with finding home range studies from a wider range of latitudes. Other issues with our home range analyses included use of the 100% MCP method instead of a kernel density estimator and the use of as few as 10 locations in the calculation of home ranges, and we are unable to ascertain how these limitations may have biased our results (Seaman et al. 1999, Börger et al. 2006). As we did not have access to raw telemetry data from most of the studies we used, we were unable to recalculate home ranges to potentially address these constraints.

Besides facilitating the mapping of density throughout the NCSO range, the variogram analysis provided useful information about the landscape ecology of fishers. The finding that autocorrelation was greatest at lag distances up to 40 km may be relevant to understanding the scale at which patches within a metapopulation (Hanski 1999) are currently assembled in the NCSO range. For a simplistic example, a circular area of 40 km diameter corresponds to an average of 83 fishers based on our results. This area is approximately 10 times larger than the minimum patch size believed necessary to support a population as determined by Olson et al. (2014). Some of the autocorrelation at smaller scales (<20 km) may be related to overlap of male and female home ranges, overlap of female home ranges, and pre-dispersal juveniles (Aubry et al. 2004, Rennie 2015). Autocorrelation in fisher density is likely driven in great part by the distribution of landscape-level habitat attributes across the study area. Other researchers have noted spatial autocorrelation in fisher occurrence and that landscape and regional patterns of habitat conditions such as tree canopy cover and precipitation are the strongest predictors of fisher occurrence in the NCSO range (Carroll et al. 1999, 2010). In our case, we demonstrated that the inclusion of canopy cover and elevation covariates reduced autocorrelation in model residuals. Nonetheless, more investigation is warranted to explain the pattern we found of density peaking in locations 40–80 km from the coast. We speculate that part of the cause may be that these areas tend to be dominated by dense, mid-elevation forests interspersed with pockets of tanoak (*Notholithocarpus densiflorus*) and other hardwoods that support high densities of fisher prey. The findings of Sweitzer and Furnas (2016) confirm that fisher

occurrence at camera stations is positively associated with co-occurrence of prey species.

Even though most (62%) camera stations we used in modeling were not rebaited, average site-level detection probability of occupancy was high (0.734) after 28 d. We controlled for reduced attraction of fishers to stations over time due to consumption of bait and weakening of the scent lure by including a covariate in our final model representing the number of days since the beginning of the survey or rebaiting (*bday*). However, we found that temporal autocorrelation in fisher visits to stations (*lag3*) was a much stronger predictor of detection probability than *bday* (Fig. 2). Furthermore, our estimate of total population size appears to be robust to differences among models explaining detection probability and whether we included camera station data from Oregon where fishers were surveyed during summer when detection probability was lower. Although there were little camera station data characterized by tree canopy cover <20% in our modeling, we do not believe this omission biased our population estimate, because the positive association we found between canopy cover and abundance resulted in negligible contribution of low canopy areas to the total population estimate.

In conclusion, we demonstrated a feasible approach to combine comparable sources of data to estimate the population size of a species over a geographic range. The RN model allowed us to accomplish this using detection/non-detection data that were efficiently collected over a large area using camera stations. The acceptance of a generally standardized camera station protocol made this task practical. It was more challenging for us to estimate the effective area of these surveys by piecing together available home range information of varying quality. For this reason, we recommend greater coordination between regional monitoring programs and local studies that collect telemetry information. Besides augmenting the types of analyses that are possible using monitoring data, these programs may be able to share data that are also useful to local studies.

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LITERATURE CITED

- Allen, M. L., B. E. Evans, and M. S. Gunther. 2015. A potential range expansion of the coastal fisher (*Pekania pennanti*) population in California. *California Fish and Game* 101:280–285.
- Ariefiandy, A., D. Purwandana, A. Seno, M. Chrismiawati, T. Jessop, and C. Ciofi. 2014. Evaluation of three field monitoring-density estimation protocols and their relevance to Komodo dragon conservation. *Biodiversity Conservation* 23:2473–2490.
- Aubry, K. B., S. M. Wisely, C. M. Raley, and S. W. Buskirk. 2004. Zoogeography, spacing patterns, and dispersal in fishers: insights gained from combining field and genetic data. Pages 201–220 in D. J. Harrison and A. K. Fuller, editors. *Martens and fisher (Martes) in human-altered environments: an international perspective*. Springer, New York, New York, USA.
- Bailey, T. C., and A. C. Gatrell. 1995. *Interactive spatial data analysis*. Prentice Hall, Harlow, UK.
- Bales, S., E. Hellgreen, D. Leslie Jr., and J. Hemphill Jr. 2005. Dynamics of a recolonizing population of black bears in Ouachita Mountains of Oklahoma. *Wildlife Society Bulletin* 33:1342–1351.
- Bechtold, W. A., and P. L. Patterson. 2005. The enhanced forest inventory and analysis program: national sampling design and estimation procedures. General Technical Report SRS-GTR-80. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina, USA. http://www.srs.fs.usda.gov/pubs/gtr/gtr_srs080/gtr_srs080.pdf
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.

- Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* 75:1393–1405.
- Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. *Journal of the American Statistical Association* 88:9–25.
- Buck, S., C. Mullis, and A. Mossman. 1983. Corral Bottom Hayfork Bally fisher study. Final Report to US Forest Service. Humboldt State University, Arcata, California, USA.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- California Fish and Game Commission. 2016. Notice of findings: fisher (*Pekania* [formerly *Martes*] *pennanti*). California Regulatory Notice Register No. 19-Z. Pages 758–764. <http://www.oal.ca.gov/files/2016/08/19z-2016.pdf>
- Carroll, C., D. S. Johnson, J. R. Dunk, and W. L. Zielinski. 2010. Hierarchical Bayesian spatial models for multispecies conservation planning and monitoring. *Conservation Biology* 24:1538–1548.
- Carroll, C., W. J. Zielinski, and R. F. Noss. 1999. Using presence-absence data to build and test spatial habitat models for the fisher in the Klamath Region, U.S.A. *Conservation Biology* 13:1344–1359.
- Ceballos, G., and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. *Science* 296: 904–907.
- Dark, S. J. 1997. A landscape-scale analysis of mammalian carnivore distribution and habitat use by fisher. Thesis. Humboldt State University, Arcata, California, USA.
- Davis, F. W., C. Seo, and W. J. Zielinski. 2007. Regional variation in home-range-scale habitat models for fisher (*Martes pennanti*) in California. *Ecological Applications* 17:2195–2213.
- Dixon, J. 1925. A closed season needed for fisher, marten and wolverine in California. *California Fish and Game* 11:23–25.
- Duquette, J. F., J. L. Belant, N. J. Svoboda, D. E. Beyer Jr., and C. A. Albright. 2014. Comparison of occupancy modeling and radiotelemetry to estimate ungulate population dynamics. *Population Ecology* 56:481–492.
- Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. Society of Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.
- Erb, L. A., L. L. Willey, L. M. Johnson, J. E. Hines, and R. P. Cook. 2015. Detecting long-term population trends for an elusive reptile species. *Journal of Wildlife Management* 79:1062–1071.
- Fiske, I. J., and R. B. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:(10).
- Furnas, B. J., and R. L. Callas. 2015. Using automated recorders and occupancy models to monitor common forest birds across a large geographic region. *Journal of Wildlife Management* 79:325–337.
- Gabriel, M. W., G. M. Wengert, and R. N. Brown. 2012a. Pathogens and parasites of *Martes* species: management and conservation implications. Pages 138–185 in K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx, and S. W. Buskirk, editors. *Biology and conservation of martens, sables, and fishers: a new synthesis*. Cornell University Press, Ithaca, New York, USA.
- Gabriel, M. W., et al. 2012b. Anticoagulant rodenticides on our public and community lands: spatial distribution of exposure and poisoning of a rare carnivore. *PLoS ONE* 7:e40163.
- Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. *Furbearing mammals of California*. Volume I. University of California Press, Berkeley, California, USA.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Hines, J. E., J. D. Nichols, J. A. Royle, D. J. MacKenzie, A. M. Gopalaswamy, N. Samba Kumar, and K. U. Karanth. 2010. Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications* 20:1456–1466.
- Jordan, M. J. 2007. Fisher ecology in the Sierra National Forest, California. Dissertation. University of California, Berkeley, California, USA.
- Karanth, K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation* 71: 333–338.
- Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- Kays, R. W., and K. M. Slauson. 2008. Remote cameras. Pages 110–140 in R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray, editors. *Non-invasive survey techniques for North American carnivores*. Island Press, Washington, D.C., USA.
- Kéry, M., B. Gardner, and C. Monnerat. 2010. Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography* 37:1851–1862.
- Kéry, M., G. Guillera-Arroita, and J. J. Lahoz-Monfort. 2013. Analysing and mapping species range

- dynamics using occupancy models. *Journal of Biogeography* 40:1463–1474.
- Kéry, M., and J. A. Royle. 2015. *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS: volume 1: prelude and static models*. Academic Press, Oxford, UK.
- Klug, R. 2014. Summary report: fisher occupancy on managed and post-fire landscape in Shasta County. Roseburg Resource Company, Weed, California, USA.
- Kucera, T. E., and R. H. Barrett. 2011. A history of camera trapping. Pages 9–26 in A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. *Camera traps in animal ecology: methods and analyses*. Springer, New York, New York, USA.
- Lawler, J. J., H. D. Safford, and E. H. Girvetz. 2012. Martens and fishers in a changing climate. Pages 371–397 in K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx, and S. W. Buskirk, editors. *Biology and conservation of martens, sables, and fishers: a new synthesis*. Cornell University Press, Ithaca, New York, USA.
- Lewis, J. C., R. A. Powell, and W. J. Zielinski. 2012. Carnivore translocations and conservation: insights from population models and field data for fishers (*Martes pennanti*). *PLoS ONE* 7:e32726.
- Lewis, J. C., and W. J. Zielinski. 1996. Historical harvest and incidental capture of fishers in California. *Northwest Science* 70:291–297.
- Linsdale, J. M. 1932. Further facts concerning losses to wild animal life through pest control in California. *Condor* 34:121–135.
- Lofroth, E. C., et al. 2010. Conservation assessment for fishers (*Martes pennanti*) in southcentral British Columbia, western Washington, western Oregon, and California. Volume I. U.S. Department of the Interior Bureau of Land Management, Denver, Colorado, USA. http://www.fws.gov/yreka/PDF/Lofroth_etal_2010.pdf
- Luck, G. W., G. C. Daily, and P. R. Ehrlich. 2003. Population diversity and ecosystem services. *Trends in Ecology and Evolution* 18:331–336.
- Luikart, G., N. Ryman, D. A. Tallmon, M. K. Schwartz, and F. W. Allendorf. 2010. Estimation of census and effective population sizes: the increasing usefulness, of DNA-based approaches. *Conservation Genetics* 11:355–373.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy estimation and modeling; inferring patterns and dynamics of species occurrence*. Academic Press, Waltham, Massachusetts, USA.
- Matthews, S. M., J. M. Higley, J. S. Yaeger, and T. K. Fuller. 2011. Density of fishers and the efficacy of relative abundance indices and small-scale occupancy estimation to detect a population decline on the Hoopa Valley Indian Reservation, California. *Wildlife Society Bulletin* 35:69–75.
- Mohr, C. O. 1947. Table of equivalent populations of North American small populations. *American Midland Naturalist* 37:223–249.
- Noon, B. R., D. D. Murphy, S. R. Beissinger, M. L. Shaffer, and D. Dellasala. 2003. Conservation planning for US National Forests: conducting comprehensive biodiversity assessments. *BioScience* 53:1217–1220.
- O'Connell, A. F., J. D. Nichols, and K. U. Karanth, editors. 2011. *Camera traps in animal ecology: methods and analyses*. Springer, New York, New York, USA.
- Olson, L. E., J. D. Sauder, N. M. Albrecht, R. S. Vinkey, S. A. Cushman, and M. K. Schwartz. 2014. Modeling the effects of dispersal and patch size on predicted fisher (*Pekania [Martes] pennanti*) distribution in the U.S. Rocky Mountains. *Biological Conservation* 169:89–98.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1–135.
- Pebesma, E. J. 2004. Multivariable geostatistics in S: the gstat package. *Computers & Geosciences* 30:683–691.
- Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Sauer. 2002. Large scales wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13:105–119.
- Popescu, V. D., P. de Valpine, and R. A. Sweitzer. 2014. Testing the consistency of wildlife data types before combining them: the case of camera traps and telemetry. *Ecology and Evolution* 2014: 933–943.
- Powell, R. A. 1993. *The fisher: life history, ecology and behavior*. Second edition. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Reed, D. H., J. J. O'Grady, B. W. Brook, J. D. Ballou, and R. Frankham. 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* 113:23–34.
- Rennie, K. M. 2015. Home range overlap and spatial-temporal interactions in female fishers on the Hoopa Indian Reservation in California. Thesis. Humboldt State University, Arcata, California, USA.
- Reno, M. A., K. R. Rulon, and C. E. James. 2008. Fisher monitoring within two industrially managed forests of northern California. Progress Report to

- California Department of Fish and Game. Sierra Pacific Industries, Anderson, California, USA.
- Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108–115.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture-recapture. Academic Press, Oxford, UK.
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations, and communities. Academic Press, Oxford, UK.
- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790.
- Schoenherr, A. A. 1992. A natural history of California. University of California Press, Berkeley, California, USA.
- Seaman, D. E., J. J. Millsaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- Seglund, A. E. 1995. The use of resting sites by the pacific fisher. Thesis. Humboldt State University, Arcata, California, USA.
- Self, S., E. Murphy, and S. Farber. 2008. Preliminary estimate of fisher populations in California and southern Oregon. Sierra Pacific Industries, Redding, California, USA, and Timber Products Company, Yreka, California, USA.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131–134.
- Slauson, K. M., J. A. Baldwin, and W. J. Zielinski. 2012. Occupancy estimation and modeling in *Martes* research and monitoring. Pages 343–368 in K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx, and S. W. Buskirk, editors. Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, Ithaca, New York, USA.
- Slauson, K. M., J. A. Baldwin, W. J. Zielinski, M. Schwartz. 2009. Estimating detection probabilities for fishers using non-invasive methods and implications for survey protocols. Draft Final Report Prepared for the U.S. Fish and Wildlife Service. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, Arcata, California, USA. https://www.fws.gov/yreka/slauson_etal_2009.pdf
- Stanley, T. R., and J. A. Royle. 2005. Estimating site occupancy and abundance using indirect detection indices. *Journal of Wildlife Management* 69: 874–883.
- Sweitzer, R. A., and B. J. Furnas. 2016. Data from camera surveys identifying co-occurrence and occupancy linkages between fishers (*Pekania pennanti*), rodent prey, mesocarnivores, and larger predators in mixed-conifer forests. Data in Brief 6:783–792.
- Sweitzer, R. A., B. J. Furnas, R. H. Barrett, K. L. Purcell, and C. M. Thompson. 2016. Landscape fuel reduction, forest fire, and biophysical linkages to local habitat use and local persistence of fishers (*Pekania pennanti*) in Sierra Nevada mixed-conifer forests. *Forest Ecology and Management* 361:208–225.
- Thompson, J. L. 2008. Density of fisher on managed timberlands in north coastal California. Thesis. Humboldt State University, Arcata, California, USA. http://humboldt-dspace.calstate.edu/bitstream/handle/2148/343/Thesis_Final_Signatures.pdf?sequence=6
- Toney, C., J. D. Shaw, and M. D. Nelson. 2009. A stem-map model for predicting tree canopy cover of Forest Inventory and Analysis (FIA) plots. In W. McWilliams, G. Moisen, and R. Czaplewski. Proceeding of Forest Inventory and Analysis (FIA) Symposium. RMRS-P-56CD. US Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- USDI Fish and Wildlife Service. 2016a. Endangered and threatened wildlife and plants; withdrawal of the proposed rule to list the west coast distinct population segment of fisher. *Federal Register* 81:22709–22808.
- USDI Fish and Wildlife Service. 2016b. Final species report, fisher (*Pekania pennanti*), west coast population. USDI Fish and Wildlife Service, Yreka, California, USA.
- Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth edition. Springer, New York, New York, USA.
- Weir, R. D., and F. B. Corbould. 2010. Factors affecting landscape occupancy by fishers in north-central British Columbia. *Journal of Wildlife Management* 74:405–410.
- Yaeger, J. S. 2005. Habitat at fisher resting sites in the Klamath province of Northern California. Thesis. Humboldt State University, Arcata, California, USA.
- Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* 16:446–453.
- Zielinski, W. J., J. A. Baldwin, R. L. Truex, J. M. Tucker, and P. A. Flebbe. 2013. Estimating trend in occupancy for the Southern Sierra fisher (*Martes pennanti*) population. *Journal of Fish and Wildlife Management* 4:3–19.
- Zielinski, W. J., and T. E. Kucera. 1995. American marten, fisher, lynx, and wolverine: survey methods for their detection. General Technical Report

PSW-GTR-157. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Arcata, California, USA. http://www.fs.fed.us/psw/publications/documents/psw_gtr157/psw_gtr157.pdf

Zielinski, W. J., R. L. Truex, G. A. Schmidt, F. V. Schlexer, K. N. Schmidt, and R. H. Barrett. 2004. Home range characteristics of fishers in California. *Journal of Mammalogy* 85:649–657.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1747/full>