UC Santa Barbara
UC Santa Barbara Electronic Theses and Dissertations

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

Permalink
https://escholarship.org/uc/item/3135g418

Author
Teton, Ben Scott

Publication Date
2018

Peer reviewed|Thesis/dissertation

eScholarship.org Powered by the California Digital Library
University of California

UNIVERSITY OF CALIFORNIA

Santa Barbara

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

A Thesis submitted in partial satisfaction of the requirements for the degree

Master of Arts in Ecology, Evolution and Marine Biology

by

Ben Scott Teton

Committee in charge:

Professor Hillary Young, Chair

Professor Carla D'Antonio

Professor Frank Davis

Professor Jesse Lewis, Arizona State University

June 2018

The thesis of Ben Scott Teton is approved.

Carla D'Antonio

Frank Davis

Jesse Lewis

Hillary Young, Committee Chair

June 2018

ACKNOWLEDGEMENTS

I am grateful to all those who assisted and supported this research and would like to specifically acknowledge the following individuals and organizations: University of California Santa Barbara faculty advisor Hillary Young (Department of Ecology Evolution and Marine Biology) and external committee members Carla D'Antonio (UCSB, EEMB), Frank Davis (UCSB, Bren School of Environmental Science Management), and Jesse Lewis (Arizona State University, College of Integrated Sciences and Arts). I would also like to thank Michael White and Bob Reid from the Tejon Ranch Conservancy for their support of this research. Additional assistance from Christina Tombach Wright (CTW Wildlife Consulting) and Luca Corlatti (University of Freiburg, Department of Wildlife Ecology and Wildlife Management) is gratefully acknowledged. This research was supported in part by the USDA Animal Plant Inspection Service in association with their National Feral Swine Damage Management Program. The views and conclusions expressed in this document are those of the author and should not be interpreted as representing the official policies of USDA-APHIS.

Finally, it is with profound gratitude that I acknowledge my friends and family who supported me throughout this process.

ABSTRACT

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

by

Ben Scott Teton

Estimating population abundance through time is an essential component of wildlife conservation and management. However, accurate population monitoring can be difficult and expensive for many elusive species occurring across large, dynamic landscapes. Thus, wildlife managers require methods that accurately estimate population abundance, while also minimizing field effort and cost. We estimated abundance of invasive wild pigs (*Sus scrofa)* on Tejon Ranch in the Tehachapi Mountains of California, using natural markings to identify individuals for mark-resight population estimation. Wild pigs in this region, like many species not traditionally identified using natural marks, are generally homogeneous in appearance with distinctive features that range dramatically in relative visibility, uniqueness and permanence. We developed a method based on standardized thresholds of image quality and animal flank distinctiveness to account for the inherent variability of natural markings between individuals. This method was tested over a fifteen-month period between March 2015 and June 2016, using an array of 48 camera traps across a 48km² survey grid. With 18.5% of wild pigs meeting our conservative standard of identifiability, we generated absolute estimates of abundance across five consecutive three-month sampling periods using the Poisson log-normal estimator under Pollocks robust design. Using left-flank photos of both naturally marked and unmarked pigs, we generated abundance estimates ranging from 352 (SE $\pm$ 56) individuals in summer 2015 to 157 (SE $\pm$ 43) individuals in spring 2016. These results suggest an overall decline in the wild pig population on Tejon Ranch from 2015 to 2016, which is supported by a simultaneous decline in Ranch-wide hunter harvest totals during this period. As this mark-resight method requires no trapping or tagging of any kind, it may be utilized as a cost and resource efficient alternative to traditional mark-resight techniques that rely on ear-tags or neck-bands for individual identification of species traditionally considered unidentifiable using natural marks alone.

INTRODUCTION

Motion-sensing camera traps are a reliable, non-invasive and relatively inexpensive method of population data collection, particularly when researching cryptic species in remote wilderness (Silveira et al. 2003). Since Karanth first used camera traps to collect population data on tigers (*Panthera tigris*) over twenty years ago (1995), this 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 (*Panthera uncia*) to giant panda (*Ailuropoda melanoleuca*), without the use of artificial markers or tags of any kind(Jackson 2006, Zheng at 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.

These natural mark-resight approaches were initially used only for species with clear and uniformly distinctive pelage patterns such as zebras (*Equua 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 concolour*) (Zero et al. 2013, Cooke et al. 2007, Kelly et al. 2008). These techniques rely on a wider range of natural identifiers such as scars, deformities and unusual pelage to distinguish individuals from the general population. While these methods initially required costly, full-frame cameras to capture the detail necessary to definitively identify individuals, the dramatic improvement in camera trap technology in recent years, both in terms of image resolution and functional reliability has made it possible to use relatively inexpensive camera traps for these approaches. Furthermore, this technological advancement allows researchers to extend these 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 this expansion of camera trap survey applications, by exploring a novel method of mark-resight population estimation using 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 private property damages, while acting as a vector for numerous human and livestock-borne diseases (Jay-Russell et al. 2012, Pimental 2007). With an estimated population between 5 and 6 million across at least 41 states, dramatic increases in wild pig population sizes and range throughout the continental United States have made the development of effective control strategies a point of focus for those local, state and federal agencies tasked with controlling the damages and liabilities associated with wild pigs (Mayer and Brisbin 2009).

Despite this heightened concern, the need remains for effective, long-term population control methods throughout much of their non-native range. This is due in large part to an inability to effectively track wild pig population change through time, as reliable population estimates are necessary to build appropriate population models and control strategies as well as test the efficacy of any ongoing control strategies (Baber & 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 discrete populations of wild pigs, but this approach is costly, labor intensive and difficult to administer across large, dynamic landscapes (Andrzejewski & Jezierski 1978, Baber & Coblentz 1986, Petit & Valière 2006). Furthermore, trapping elusive, territorial animals like wild pigs potentially introduces bias as capture-probabilities can be influenced by age, sex and social standing (Ebert et. al. 2012). Other non-invasive methods for estimating wild pig populations have shown promise, such as CMR approaches that rely on fecal DNA or hair trap sampling. However, neither approach has been demonstrated to accurately represent population abundance and structure through time in a species such as wild pigs, with a low defection rate relative to other ungulates and behaviors that vary dramatically based on maturity and group status (Ebert at al. 2012, Ebert et al. 2010). For example, heterogeneity in wild pig behavior around hair traps has been shown to misrepresent overall population structure in wild pigs and certain climate conditions limit fecal sample persistence in the field, making it difficult to acquire an adequate sample size to accurately estimate population (Ebert 2009, Ebert et al. 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 faced with real-time management decisions. Camera trapping provides an alternative option to improve on these inefficiencies and provide a low-cost, non-invasive method of wild pig population estimation that can be easily adopted across the wide range of habitats these animals currently occupy.

Here we test an approach through which wild pig population estimates can be generated from camera trap photo data alone. 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. We used baseline standards of both image quality and animal flank distinctiveness to systematically catalogue wild pig photos captured over that period and individually identify a significant subset of the population using a wide range of naturally occurring marks. Encounter data from these naturally marked and unmarked individuals were analyzed using mark-resight models, which generated estimates of abundance and other population parameters through time. By incorporating individual flank distinctiveness as an ordinal covariate into this analysis, 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.

The specific questions addressed by this study are: (1) can naturally occurring marks be used to reliably identify individual wild pigs? And (2) can this approach to individual identification be incorporated into mark-resight models to estimate population abundance through time? We test the hypothesis that naturally occurring marks can be used as a non-invasive alternative to identify individuals within a population of wild pigs, such that population estimates can be generated from mark-resight analysis of camera trap photos alone. We further assess the effectiveness of our baseline standards of image quality and flank distinctiveness by determining how the relative level of flank distinctiveness among naturally marked individuals affects heterogeneity of resighting rates between individuals.

METHODS

Study Area and Design

This research was conducted at Tejon Ranch in the Tehachapi Mountains of Southern California (Kern County, 35° 01'N, -118° 44'W). At 1093 km², Tejon Ranch represents a substantial piece of the open space corridor connecting the Los Padres and Angeles National Forests with the Sequoia National Forest and the southern Sierra Nevada. This region spans a strong elevational gradient and thus a wide range of climatic conditions; however, the ranch is 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 degrees respectively (Diamond et al. 2013). The majority of Tejon Ranch, some 970 km^2, is undeveloped and protected by conservation easements stemming from a land-use agreement established in 2008. These easements allow the land owner to retain certain land-use rights that include hunting and cattle ranching. 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, as their extensive rooting and wallowing across all habitats have disrupted floral and faunal communities while acting as a vector for invasive vegetation (Kunkel 2013).

Our study area was defined by a 6 by 8 km survey grid, broken into 48 individual 1 km^2 grid cells that ranged in elevation from 1100 to 2100 meters. The study grid was located within the Tunis Creek, and El Paso Creek watersheds, which are considered to provide perennial, high quality habitat for wild pigs (Figure 1). Vegetation in this area is characterized predominantly by oak woodland and mixed hardwood-conifer forest types, with significant patches of open grassland occurring across south facing slopes.

Camera trap photo data was collected over fifteen months between March 2015 and July 2016, and was delineated into five consecutive, three-month sampling intervals. During this time wild pigs were actively hunted across the Ranch, including our survey area, with reduced hunting pressure in August 2015 and February 2016 when hunting was severely, although not entirely, restricted.

We selected a grid cell size of $1km^2$ 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 the sexes of wild pigs and across habitat conditions, but a rough estimate of home range size for wild pigs in California was estimated by Switzer et al. (2000) to be around $4km^2$. Within each 1 x 1 km cell, one white-flash camera trap (Reconyx Hyperfire 550) was installed and set to capture wildlife activity in 5-image bursts, 24 hours a day. Within each cell, camera sites were placed 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.

Cameras were set approximately 60 to 100 cm off the ground and 2 to 4 meters from the anticipated travel path. We set cameras at 90^o angles to this anticipated path to maximize the likelihood of capturing clear images of animals’ flanks. Wherever possible, cameras were oriented northward to avoid false triggers related to interference from direct sunlight and framed against a hillside or other solid backdrop (as opposed to open landscape) to improve flash performance during nighttime captures. With few exceptions, cameras were drilled into existing natural structure (trees or snags) and were protected by a steel bear-box. Cameras were placed a minimum distance of 100 meters away from potential attractants like active wallowing areas that were likely to concentrate wild pigs. Cameras were checked and photo data were retrieved 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 ensure that all identified individuals were equivalently detectable, 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, photo data were retrieved and sorted by species. All wild pig images were grouped 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 at al. 2002). All images in each encounter were then assessed by a single trained observer 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 if 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 at least one image captured within an encounter, the image or images were imported into a photo-ID (PID) catalogue. These images were then compared against all other known individuals to determine if 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 at least one additional independent observer.

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. This baseline assumes that for a photo to be usable for mark-resight population estimation, it must be of high enough quality to confirm the identity of the *least* distinctive individual in the catalogue, were that individual to be hypothetically transposed into the image (Figure 2). We defined six 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 meters); (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, catalogue photos were categorized 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. All other wild pig photos were considered eligible for entry into the PID catalogue. Additionally, particularly high-quality images of marked individuals, containing most or all of the six parameters described above, were flagged for use as stock photos to confirm future resights.

Flank Distinctiveness

Distinctiveness refers to overall identifiability and was assessed independently for each flank of an individual entering the PID catalogue. Distinctiveness was assessed 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 (Negroes 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 three of these criteria. If an individual's features met or surpassed all distinctiveness standards, primary features were described and descriptive notes (including secondary feature descriptions, sex and sounder associations) were imported into the PID catalogue along with the encounter photos used to establish its identity. Encounter photos used to resight known individuals were similarly imported into the PID catalogue, creating an easily accessible photographic record of the individual's complete capture history. Since this was the first attempt to track natural markers of wild pigs over time, 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 was processed and confirmed. All animals that did not meet our standardized baseline of distinctiveness for this survey were classified 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 (Figure 3). Only clearly identifiable flanks, categorized by a distinctiveness value ≥ 3, were considered uniquely marked and entered in the PID mark-resight catalogue. This ordinal scoring system allowed us to test the heterogeneity of resighting probabilities based on distinctiveness, and to determine if, despite our baseline standards, those most distinctive individuals were disproportionately resighted due to the unusual visibility of their identifiable marks. This assessment was independently conducted for both the left and right flanks of individuals entering the catalogue, however only left-flank photo data were analyzed for this study.

Photo-ID Catalogue

We used Adobe Photoshop Lightroom 5 to organize and catalogue resight photographs and individual capture histories through time. This 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 if 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, an archive specific to that individual was set-up to contain the full capture history of the individual, and a profile based on the individuals' identifiable fe7atures was established and embedded into the image(s) as metadata. If an incoming image was identified as a resight of an individual already in the PID catalogue, the image(s) were embedded with that individual's metadata profile and catalogued 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 at al. 2015, McClintock and White 2012). We developed this model using RMark, an application within R that enabled us to build and compare models from Program MARK (Burnham and White 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 this resight data collected throughout our sampling window was modelled as five consecutive, three-month primary sampling intervals, within which geographic and demographic transition would be limited. However, as our survey grid was unbounded and surrounded by viable habitat, and our population was actively hunted, we could not assume complete geographic or demographic closure, even within our discrete seasonal sampling intervals. As naturally identifiable individuals are distributed randomly across the population, and are discovered as opposed to intentionally distributed, 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). From this model estimates were generated for abundance (N), apparent survival (φ), and transition rates between observable and unobservable states (γ' and γ"). Abundance estimates and overall mean resighting rates (λ) for each seasonal sampling interval were derived from the total number of sightings of unmarked individuals, the capture histories of each marked individual resighted at least once and the 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 as 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 also potentially influence resighting rates, as males are known to travel more and occupy significantly larger home-ranges than females (Sweitzer 2000). Using an approach fist 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 while 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 this initial analysis was to determine if our method of data collection could be used to generate unbiased estimates of 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 seasonal sampling interval U to change, while 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 fixed across all primary sampling intervals. Since our survey area was not geographically closed, abundance estimates generated from these models reflect the super population size ($\hat{\hat{N}}$), or the total number of individuals that occupied our sampling grid throughout the sampling window.

Model selection was based on Akaike's Information Criterion (AIC) values adjusted for small sample sizes(AIC_c). These values, generated by program MARK, were used to rank the 10 resight models used for this analysis based on overall fit and complexity while a delta cut-off value of ≤ 2 was selected, within which contending models were averaged (Burnham and Anderson 2002).

RESULTS

Over the 15-month survey period from March 2015 through May 2016, our camera trap array recorded 3204 independent encounters with wild pigs which included 4556 sightings of individual adults and 648 sightings of piglets and subadults. Of those adult encounters, 2545 individuals were sighted with their left flanks oriented to the camera. Of those left flank sightings, 2152 (84.6%) met all our standards for image quality and were considered eligible for mark-resight analysis. During this period, catalogue profiles were established, and capture histories were recorded 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 a total of 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 number 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 over 80% of marked individuals identified within the first two seasonal sampling intervals (Figure 4).

Model selection results based on AICc values of the 10 mark-resight estimators used in this study are reported in table 1. For the top three ranked models that fell within our delta cut-off value of ≤ 2, their relative weights indicate there is minimal evidence to support any one above the others. To account for this, we selected a model averaging approach based on the results of these three models to estimate absolute abundance $\bar{\hat{N}}$, standard deviation and 95% confidence across our five seasonal sampling intervals (Figure 5). Within each of these top three ranked models, seasonal sampling interval (time) was associated with α, while flank-distinctiveness was only included in the third, and least parsimonious model used for averaging. Overall mean resighting rates (λ) were estimated as 2.513 (SE = 0.519; 95% CI = 1.684-3.751), 1.829 (SE = 0.313; 95% CI =

1.311-2.550), 1.995 (SE = 0.362; 95% CI = 1.315-2.704), 1.272 (SE = 0.284; 95% CI = 0.986-2.195) and 0.934 (SE = 0.257; 95% CI = 0.479-1.492) for seasons 1-5 respectively, while heterogeneity of individual resighting rates (σ) was estimated at 0.949 (SE = 0.084; 95% CI = 0.798 – 1.129).

Individual encounter totals fluctuated significantly across seasonal sampling intervals and declined precipitously between Spring 2015 to Spring 2016. Between these two 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.

DISCUSSION

Abundance Estimates

In this study we demonstrate that natural pelage markings can be used to generate robust estimates of wild pig abundance with reasonably low coefficients of variation. This tool provided the first estimate of wild pig abundance using a standardized methodology to identify and resight individuals from camera trap data alone and the first estimate of their abundance in the Tehachapis. Our results suggest that the Tejon Ranch supports a large population of wild pigs and that this population may be in decline. While seasonal abundance estimates indicate that the wild pig population was in decline across our study area following Summer 2015, these estimates did not reflect the 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 four seasonal sampling intervals, the coefficient of variation(CV) ranged from 17-19%; while in Spring 2016 this measure increased to 27%. 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 use of natural marks around baited camera traps, to improve the accuracy of population estimates, sampling design should seek to maximize individual detections around multiple camera sites. 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.

This lack of precision around abundance estimates, particularly in Spring 2016, suggests that declines in resighting rates might be due to seasonal variation in behavior as opposed to population decline. However, overall mean resighting rates fell from a high of 2.513 (SE = 0.519; 95% CI = 1.684-3.751) in Spring 2015 to a low of 0.934 (SE = 0.257; 95% CI = 0.479-1.492) in Spring 2016, indicating a decline that cannot be completely explained by seasonal variation. Furthermore, there is significant anecdotal evidence that suggests Tejon's wild pig population was in decline during this period, as hunter harvest across the property dropped markedly despite consistent hunter effort (Figure 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, this does suggest a Ranch-wide decline of a population that was, at least recently, well into the thousands of individuals.

Wild pig fecundity and range size are known to vary significantly in response to changes in environmental conditions and resource availability (Bieber and Ruff 2005). 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 Anchukaitus 2014, Espelta et al. 2008). As acorns are a major staple in the diet of wild pigs on Tejon, it is reasonable to assume that this lack of primary production contributed, at least in part, to their population decline during this period (Robeson et al. 2017).

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 2009). As our method relies on a wide range of variable marks to identify individuals, 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 equivalently 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 selected 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 1-3 respectively), suggesting that our covariates (gender and distinctiveness) were not major drivers of resighting probability. Furthermore, the only selected 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 dataset, 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 dataset to higher quality images, observers were able to process photo data more efficiently without having to substantially enhance or cross-refence partially identifiable individuals from poor quality images.

Overall, we prioritized efficiency and conservatism when applying this method to wild pigs on Tejon. 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

This natural mark-resight method, 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 non-invasive alternative to trapping and tagging. Wild pigs on Tejon Ranch provided an excellent opportunity to test the potential of this approach, as wild pig population parameters are notoriously difficult to estimate, particularly across densely vegetated and topographically dynamic landscapes (Ebert 2009). This 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. As this method relies solely on data generated from camera traps and requires minimal fieldwork consisting only of camera trap installation and routine maintenance, it can be implemented across landscapes that would otherwise be economically or logistically impractical to survey. It required 8-10 field days a month for a technician to maintain our 48-camera survey grid, while a single trained observer could process an entire month's survey data in a period of 6 to 8 hours. We believe these survey implementation and data processing requirements compare favorably with other field monitoring techniques currently used to survey wildlife populations in remote settings. 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.

REFERENCES

1. Acevedo, P., J. Vicente, U. Höfle, J. Cassinello, F. Ruiz-Fons, and C. Gortazar. 2007. Estimation of European wild boar relative abundance and aggregation: A novel method in epidemiological risk assessment. Epidemiology and Infection 135:519–527.

2. Alonso, R. S., B. T. McClintock, L. M. Lyren, E. E. Boydston, and K. R. Crooks. 2015. Mark-recapture and mark-resight methods for estimating abundance with remote cameras: A carnivore case study. PLoS ONE 10:1–13.

3. Andrzejewski, R., and W. Jezierski. 1978. Management of a Wild Boar Population and its Effects on Commercial Land. Acta Theriologica 23:309–339.

4. Babber, D., and B. E. Coblentz. 1986. Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina island. Journal of Mammalogy 67:512–525.

5. Berger, J. O. 2006. Bayes Factors. Encyclopedia of Statistical Sciences 90:773–795.

6. Bieber, C., and T. Ruf. 2005. Population dynamics in wild boar Sus scrofa: Ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. Journal of Applied Ecology 42:1203–1213.

7. Chen, P., Y. Gao, J. Wang, Q. Pu, C. Lhaba, H. Hu, J. Xu, and K. Shi. 2016. Status and conservation of the Endangered snow leopard Panthera uncia in Qomolangma National Nature Reserve, Tibet. Oryx 51:1–4.

8. Conservancy, T. R., K. Kunkel, M. Thinking, C. Science, and G. Gateway. 2013. Tejon Ranch Wildlife Assessment and Recommendations.

9. Cooke, J. G., D. W. Weller, A. L. Bradford, A. M. Burdin, and R. L. Brownell. 2006. Population assessment of Western Gray Whales in 2006. Presented to the International Whaling Commission Scientific Committee SC/58/BRG3:1–10.

10. Corlatti, L., A. Gugiatti, and L. Pedrotti. 2016. Spring spotlight counts provide reliable indices to track changes in population size of mountain-dwelling red deer *Cervus elaphus*. Wildlife Biology 22:268–276.

11. Diamond, H. J., T. R. Karl, M. A. Palecki, C. B. Baker, J. E. Bell, R. D. Leeper, D. R. Easterling, J. H. Lawrimore, T. P. Meyers, M. R. Helfert, G. Goodge, and P. W. Thorne. 2013. U.S. climate reference network after one decade of operations status and assessment. Bulletin of the American Meteorological Society 94:485–498.

12. Ebert, C., D. Huckschlag, H. K. Schulz, and U. Hohmann. 2010. Can hair traps sample wild boar (Sus scrofa) randomly for the purpose of non-invasive population estimation? European Journal of Wildlife Research 56:583–590.

13. Ebert, C., F. Knauer, B. Spielberger, B. Thiele, and U. Hohmann. 2012. Estimating wild boar *Sus scrofa* population size using faecal DNA and capture-recapture modelling. Wildlife Biology 18:142–152.

14. Ebert, C., F. Knauer, I. Storch, and U. Hohmann. 2010. Individual heterogeneity as a pitfall in population estimates based on non-invasive genetic sampling: a review and recommendations. Wildlife Biology 16:225–240.

15. Griffin, D., and K. J. Anchukaitis. 2014. How unusual is the 2012 – 2014 California drought? Geophysical Research Letters 41:9017–9023.

16. Jackson, R. M., J. D. Roe, R. Wangchuk, and D. Hunter. 2006. Estimating Snow Leopard Population Abundance Using Photography and Capture – Recapture Techniques Estimating Snow Leopard Population Abundance Using Photography and Capture – Recapture Techniques. Wildlife Society Bulletin 34:772–781.

17. Karanth, K. U. 1995. Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. Biological Conservation 71:333–338.

18. Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, and Y. E. Di Blanco. 2008. Estimating Puma Densities from Camera Trapping across Three Study Sites: Bolivia, Argentina, and Belize. Journal of Mammalogy 89:408–418.

19. Lewis, J., and S. Vandewoude. 2015. THE EFFECTS OF URBANIZATION ON POPULATION DENSITY, OCCUPANCY, AND RESIGHTING PROBABILITY OF WILD FELIDS The effects of urbanization on population density, occupancy, and resighting probability of wild felids. 25:1880–1895.

20. Maria, J., P. Cortés, R. Molowny-horas, B. Sánchez-, and J. Retana. 2018. Masting Mediated by Summer Drought Reduces Acorn Predation in Mediterranean Oak Forests Published by: Wiley on behalf of the Ecological Society of America Stable 89:805–817.

21. Mayer, John, and Brisbin, I. Lehr. Wild Pigs: Biology, Damage, Control Techniques and Management. United States: N. p., 2009.

22. Mcclintock, B. T., J. M. Hill, L. Fritz, K. Chumbley, K. Luxa, and D. R. Diefenbach. 2014. Mark-resight abundance estimation under incomplete identification of marked individuals. Methods in Ecology and Evolution 5:1294–1304.

23. McClintock, B. T., and G. C. White. 2012. From NOREMARK to MARK: Software for estimating demographic parameters using mark-resight methodology. Journal of Ornithology 152:641–650.

24. McClintock, B. T., G. C. White, M. F. Antolin, and D. W. Tripp. 2009. Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. Biometrics 65:237–246.

25. Negrões, N., P. Sarmento, J. Cruz, C. Eira, E. Revilla, C. Fonseca, R. Sollmann, N. M. Tôrres, M. M. Furtado, A. T. A. Jácomo, and L. Silveira. 2010. Use of Camera-Trapping to Estimate Puma Density and Influencing Factors in Central Brazil. Journal of Wildlife Management 74:1195–1203.

26. O'Brien, T. G., M. F. Kinnaird, and H. T. Wibisono. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6:131–139.

27. Petit, E., and N. Valiere. 2006. Estimating Population Size with Noninvasive\nCapture-Mark-Recapture Data. Conservation Biology Volume 20: 62–1073.

28. Pimental, D. 2007. Environmental and Economic Costs of Vertebrate Species Invasions into the United States. Managing Vertebrate Invasive Species 1–8.

29. Silveira, L., A. T. A. Jácomo, and J. A. F. Diniz-Filho. 2003. Camera trap, line transect census and track surveys: A comparative evaluation. Biological Conservation 114:351–355.

30. Kenneth P . Burnham , David R . Anderson and Jeffrey L . Laake. 2018. Efficiency and Bias in Strip and Line Transect Sampling. Wiley on behalf of the Wildlife Society Stable. 49:1012–1018.

31. Sweitzer, R. A., D. Van Vuren, I. A. Gardner, W. M. Boyce, and J. D. Waithman. 2000. Estimating Sizes of Wild Pig Populations in the North and Central Coast Regions of California. The Journal of Wildlife Management 64:531.

32. Taylor, W. P. 1943. the Wildlife Society. Science (New York, N.Y.) 98:185–188.

33. USDA-APHIS. 2015. Final Environmental Impact Statement. A National Approach. 524.

34. White, G. C., and K. P. Burnham. 1999. Program mark: Survival estimation from populations of marked animals. Bird Study 46:S120–S139.

35. Zero, V. H., S. R. Sundaresan, T. G. O'Brien, and M. F. Kinnaird. 2013. Monitoring an Endangered savannah ungulate, Grevy's zebra Equus grevyi: Choosing a method for estimating population densities. Oryx 47:410–419.

36. Zheng, X., M. A. Owen, Y. Nie, Y. Hu, R. R. Swaisgood, L. Yan, and F. Wei. 2016. Individual identification of wild giant pandas from camera trap photos – a systematic and hierarchical approach. Journal of Zoology 300:247–256.

Table 1**:** Model selection results from ZPNE mark-resight models used for population estimation of invasive wild pigs on Tejon Ranch. Models used data collected from camera trap photos of naturally marked and unmarked wild pigs occurring across a 48km^2 survey grid from March 2015 through May 2016. The table reports values of Akaike's information criterion corrected for small sample size (AICc), differences in AICc (ΔAICc) between each model and the model with the lowest AICc, the Akaike's weights (Weight) and number of parameters (Num. pars.). Models selected for averaging are in bold.

Model	AICc	ΔAICc	Weight	Num. Pars.
α (season + sex) σ (.) U (season) γ' (.) γ"(.) φ (.)	**1096.62**	**0.00**	**0.272**	**14**
α (season) σ (.) U (season) γ' (.) γ"(.) φ (.)	**1096.78**	**0.15**	**0.252**	**13**
α (season + sex + LFD) σ (.) U (season) γ' (.) γ"(.) φ (.)	**1098.40**	**1.78**	**0.112**	**15**
α (season + LFD) σ (.) U (season) γ' (.) γ"(.) φ (.)	1098.90	2.28	0.087	14
α (season + sex X LFD) σ (.) U (season) γ' (.) γ"(.) φ (.)	1098.99	2.37	0.083	16
α (.) σ (.) U (season) γ' (.) γ"(.) φ (.)	1099.39	2.76	0.068	9
α (sex) σ (.) U (season) γ' (.) γ"(.) φ (.)	1099.67	3.05	0.059	10
α (sex + LFD) σ (.) U (season) γ' (.) γ"(.) φ (.)	1101.19	4.56	0.028	11
α (LFD) σ (.) U (season) γ' (.) γ"(.) φ (.)	1101.29	4.66	0.026	10
α (sex X LFD) σ (.) U (season) γ' (.) γ"(.) φ (.)	1102.73	6.10	0.013	12

Table 2: Population estimates averaging all models with delta AICc values ≤ 2 (**α (season + sex) σ (.) U (season) γ' (.) γ"(.) φ (.); α (season) σ (.) U (season) γ' (.) γ"(.) φ (.);α (season + sex + LFD) σ (.) U (season) γ' (.) γ"(.) φ (.))** Table reports estimates of superpopulation ($\hat{N}$) across 5 three-month sampling intervals, the standard error of those estimates, the 95% confidence intervals of those estimates and their associated coefficient of variation.

Sampling Interval	N-hat	Standard Error	Lower 95% CI	Upper 95% CI	CV
Spring2015	204	39	141	295	0.19
Summer2015	352	56	258	479	0.16
Fall2015	296	49	212	408	0.17
Winter2015	178	34	122	256	0.19
Spring2018	157	43	92	264	0.27

Figure 1: Map of survey grid within Tejon Ranch in the Tehachapi Mountains of California. Each 1x1 kilometer grid cell contained one camera station collecting mark-resight data for invasive wild pig population estimation.

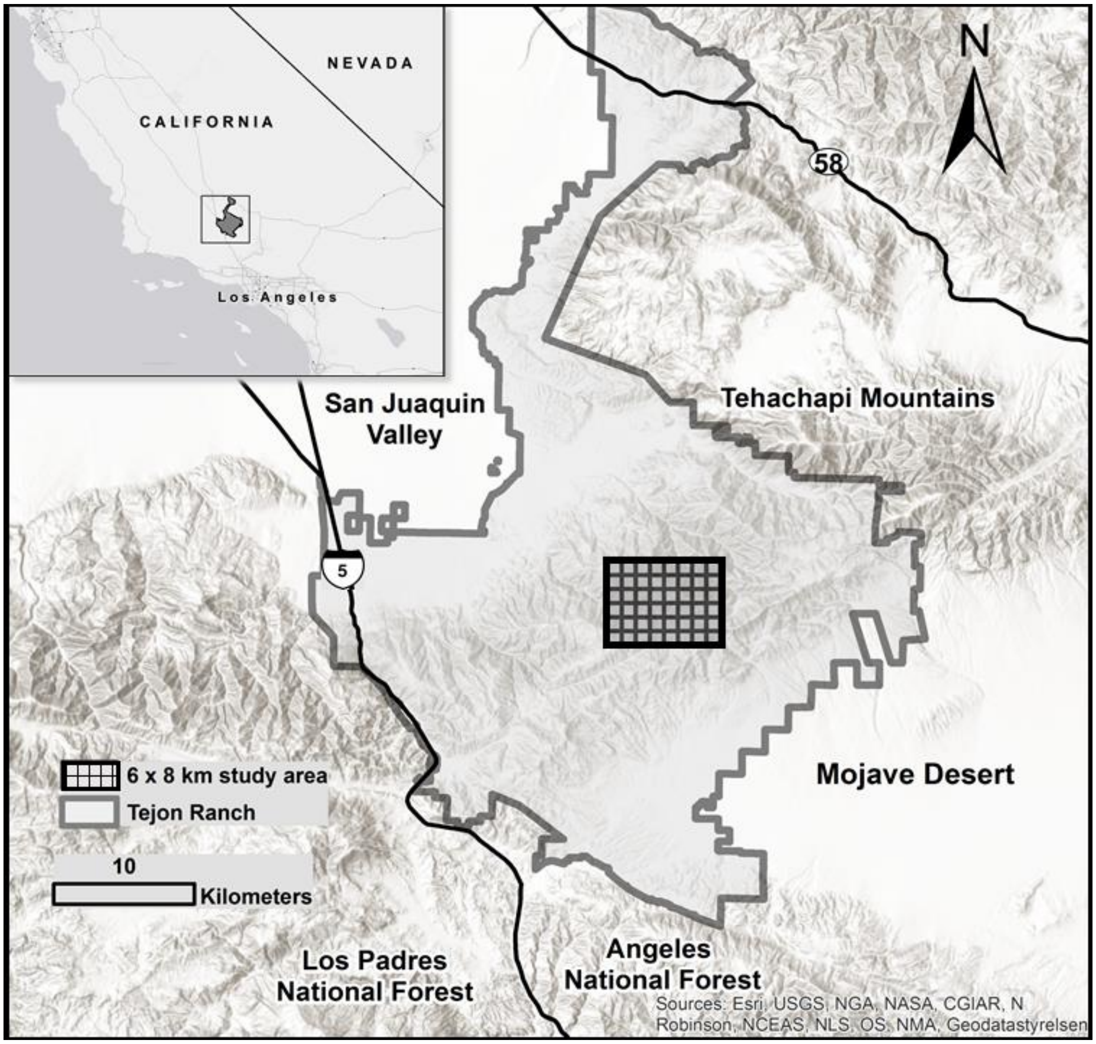

Figure 2: Photos A-D were used to identify and resight wild pig M02 over a period of nine months across multiple camera stations within our survey grid on Tejon Ranch. Photo A represents a high-quality image containing all six parameters that contribute to image quality. Images of this quality should 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 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 as this image is of inadequate quality to (hypothetically) identify all individuals included in our mark-resight catalogue.

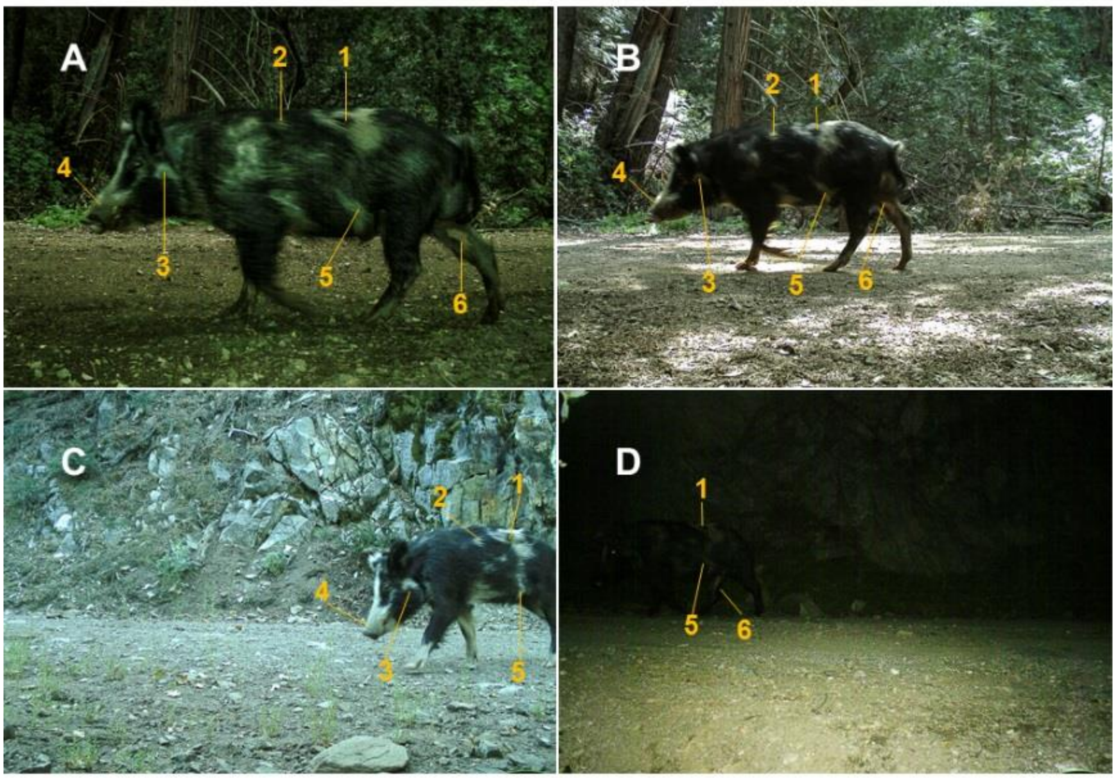

Figure 3: Variable levels of flank distinctiveness standardized as an ordinal covariate for analysis. Distinctiveness values (DV) are based on broad categories of appearance based on the relative visibility, uniqueness and permanence of marks used to identify individuals. Based on our intentionally conservative standard, only individuals above DV2 were considered marked and included in the PID catalogue.

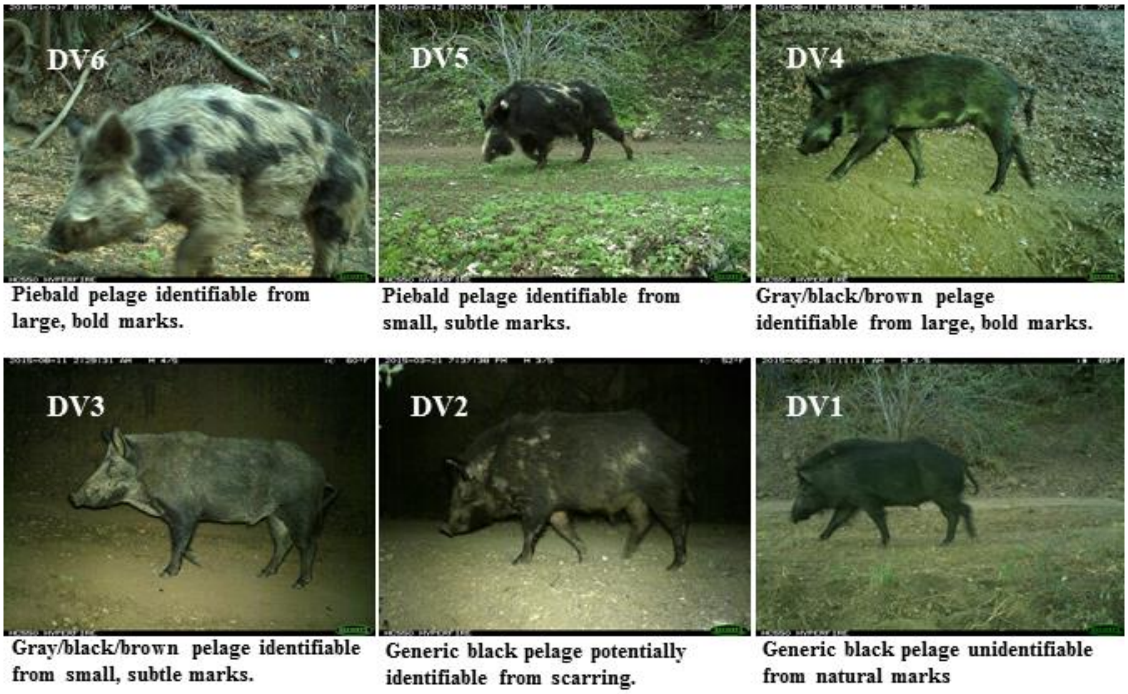

Figure 4: Discovery curve of newly identified wild pigs during five consecutive seasonal sampling intervals across our 48 km^2 survey grid on Tejon Ranch.

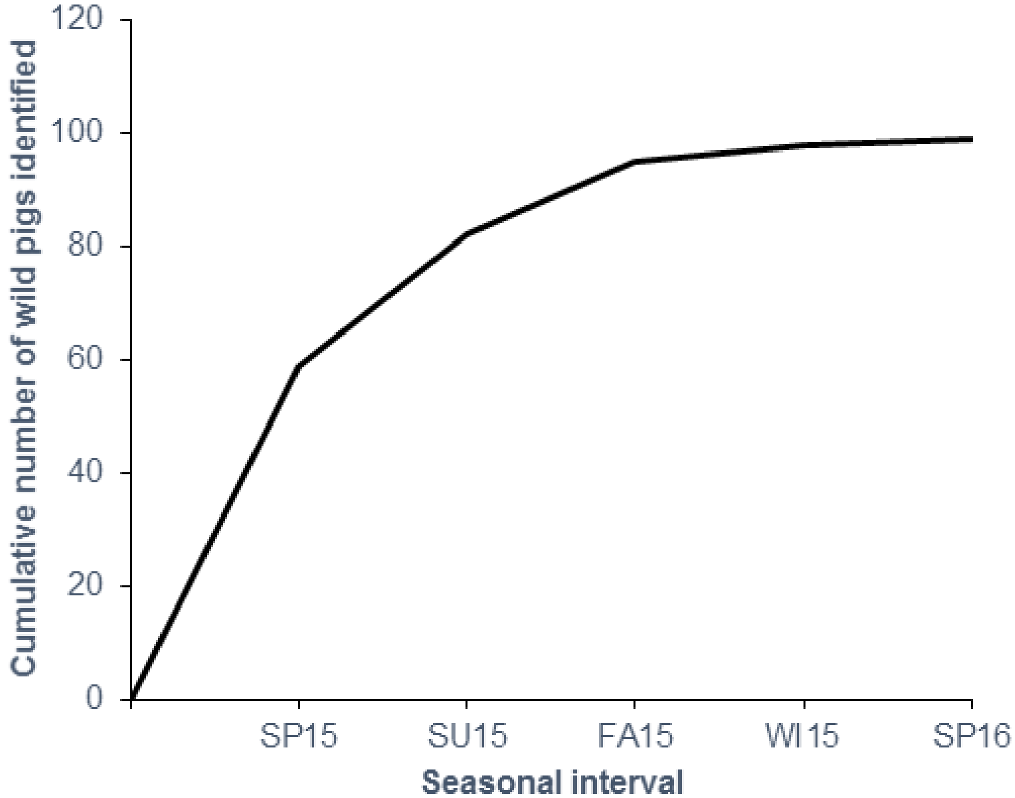

Figure 5: Comparing estimators and indices of wild pig abundance across Tejon Ranch. Mark-resight estimates (vertical bars represent 95% CI) of wild pig abundance across our 48km^2 survey grid are compared with total wild pig harvest across Tejon Ranch. Data collected across 5 consecutive seasonal sampling 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 AICc 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.