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Original article

Camera trapping estimates of density and survival of fishers *Martes pennanti*

Mark J. Jordan, Reginald H. Barrett & Kathryn L. Purcell

Developing efficient monitoring strategies for species of conservation concern is critical to ensuring their persistence. We have developed a method using camera traps to estimate density and survival in mesocarnivores and tested it on a population of fishers *Martes pennanti* in an area of approximately 300 km^2 of the southern Sierra Nevada mountains in California. Fishers in this region are isolated from other populations by a gap of approximately 400 km, and the status of individual populations in the southern Sierra Nevada is poorly understood, making management decisions difficult. We caught fishers in live traps, marked them with ear tags, and resighted them with camera traps. We measured latency to first detection and detection rate to compare our results to previous camera trapping studies of fishers. We used the robust design Poisson log-normal mixed-effects mark-resight model to obtain annual estimates of density and apparent survival. Our values for latency to first detection and detection rate were slightly lower than those obtained by previous studies. Fishers in this isolated region occur at lower densities than at other locations across their range with only approximately 6-11 animals/100 km^2. Their average annual, adult survival rate (0.94) was comparable to that found in other studies, though this parameter had very low precision. We experienced relatively high levels of tag loss in our study, suggesting our estimates of abundance are biased upward. We provide recommendations for improving the precision and accuracy of results obtained from this type of study. Our results demonstrate a novel application of mark-resight methods to estimate density and survival for mesocarnivores. These estimates provide timely information to managers about fishers at the local population level in the southern Sierra Nevada mountains.

Key words: camera trapping, density estimation, fisher, mark-resight, Martes pennanti, mesocarnivore, Sierra Nevada, survival rate estimation

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Effective recovery of species of conservation concern requires an understanding of the causes of the species' decline and the impact of human activities on its populations (Caughley 1994). To better understand these causes, a population should be monitored in a systematic way to assess the impacts of management actions that may affect it (Nichols & Williams 2006). However, without reliable estimates of demographic parameters such as density and survival, it is difficult to draw conclusions about treatment effects.

Capture-recapture studies are commonly used to

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obtain detailed population parameter estimates (Otis et al. 1978, Pollock et al. 1990, Seber & Schwarz 2002). In these studies, animals are captured, given some identifying mark, and released. In subsequent sampling periods, animals are recaptured. The proportion of marked animals in this sample can be used to estimate abundance, and the capture histories of individuals can provide estimates of population vital rates.

One variation on the capture-recapture approach is to use a mark-resighting method where a group of animals is captured during an initial marking phase and given distinguishing marks, such as ear tags or radio-transmitters (Arnason et al. 1991). The animals are then resighted using a different 'capture' technique, but are generally not physically handled again. The mark-resight method has several advantages over traditional capture-recapture sampling. These studies can be less labour intensive because resighting often requires less effort than initial capture and handling. Because the animals are not physically restrained during resighting, the risks to individual animals are reduced (Minta & Mangel 1989). Also, because the capture and resighting phases of the study use different techniques for capturing the animal, the risk of a behavioural response to trapping affecting recapture rate is reduced (Otis et al. 1978, Minta & Mangel 1989).

Camera traps are a good alternative to many traditional wildlife survey methods because cameras can detect animals at all times of day and night, and they do not need to be checked daily (Kucera et al. 1995). Camera trapping has been used to monitor a variety of mesocarnivore species, including fishers *Martes pennanti* (Fuller et al. 2001, Long et al. 2007), eastern spotted skunks *Spilogale putorius* (Hackett et al. 2007) and ocelots *Leopardus pardalis* (Trolle & Kéry 2003, Maffei & Noss 2008). Camera trapping can be used to obtain demographic information in a capture-recapture framework when the study organisms have some form of individually identifying marks, either applied by biologists (e.g. ear tags on grizzly bears *Ursus arctos*; Mace et al. 1994) or a naturally occurring, unique pelage or colouring pattern (e.g. stripes of tigers *Panthera tigris*; Karanth et al. 2006). Most camera capture-recapture studies have used the latter approach, focusing primarily on felids (Jackson et al. 2006, Karanth et al. 2006, Maffei & Noss 2008, Marnewick et al. 2008, Sarmento et al. 2009).

The goal of our study was to conduct an intensive, mark-resight study using camera traps to estimate population parameters (density and survival) for a population of fishers in the southern Sierra Nevada mountains in California. We chose this species due to concern over its status in the state because its range has been greatly reduced in California, and it now exists in two isolated populations separated by $>$ 400 km (Zielinski et al. 2005). The U.S. Fish and Wildlife Service has deemed the Pacific state populations of the fisher to be 'warranted but precluded'; for listing under the U.S. Endangered Species Act (Federal Register 2004), meaning that these populations should be listed, but the Service currently lacks the resources to meet the requirements of the listing process. We designed our study to provide critical density and vital rate estimates to inform management decisions about this species, while also providing insights into methods for monitoring mesocarnivores in general.

Material and methods

Field methods

We conducted field work in the Kings River region of the southern Sierra Nevada mountains in Fresno County, California, USA (37°1'N, 119°9'W) in an area that included a mix of public and private land. The U.S. Forest Service managed the public land, while the most significant private land holder within our study area boundaries was the utility company Southern California Edison. The predominant forest cover types in this area are Ponderosa pine *Pinus ponderosa* and Sierran Mixed Conifer (Mayer & Laudenslayer 1989). Our study area covered an elevation gradient corresponding to fisher occurrence in the region (1,200-2,400 m a.s.l.; Jordan et al. 2002), roughly corresponding to forest types preferred by fishers in this region (Zielinski et al. 2006, Purcell et al. 2009). This elevational band was particularly narrow at the northern and southern boundaries of our study area in the drainages formed by the San Joaquin River to the north and the Kings River to the south.

We divided our study area into a trapping grid composed of 317 1×1 km cells (Fig. 1). Three of the 317 potential cells were not used; one cell was not trapped because it was entirely within private land to which we did not have access, and the two other cells were unused because they contained a busy campground and private summer cabins.

Live trapping occurred in July and August during 2002-2004. We built live traps by attaching Toma-

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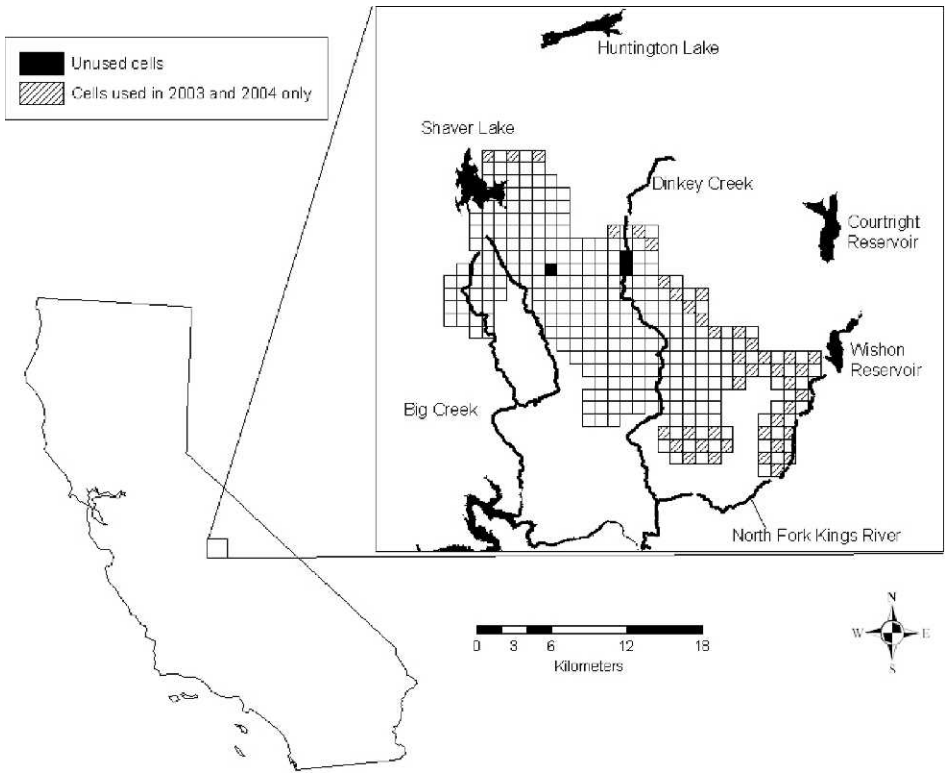


Figure 1. The Kings River Fisher Project study area was located in the Sierra Nevada Mountains of Fresno County, California, USA. The 317 km^2 study area was divided into 1×1 km cells. Of the 317 cells, three (shaded black) were not used (see text).

hawk collapsible single-door live traps (Model 207, $81.3 \times 25.4 \times 30.5$ cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) to a plywood box (Wilbert 1992). We placed one live trap in every other cell within the trapping grid. We attempted to place traps near the center of a given cell, though this was not always practical. Important microhabitat characteristics in trap site selection within a cell included high sawlog density (trees with $>$ 60 cm dbh), proximity to a stream (or dry watercourse), high canopy cover and downed woody debris. These characteristics are important features of habitats used by fishers in the Sierra Nevada (Zielinski et al. 2004, Zielinski et al. 2006, Purcell et al. 2009). We baited traps with a piece of raw chicken securely tied to the inside of the trap and a commercial lure ('Gusto'; Minnesota Trapline Products, Pennock, Minnesota, USA) poured onto a nearby tree or log.

Because of limited resources and personnel, we did not have traps open over our entire study area during each trapping session. Instead, we divided our study area into four regions, using ridges between watersheds to isolate each region. We then trapped each region sequentially, starting in the northeast of the study area. After eight trap nights, we collected the traps and moved them to the next region. We baited and opened all traps within a region on the same day. We used the same rotation of trap locations every year.

We processed all live-caught fishers the first time they were captured each year. Fishers that were processed were coaxed into a metal handling cone and sedated with a Ketamine hydrochloride and Diazepam mixture (1 mg Diazepam/200 mg Ketamine) injected intramuscularly at a dosage of 11-24.2 mg Ketamine/kg of estimated body weight. Further details of the fisher processing procedure and measurements taken can be found in Jordan (2007).

Fisher pelage is not distinct enough to distinguish individual animals, so live trapping and marking with uniquely coloured ear tags was an integral part of our study. We double-marked every fisher to reduce the likelihood of the complete loss of tags. Each fisher received an implanted passive integrated transponder (PIT) microchip tag (125 kHz, TX 1405L; Biomark, Boise, Idaho, USA) in the nape for permanent and unique identification. A unique

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combination of coloured ear tags and reflective tape (Coloured Rototag; Dalton Group Limited, Dalton House, Nettlebed, Oxfordshire, England) was fastened to each ear to identify animals resighted at camera stations. When we recaptured an animal that had lost its ear tags, we replaced them with an identically-coloured pair.

Camera resighting occurred during September and October of each year of our study, following live trapping. We used dual-sensor remote camera systems (Trailmaster Trail Monitor, Model TM 1550; Goodson and Associates, Inc., Lenexa, Kansas, USA) to trigger a 35-mm camera when an infrared beam was broken (Kucera et al. 1995). The camera trap consisted of a corrugated plastic box ($81.3 \times 26 \times 26$ cm) attached to a camera with an infrared trigger oriented so that the infrared beam crossed the entrance of the box. With this orientation, we were able to identify fishers in photographs by their ear tags. Animals available for resighting included those live-captured and marked during our study as well as those that were caught in 2000 and 2001 as part of a radio-telemetry study of this population (Mazzoni 2002, Purcell et al. 2009).

We placed camera traps in cells adjacent to those used for live trapping, following the same criteria for placement within a cell as for live trapping. As with live trapping, we did not have enough resources to place camera traps throughout our entire study area at the same time. In this case, we divided our study area into three regions that we trapped sequentially. After 12 days, we moved the traps to the next region. In 2002, however, we did not place camera traps on the eastern edge of our study area due to time constraints (see Fig. 1). We baited the stations with raw chicken and a commercial lure. We opened half of the traps in a region on the first day of the trapline and the other half on the next, and we checked each trap every other day.

We received approval for our field methods from the Animal Care and Use Committee of the University of California, Berkeley, USA (Permit No. R139-1204) and the California Department of Fish and Game (Scientific Collecting Permit No. 803043-03).

Parameter estimation

The robust design is a capture-recapture study design that allows for the joint estimation of abundance and apparent survival rates. This design estimates abundance within each trapping season ('primary occasion'), then combines all of the data within each primary occasion to estimate survival and temporary emigration probabilities across years, reducing overall variance in parameter estimates (Kendall & Pollock 1992, Kendall et al. 1997, Kendall & Nichols 2002). We used a new, mark-resight implementation of the robust design called the robust design Poisson log-normal mixed-effects mark-resight model (RDPNE; McClintock & White 2009). This model allows for estimation of the number of unmarked animals in the population, and derives an estimate of abundance for each year from the total number of unmarked and marked animals. It also estimates a variance component of the resighting rate due to individual heterogeneity and uses this to estimate a mean resighting rate for all animals within a given year. The model also estimates the 'open population' parameters apparent survival and probability of temporary movement out of (γ'') and back into the study area ($1\text{-}\gamma'$) (Kendall et al. 1997).

The number of times marked and unmarked animals are resighted within a given year is used to estimate parameters in the RDPNE. This model does not require that resighting data be broken down into discrete time intervals, as with other capture-recapture data structures based on capture histories (Otis et al. 1978). However, because an animal could be photographed multiple times in a single visit to one of our camera traps, we needed to determine an appropriate way to handle these photos to ensure independence of resighting events. This was compounded by the fact that we could not distinguish among unmarked fishers, so we could not determine if multiple photographs of unmarked animals were the same or different individuals.

Previous studies have addressed this problem by breaking down resighting phases into 24-hour periods (e.g. Marnewick et al. 2008, Sarmento et al. 2009). However, this approach presents a different problem. If midnight is the boundary between 24-hour intervals and the same animal is photographed at 23:58 and four minutes later at 00:02, this will be counted as two resightings. However, if this occurs at 10:00, it will be treated as a single capture. This 'midnight problem', coupled with our inability to distinguish among unmarked fishers, led us to treat all photographs as separate captures.

The RDPNE allows for parameter estimation in a generalized, maximum-likelihood framework based on selection of a best-fitting model from a set of candidate models (Lebreton et al. 1992, McClintock

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& White 2009). We chose the model that best fit the data using Akaike's Information Criterion with a small sample size correction (AIC_c; Burnham & Anderson 2002). Following McClintock & White (2009), we first selected the best-fitting model structure for the intercept (log scale) of the resighting rate (α) and the estimate of individual heterogeneity (σ). These two parameters are combined to estimate the mean resighting rate. We compared models for all possible combinations that held α constant or allowed it to vary by time while holding σ constant, allowing it to vary by time, or assuming no individual heterogeneity in resighting rate by fixing σ at 0. During this step, we made the number of unmarked animals and apparent survival fully time-dependent, while temporary emigration was random ($\gamma'' = \gamma'$) so that all parameters were identifiable (Kendall et al. 1997, McClintock & White 2009).

We used the best-fitting structure from the above step to develop less parameterized models to estimate derived resighting rate, abundance, apparent survival and temporary emigration. We developed models for all possible combinations of time-dependent and constant number of unmarked animals and apparent survival. We also tested all of these models under random emigration or no emigration ($\gamma'' = \gamma' = 0$). We could not separately model the effect of sex on abundance because we could not distinguish male from female unmarked fishers in photographs. We did investigate models with sex-specific differences in survival, which is conditioned solely on marked animals. Model selection and parameter estimation were performed in Program MARK (White & Burnham 1999).

Because male fishers have larger home ranges, we used the average home-range size of males for our buffer. This increased the likelihood that our effective sampling area included all target animals. Male home ranges in the Kings River area had an average radius of 2.64 km based on a 100% minimum convex polygon (Mazzoni 2002). Using this as a buffer and truncating for elevation produced an effective sampling area of 367 km^2 in 2002 and 430 km^2 in 2003 and 2004. Because we used data from a radio-telemetry study to estimate home-range size, the calculation of effective study area does not suffer from some of the theoretical limitations inherent in calculating effective study area when using trapping data, such as the mean maximum distance between captures (Parmenter et al. 2003). We calculated density by taking abundance estimates for each year, then dividing these point estimates and the upper and lower bounds of their confidence intervals by the estimate of the effective sampling area. They were then normalized to estimate the number of fishers/100 km^2.

To compare our camera trapping results to previous studies, we calculated two separate metrics from photographic data. We determined the latency to first detection for camera traps (Foresman & Pearson 1998), which is a measure of the number of days elapsed from the opening of a trap to the first day that an animal is detected at it. We measured this parameter using the time-date stamp on photographs. We also estimated the detection rate (e.g. Long et al. 2007), which is the proportion of traps that detected a fisher.

Results

We defined an active trap night as one that was not lost to some form of disturbance, the most common of which resulted from the trap being closed with no animal inside it or damage by black bears *Ursus americanus*. Over the three years of our study, we had 3,799 live trap nights, of which 629 (16.6%) were lost to disturbance, leaving 3,170 active live trap nights. Although we could not count exactly how many trap nights we lost to bears, we approximated this number based on circumstantial evidence such as traps that were rolled away from the site and damaged. We estimated that bear damage accounted for approximately 35% of the total number of lost trap nights, or $\sim$ 6% of all trap nights. No traps with an animal inside of them were damaged by bears.

We caught 15 mammal species in live traps (Jordan 2007), and we caught fishers on between 1.3% and 2.0% of active trap nights from 2002-2004 (Table 1). Of the non-fisher carnivores, ringtails *Bassariscus astutus* were the most frequently captured. These data do not include occurrences of black bear disturbance of sites, which exceeded the capture rate for fishers. Fisher captures covered nearly the entire elevational range of available traps, with our highest capture occurring at 2,282 m a.s.l. However, most fishers were caught at elevations between 1,200 and 1,800 m a.s.l. (Fig. 2).

Out of 4,448 camera trapping nights, we lost 538 (12.1%) to some form of disturbance. We caught 18 mammal species at camera traps, including representatives of all species captured in live traps (Jordan 2007). Among carnivores, black bears were the only species photographed more frequently than

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Table 1. Live and camera capture results for fishers in the Sierra National Forest, Fresno County, California, USA from 2002 to 2004. Capture rate is the percentage of active trap nights that a capture occurred. Latency is the average number of trap nights before a capture occurred, and does not include traps with no captures.

		All species			Fishers		
Year	Trap type	Captures	Capture rate	Latency	Captures	Capture rate	Latency
2002	Live	37	3.7	3.28	13	1.3	3.38
	Camera	381	31.2	2.64	90	7.4	4.35
2003	Live	36	3.2	4.64	20	1.8	5.11
	Camera	300	18.4	3.75	75	4.6	4.79
2004	Live	48	4.6	4.40	21	2.0	5.00
	Camera	393	24.6	3.61	62	3.9	5.03

fishers, accounting for 24% of all camera captures. However, in most of these cases, they also disabled the station. We attributed 64% (346 out of 538) of lost camera trap nights to bear damage. Western spotted skunks *Spilogale gracilis* and ringtails were also commonly captured with camera traps.

Capture rates of fishers were considerably higher with camera traps than live traps (Fisher's exact test: $P < 0.001$; see Table 1). Elevation ranges of camera trap captures of fishers were similar to those for live trapping ($t = 0.868$, $df = 233$, $P = 0.39$; see Fig. 2). Latency to detection was not significantly different for live and camera traps ($t = 0.668$, $df = 6$, $P = 0.53$; see Table 1). The detection rate of fishers was 34%, 20% and 22% for 2002, 2003 and 2004, respectively.

We had 20, 23 and 27 resightings of marked fishers in 2002, 2003 and 2004, respectively, representing 12, 13 and 14 distinct individuals. We had an additional 84, 51 and 34 photographs of unmarked animals in these years, along with eight, 13 and eight photographs of marked animals that we were unable to identify, primarily because the animal was not oriented properly toward the camera or glare from the flash made it difficult to discern the colours of the ear tags and reflective tape. In cases where we could distinguish among fishers, we had seven instances where two different, marked fishers were detected at a camera between investigator visits, and a further seven where both a marked and an unmarked fisher were detected during that span. Finally, over the three years of our study, we had seven, seven and six photographs of fishers, respectively, whose marking status we could not determine, primarily because the animal's head was outside of the box when photographed. We excluded these individuals from further analyses.

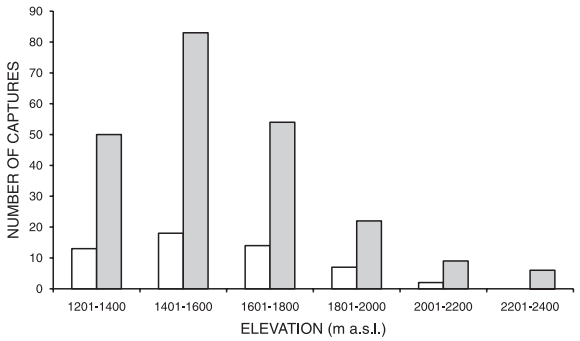


Figure 2. Elevations of fisher captures in live (□) and camera traps (■) in the Sierra National Forest, Fresno County, California, USA. Data are combined for surveys conducted from 2002 to 2004.

The model that held α and σ constant accounted for 73% of the AIC_c weights, so we used this structure for all subsequent modeling. Of the top five models, three indicated some effect of sex on survival, either independently or in an additive or interactive combination with time. While these models yielded lower point estimates of survival for males than for females, the variance of these estimates was so high as to make inferences meaningless (M.J. Jordan, unpubl. data). We therefore removed the effect of sex on survival from subsequent analyses.

The two best remaining models accounted for 95% of the overall AIC_c weights and varied only in their treatment of apparent survival (Table 2). Both of these models allowed for an annual difference in the number of unmarked fishers and allowed for some degree of temporary emigration (see Table 2). There was some support among these models for annual variation in apparent survival.

The model-averaged abundance estimates for 2002-2004 were 40, 29 and 27 fishers, respectively (95% CI: 29-51 (2002), 22-36 (2003) and 20-33 (2004)). Confidence interval length was 0.55, 0.48 and 0.48 times the point estimate of abundance for 2002, 2003 and 2004, respectively. After dividing our abundance estimates by the effective sampling

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Table 2. Model selection results under the robust design Poisson log-normal mixed-effects mark-resight model from camera trapping data in the Sierra National Forest, Fresno County, California, USA from 2002 to 2004. Model symbols are: α = uncorrected resighting rate, σ = variance due to individual heterogeneity, U = number of unmarked individuals in the population, φ: apparent survival rate and γ = temporary emigration rate. Parameter varies by: $_t$ time, . parameter constant, $_0$ set to 0.

Model	AIC_c	ΔAIC_c	AIC_c weights	No. of parameters	Deviance
$\alpha.\ \sigma.\ U_t\ \varphi.\ \gamma.$	225.9	0.0	0.739	7	209.9
$\alpha.\ \sigma.\ U_t\ \varphi_t\ \gamma.$	228.4	2.5	0.215	8	209.8
$\alpha.\ \sigma.\ U.\ \varphi.\ \gamma.$	232.0	6.1	0.035	5	221.0
$\alpha.\ \sigma.\ U.\ \varphi_t\ \gamma.$	234.3	8.4	0.011	6	220.8
$\alpha.\ \sigma.\ U_t\ \varphi.\ \gamma_0$	270.2	44.3	0.000	6	256.8
$\alpha.\ \sigma.\ U_t\ \varphi_t\ \gamma_0$	272.5	46.6	0.000	7	256.5
$\alpha.\ \sigma.\ U.\ \varphi.\ \gamma_0$	4346.7	4120.8	0.000	4	4388.0
$\alpha.\ \sigma.\ U.\ \varphi_t\ \gamma_0$	4347.7	4121.8	0.000	5	4336.7

area for each year, we obtained density estimates of 10.9, 6.7 and 6.3 fishers/100 km^2 in 2002-2004, respectively (95% CI: 7.9-13.9 (2002), 5.1-8.4 (2003) and 4.7-7.7 (2004)).

After taking the number of marked but unidentified fishers into account, we obtained model-averaged mean resighting rate estimates of 3.1, 3.4 and 3.0 times per animal for 2002, 2003 and 2004, respectively. Our estimates of apparent survival had very low precision. Averaging across models, we estimated apparent survival as 0.95 (95% CI: 0.01-1.0) between 2002-2003 and 0.93 (95% CI: 0.04-1.0) between 2003-2004. Temporary emigration rates were 0.40 (95% CI: 0.15-0.71) in both intervals.

We conducted the same analysis with a data set that used investigator visits to the camera station as the cut-off between distinct captures. All photographs of the same animal between visits were collapsed into a single resighting for analysis. The relative ranking of models based on this treatment of the data was identical to the data set with no cut-off time between captures, though ΔAIC_c values were slightly lower among the top models. We obtained abundance estimates similar to those from the analysis with no cut-off time, though they had higher standard errors.

Discussion

Our results show that photographic mark-resight methods can be applied to mesocarnivores that do not have individual markings. A previous study in Massachusetts also estimated density in fishers using camera traps in a mark-resight context (Fuller et al. 2001). We obtained similar, though slightly lower, mean abundance estimates to this study, however, our confidence intervals were slightly wider. One substantial difference between this study and ours is that their study area was approximately half the size of ours, and therefore contained roughly 2-3 times the density of fishers (21-25/100 km^2). Further, they had 2-3 times as many fishers that were marked and available for each resighting phase.

The point estimates of survival from our study are comparable to previously reported values (Krohn et al. 1994), although there have been relatively few studies estimating this parameter in fishers. However, the uncertainty around this value makes it difficult to make projections of future population trajectory with confidence.

The values we obtained for latency to detection and detection rate were comparable to other camera trapping studies of fishers. Our average value of 3.3 camera trap nights for trap latency is slightly lower than that obtained in two different studies in the northeastern U.S. ($\sim$ 5; Gompper et al. 2006 and 6.6; Long et al. 2007). This result suggests that our method was slightly more efficient at detecting fishers. However, we also obtained detection rates that were slightly lower than those reported in these two studies, likely due to our population's low density.

To increase confidence in our results, we should determine if our study design met the assumptions of the analysis method. The RDPNE first assumes that the population is closed (i.e. no dispersal or mortality) within each primary sampling occasion (McClintock & White 2009). We assumed that our population was closed during each primary occasion because most dispersal takes place after our trapping season (Arthur et al. 1993), and we caught very few juveniles that might have been dispersing or about to disperse.

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Our relatively high estimates of temporary emigration may suggest that the population was not geographically closed. Although, we used ecological and topographical boundaries to attempt to establish a study area perimeter that reduced the number of animals with home ranges extending beyond its boundaries, radio-telemetry data collected for another study (Mazzoni 2002, Purcell et al. 2009) showed that some animals, particularly males, occasionally ranged outside of our study area.

Recent models allow for analysis of capture-recapture data in a spatially explicit way, allowing models to account for unequal capture probabilities due to movement beyond study area boundaries (e.g. Borchers & Efford 2008, Royle et al. 2009). Our data were not amenable to this type of analysis because it requires that all individuals (marked and unmarked) be individually identifiable (Efford et al. 2009). However, this is a potentially fruitful area of research for mark-resight modeling.

The RDPNE, like all models based on marked animals, assumes that no marks are lost during the study (Pollock et al. 1990, McClintock & White 2009). We estimated the extent of tag loss from live capture data. Out of nine fishers that were caught in live traps more than once and at least one year apart, four had lost their ear tags by the following year. Assuming that tags are lost at a constant rate, this suggests a rate of 4% of fishers losing their tags every month, or approximately 1-2 fishers losing tags in the two months between the end of live capture and the end of camera resighting each year.

Lost tags will bias upward an abundance estimate from capture-recapture data while biasing downward estimates of apparent survival (Arnason & Mills 1981, McDonald et al. 2003). Jordan (2007) simulated data using a different estimator of abundance (Bowden & Kufeld 1995) based on the data collected for our study and found that abundance estimates could be biased upward by as much as 10% given the level of tag loss that we observed in our study. Corrections for this bias have typically been *ad hoc* (e.g. Nichols & Hines 1993, Diefenbach & Alt 1998), although it has been incorporated into Jolly-Seber (Cowen & Schwarz 2006) and band recovery (Kremers 1988) models. Further research is needed into the extent to which tag loss rates such as we observed affect the accuracy of abundance and apparent survival estimates under the RDPNE model.

The third assumption of the RDPNE is that there are no errors distinguishing marked from unmarked animals (McClintock & White 2009). This was not always the case in our study, as we had photographs of animals with their heads outside of the box when they triggered the camera. This happened in roughly 10% of the photographs each year. We excluded these events from the analysis so they did not bias our results.

Related to the above issue, the RDPNE assumes independent and identically distributed resighting probabilities for marked and unmarked animals. We could not individually identify unmarked animals, so to reduce the impact of making assumptions about the capture process for unmarked fishers, we treated every photograph as an independent capture rather than resort to arbitrary, temporal cut-offs between photographs. We felt that this was the safest approach given that we observed 14 confirmed cases of two different animals visiting a station between investigator visits, and there was an unknown number of other cases such as those when both animals were unmarked. Further, model selection results based on a cut-off of investigator visits spaced approximately 48 hours apart suggested that the approach we used did not alter our estimates of abundance.

One way to increase the number of marked individuals, and thus improve precision of both abundance and apparent survival estimates, would be to increase the duration of the marking phase of the study within each primary sampling occasion. To most efficiently accomplish this, we recommend researchers use a method such as a discovery curve, which estimates the proportion of the population that has been captured by plotting the cumulative number of new individuals observed against time (Colwell et al. 2004, Baker et al. 2006). As the season progresses, more and more individuals will be recaptures from within that year, and eventually the curve should reach an asymptote representing the abundance of the population. We recommend periodic development of a new discovery curve in order to determine approximately what proportion of the population has been marked, using a cut-off of at least 60% of the population being marked to yield reasonably precise estimates of abundance.

The method of iteratively checking field data using discovery curves can allow researchers to estimate the percentage of the population marked and identify a stopping point for live trapping. However, to most efficiently mark the population,

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one should also consider how to increase capture rates for each individual trap night. A number of modifications to our field method could have increased rates of initial capture and resighting. For example, prebaiting by leaving traps baited and open, but not set, is a common technique to enhance capture rates at live traps (Schemnitz 1994). Researchers can also conduct trapping at a different time of year than we did. Capture rates were higher in our study area in the winter than in the summer or fall (M.J. Jordan, unpubl. data), so moving the trapping season to that time of year could enhance both capture and resighting rates.

One issue that had a large impact on our capture success was the problem of black bear damage to traps. In most cases of bear visits to camera traps, the bears disabled the station, and most lost trap nights could be blamed on damage caused by bears. Although it was often possible to repair the stations in the field, this was still a significant loss of trapping ability. We recommend incorporating a loss rate of 10-15% of trap nights for any power analyses conducted prior to commencing this sort of study. One way to avoid bear damage would be to trap during the winter when bears are not active. As mentioned above, this also has the potential to increase fisher capture and resighting rates. We suggest future research examine the impact of tag loss on the accuracy of parameter estimates from mark-resight data as well as test methods to reduce the likelihood of lost tags. One potential remedy is to use a resighting device that can read PIT tags (M. Higley & S. Matthews, pers. comm.), which are implanted and thus unlikely to be lost. While we implanted these tags in all live-caught fishers, we did not test such a recapture device.

In addition to the considerations outlined above, there are certain practical issues to address before planning a survey such as this. The first concern for many managers will be the cost. Each station requires a one-time capital expenditure to buy the infrared device and camera, which is higher than the cost of many other types of survey devices like live traps or hair snares. The operating costs for bait, film, minor repairs and film developing were comparable to the equivalent costs for live trapping, although some of these costs might be reduced by using digital cameras. At the outset of this study, there were no mass-marketed, active infrared digital camera systems available, although many passive infrared systems were. Finally, labour costs should be considered; this study employed four people full time for four months every year, which included two months of live trapping and marking prior to camera trapping. Our results show that this study duration may not be sufficient to obtain precise density or survival estimates with a desired level of precision.

While previous studies have used cameras to monitor populations of fishers, most of them have focused on determining the presence of this species without developing estimates of density or vital rates. What sets the current study apart are our demographic estimates for a population of fishers using these methods. State and federal agencies need current information to make decisions about land management actions, such as fuel reduction treatments, that will affect this species. Our study highlights the importance of a significant investment of resources and a commitment to long-term research to generate the data needed to effectively make conservation decisions.

Recent models show that fishers occupy a relatively narrow band of habitat throughout the southern Sierra Nevada and that the total population in the region is probably < 300 individuals (Spencer et al. 2011), a finding compatible with our study. Further, our estimates of population density are lower than most published estimates of this parameter (Powell 1993, Fuller et al. 2001, Weir & Corbould 2006). Although the confidence intervals overlap, our data also suggest a decline in abundance over the three years of our study. Our results provide a starting point for developing more proactive management objectives for fishers in California as well as general guidelines for planning camera trapping studies of mesocarnivore populations.

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