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Original Article

Using Natural Pelt Patterns to Estimate Population Abundance with Mark–Resight Models

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ABSTRACT To estimate population abundance of wide-ranging and elusive species, wildlife managers require practical data-collection methods that are efficient, accurate, and cost-effective. Natural abundance marking can provide a useful solution, but it has largely been utilized only for conservation monitoring of species with very high distinctiveness. We estimated abundance of invasive wild pigs (*Sus scrofa*), a widespread pest species with low to moderate distinctiveness, in the Tehachapi Mountains of California, USA. Wild pigs are increasingly recognized as a major threat to wildland communities throughout the United States, but we still lack cost-effective ways to track their populations. We used natural markings to identify individuals for mark–resight population estimation, developing a method based on standardized thresholds of image quality and animal flank distinctiveness to account for the inherent variability of natural markings among individuals. We tested our method over a 15-month period during 2015 and 2016, using an array of 48 camera traps across a 48-km^2 survey grid. With 18.5% of wild pigs meeting our conservative standard of identifiability, we estimated abundance using standard mark–resight methods that ranged from 506 (±69 [SE]) individuals in summer 2015 to 184 (±44) individuals in spring 2016. We were able to detect a likely decline in the wild pig population from 2015 to 2016, which was supported by a simultaneous decline in hunter harvest totals in the region during the same period. Our approach requires no trapping or tagging of any kind, so it may be utilized as an efficient alternative to techniques that rely on physically capturing animals to apply ear-tags or neck-bands for individual identification. © 2020 The Wildlife Society.

KEY WORDS abundance estimation, California, camera trap, invasive species, natural mark identification, Poisson log-normal, *Sus scrofa*, Tehachappi Mountains, wild pig.

Motion-sensing camera traps are a reliable, noninvasive, and relatively inexpensive method of population data collection, particularly when researching cryptic species in remote wilderness (Silveira et al. 2003). Since Karanth (1995) first used camera traps to collect population data on tigers (*Panthera tigris*) >20 years ago, the technology has emerged as a powerful survey tool for wildlife managers and population ecologists. Researchers have used camera-trap photo data and mark–resight techniques to successfully estimate population parameters for species ranging from snow leopards (*Uncia uncia*) to giant panda (*Ailuropoda melanoleuca*), without the use of artificial markers or tags of any kind (Jackson et al. 2006, Chen et al. 2016). This was accomplished by using the animals' unique natural pelage patterns to identify individuals, from which capture histories were generated and incorporated into statistical models for population estimation.

Mark–resight approaches using natural marks initially evaluated species with clear and uniformly distinctive pelage patterns, such as zebras (*Equus quagga*), but have advanced to include a range of other species with less distinctive natural markers, such as gray whales (*Eschrichtius robustus*) and mountain lions (*Puma concolor*; Cooke et al. 2007, Kelly et al. 2008, Zero et al. 2013). Mark-resight techniques rely on a wider range of natural identifiers such as scars, deformities, and unusual pelage to distinguish individuals. Improvement in camera-trap technology in recent years, both in terms of image resolution and functional reliability, has made it possible to use camera traps efficiently to

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evaluate wildlife populations. Furthermore, technological advance's allow researchers to extend methods to an even broader range of species by incorporating more subtle marks to establish or confirm an individual's identity (Kelly et al. 2008). Our study continues the expansion of camera-trap survey applications by exploring a novel method of using mark–resight population estimation for naturally identifiable individuals from a population of invasive wild pigs (*Sus scrofa*), a species generally characterized by indistinct pelage.

Invasive wild pigs have become an increasingly problematic species throughout much of the United States, causing extensive ecological, agricultural, and property damage while acting as a vector for numerous human and livestock-borne diseases (Pimental 2007, Jay-Russell et al. 2012). With an estimated population of approximately 7 million across ≥41 states, expanding wild pig populations throughout the continental United States have made the control and management of increasing populations a priority across local, state, and national levels (Mayer and Brisbin 2009). Despite the recognized need, we still lack effective, long-term population-control methods throughout much of their nonnative range. Control methods are limited due in large part to a continued inability to effectively track wild pig population change through time, because reliable population estimates are necessary to build appropriate population models and test the efficacy of any ongoing control strategies (Baber and Coblentz 1986, Sweitzer et al. 2000, Acevedo et al. 2007). A small number of traditional capture–mark–recapture (CMR) studies have generated density estimates for populations of wild pigs, but this approach requires capturing and marking animals, which is costly, labor-intensive, and difficult to administer across large landscapes (Andrzejewski and Jezierski 1978, Baber and Coblentz 1986, Petit and Valiere 2006). Noninvasive methods for estimating wild pig populations have shown promise, such as CMR approaches that rely on fecal DNA or hair-trap sampling. However, usefulness of all approaches are potentially limited by varying rates of sample collection among age and sex classes (Ebert et al. 2010*a*, 2012). Furthermore, DNA analysis for hair and fecal sampling approaches are time-consuming and expensive (both in the field and the lab), making this approach untenable for many wildlife managers confronting real-time management decisions. Camera trapping provides an alternative option to improve on these inefficiencies and provide a low-cost, noninvasive method of wild pig population estimation that can be easily adopted across the wide range of landscapes these animals currently occupy.

We tested an approach to estimate wild pig population size using only natural marks documented through wildlife cameras. We established a camera-trap survey grid to collect photo data over a 15-month period from March 2015 through May 2016 at the Tejon Ranch in the Tehachapi Mountains of California, USA. We used baseline standards of image quality and animal flank distinctiveness to catalogue wild pig photos systematically and individually identify a subset of the population using a diversity of naturally occurring marks. We analyzed encounter data from naturally marked and unmarked individuals using mark–resight models, which estimated abundance through time. By incorporating individual flank distinctiveness as a covariate, we estimated heterogeneity in resighting rates between marked individuals with variable distinctiveness, thereby testing the effectiveness of our baseline standards in mitigating resighting bias associated with this novel method of individual identification. Our specific objectives were to evaluate 1) the use of naturally occurring marks to reliably identify individual wild pigs, and 2) whether this approach to individual identification can be used with mark–resight models to estimate population abundance through time.

STUDY AREA

Our research was conducted at Tejon Ranch in the Tehachapi Mountains of southern California, USA (Fig. 1). At 1,093 km^2, Tejon Ranch represented an important open-space corridor connecting the Los Padres and Angeles National Forests with the Sequoia National Forest and the southern Sierra Nevada (Kern County, 35°01′N, −118°44′W). The region spanned a strong elevational gradient and a wide range of climatic conditions; however, the ranch was generally characterized by a Mediterranean climate, with an average annual rainfall of 164 mm that falls between October and May. Average minimum and maximum temperatures are 6° and 36° C, respectively (Diamond et al. 2013). Since at least 1990, Tejon Ranch has been occupied by a population of wild pigs. In recent years, wild pigs have been identified as one of the primary threats to the native ecology of the region because their extensive rooting and wallowing across all habitat types have disrupted floral and faunal communities while acting as a vector for invasive vegetation (Kunkel 2013).

METHODS

We collected camera-trap photo data over 15 months between March 2015 and May 2016, and delineated our data into 5 consecutive, 3-month sampling intervals. During this time, wild pigs were actively hunted across the Tejon Ranch, including our survey area, with reduced hunting pressure in August 2015 and February 2016 when the Tejon Ranch Company restricted access to the majority of their hunt club members.

We selected a grid cell size of 1 km^2 to ensure that multiple camera locations were present within the known home range of wild pigs. Movement patterns and territoriality are known to vary between sexes of wild pigs and across habitat conditions, but a rough estimate of home range size for wild pigs in California was estimated by Sweitzer et al. (2000) to be approximately 4 km^2. Within each 1×1 km cell, we installed one white-flash camera trap (Reconyx Hyperfire 550, Holmen, WI, USA) and set it to capture wildlife activity in 5-image bursts, 24 hours/day. Within each cell, we placed camera sites along travel corridors for wild pigs. Specifically, we aimed to place cameras within each cell at pinch points on the landscape that constrained animal movement along roads or game trails.

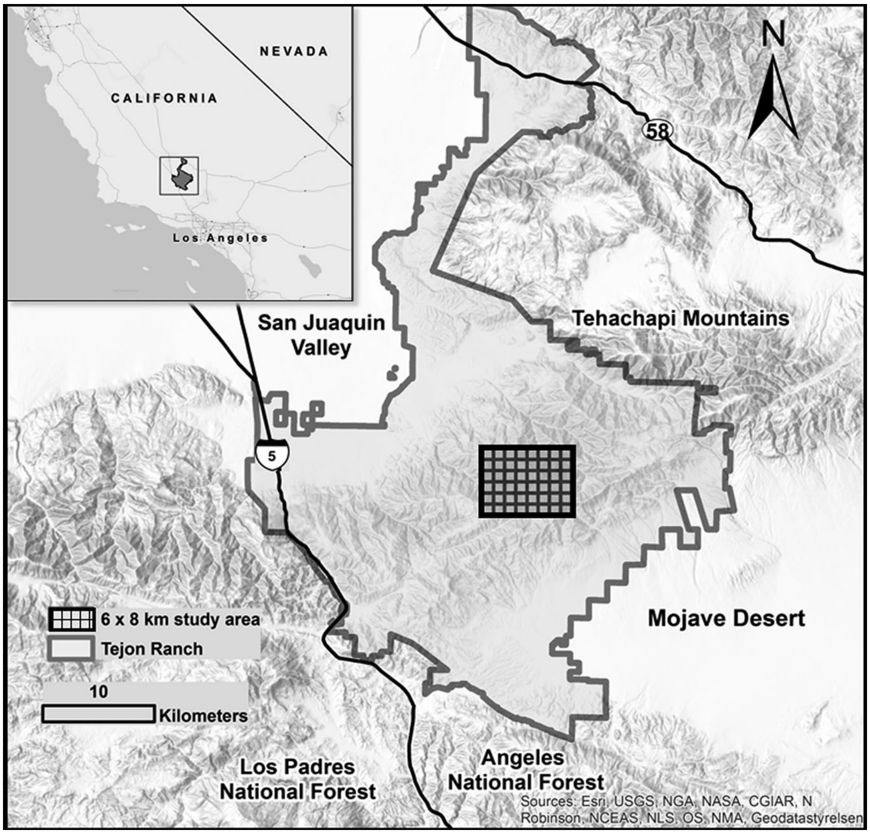

Figure 1. Map of survey grid used to identify and resight wild pigs within Tejon Ranch in the Tehachapi Mountains of California, USA (Kern County, 35°01′N, −118°44′W). Each 1 × 1-km grid cell contained one camera station collecting mark–resight data for invasive wild pig population estimation.

We set cameras approximately 60–100 cm off the ground and 2–4 m from the anticipated travel path. We set cameras at 90° angles to the anticipated path to maximize the likelihood of capturing clear images of animals' flanks. Wherever possible, we oriented cameras northward to avoid false triggers related to interference from direct sunlight and framed field of view against a hillside or other solid backdrop (as opposed to open landscape) to improve flash performance during nighttime captures. We placed cameras a minimum distance of 100 m away from potential attractants, such as active wallowing areas, that were likely to concentrate wild pigs. We checked cameras and retrieved photo data at monthly intervals to ensure cameras were operational and photo frames unobstructed throughout the survey period.

Photo-ID

Wild pigs on Tejon Ranch present a wide range of heterogeneous marks and pelage patterns. To standardize the identification of individuals, we established a system to account for the variability of image quality and animal flank distinctiveness, based on a similar protocol developed by Cooke et al. (2007) to estimate populations of Atlantic gray whales from boat-based photographic surveys.

Following each camera check throughout the 15-month survey period, we retrieved photo data and sorted by species. We grouped all wild pig images into sets of independent encounters defined by a 30-minute quiet period of inactivity before and after wild pigs encountered a given camera (O'Brien et al. 2002). A single trained observer then assessed all images in each encounter to determine if 1) the animal in the photograph was an adult (piglets and subadults, defined by size and distinctive juvenile pelage, were not included as part of our analysis); 2) the image was of sufficient quality (see image quality below) to determine whether the animal photographed was marked or unmarked; and 3) the exposed flank captured within the image was sufficiently distinctive to establish or confirm the individual's identity (see flank distinctiveness below). If these conditions were met for ≥1 image captured within an encounter, we imported the image or images into a photo-ID (PID) catalogue. We then compared images against all other known individuals to determine whether they represented a resight of a known individual or the initial capture of an identifiable individual new to the PID catalogue. All resight data used to estimate population abundance were confirmed by ≥1 additional independent observer.

Image Quality and Flank Distinctiveness

Image quality.—To standardize image quality, we established a baseline threshold that defined the lower limit on quality for all images entering the PID catalogue. The baseline assumes that for a photo to be usable for mark–resight population estimation, it must be of high enough quality to

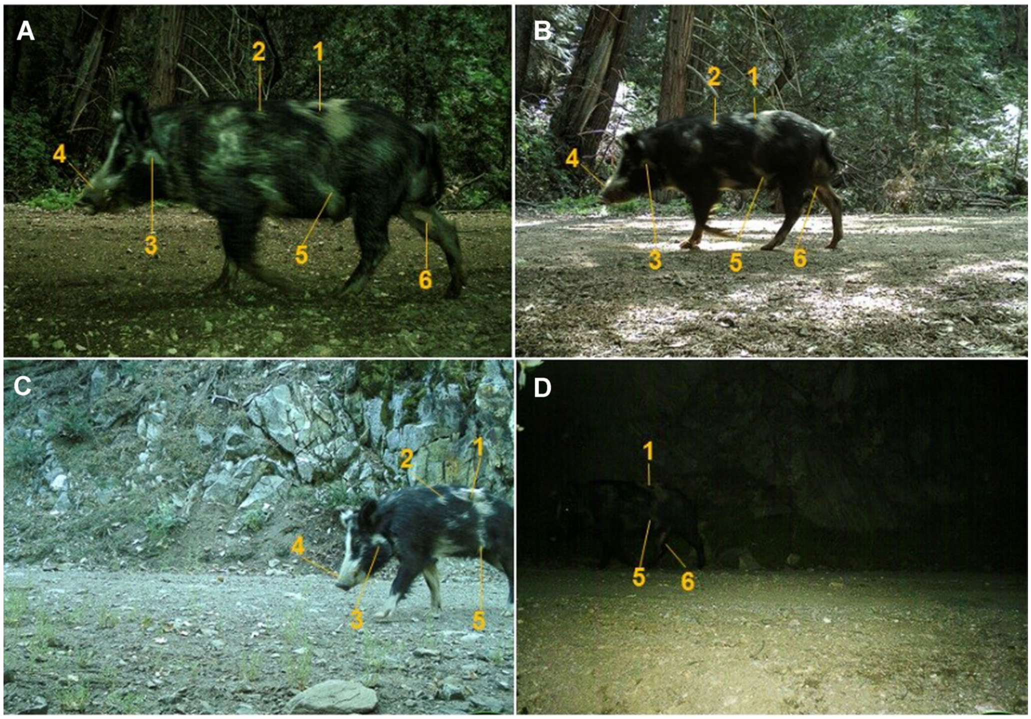

Figure 2. As example of criteria of image quality we show 4 photos (A–D) that were used to identify and resight wild pig M02 over a period of 9 months across multiple camera stations within our survey grid on Tejon Ranch, California, USA, during 2015–2016. Photo A represents a high-quality image containing all 6 parameters that contribute to image quality. Images of this quality should be used to confirm future resights of this individual. Photos B and C do not include all 6 parameters that contribute to image quality, but are of adequate quality to definitively confirm the identity of this individual, and (hypothetically) all other identifiable individuals included in our mark–resight catalogue. Note that the physical condition of this individual has visibly changed, and yet identifiable marks persist. Photo D is of poor quality and can only definitively confirm the identity of the most distinctive individuals featured in our mark–resight catalogue. This resight will not be included in our analysis because this image is of inadequate quality to (hypothetically) identify all individuals included in our mark–resight catalogue.

confirm the identity of the least distinctive individual in the catalogue, were that individual to be hypothetically transposed into the image (Fig. 2). We defined 6 parameters that contributed to overall image quality: 1) aspect (featured animal's left or right flank) is an appropriate distance from the camera, (2–4 m); 2) aspect is photographed at an approximate 90° angle to the camera; 3) aspect is completely within frame and within flash radius; 4) image is without blurring due to rapid animal movement; 5) image is without environmental disturbance (mud, rain, fog, dust, snow, etc.); and 6) image is without camera malfunction (overcompensation, flash fail, etc.). Based on these parameters, we categorized catalogue photos by quality. Wild pig encounters containing only poor-quality images, in which the mark status of the individual captured was indeterminate, were not included in the PID catalogue or used for mark–resight population estimation. We considered all other wild pig photos eligible for entry into the PID catalogue. Additionally, we flagged particularly high-quality images of marked individuals, containing most or all of the 6 parameters described above, for use as stock photos to confirm future resights.

Flank distinctiveness.—Distinctiveness refers to overall identifiability and we assessed it independently for each flank of an individual entering the PID catalogue. We assessed distinctiveness as a combination of 1) visibility, 2) uniqueness, and 3) permanence of the features (e.g., pelage patterns, scars, ear tears, tail kinks, rub marks, deformations) used to identify an individual. Visibility refers to how discernible a feature would appear in images of different quality (e.g., only features with high visibility are discernible in images of poor quality). However, there were also many highly visible features that were so common within the population that they contributed little to confirming the identity of an individual. Uniqueness is a generalized assessment of how common certain features were within the entire pig population. Permanence refers to the reliability of features and attempts to account for the rate at which certain features changed over time (Negrões et al. 2010).

For an individual to be considered adequately distinct for entry into the PID catalogue, they had to possess a feature or collection of features that met baseline standards for all 3 criteria. If an individual's features met or surpassed all distinctiveness standards, we described primary features and imported descriptive notes (including secondary feature descriptions, sex, and sounder associations) into the PID catalogue along with the encounter photos used to establish its identity. We similarly imported encounter photos used to resight known individuals into the PID catalogue, creating an easily accessible photographic record of the individual's complete capture history. This was the first attempt to track natural markers of wild pigs over time; therefore, we were unsure of how quickly certain features like scars and rub marks would change over time. To be conservative, we focused only on larger, easily distinguished markers that we were confident would remain consistent across the 3-month sampling intervals used for our analysis. This approach also increased the overall efficiency with which wild pig photo data were processed and confirmed. We classified all animals that did not meet our standardized baseline of distinctiveness for this survey as unmarked individuals.

To include distinctiveness as a covariate during analysis, we associated each individual's flanks with an ordinal distinctiveness value (DV) based on distinctiveness relative to the entire population of marked individuals. This value was based on general appearance categories that distinguished extremely distinctive piebald individuals from those characterized by more common black, gray, and brown pelages (Fig. 3). We considered only clearly identifiable flanks, categorized by a distinctiveness value ≥3, to be uniquely marked and entered these in the PID mark–resight catalogue. The ordinal scoring system allowed us to test the heterogeneity of resighting probabilities based on distinctiveness, and determine whether, despite our baseline standards, those most distinctive individuals were disproportionately resighted as a result of the unusual visibility of their identifiable marks. We independently conducted the assessment for both the left and right flanks of individuals entering the catalogue; however, we analyzed only left-flank photo data for this study.

Photo-ID Catalogue

We used Adobe Photoshop Lightroom 5 to organize and catalogue resight photographs and individual capture histories through time. The platform allowed us to embed searchable keywords and other pertinent metadata into individual photographs based on the specific features, or feature types, used to identify the individual contained within the image. Through these searchable keywords, we were able to efficiently process photo data by comparing incoming pig photos with only those individuals sharing similar diagnostic features, thus, dramatically decreasing the observer effort required to determine whether incoming images represented a resight of a previously identified individual or the first encounter of an individual new to the PID catalogue.

When an incoming image was determined to represent an individual new to the PID catalogue, we set-up an archive specific to that individual to contain the full capture history of the individual, and established a profile based on the individuals' identifiable features and embedded it into the image(s) as metadata. If an incoming image was identified as a resight of an individual already in the PID catalogue, we embedded the image(s) with that individual's metadata profile and catalogued it within the individual's existing capture history folder.

Mark–Resight Analysis

We applied the Poisson log-normal estimator under robust design to estimate population abundance using left-flank photo data from both marked and unmarked wild pigs collected across our 15-month sampling window (PNE; McClintock et al. 2009, Alonso et al. 2015, McClintock and White 2012). We developed our model using RMark

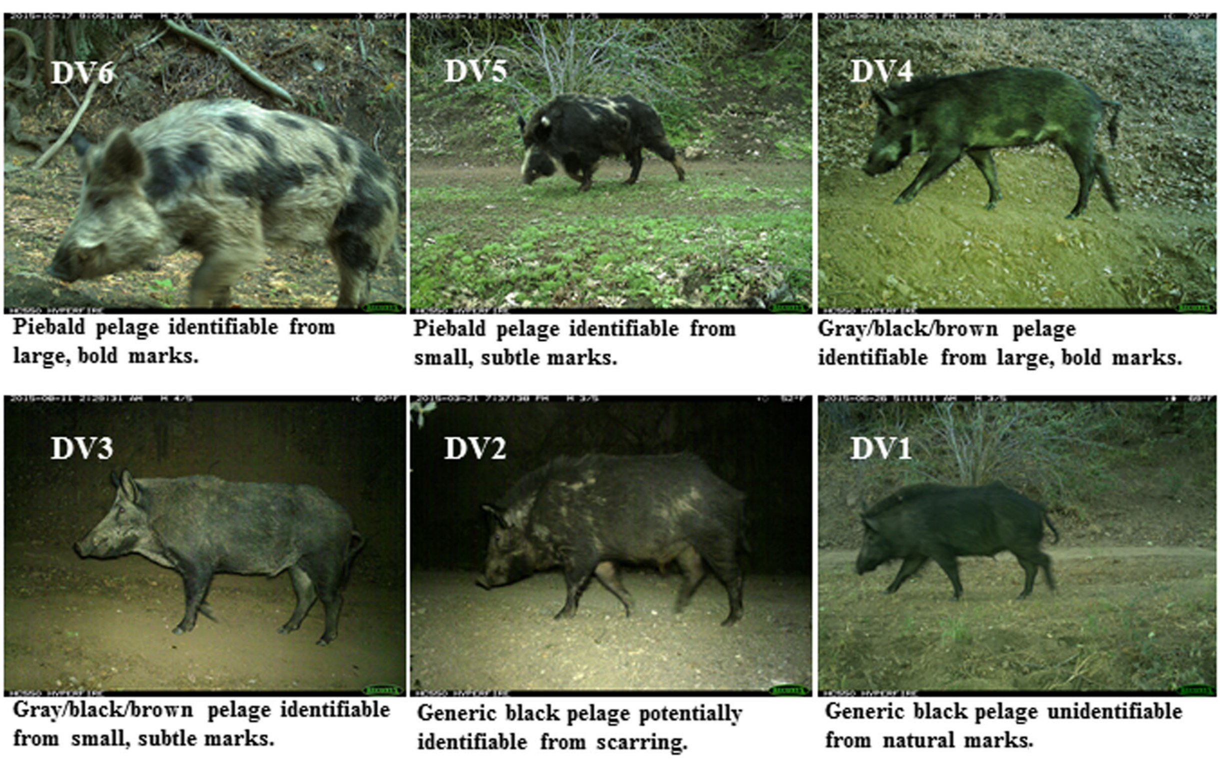

Figure 3. Variable levels of flank distinctiveness standardized as an ordinal covariate for analysis of photos used to identify and resight wild pigs using multiple camera stations on Tejon Ranch, California, USA, during 2015–2016. Distinctiveness values (DV) are based on broad categories of appearance based on the relative visibility, uniqueness, and permanence of marks used to identify individuals. Based on our intentionally conservative standard, only individuals above DV2 were considered marked and included in the PID catalogue.

(Laake 2013), an application within Program R (R Core Team 2017) that enabled us to build and compare models from Program MARK (White and Burnham 1999). Conventional mark–recapture analyses assume a geographically (immigration and emigration) and demographically (births and deaths) closed population within which sighting probabilities are equivalent between all individuals. To account for these resight data collected throughout the study, we modelled our sampling window as 5 consecutive, 3-month primary sampling intervals, within which geographic and demographic transition would be limited. However, our survey grid was unbounded and surrounded by viable habitat, and our population was actively hunted; therefore, we could not assume complete geographic or demographic closure, even within our discrete seasonal sampling intervals. Naturally identifiable individuals are distributed randomly across the population, and discovered as opposed to intentionally distributed, so the exact number of marked individuals using our study grid was unknown. A zero-truncated Poisson log-normal estimator (ZPNE; McClintock et al. 2009) applied under robust design accounts for unknown marked individuals, as well as individual heterogeneity and simple random sampling with replacement (as was the case across our continuously operating camera-trap array on Tejon Ranch). We generated estimates for abundance (N), apparent survival (φ), and transition rates between observable and unobservable states (γ' and γ'') from this model. We derived abundance estimates and overall mean resighting rates (λ) for each seasonal sampling interval from the total number of sightings of unmarked individuals, capture histories of each marked individual resighted at least once, and mean resighting rates for all individuals (α) together with the individual heterogeneity of resighting rates between individuals (σ).

Additionally, in (Z)PNE individual covariates can be incorporated to more accurately model mean resighting rates and individual heterogeneity. This was particularly relevant for our study because we were relying on untested baseline standards to account for potential resighting bias related to the wide range of marks used to identify individuals. By incorporating relative distinctiveness values (DV 1–6) as an ordinal covariate into our model, we were able to account for its potential influence on resighting probabilities between individuals. We also included sex as a binary covariate (males = 0 females = 1) that could potentially influence resighting rates, because males are known to travel more and occupy significantly larger home ranges than females (Sweitzer et al. 2000). Using an approach first developed by Corlatti et al. (2016), we considered a series of parameter combinations of increasing complexity where the simplest model assumed mean resighting rate (α) remained constant, whereas the most complex model assumed α was a function of the interaction between sex and level of distinctiveness, in addition to seasonal sampling interval. The primary goal of our analysis was to determine whether our method of data collection could be used to estimate population abundance. Based on this objective, we limited our analyses of parameter combinations to 10 models that allowed the number of unmarked individuals in the population during each season (U) to change. Further, the level of heterogeneity for individual resighting rates (σ), apparent survival between primary sampling intervals (φ), and transition rates between observable and unobservable states (γ' and γ'') was constant across primary sampling intervals. Our survey area was not geographically closed, so abundance estimates generated from these models reflect the super population size ($\hat{N}$), or the total number of individuals that occupied our sampling grid throughout the sampling window.

We evaluated competing models using Akaike's Information Criterion (AIC) values adjusted for small sample sizes (AIC_c) and weight (w_i). We used these values to rank the 10 resight models used for this analysis based on overall fit and complexity (Table 1), from which we derived parameter estimates through model-averaging (Anderson and Burnham 2002).

RESULTS

Over the 15-month survey period from March 2015 through May 2016, our camera-trap array recorded 3,204

Table 1. Mark–resight model rankings used for population estimation of invasive wild pigs on Tejon Ranch, California, USA, derived from camera trap photos of naturally marked and unmarked wild pigs from March 2015 through May 2016.

Model[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	No. of parameters
α (season + sex) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,096.62	0	0.27	14
α (season) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,096.78	0.15	0.25	13
α (season + sex + DV) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,098.40	1.78	0.11	15
α (season + DV) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,098.90	2.28	0.09	14
α (season + sex × DV) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,098.99	2.37	0.08	16
α (.) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,099.39	2.76	0.07	9
α (sex) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,099.67	3.05	0.06	10
α (sex + DV) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,101.19	4.56	0.03	11
α (DV) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,101.29	4.66	0.03	10
α (sex × DV) σ (.) U (season) γ' (.) γ'' (.) φ (.)	1,102.73	6.10	0.01	12

[a] Zero-truncated Poisson log-normal mark–resight models ranked using Program MARK. Variables: ordinal distinctiveness value of each individual's flanks (DV), no. of unmarked individuals in the population during each season (U), mean resighting rates for all individuals (α), individual heterogeneity of resighting rates between individuals (σ), transition rates between observable and unobservable states (γ' and γ''), and apparent survival (φ).
[b] AIC_c = Akaike's information criterion corrected for small sample size.
[c] ΔAIC_c = differences in AIC_c between each model and the model with the lowest AIC.
[d] w_i = model wt calculated using AIC_c, indicating the relative support for the given model.

independent encounters with wild pigs, which included 4,556 sightings of individual adults and 648 sightings of piglets and subadults. Of those adult encounters, 2,545 individuals were sighted with their left flanks oriented to the camera. Of those left-flank sightings, 2,152 (84.6%) met all our standards for image quality and were considered eligible for mark–resight analysis. During this period, we established catalogue profiles, and recorded capture histories for the 73 individuals considered identifiable from natural marks (visible from a left-flank orientation), based on our standard of flank distinctiveness. These 73 individuals consisted of 38 females and 35 males and were resighted 398 times, representing 18.5% of adult left-flank encounters. The mean number of resightings for marked individuals was 5.45, with a range of 1–37 (median = 3). On average, males were resighted 63% more often than females (average no. of resightings for males = 6.83, females = 4.18). A discovery curve across all 5 seasonal sampling intervals suggests a leveling-off of newly identified individuals entering the PID catalogue, with >80% of marked individuals identified within the first 2 seasonal sampling intervals (Fig. 4).

Model rankings based on AIC_c values of the 10 models demonstrated no definitive top model. To account for this, we model-averaged estimates of abundance ($\hat{N}$) and 95% confidence across our 5 seasonal sampling intervals (Fig. 5). Seasonal sampling interval (time) was associated with α in all 5 of our top-ranked models, while flank-distinctiveness was included in the third, fourth, and fifth of these top-ranked models. Overall mean resighting rates (λ) were estimated as 2.183 (SE = 0.397, 95% CI = 1.539–3.116), 2.010 (SE = 0.342, 95% CI = 1.449–2.804), 1.953 (SE = 0.325, 95% CI = 1.416–2.704), 1.439 (SE = 0.267, 95% CI = 1.008–2.073), and 1.023 (SE = 0.234, 95% CI = 0.669–1.614) for seasons 1–5 respectively, while heterogeneity of individual resighting rates (σ) was estimated at 0.952 (SE = 0.084, 95% CI = 0.801–1.132).

Individual encounter totals fluctuated across seasonal sampling intervals and declined precipitously from Spring 2015 to Spring 2016. Between these 2 sampling intervals individual encounter totals (adults only, left- and right-flank encounters) declined almost 78% and left-flank encounters used for this analysis declined from 663 in Summer 2015 to 135 in Spring 2016. A significant birth pulse appeared to have occurred in Spring 2015, with 446 individual piglet/juveniles sighted; by contrast, only 55 were sighted in Spring 2016 (includes both left- and right-flank sightings). There were no piglet/juveniles sighted from November 2015 through February 2016.

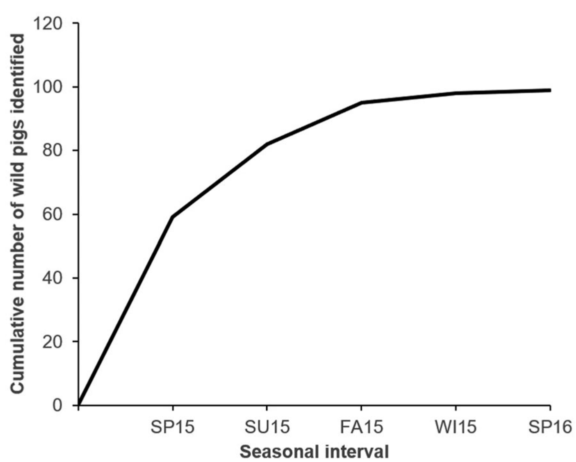

Figure 4. Discovery curve of newly identified wild pigs during 5 consecutive seasonal sampling intervals across our 48-km^2 survey grid on Tejon Ranch, California, USA, during 2015–2016.

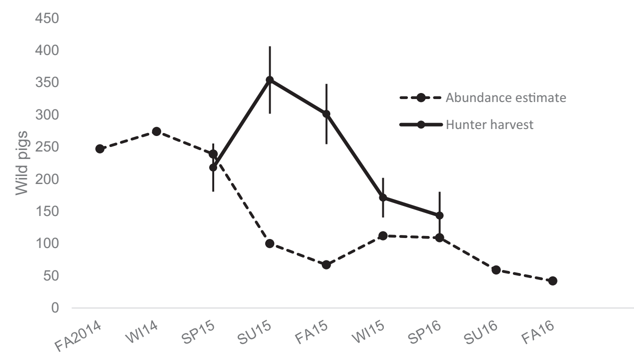

Figure 5. Comparing estimators and indices of wild pig abundance across Tejon Ranch, California, USA. Mark–resight estimates (vertical bars represent 95% CI) of wild pig abundance across our 48-km^2 survey grid are compared with total wild pig hunter harvest across Tejon Ranch. Data collected across 5 consecutive seasonal sampling intervals from March 2015 through May 2016 were analyzed using the Poisson log-normal estimator under robust design. Estimates represent averages of competing models with delta AIC_c values ≤2. Seasonal harvest totals for wild pigs hunted across Tejon Ranch from September 2014 through November 2016 appear as reported by the Tejon Ranch Company. Both metrics suggest the wild pig population on Tejon Ranch was in decline from 2015 to 2016.

DISCUSSION

Abundance Estimates

We demonstrate that natural pelage markings can be used to generate robust estimates of wild pig abundance with reasonably low coefficients of variation. Our approach provided the first estimate of wild pig abundance using a standardized methodology to identify and resight individuals using natural marks from wildlife cameras and the first estimate of their abundance on Tejon Ranch. Our results suggest that the Tejon Ranch supports a large population of wild pigs and that the population was likely in decline during the study. Seasonal abundance estimates were in decline across our study area following Summer 2015, and although movement patterns and distribution of wild pigs are known to naturally fluctuate throughout the year, a direct comparison of springtime estimates from 2015 and 2016 indicate this trend may not be entirely explained by seasonal variation. Additionally, overall mean resighting rates fell from a high of 2.183 (SE = 0.397, 95% CI = 1.539–3.116) in Spring 2015 to a low of 1.023 (SE = 0.234, 95% CI = 0.669–1.614) in Spring 2016, further indicating a decline that cannot be completely explained by seasonal variation in distribution. Furthermore, there is significant

Table 2. Estimates of superpopulation ($\hat{N}$) of invasive wild pigs on Tejon Ranch, California, USA, from March 2015 through May 2016 across 5 3-month sampling intervals, the standard error (SE) of those estimates, the 95% confidence intervals (CI) of those estimates and their associated coefficient of variation (CV), averaged across all contending models.

Sampling interval	$\hat{N}$	SE	Lower 95% CI	Upper 95% CI	CV
Spring 2015	218	37	156	305	0.17
Summer 2015	354	52	266	473	0.15
Autumn 2015	301	47	223	408	0.16
Winter 2015	171	31	121	243	0.18
Spring 2016	143	37	88	236	0.26

anecdotal evidence that suggests Tejon Ranch's wild pig population was in decline during the study period, as hunter harvest across the property dropped markedly despite consistent hunter effort (Fig. 5). The Tejon Ranch Company's wild pig hunting program, one of the largest in California, harvested 1,188 pigs in 2014, 616 in 2015, and only 305 in 2016. Although annual hunter harvest rates may fluctuate for many reasons other than population density (data on hunting effort were not available), our results suggest a ranch-wide decline of a population that was, at least recently, well into the thousands of individuals.

However, the decline in our estimates did not reflect the outright collapse that raw encounter totals would suggest. Rather, the reduction in overall input data in Spring 2016 resulted in a substantial loss in precision relative to the other seasonal sampling intervals (Table 2). For the first 4 seasonal sampling intervals, the coefficient of variation (CV) ranged from 15% to 18%; whereas in Spring 2016 this measure increased to 26%. Thus, abundance estimates for Spring 2016 are more variable relative to the mean, and thereby less reliable, than estimates of all other seasonal sampling intervals analyzed for this study. This uncertainty reduces our ability to make confident empirical statements about population trends and may limit the potential application of this method in areas where wild pig abundance is low. As Keiter et al. (2017) proposed in their comparison of density estimators used to assess wild pig populations, including the short-term use of natural marks around baited camera traps, sampling design should seek to maximize individual detections around multiple camera sites to improve the accuracy of population estimates. This can be accomplished by increasing the number of camera traps within a given survey area, relative to the average home-range size of the subject species. A greater understanding of site-specific home-range size would improve our ability to design a survey grid that maximizes individual detection potential for wild pigs in this part of the Tehachapis.

Wild pig fecundity and range size are known to vary significantly in response to changes in environmental conditions and resource availability (Bieber and Ruf 2005). The years of 2015 and 2016 represented the fourth and fifth year of sustained drought conditions in southern California. This extended drought visibly depressed many ecological communities on Tejon, as evidenced by wide-spread conifer die-off and poor acorn production across all oak species (Griffin and Anchukaitis 2014). Acorns are a major staple in the diet of wild pigs on Tejon Ranch, so it seems likely this lack of primary production contributed, at least in part, to the apparent population decline during this period (Espelta et al. 2008).

Data Processing and Baseline Standards

Mark–resight models under robust design provide flexibility when analyzing photo data captured using a variety of field methods. There are, however, important assumptions that must be met to produce unbiased estimates (McClintock and White 2012, McClintock et al. 2014). Our method relies on a wide range of variable marks to identify individuals; therefore, it was critical that we could account for and standardize the relative distinctiveness of these marks to meet the assumption that all marked individuals within the population are equally detectable. By using generalized descriptors and broad categorical assessments of natural marks, we were able to incorporate distinctiveness as an ordinal covariate into our analysis and assess its influence on resighting rates. Among all our top models, heterogeneity of individual resighting rates was roughly equivalent (0.945, SE = 0.084, 95% CI = 0.794–1.124; 0.958, SE = 0.084, 95% CI = 0.807–1.138; and 0.941, SE = 0.084, 95% CI = 0.79–1.121 for models ranked 1–3, respectively), suggesting that our covariates (gender and distinctiveness) were not major drivers of resighting probability. Furthermore, the only highly ranked model that included distinctiveness as a covariate was outperformed by a more parsimonious model, indicating that distinctiveness was uninformative as a covariate and thus had little or no effect on resighting rates among our marked population. This suggests that by excluding low-quality images from the data set, we were able to include less distinctive individuals into the PID catalogue without introducing resighting bias favoring more distinctive individuals. Strict image-quality standards also minimize misidentification errors related to demographic information such as sex and age class, which can be difficult to discern in poor-quality images. Additionally, by limiting our data set to higher quality images, observers were able to process photo data more efficiently without having to substantially enhance or cross-reference partially identifiable individuals from poor quality images.

Overall, we prioritized efficiency and conservatism when applying this method to wild pigs on Tejon Ranch. This is reflected in our conservative baseline standard for flank-distinctiveness used to qualify individuals as marked. If we were to lower these standards, a greater percentage of the overall population would be considered identifiable, and the image quality standard required to identify these less distinctive individuals would increase. We expect this increase in the proportion of marked to unmarked individuals in the population would result in greater precision around abundance estimates. However, this would also limit the total number of encounter photos used in the analysis and potentially increase the time needed to process the remaining photo data. Comparative methods testing is required to determine the range of image and distinctiveness standards within which precision and efficiency are maximized.

MANAGEMENT IMPLICATIONS

Our method of identifying naturally marked individuals, based on standards of image quality and flank distinctiveness, was developed as a flexible template that could be broadly applied across a range of species and habitats as a noninvasive alternative to trapping and tagging. Wild pigs on Tejon Ranch provided an excellent opportunity to test the potential of this approach because wild pig population parameters can be difficult to estimate, particularly across densely vegetated and topographically dynamic landscapes; and wild pigs are an ecologically important pest species across a wide range of areas (Ebert et al. 2010*b*). Our study demonstrates that a standardized analysis of camera trap photo data can successfully identify a substantial proportion of individuals within populations characterized by generally indistinct pelage. Our method relies solely on data generated from camera traps and requires minimal fieldwork consisting only of camera-trap installation and routine maintenance; therefore, it can be implemented across landscapes that would otherwise be economically or logistically impractical to survey. It required 8–10 field days/month for a technician to maintain our 48-camera survey grid, whereas a single trained observer could process an entire month's survey data in a period of 6–8 hours. These survey implementation and data processing requirements compare favorably with other field monitoring techniques currently used to survey wildlife populations in remote settings. Furthermore, recent advancements in automated computer learning software capable of sorting thousands of images per minute by species, and in some cases demographic class, will only enhance the potential of population estimators that rely on camera-trap data alone (Tabak et al. 2019). For many wildlife managers facing resource constraints, this simple monitoring approach can be used to efficiently estimate real-time changes in population dynamics to inform effective wildlife conservation and control strategies.

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