



## Original Article

# 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

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**ABSTRACT** We used a mark–resight design to calculate density estimates of fisher (*Martes pennanti*), a candidate for listing under the United States Endangered Species Act, on the Hoopa Valley Indian Reservation in northwestern California, USA in order to determine population status in 1998 and 2005. Our density estimation results and simultaneous population-monitoring data provided a post hoc opportunity to evaluate the relative efficacy of 3 classical indexing techniques (catch-per-unit-effort, frequency of detection at camera stations, and frequency of detection at track-plate stations) and small-scale occupancy estimation to accurately detect population change. We calculated densities (and 95% CI) of 52 (43–64) and 14 (13–16) fishers/100 km<sup>2</sup> in 1998 and 2005, respectively. We detected a decline in the relative abundance of fishers between 1998 and 2005 using catch-per-unit-effort indices ( $\chi^2 \geq 10.18$ ,  $P \leq 0.007$ ), but not in magnitude similar to our density estimates. We detected an increase ( $\chi^2 = 4.23$ ,  $P = 0.040$ ) and no difference ( $\chi^2 = 1.38$ ,  $P = 0.240$ ) in the relative abundance of fishers between surveys using frequency of detection indices at camera stations and at track-plate stations, respectively. Occupancy estimates did not differ between 1998 and 2005. We speculate changes in prey habitat, increases in predation, disease, or some combination of these potential causes, were responsible for the population decline. Our results reinforce the importance of careful thought given to the study goals and potential limitations of any technique. For populations deemed valuable (e.g., at risk or sensitive), we suggest managers consider adopting more defensible, large-scale occupancy estimation or mark–recapture methods to monitor changes in population sizes. © 2011 The Wildlife Society.

**KEY WORDS** cameras, capture, fisher, *Martes pennanti*, occupancy, relative abundance index, track-plate.

Managing small and isolated populations of imperiled species often involves accurately assessing changes in population sizes to evaluate extinction risk, identifying population-level threats, and determining the success of conservation measures. Often, abundance or density is the metric by which population changes are measured. However, estimation of abundance and density often require substantial effort, leading some to view indices of relative abundance

(e.g., Wood 1959, Roughton and Sweeny 1982, Conner et al. 1983, Kohn et al. 1993, Sargeant et al. 2003) and occupancy estimation (MacKenzie et al. 2006, Long and Zielinski 2008) as surrogates for abundance and appropriate methods for population monitoring.

Classical indexing methods commonly involve deploying scent stations or other detection devices throughout a study area, estimating frequency of detection (no. of animal visits/no. of station-nights), and assuming that frequency of detection is related to the number of individuals in the area (Long and Zielinski 2008). However, doubt about the relationship between classical indices and abundance has led to these indices being eclipsed by more defensible detection-history methods for estimating occupancy (MacKenzie et al. 2002, 2006; Anderson 2003; Sargeant et al. 2003; Long and Zielinski 2008). Modern occupancy estimation methods are used to estimate the proportion of a large-scale survey

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area that is occupied or used by the species of interest (Mackenzie et al. 2006, Long and Zielinski 2008). Occupancy estimation methods provide for the estimation of detectability directly and use it to adjust occupancy estimates to account for sites where the species was likely present but not detected (MacKenzie et al. 2002, 2006; Long and Zielinski 2008).

However, few classical indices (e.g., Sargeant et al. 2003, Choate et al. 2006) or occupancy estimates (e.g., Sileshi et al. 2006, Gopal et al. 2010, Zylstra et al. 2010) have been applied simultaneously to populations with abundance- or density-based estimates of a change in population size. Two independent research efforts (1997–1998 and 2004–2005) on fishers (*Martes pennanti*) on the Hoopa Valley Indian Reservation (hereafter Reservation) in northwestern California, USA provided a post hoc opportunity to compare estimates of relative fisher abundance and occupancy to estimates of fisher population density at 2 points in time. Accurate monitoring of fisher populations is of particular conservation concern because of the candidate status of populations in Washington, Oregon, and California (USA) under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2004). We calculated estimates of fisher population size using a mark–resight design on the Reservation in 1998 and 2005. We simultaneously evaluated the relative efficacy of 3 indexing techniques and occupancy estimation in detecting a change in relative fisher abundance between 1998 and 2005. The indexing techniques were 1) catch-per-unit-effort, 2) frequency of fisher detections at camera stations, and 3) frequency of fisher detections at track-plate stations.

## STUDY AREA

Our study was conducted on 90 km<sup>2</sup> in the southeast corner of the 366-km<sup>2</sup> Reservation (Fig. 1). The area was located within the Klamath physiographic province (Küchler 1977) and elevations ranged between 98 m and 1,170 m. Mean daily maximum and minimum temperatures were 22° C and 6° C, respectively, and mean annual precipitation, primarily

rain, was 138 cm (National Climate Data Center, <http://www.ncdc.noaa.gov/oa/ncdc.html>, accessed 15 Jan 2011). The urban zone of the Reservation occupied 25 km<sup>2</sup> on the western border of our study area and was the location of infrastructure for the Reservation's 2,600 human inhabitants (Fig. 1; Hoopa Valley Tribe, <http://www.hoopansn.gov/documents/2000Census.pdf>, accessed 23 Jan 2011).

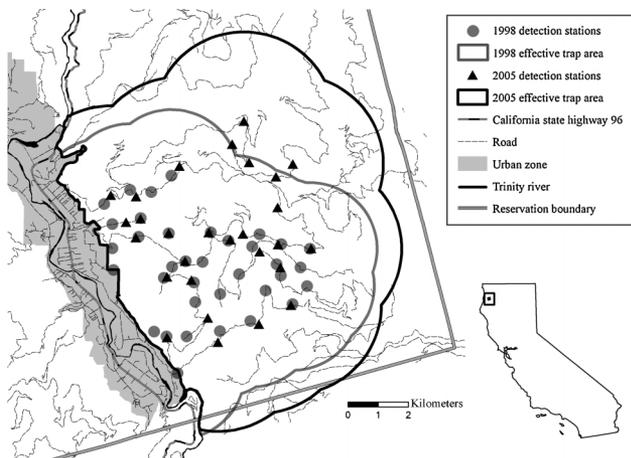
Forests generally had an overstory dominated by Douglas-fir (*Pseudotsuga menziesii*) and a midstory dominated by hardwood trees including tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), Oregon white oak (*Quercus garryana*), California black oak (*Q. kelloggii*), and canyon live oak (*Q. chrysolepis*). Pure hardwood stands occurred in some areas. Past and current timber harvests created a mix of mature–old growth and early seral forests. Between 1998 and 2005 abrupt changes in habitat conditions occurred on 3% of the study area by way of timber harvest (198 ha) and wildfire (68 ha). Less obvious changes occurred through succession, as previously harvested stands grew from a brushy condition into a stem-exclusion stage of dense young conifer and hardwood trees.

## METHODS

We applied the theoretical framework of a mark–resight model (Seber 1982, Bowden 1993, Bowden and Kufeld 1995) adjusted for density (Wilson and Anderson 1985, Maffei et al. 2004, Silver et al. 2004, Soisalo and Cavalcanti 2006, Maffei and Noss 2008) to estimate fisher population density in 1998 and 2005. Capture and handling methods were approved by the Institutional Animal Care and Use Committee of Humboldt State University, protocol 04104.W.42.A.

We selected 36 and 28 locations to place traps, cameras, and track-plates in 1998 and 2005, respectively. Selection was based on our knowledge of fisher habitat, time of year of trapping, effective coverage of the study area, road availability, and access. The goal of the selection process was to maximize the detection probability of each fisher present on the study area. Effective coverage of the study site involved maximizing the likelihood  $\geq 1$  location was placed in each potential female fisher home range (Karanth and Nichols 1998, Fuller et al. 2001, Maffei et al. 2004, Silver et al. 2004, Yaeger 2005; Fig. 1). The reduction in the number of stations between 1998 and 2005 was based on an observed increase in home range size of adult female fishers on the study area between the 2 time periods (168  $\pm$  17 ha in 1998 and 728  $\pm$  85 ha in 2005, mean  $\pm$  SE; Yaeger 2005, S. M. Matthews, Hoopa Valley Tribe, unpublished data). Thus, fewer stations were required in 2005 to maintain effective coverage of the study area.

We used Tomahawk live traps (model 207; Tomahawk Live Trap Company, Tomahawk, WI) baited with chicken legs and modified with a plywood cubby box to capture fishers (Wilbert 1992, Seglund 1995). Initial trapping occurred between 1 October 1997 and 14 March 1998 over an area of 26.0 km<sup>2</sup>. Trapping also occurred between 8 December 2004 and 11 March 2005 over an area of



**Figure 1.** Locations of trap, camera, and track-plate stations and the effective trap areas in 1998 and 2005 on the Hoopa Valley Indian Reservation, Humboldt County, California, USA.

36.8 km<sup>2</sup> that overlapped the area trapped in 1997–1998 (Fig. 1).

We anesthetized captured fishers with ketamine hydrochloride (40 mg/kg) and diazepam (0.25 mg/kg) and handled them using standard protocols (Aubry and Raley 1996, Yaeger 2005). We marked each fisher with uniquely colored plastic ear tags (Nasco Standard Rototag Blank; Nasco, Modesto, CA) in both ear pinnae for future individual identification. We fitted all adult and subadult female fishers and select male fishers with radiotransmitters (Telonics MOD80 or MOD125 [Telonics, Inc., Mesa, AZ] in 1998; and Holohil model MI-2 [Holohil Systems Ltd., Carp, ON, Canada] or Telonics model MOD80 in 2005) to determine the mean maximum distance moved to establish an effective trap area (Wilson and Anderson 1985, Maffei et al. 2004, Silver et al. 2004, Soisalo and Cavalcanti 2006, Maffei and Noss 2008). We released all fishers after recovery from anesthesia at their sites of capture.

Resighting devices used in 1998 included both a remote camera and a track-plate housed in a single rectangular, plywood box that was open on one end (Fowler and Golightly 1994, Zielinski 1995). The cameras were converted 35-mm cameras (Olympus Infinity Mini DLX; Olympus, Melville, NY) and were triggered by a magnetic reed-switch (HE500-ND; Hamlin, Inc., Lake Mills, WI) mounted on a treadle attached to the track-plate. In 2005 we housed the cameras and track-plates as separate devices. The converted 35-mm cameras were triggered by infrared door alarms (Radio Shack Mini PIR Alarm Catalog no. 49-425 [Radio Shack Corp., Fort Worth, TX]; Matthews et al. 2008) and housed in 119-cm-long and 38.7-cm-diameter polyvinyl chloride culvert pipes. Camera stations used in 1998 and 2005 required an animal to enter the device in order for the camera to be triggered and were baited with a chicken leg tied to the floor with fishing line. In 2005 we housed track-plates in corrugated plastic (rather than plywood) boxes of the same dimensions as those used in 1998. We examined bait, film, and track-plates every other day.

Because of equipment limitations, we conducted multiple sessions during 1998 and 2005, moving devices to alternate locations for each session. In 1998 we placed camera-track-plate devices at 12 locations for 13 nights (13–26 Mar 1998), then at 12 locations for 10 nights (30 Mar–9 Apr 1998), and the remaining 12 locations for 10 nights (13–23 Apr 1998). In 2005 we placed remote cameras at 14 locations and track-plates at the other 14 locations for 12 nights (20 Mar–1 Apr 2005) and then moved cameras to track-plate locations and vice versa for another 12 nights (1–13 Apr 2005).

We calculated fisher abundance for 1998 and 2005 using the Bowden estimator of population size (Bowden 1993, Bowden and Kufeld 1995) in the software Program NOREMARK (White 1996). We defined an independent resighting of the same individual as any photograph separated by >24 hr, or any individual fisher resighted at  $\geq 2$  camera stations within 24 hr (Mace et al. 1994). We generated a density estimate by dividing fisher abundance by the effective trap area (Soisalo and Cavalcanti 2006, Maffei and Noss 2008). The effective trap area included a circular buffer

around each detection station location, minus the urban zone of the Reservation. The radius of the buffer was the mean maximum distance moved (MMDM) between female fisher locations (Soisalo and Cavalcanti 2006, Maffei and Noss 2008). Fisher locations used to calculate MMDM were collected using ground-based radiotelemetry, trap, and camera locations (Soisalo and Cavalcanti 2006, Maffei and Noss 2008).

We calculated catch-per-unit-effort in 1998 and 2005 as the frequency of fisher captures at trap sites for unmarked fishers (no. of unmarked fisher captures/no. of trap-nights) and for any fisher, including recaptured individuals that we had previously marked (no. of total fisher captures/no. of trap-nights). We calculated the frequency of fisher detections at camera and track-plate stations (no. of fisher detections/no. of station-nights) in 1998 and 2005. In order to simulate relative abundance index methods, which would not include a previous marking effort, we included all detections of fishers in calculating frequencies of detection, irrespective of marked status. Binomial proportions tests were used to test for significant differences between 1998 and 2005 estimates of relative abundances for each technique using the STATS package in Program R version 2.10.1 (R Development Core Team 2008).

Although we designed our study to estimate fisher density, upon reviewer suggestion, we retrospectively developed an occupancy design from our data to compare to our density results. Occupancy estimation is used as a monitoring technique at larger spatial scales, following from the assumption that detection of species and detection histories at each location are independent (MacKenzie et al. 2006). We initially discounted occupancy estimation as a population monitoring method because of the small size of our study area (90 km<sup>2</sup>) compared to estimates of average female fisher home ranges (168  $\pm$  17 ha in 1998 and 728  $\pm$  85 ha in 2005, mean  $\pm$  SE; Yaeger 2005; S. M. Matthews, unpublished data). This relationship led to violations of the above independence assumption while maintaining an effective number of sample locations. Thus, our results are more an expression of “use” of the space that was sampled than of true occupancy.

We analyzed detection histories as if each station was a sample unit and by combining stations with the next closest station into 2-station sample units. We acknowledge that even by combining stations our design still violates the independence assumption and the precision of our occupancy estimates are probably overstated (MacKenzie et al. 2006). The 1998 effort had a single device that contained both a camera and track-plate. Overall the cameras recorded many more unique detections than did the track-plates. However, for each visit the occupancy data would include a 0 or a 1 (not detected or detected); therefore, even if the camera recorded 2 or more distinct detections of fishers they would be consolidated into a 1 in the detection history for the sample unit. Thus, we elected to use only the track detection data to develop detection histories for the 6 visits in 1998. The 2005 detection devices were separated into a stand-alone camera station and a track-plate device. Detection histories were developed for both camera and track-plate data and analyzed

separately for the 8 visits in 2005. Occupancy analyses were conducted in Program Presence 2.3 (Hines 2006).

## RESULTS

We captured 29 individual fishers (21 F, 8 M) on 67 occasions during 451 trap-nights during the 1997–1998 trapping effort (Table 1). Fourteen individual fishers (8 F, 6 M) were captured on 49 occasions during 605 trap-nights during the 2004–2005 trapping effort (Table 1). The measures of MMDM by female fishers in 1998 and 2005 were 2,220 m and 2,997 m, respectively. Buffering each camera location used in 1998 by 2,220 m and those used in 2005 by 2,997 m resulted in effective trap areas of 66.8 km<sup>2</sup> and 102.5 km<sup>2</sup> during 1998 and 2005, respectively (Fig. 1). We calculated density estimates (and 95% CI) of 52 (43–64) and 14 (13–16) fishers/100 km<sup>2</sup> during 1998 and 2005, respectively, indicating a population decline of 73% (Table 1).

The frequency of detection of unmarked fishers and all fishers at trap sites was greater in 1998 than in 2005, indicating a decline in relative abundance (Table 1). Fishers were detected at camera stations less frequently in 1998 than in 2005, indicating an increase in relative abundance (Table 1). Fishers were detected at track-plate stations with equal frequency in 1998 and 2005, indicating no change in relative abundance (Table 1).

Our 1998 and 2005 occupancy estimates based on either single-station or 2-station sample units did not differ based on the overlap of our 95% confidence intervals (Tables 2

and 3). There was no structure on the occupancy portions of our models and only minor structure on the detection probability portions. The structure on the detection probabilities varied from one data set to the other; however, a time trend or quadratic trend was included in the top 2 models in all cases and was competitive with the top model if it was not number one based on Akaike's Information Criterion values and weights. Estimates of occupancy were essentially identical regardless of detection probability structure. In addition, the estimates of occupancy were incredibly close to the naïve estimates (Tables 2 and 3). Detection probabilities were also fairly high, with the top models for all the data sets including a time trend or quadratic trend. Detection probabilities estimated by the simplest model (constant or dot) resulting in a single probability estimate were 0.51, 0.75, and 0.71 for the 1998 track, 2005 photo, and 2005 track data sets respectively.

## DISCUSSION

The 3 relative abundance indices and occupancy estimation were inconsistent in detecting an apparent 73% decline in fisher population density, which cast doubt on the reliability of these types of indices to detect large changes in population size at small scales. Our estimate of a 73% decline in fisher density was supported by a 4-fold increase in female home range sizes between 1998 and 2005. Benson et al. (2006) identified a similar relationship between density and home range size for bobcats (*Lynx rufus*). They documented that bobcat population density explained 56% of the variation in

**Table 1.** Changes in frequency of detection of fishers compared using binomial proportions tests to evaluate the relative efficacy of 3 indexing techniques (catcher-unit effort, camera stations, and track-plate stations) to detect an apparent 73% fisher population decline determined using a mark-resight design in 1998 and 2005 on the Hoopa Valley Indian Reservation, Humboldt County, California, USA.

Index technique	Detections		Trap-nights		Frequency of detection (%)					
	1998	2005	1998	2005	1998	2005	$\Delta$ (%)	$\chi^2$	<i>P</i>	Trend
Traps: unmarked fishers	29	14	451	605	6.4	2.3	-4.1	10.18	0.001	Decline
Traps: all fishers	67	49	451	605	14.9	8.1	-6.8	11.38	0.007	Decline
Cameras	149	146	416	336	35.8	43.5	7.7	4.23	0.040	Increase
Track-plates	100	76	229	202	43.7	37.6	-6.1	1.38	0.240	No change

**Table 2.** Estimates of fisher occupancy and 95% confidence intervals (CI) based on track or photo detections collected at single-station sample units in 1998 (6 visit detection histories) and 2005 (8 visit detection histories) on the Hoopa Valley Indian Reservation, Humboldt County, California, USA.

Data set	Sample units	Naïve estimate	$\psi$	95% CI	
				Lower	Upper
1998 track	36	0.861	0.872	0.709	0.950
2005 track	28	0.571	0.572	0.387	0.738
2005 photo	28	0.643	0.643	0.454	0.796

**Table 3.** Estimates of fisher occupancy and 95% confidence intervals (CI) based on track or photo detections collected at 2 station sample units in 1998 (6 visit detection histories) and 2005 (8 visit detection histories) on the Hoopa Valley Indian Reservation, Humboldt County, California, USA.

Data set	Sample units	Naïve estimate	$\psi$	95% CI	
				Lower	Upper
1998 track	18	0.842	0.852	0.694	0.936
2005 track	14	0.714	0.714	0.440	0.889
2005 photo	14	0.786	0.786	0.506	0.929

female home range size, whereas food availability and body weight failed to explain observed changes in bobcat home range size.

Of the 3 relative abundance indices we considered, only the results from catch-per-unit-effort for both unmarked and total fisher captures indicated the presence of a decline (but not the magnitude) in fisher density on the study area. Fisher detection rates at camera stations were significantly greater in 2005 than in 1998, indicating an increase rather than the actual significant decrease in population size. Our occupancy estimation results illustrate the point that a purely occupancy-based approach may not be as sensitive to a population change as a more intensive mark-resight approach. Occupancy methods are better suited for long-term, large-scale monitoring where dramatic changes in occupancy of areas might be expected due to large-scale disturbances (Mackenzie et al. 2006, Long and Zielinski 2008).

We suspect the proximity of detection stations ( $\geq 1$  in each potential *F* fisher home range) did not allow us to evaluate whether visitation rates were a function of population size or repeat visitation by the same animal(s) (Zielinski and Stauffer 1996, Sargeant et al. 2003, Long and Zielinski 2008). Variation in individual fisher detection probabilities probably influenced our results. Although we considered each fisher unmarked when totaling the number of fisher visits, marked status enabled us to confirm that 3 individual fishers made up nearly 90% of marked fisher detections in 2005, whereas in 1998 the 3 most frequently detected marked fishers only made up 45% of marked fisher detections. Similarly, Sargeant et al. (2003) found density-dependent visitation rates (visitation rates were greater when population sizes were low) to scent stations by kit foxes (*Vulpes macrotis*) and swift foxes (*V. velox*) in a comparison of scent-station population indices to concurrent and independent measures of population sizes.

Our results support the conclusions of other studies (as articulated by Ray and Zielinski [2008]) that relative indices from classical detection station designs have low resolution because reliable inferences require independent and large samples (Zielinski and Stauffer 1996, Sargeant et al. 2003). These results do not diminish the value of methods involving remote cameras or track-plate stations, but in fact reinforce the importance of giving careful thought to the study goals and potential limitations of any technique. For populations deemed important (e.g., at risk or sensitive), we caution managers considering classical relative abundance indices to consider more defensible detection-history methods for estimating occupancy at an appropriate spatial scale or a mark-recapture or mark-resight design (MacKenzie et al. 2002, 2006; Sargeant et al. 2003; Long and Zielinski 2008; Ray and Zielinski 2008).

Our estimates of fisher density fall within (2005) and above (1998) the upper limit of the range of estimates (5–38 fishers/100 km<sup>2</sup>) from across the regional distribution of fishers (Powell 1993). Two California studies used camera-recapture methods similar to ours to estimate fisher density for 2 unharvested populations in different portions of the California range. On industrially managed timberlands in

northwestern, coastal California, Thompson (2008) reported fisher density estimates ranging from 15 individuals/100 km<sup>2</sup> to 21 individuals/100 km<sup>2</sup>. On the west slope of the southern Sierra Nevada in the Sierra National Forest, Jordan (2007) reported fisher densities for an untrapped population ranging from 5.3 individuals/100 km<sup>2</sup> to 25.3 individuals/100 km<sup>2</sup>.

Unfortunately, research activity to determine the cause of the decline did not occur on the Reservation between 1998 and 2005. Thus, we are left to speculate that changes in prey habitat, increases in predation, disease, or some combination of these potential causes, were responsible for the population decline. It is possible that habitat change adjacent to the Reservation resulting from catastrophic wildfire may have contributed to increased fisher predation risk and population declines on the Reservation. In 1999 the Megram fire burned over 505 km<sup>2</sup> on the southeastern border of the Reservation (Jimerson and Jones 2003). Over 63 km<sup>2</sup> of old-growth and late-mature forest was affected by high-severity fire (>80% tree mortality), returning these areas to shrub-forb vegetation community (Jimerson and Jones 2003). Since 1999 reports of incidental sightings of bobcats have increased throughout the Reservation (J. M. Higley, Hoopa Tribal Forestry, unpublished data). Witmer and deCalesta (1986) reported bobcats used Douglas-fir-dominated forest cover during the day while they were most inactive, and clear-cut units at night while they were most active (presumably hunting).

Predation generally has not been considered a limiting factor for fisher populations based on research conducted in New England and Great Lakes regions (Powell 1993, Kurta 1995), but recent research on west coast fisher populations indicates that predation, especially by bobcats, is a common source of mortality (G. Wengert, University of California Davis, unpublished data). An increase in bobcat predation on fishers might also explain the observed sex ratio change. Smaller body size might make female fishers more susceptible to bobcat predation to the point of skewing fisher population sex ratios.

## MANAGEMENT IMPLICATIONS

The use of classical relative abundance indices and occupancy estimation are particularly attractive to managers because of their relative low cost and the belief they are effective in monitoring relative change in abundance over time. Our results cast doubt on the efficacy of these indices and small-scale occupancy estimation to adequately detect significant population change and reinforce the importance of careful thought given to the study goals and potential limitations of any technique. Managers should consider adopting more defensible large-scale occupancy estimation or mark-recapture techniques as methods to monitor changes in wildlife population sizes, especially when responsible for at-risk populations. With the absence of long-term monitoring on the Reservation between 1998 and 2005, the cause(s) of the fisher population decline will never be known. However, our results illustrate the value in establishing long-term, accurate programs to monitor populations of

imperiled species, which strive to determine cause and effect relationships resulting in changes in populations and which, ultimately, model habitat fitness.

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## LITERATURE CITED

- Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. *Wildlife Society Bulletin* 31:288–291.
- Aubry, K. B., and C. M. Raley. 1996. Rogue River fisher study, study plan and sampling protocols August 1996. U.S. Forest Service, Pacific Northwest Research Station, Olympia, Washington, USA.
- Benson, J. F., M. J. Chamberlain, and B. D. Leopold. 2006. Regulation of space use in a solitary felid: population density or prey availability? *Animal Behaviour* 71:685–693.
- Bowden, D. C. 1993. A simple technique for estimating population size. Colorado State University, Department of Statistics Technical Report 93/12, Fort Collins, USA.
- Bowden, D. C., and R. C. Kufeld. 1995. Generalized mark–resight population size estimation applied to Colorado moose. *Journal of Wildlife Management* 59:840–851.
- Choate, D. M., M. L. Wolfe, and D. C. Stoner. 2006. Evaluation of cougar population estimators in Utah. *Wildlife Society Bulletin* 34:782–799.
- Conner, M. C., R. F. Labisky, and D. R. Progulski, Jr., 1983. Scent-station indices as measures of population abundance for bobcats, raccoons, gray foxes, and opossums. *Wildlife Society Bulletin* 11:146–152.
- Fowler, C. H., and R. T. Golightly. 1994. Fisher and marten survey techniques on the Tahoe National Forest. Final Report to the U.S. Forest Service, Agreement no. PSW-90-0034CA. Humboldt State University, Arcata, California, USA.
- Fuller, T. K., E. C. York, S. M. Powell, T. A. Decker, and R. M. DeGraaf. 2001. An evaluation of territory mapping to estimate fisher density. *Canadian Journal of Zoology* 79:1691–1696.
- Gopal, R., Q. Qureshi, M. Bhardwaj, R. K. J. Singh, and Y. V. Jhala. 2010. Evaluating the status of the endangered tiger *Panthera tigris* and its prey in Panna Tiger Reserve, Madhya Pradesh, India. *Oryx* 44:383–389.
- Hines, J. E. 2006. PRESENCE2—software to estimate patch occupancy and related parameters. U.S. Geological Survey–Patuxent Wildlife Research Center. <<http://www.mbr-pwrc.usgs.gov/software/presence.html>>. Accessed 15 Dec 2010.
- Jimerson, T. M., and D. W. Jones. 2003. Megram: blowdown, wildfire, and the effects of fuel treatment. Tall Timbers Research Station, Miscellaneous Report Number 13:55–59.
- Jordan, M. J. 2007. Fisher ecology in the Sierra National Forest, California. Dissertation, University of California Berkeley, Berkeley, USA.
- Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- Kohn, B. E., N. F. Payne, J. E. Ashbrenner, and W. A. Creed. 1993. The fisher in Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin no. 183, Madison, USA.
- Küchler, A.W. 1977. Appendix: the map of the natural vegetation of California. Pages 909–938 in M. G. Barbour and J. Major, editors. *Terrestrial vegetation of California*. John Wiley and Sons, New York, New York, USA.
- Kurta, A. 1995. *Mammals of the Great Lakes Region*. University of Michigan Press, Ann Arbor, Michigan, USA.
- Long, R. A., and W. J. Zielinski. 2008. Designing effective noninvasive carnivore surveys. Pages 8–44 in R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray, editors. *Noninvasive survey methods for carnivores*. Island Press, Washington, D.C., USA.
- Mace, R. D., S. C. Minta, T. L. Manley, and K. E. Aune. 1994. Estimating grizzly bear population size using camera sightings. *Wildlife Society Bulletin* 22:74–83.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- 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, Burlington, Massachusetts, USA.
- Maffei, L., and A. J. Noss. 2008. How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. *Biotropica* 40:71–75.
- Maffei, L., E. Cuéllar, and A. Noss. 2004. One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology* 262:295–304.
- Matthews, S. M., R. T. Golightly, and J. M. Higley. 2008. Mark–resight density estimation for American black bears in Hoopa, CA. *Ursus* 19:13–21.
- Powell, R. A. 1993. *The fisher: life history, ecology and behavior*. Second edition. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Ray, J. C., and W. J. Zielinski. 2008. Track stations. Pages 75–109 in R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray, editors. *Noninvasive survey methods for carnivores*. Island Press, Washington, D.C., USA.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <<http://www.R-project.org>>. Accessed 20 Jan 2011.
- Roughton, R. D., and M. W. Sweeney. 1982. Refinements in scent-station methodology for assessing trends in carnivore populations. *Journal of Wildlife Management* 46:217–229.
- Sargeant, G. A., P. J. White, M. A. Sovada, and B. L. Cypher. 2003. Scent station survey techniques for swift and kit foxes. Pages 99–105 in M. A. Sovada and L. Carbyn, editors. *Ecology and conservation of swift foxes in a changing world*. Canadian Plains Research Center, University of Regina, Saskatchewan, Canada.
- Seber, G. A. 1982. *The estimation of animal abundance*. Second edition. Charles Griffin, London, United Kingdom.
- Seglund, A. E. 1995. The use of resting sites by the Pacific fisher. Thesis, Humboldt State University, Arcata, California, USA.
- Sileshi, G., G. Hailu, and P. L. Mafongoya. 2006. Occupancy-abundance models for predicting densities of three leaf beetles damaging the multipurpose tree *Sesbania sesban* in eastern and southern Africa. *Bulletin of Entomological Research* 96:61–69.
- Silver, S. C., L. E. T. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gomez, and G. Ayala. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx* 38:148–154.
- Soisalo, M. K., and S. M. C. Cavalcanti. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* 129:487–496.
- Thompson, J. L. 2008. Density of fishers on managed timberlands in north coastal California. Thesis, Humboldt State University, Arcata, California, USA.
- U.S. Fish and Wildlife Service. 2004. Twelve-month finding for a petition to list the west coast distinct population segment of the fisher (*Martes pennanti*). Federal Register 69:18770–18792.
- White, G. C. 1996. Program NOREMARK software reference manual. Department of Fisheries and Wildlife, Colorado State University, Fort Collins, Colorado, USA.

- Wilbert, C. J. 1992. Spatial scale and seasonality of habitat selection by martens in southeastern Wyoming. Thesis, University of Wyoming, Laramie, USA.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.
- Witmer, G. W., and D. S. deCalesta. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. *Canadian Journal of Zoology* 64:2333–2338.
- Wood, J. E. 1959. Relative estimates of fox population levels. *Journal of Wildlife Management* 23:53–63.
- Yaeger, J. S. 2005. Habitat at fisher resting sites in the Klamath Province of northern California. Thesis, Humboldt State University, Arcata, California, USA.
- Zielinski, W. J. 1995. Track plates. Pages 67–89 in W. J. Zielinski and T. E. Kucera editors. American marten, fisher, lynx, and wolverine: survey methods for their detection. U.S. Forest Service Pacific Southwest Research Station General Technical Report PSW-GTR-157, Albany, California, USA.
- Zielinski, W. J., and H. B. Stauffer. 1996. Monitoring *Martes* populations in California: survey design and power analysis. *Ecological Applications* 6:1254–1267.
- Zylstra, E. R., R. J. Steidl, and D. E. Swann. 2010. Evaluating survey methods for monitoring a rare vertebrate, the Sonoran desert tortoise. *Journal of Wildlife Management* 74:1311–1318.

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