Research Article

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Multi-level movement response of invasive wild pigs (*Sus scrofa*) to removal

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Abstract

BACKGROUND: Lethal removal of invasive species, such as wild pigs (*Sus scrofa*), is often the most efficient approach for reducing their negative impacts. Wild pigs are one of the most widespread and destructive invasive mammals in the USA. Lethal management techniques are a key approach for wild pigs and can alter wild pig spatial behavior, but it is unclear how wild pigs respond to the most common removal technique, trapping. We investigated the spatial behavior of wild pigs following intensive removal of conspecifics *via* trapping at three sites within the Savannah River Site, SC, USA. We evaluated changes in wild pig densities, estimated temporal shifts in home-range properties, and evaluated fine-scale movement responses of wild pigs to removal.

RESULTS: We observed a significant reduction in the density of wild pigs in one site following removal *via* trapping while a qualitative reduction was observed in another site. We found little evidence of shifts in pig home-ranging behavior following removal. However, we did observe a nuanced response in movement behavior of wild pigs to the removal at the scale of the GPS locations (4 h), including increased movement speed and reduced selection for vegetation rich areas.

CONCLUSION: Our work provides a better understanding of the impact of removal *via* trapping on wild pig movement and its implications for management. The lack of shift in home-range characteristics observed illustrates how targeted trapping could be used to provide temporary relief for species sensitive to wild pig consumption such as ground nesting birds or agricultural crops.

Supporting information may be found in the online version of this article.

Keywords: animal movement; GPS telemetry; step-selection functions (SSF); spatially-explicit-capture-recapture (SECR); swine; wild boar

1 INTRODUCTION

Non-native invasive species are a global issue with far reaching impacts to biodiversity, ecosystem health, biosecurity, and commodities.[1,2] Although non-lethal techniques can be effective for controlling some species at localized scales, lethal removal of individuals is the most efficient approach to reduce the negative impact and spread of most invasive pests.[3,4] However, information is lacking on behavioral change of individuals remaining during or after incomplete eradication efforts and how such changes could impact the effectiveness of additional management or monitoring activities. Remaining individuals may redistribute themselves within the area according to resource availability (*i.e.* as predicted from the ideal-free distribution theory).[5] Alternatively, for territorial species the repopulation of areas where control has occurred could be largely influenced by the number or characteristics (*e.g.*, dominance status) of individuals remaining in and/or recolonizing the area (*i.e.* ideal despotic distribution).[6] For example, whether dominant or sub-dominant animals were removed could influence how quickly the area is repopulated. These interactions might be further influenced by the social structure of the population, particularly if remnant group members are able to maintain territories and dampen colonization or if individuals are more tolerant of colonization by some conspecifics than

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others, or with remaining individuals actively seeking conspecifics.[7]

Removal efforts can also alter animal behavior by eliciting behaviors to reduce the risk of being 'removed', akin to antipredator behavioral responses.[8] Numerous studies have shown that animals can adjust their behavior in response to risk from humans across a range of circumstances including seasonal hunting,[9] poaching,[10] and targeted removal programs.[7,11] While the range of these antipredator behavioral responses is well documented, the cues animals use to assess risk are more ambiguous.[12] Especially lacking is an understanding of how invaders respond to and assess a new or sporadic source of risk (such as a removal program) spatially, and the temporal scale of the response following the disappearance of the threat. Some animals are not affected by risk, some adjust behaviors to the current and immediate risk without being affected by its magnitude,[13] while others use cognition including memory and learning to adjust their behavior based on the extent of their exposure to this novel risk.[14] Altogether, the consequences of removal on the behavior of remaining individuals is difficult to predict, yet critical to evaluating removal effectiveness.

Wild pigs (*Sus scrofa*) have established invasive populations throughout much of their introduced range (*e.g.*, Australia, North America) through a combination of intentional introductions, escapes, and natural expansion, and removal is a key management strategy used to reduce the detrimental effects of wild pigs on property, livestock, sensitive habitats, and native species.[15] Complete removal of wild pig populations is extremely challenging due to their high reproductive potential, cryptic nature, and recreational and economic value.[16–18] The reality is that in most invasive species management situations a portion of the population survives eradication programs[19,20] and it is unclear how wild pigs respond spatially and temporally to variation in removal risk. Wild pig spatial behavior is sensitive to changes in forage availability,[21] and vacant niche space created by removals can cause remaining animals to shift home ranges towards high quality resources.[22] Intrusive lethal management techniques (*e.g.*, aerial gunning, drive hunts, hunting with dogs) have been shown to cause short-term increases in movement and shifts in wild pig home ranges,[11,23,24] but, to our knowledge, changes in spatial behavior have not been assessed during and following the most common removal technique, trapping.[16]

We investigated the spatial behavior of wild pigs in response to removal of conspecifics at three sites that varied in terms of resource richness within the Savannah River Site (SRS), SC, USA. Using camera traps and GPS collars, we evaluated how wild pig abundance and space use varied before, during, and after removal programs at different spatial scales by monitoring changes in density, home range characteristics, and fine-scale resource selection estimated from mechanistic movement models. In doing so, we also evaluated what cues or proxies of removal risk wild pigs potentially responded to (*i.e.* current risk, cumulative risk on the landscape, or cumulative exposure to risk from the individual perspective). We expected removal programs to create vacant niche space resulting in increased home range sizes or shifts towards removal areas at varying temporal scales. Similarly, we expected wild pigs to adjust fine-scale movement in response to the cumulative risk on the landscape (*i.e.* how many wild pigs were removed in an area) and to have biased movement towards lower density areas post removal (including areas of removal). Overall, our work provides a multi-scale understanding of the impact of trapping on wild pig movement and offers insights into the cognitive processes at play in their behavioral response.

2 MATERIALS AND METHODS

2.1 Study area

We conducted this study at the SRS, a US Department of Energy facility located near Aiken, South Carolina (33.344088, −81.741207, elevation 20–130 m). The SRS is a 780-km^2 (Fig. 1 (a)) limited-access nuclear production and research facility owned and operated by the U.S. Department of Energy. The climate of the SRS is classified as humid subtropical with precipitation distributed evenly throughout the year and averaging approximately 1200 mm annually. Average temperatures range from 26.7 °C in July to 1.7 °C in January.[25] The SRS is primarily composed of upland pine forest interspersed with riparian bottomland hardwood and swamp.[25] We monitored wild pigs at three areas within the SRS including the 12-km^2 Three Rivers Solid Waste Authority Regional Landfill (hereafter referred to as the landfill) where the active landfill is unfenced and thus used extensively by wild pigs (Fig. 1(b)). The two other study areas, referred to as natural areas 1 and 2 (Fig. 1(c) and 1(d)), had reduced anthropogenic impacts compared to the landfill site, with no supplemental food resources.

We captured wild pigs in the area surrounding the landfill from November 2015 through February 2016, from January through March 2016 at natural area 1, and from February through May 2017 at natural area 2 (Fig. 2) using a combination of corral traps and remote chemical immobilization over bait piles. For both trapping and darting, wild pigs were immobilized using a combination of Telazol® (4.4 mg/kg; MWI Veterinary Supply, ID) and Xylazine (2.2 mg/kg; Wildlife Pharmaceuticals Inc., CO). We marked wild pigs with individually numbered ear tags (Y-Tex, Cody, WY) and attached GPS collars (Lotek Globalstar or LiteTrack, Newmarket, Ontario, Canada; Telonics TGW4501 and TGW4600, Mesa, AZ, USA). Globalstar and Telonics collars were programed to take a location every 1 or 2 h. LiteTrack collars recorded a location every 4 h and were programed to automatically release after 6 months. We designed trapping protocols to capture family groups, which are primarily composed of adult females and their dependent offspring. We deployed multiple collars within some groups (range = 1–3 collars/group, average = 1.7). Females were also captured and collared *via* darting over bait piles where trapping proved ineffective. We also collared adult males opportunistically when captured with female groups. Capture and handling procedures were approved by the University of Georgia's Institutional Animal Care and Use Committee (IACUC approval # A2015 05-004-Y3-A5). The analysis at the National Wildlife Research Center was done under quality assurance protocol number 2253.

Collared wild pigs were monitored for approximately 2–7 months prior to removal efforts to establish baseline information on local density and space use. Based on the distribution of collared wild pigs, we subsequently conducted wild pig removal programs at the landfill, natural area 1, and natural area 2, (Fig. 2). We concentrated removals within the central areas of each study site to maximize the number of collared wild pigs whose home ranges intersected with the removal area. Wild pigs were removed from an area of approximately 0.5 km^2 at the landfill, from an area of approximately 2.1 km^2 at natural area 1, and from an area of approximately 9 km^2 at natural area 2 (Fig. 1) using a combination of trapping and the opportunistic shooting of individuals as they traveled to the landfill. We euthanized all wild pigs

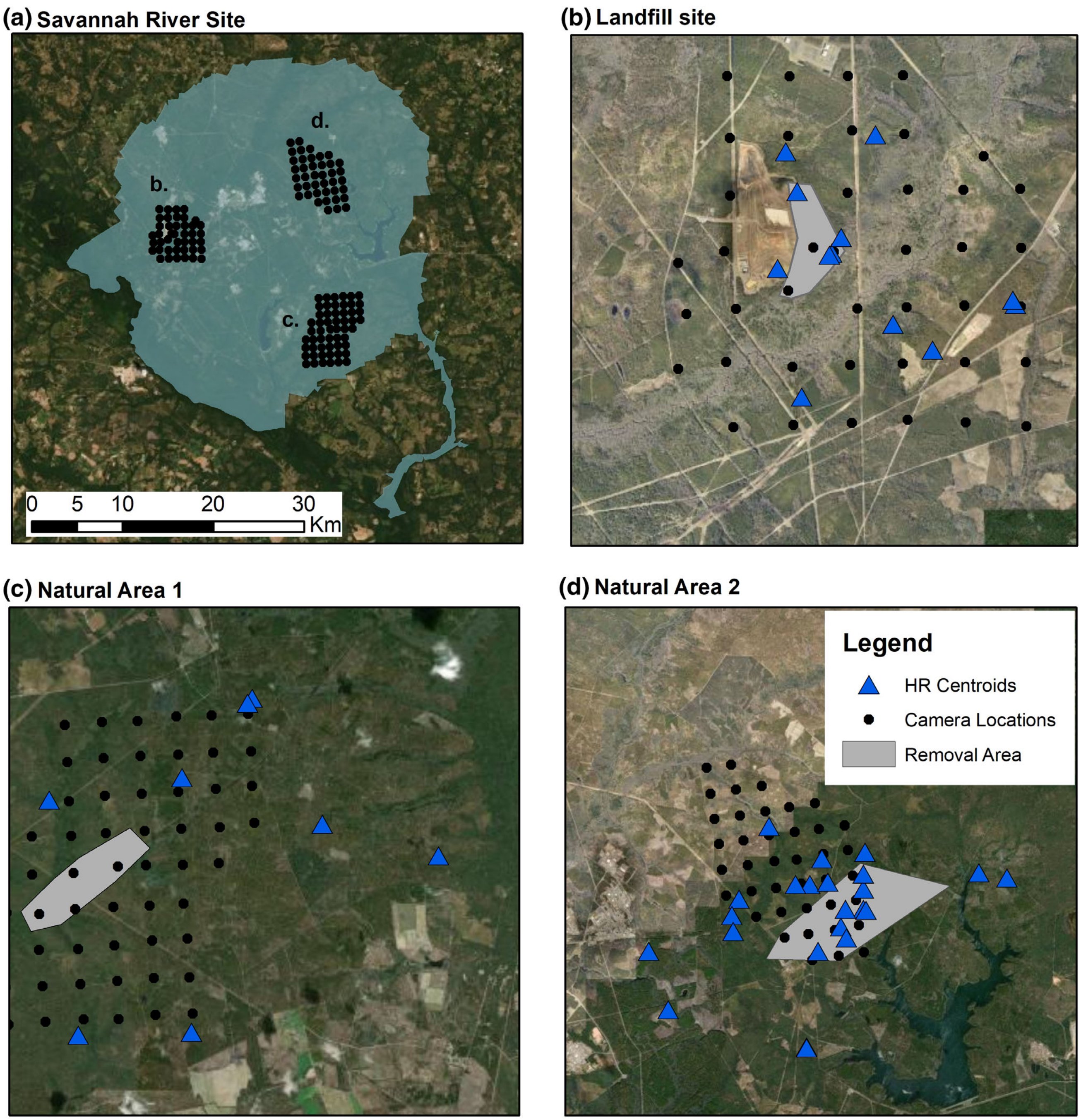

Figure 1. Location of baited camera grids within the Savannah River Site, SC (a). We placed cameras at the Landfill (b) and Natural Area 1 (c) before (Landfill = March 2016; Natural Area 1 = April 2016) and after (Landfill = August 2016; Natural Area 1 = September 2016) removal programs. We also placed cameras before (December 2016) removal programs at Natural Area 2. We set cameras approximately 750 m (b and c) or 1000 m (d) apart in areas expected to maximize the likelihood of detecting wild pigs. For each study site (b–d), we also indicate home-range centroids of wild pigs tracked using GPS telemetry relative to removal areas.

caught in traps, including collared individuals *via* gunshot to the head.

Camera traps were deployed for 10-day periods before and after removal efforts at the landfill (11 March 2016–2021 March 2016 and 3 August 2016-8-13/2016) and natural area 1 (8 April 2016–2018 April 2016 and 9 September 2016–2019 September 2016), and before the removal program at natural area 2 (4 December 2016–2114 December 2016). At all sites we deployed an array of motion-activated white-flash cameras (RECONYX, Holmen, WI) programmed to take a burst of three photos followed by a 1 min quiet period when triggered. At the landfill (n = 42) and natural area 1 (n = 54), camera locations were based on a predetermined grid with 750 m spacing (Fig. 1(b) and (c)); cameras were placed within 75 m of grid locations in areas expected to maximize detection of pigs (*i.e.* near trails or fresh wild pig sign). A similar grid (n = 41) was placed at natural area 2 (Fig. 1(d).) with the cameras placed within 100 m of a predetermined 1,000 m grid. At all sites, cameras were placed on trees or

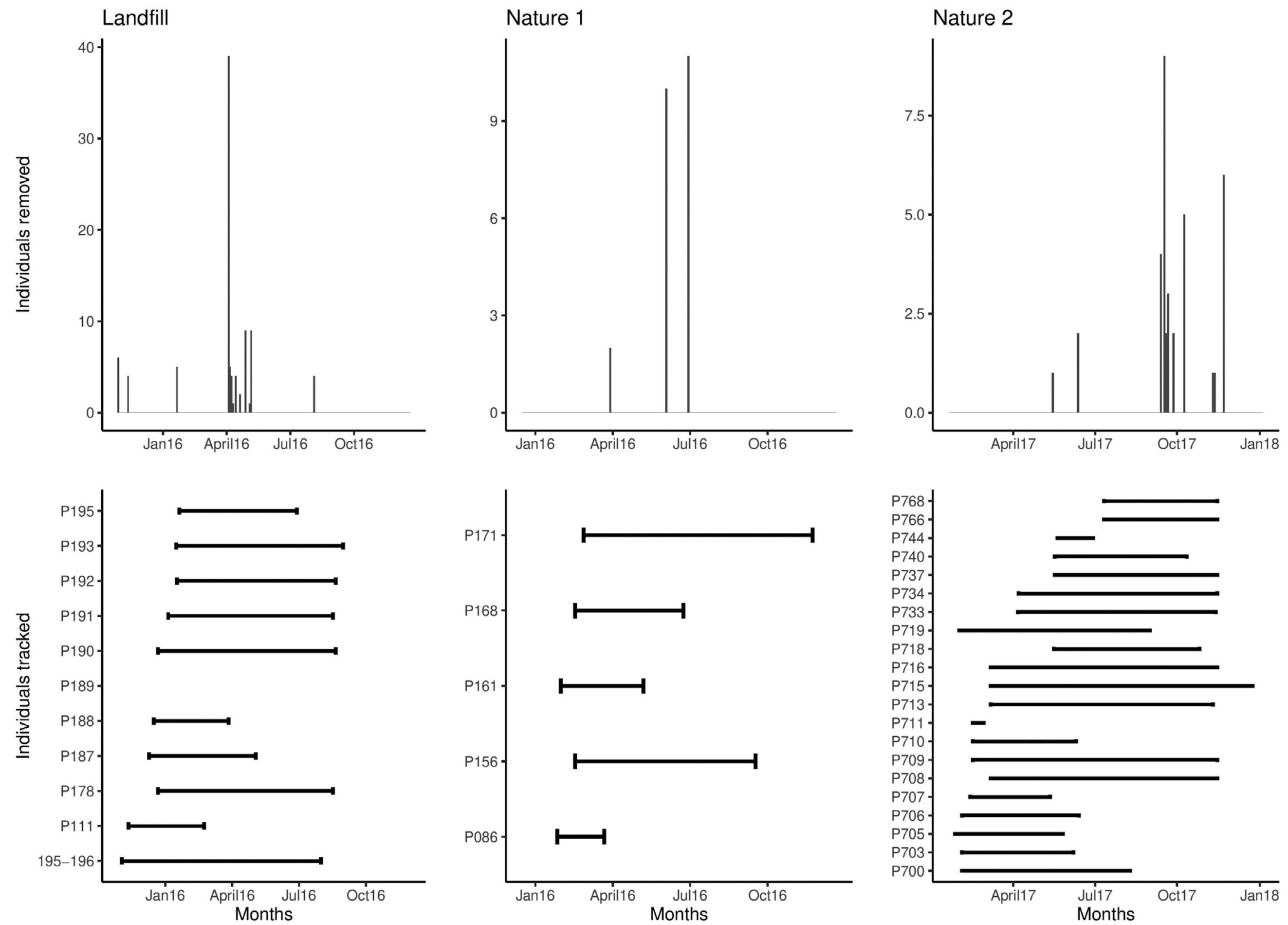

Figure 2. Number of wild pigs removed per day (top row) and duration of monitoring for pigs tracked with GPS collars (bottom row) in three sites within the Savannah River Site, SC.

steel t-posts approximately 1 m off the ground and directed at 12 kg of whole kernel corn placed on the ground 3–4 m away on the same day. Revisits by wild pigs were encouraged by the additional placement of 12 kg of corn on day 5. Although randomly placed cameras may be a less biased way to monitor wildlife,[26,27] our study design increased the likelihood of repeated detections of individuals within the 10-day sampling window allowing for density estimates.[28]

2.2 Statistical analyses

2.2.1 Spatially-explicit capture-recapture

We compared wild pig density before and after removal using spatially-explicit capture-recapture models (SECR) with an unknown number of marked individuals. We defined independent detections of wild pigs as visits to camera sites with a minimum 4 h quiet period. At the SRS, a large portion of wild pigs had distinct black and white spotted pelage and many red /brown individuals with distinct black spotting. We used a combination of natural marks and ear tags to individually identify the majority of wild pigs within detections. We estimated density before and after removal at the landfill and natural area 1 and before removal at natural area 2. Wild pigs were classified into three age groups from camera trap images based on body size, body shape, and the presence of natal stripping patterns. Piglets were < 10 kg with little to no body fat, commonly had prominent natal stripping, and traveled exclusively with their natal group. Juveniles did not display sexual dimorphism, and were still detected with their natal family group, but could travel independently for extended periods of time. Adults were any individuals estimated to be >35 kg and had the potential to be reproductively active. Piglets were not included in the analyses since they are not independent from adult pigs.[29] Model selection based on Akaike information criteria (AIC)[30] and plots of effective sampling area were used to select the best detection function (and buffer distance) and AIC model selection was also used to evaluate if density and/or detection probability was influenced by age and sex. This analysis was performed using package 'secr'[31] in Program R.[32]

2.2.2 Home-range characteristics

To evaluate the effect of a removal event on wild pig broad-scale space use, we estimated home ranges properties pre-, during, and post-removal at the landfill site. We focus on the landfill site as it was the site with the longest duration of monitoring prior to and following the removal. The amount of available GPS data varied among individuals based on capture date and when collars were released. We excluded individuals with <45 days of monitoring before and after the removal period, respectively. Using a 7-day moving window, we created kernel density home ranges[33] at a 95% contour level using package adehabitatHR[34] in program R.[32] Moving window home ranges incorporated each day as well as the 3 days before and after. From these home ranges we calculated home range size (km^2) and the Euclidean distance from the home range centroid to the removal area. In addition, we estimated the volume of intersection (VI)[35] between all pre-removal locations and 7-day home ranges during and post-removal period to detect expansion of home ranges into previously unoccupied space.

We fitted a piecewise generalized least square (GLS) regression to detect continuous breaks in time-series of home-range size, distance to removal area, and volume of intersection for each individual.[36] We used GLS to account for temporal autocorrelation by adding a first-order auto-regressive correlation matrix (AR1).[37] We compared the piecewise regression with an intercept-only GLS and a constant-slope GLS using a likelihood ratio-test.[38] When a significant break was detected during or shortly following the period of removal (removal happened during days 95–121), we evaluated the direction of changes in the trends. A break detected during the removal or shortly following the removal period was considered an indication that the removal impacted home-ranging behavior for that individual. These analyses were conducted using the package 'nlme'.

2.2.3 Step-selection functions

We evaluated fine-scale (at the scale of the movement location) response of wild pig fitted with GPS collars to localized removal of conspecifics. We used step-selection functions (SSFs)[39] to evaluate the influence of pig removal on fine-scale habitat selection and movement. SSFs use conditional logistic regression to compare attributes associated with observed movement steps to potential, randomly generated, movement steps an individual could have performed. We generated 50 random steps for every observed step based on a gamma distribution for step length and a uniform distribution for turning angles.[40] We evaluated the influence of elevation (acquired from the Shuttle radar topography mission, SRTM), 16-day Normalized Vegetation Difference Index (NDVI; acquired from the Modis Terra satellite), and land-cover (acquired from the USDA cropland data layer) that we reclassified into five categories (crops, barren, forest, shrubs, and wetland [reference category]). Speed (step length) and turning angles were also included as covariates. All layers were acquired using Google Earth Engine.

We measured the effects of spatio-temporal removal strength by including three additional covariates representing measures of risk: instantaneous strength on the landscape, cumulative strength on the landscape, and individual-level cumulative strength (exposure). Location and timing of removed pigs were used to generate a daily spatio-temporal kernel representing the magnitude of removal in space and time. This variable represents a time-specific removal strength and thus tests the effects of instantaneous removal intensity on movement behavior. By combining all removal strength surfaces, we derived the cumulative removal strength surface for the study area. This was done by adding all previous temporal snapshots of the spatio-temporal kernel for each specific date to obtain the cumulative snapshots for each date. Lastly, we evaluated the individual-level cumulative strength or cumulative exposure to removal experienced by individual pigs by adding the current removal strength over time based on the locations visited by the pigs. To simplify interpretation, account for potential non-linearity in response, and improve interpretability of model averaging among individuals (see below), we categorized each measurement of removal strength into three categories (low, medium, high). The 'low' category represents values associated with null removal strength or exposure (whether current or cumulative). The 'high' category contained values that were above the mean strength or exposure (whether current or cumulative). The 'medium' category contained values not included in low and high categories. The distribution of each variable associated with removal were heavily right-skewed, leading to the high category having the least entries. We tested for interactions between time-specific and cumulative removal strength and cumulative exposure and other covariates using model selection based on AIC. We also tested for an interaction between cumulative exposure and current removal strength to test for a potentially learned response.

Only individuals overlapping temporally with periods of removal in each study site were kept for the step-selection function analysis. All continuous covariates were centered and scaled (by dividing by one standard deviation) to facilitate interpretability.[41] Given possible variation among individuals in selection and movement, we performed conditional logistic regression separately for each individual to estimate individual-level coefficients[42] that could then be combined into population-level coefficients.[43] We performed model selection at the population level by adding up individual model log-likelihoods[43] and then using AIC.[30] We tested if individual responses (based on coefficients) were different between sexes and among age classes and sites using univariate linear models in which age, sex, or site were a categorical independent variable and each individual coefficient the response variable. Each observation was weighted by the inverse of the squared standard error associated with the coefficient ($1/SE^2$). This part of the analysis was performed using R packages 'MASS', 'survival', 'spatstat', 'sparr', 'hab', and 'indRSA'.

3 RESULTS

During initial trapping efforts, we captured 126 wild pigs across our three study areas. We placed ear tags on all captured wild pigs and fitted 37 juveniles and adults with GPS collars (Table 1), yielding a total of 57 593 locations. A total of 127 wild pigs were euthanized during removal efforts. The landfill sites had the highest number ($n = 76$) of wild pigs removed (14 adults, 58 juveniles, and four piglets; 37 females and 39 males). We removed 21 wild pigs from natural site 1 (six adults and 15 juveniles; 12 females and nine males) and 30 from natural site 2 (13 adults, 11 juveniles, and six piglets; 11 females and 19 males). Of the 37 collared wild pigs, 18 (12 females, five males, and one unknown, see Table 1) had GPS data that overlapped with the removal areas for a minimum of 45 days before and after and were included in fine-scale step selection function analyses. Only wild pigs from the landfill site were included in the home-range analysis.

3.1 Spatially-explicit capture-recapture

We captured 13 750 images of wild pigs and identified 165 juvenile and adult individuals at the landfill, captured 12 086 images of wild pigs and identified 85 juvenile and adult individuals at natural site 1, and captured 5186 images of wild pigs and identified 54 juvenile and adult individuals at natural site 2. For each site, the most supported SECR models used a half-normal discounting function for detection probability, included an age-sex covariate and animal-site effect for detection probability, and age-sex covariate for density. Estimated adult and juvenile density (not including piglets) ranged from 1 pig/km^2 in the two natural sites up to 6 pigs/km^2 in the landfill site (Fig. 3). Density was significantly lower in the landfill site following removal, mostly due to

Table 1. Summary information on pig collaring and removal efforts. Duration of removal and monitoring are given in days. Core removal periods reflect the period when 50% of the pigs were removed. Number of pigs included in each analysis and total number of pigs removed from each study site are also given. For number of pigs collared or included, number of females (F), males (M), adults (A), subadults (S), or unknown (U) were given. Further details about the timing of removal relative to collaring effort are presented in Fig. S2, Supplementary material

Sites (Area)	# Collared Individuals	Duration core removal (90% of individuals removed)	Monitoring prior to core removal (range)	Monitoring after core removal (range in days)	#Included H-R analysis	#Included SSFs analysis	# Removed
Landfill ($21 km^2$)	11 (5FA, 1MA, 4FS, 1 U)	16(190)	103(71, 154)	84.8 (−58, 228	11 (5FA, 1MA, 4FS, 1 U)	7 (3FA, 1MA, 2FS, 1 U)	76
Nature 1 ($98 km^2$)	5 (3 MS, 2 U)	26(87)	113(98, 129)	12.4 (−100, 145	0	0	21
Nature 2 ($137 km^2$)	21 (8FA, 7 MA, 5FS, 1MS)	23(162)	176(67, 233)	−31.7 (−224, 75)	0	11 (5FA, 4MA, 2FS)	30

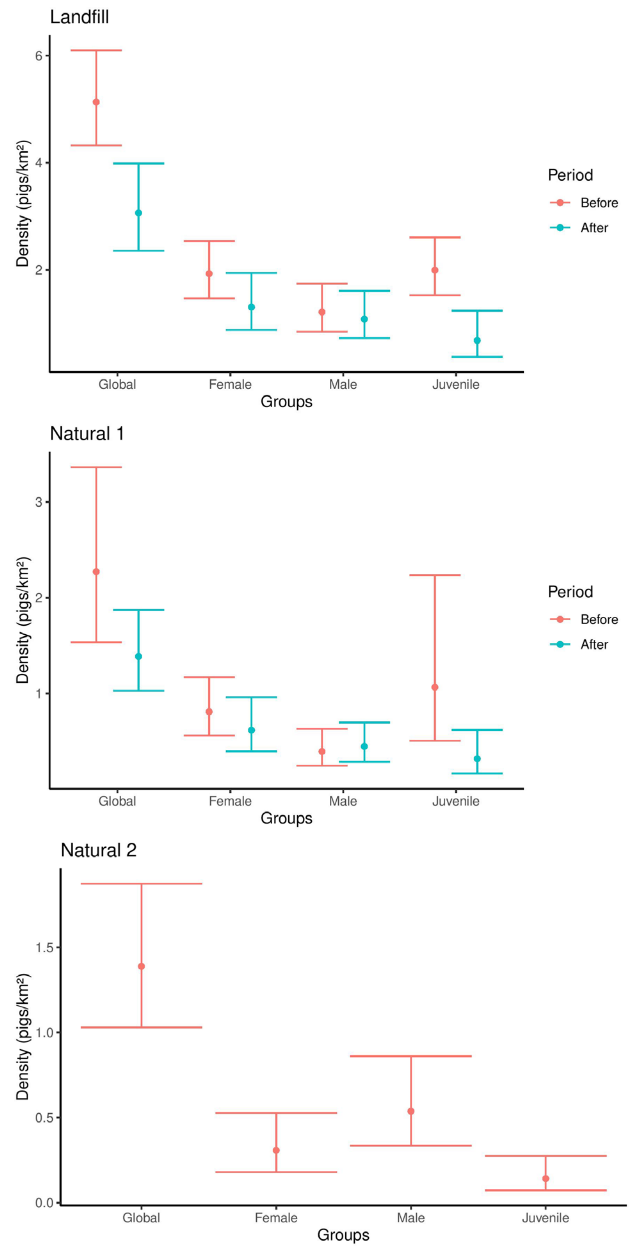

Figure 3. Predicted density (with 95% CI) of feral pigs in three different sites. Density was estimated globally, but also specifically for female, male, and juvenile, before and after the removal of pigs for the landfill and natural area 1. Density was estimated only before for the natural area 2 site. Piglets are not included in the global density estimate.

reduction in juvenile density (Fig. 3). A similar trend was qualitatively observed in the natural area 1, although observed differences were not significant (Fig. 3). The proportion of wild pigs removed varied from a 60% global reduction to a reduction of less than 10% for adults in the landfill and natural area 1.

3.2 Home-range

Weekly variation existed in home-range size but it was not strongly associated with removal or sex (Fig. 4). Two of the individuals closer to the removal (one male and one female) showed a decrease in home-range size following the removal as judged by piecewise regression and two of the female wild pigs that were the farthest from the landfill also had a decrease in their distance

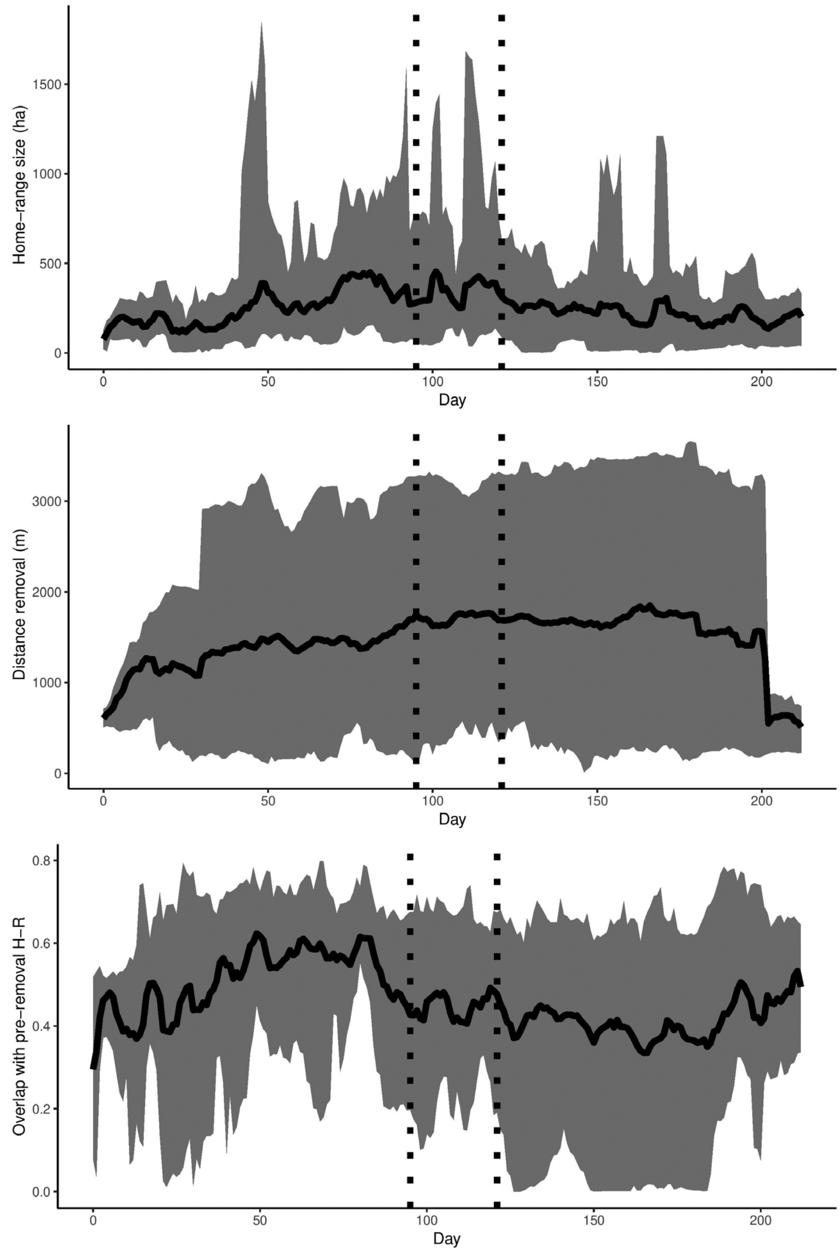

Figure 4. Temporal changes in home-range properties (home-range size, home-range distance to the removal, and home-range overlap with pre-removal home-range) for 11 wild pigs in the landfill site. Dark line represents average among individual pig home-range properties while shaded gray area represents the extent of individual variation. Vertical dashed line represents period of core removal in the landfill site.

to the landfill site following the removal. For all other individuals, the piecewise regression analysis did not detect significant changes associated with the removal period (Table S1).

3.3 Step-selection function

A total of 18 individual wild pigs from the three sites were included in the fine-scale movement analysis for a total of 41 439 locations (range per individual = 120–3236). AIC model selection indicated that an interaction of all covariates with the categorized cumulative exposure to removal covariate offered the best fit (delta AIC > 15 for all other models). Population-level results indicated that when not exposed to any removal wild pigs generally underused crops, forest and shrub areas (relative to selection for wetlands, Table 2). This underuse remained under medium exposure to removals, though wild pigs started moving faster under medium exposure. When reaching higher removal exposure, wild pigs only avoided vegetation-rich areas (based on NDVI), and demonstrated the highest speeds recorded (Table 2). Despite being included in the top model, the cumulative exposure to removal did not influence the selection or avoidance of area with current removal at the population level.

Despite obvious population-level responses for some variables, strong individual variation existed in wild pig response to all covariates (Fig. 5), with some individual wild pigs displaying opposite movement and habitat selection responses relative to the rest of the population. Overall, individual variation was weakly structured by sex (Fig. S1) and age (Fig. S2), with very few covariates showing significant patterns and moderately structured by site with some

Table 2. Population-level coefficients (with 95% CI) evaluating changes in fine-scale selection of 18 feral pigs in response to removal of nearby pigs based on a step-selection function. Coefficients represent the absolute strength of the selection of avoidance of a covariate based on their cumulative level of exposure to the removal (low, medium or high). Coefficients in bold indicate covariates where confidence intervals excluded zero

Cumulative exposure	Covariate	Coefficients
Low (null)	Current removal	NA
	Barren	−0.408 (−0.974, 0.158)
	Crops	**−1.649 (−2.254, −1.045)**
	Speed	0.018 (−0.023, 0.06)
	Elevation	0.263 (−0.001, 0.527)
	Forest	**−0.655 (−0.971, −0.338)**
	NDVI	**0.362 (0.174, 0.551)**
	Shrubs	**−0.417 (−0.672, −0.163)**
Medium	Current removal	0.022 (−0.022, 0.066)
	Barren	**−0.606 (−0.872, −0.34)**
	Crops	**−0.547 (−0.785, −0.31)**
	Speed	**0.08 (0.038, 0.123)**
	Elevation	0.121 (−0.044, 0.287)
	Forest	**−0.454 (−0.614, −0.294)**
	NDVI	−0.02 (−0.157, 0.117)
	Shrubs	**−0.381 (−0.548, −0.214)**
High	Current removal	0.044 (−0.004, 0.091)
	Barren	0.178 (−0.331, 0.687)
	Crops	0.536 (−0.11, 1.181)
	Speed	**0.153 (0.04, 0.266)**
	Elevation	−0.351 (−0.741, 0.038)
	Forest	−0.013 (−0.642, 0.616)
	NDVI	**−0.103 (−0.202, −0.003)**
	Shrubs	0.177 (−0.263, 0.617)

variables showing differences. Male wild pigs avoided areas with higher elevation less strongly than females and moved faster when their cumulative exposure to removal was at a medium level, and female pigs avoided shrub areas more strongly when at high and low cumulative levels of exposure (Fig. S1). Adult wild pigs avoided elevation and crop areas more strongly and moved faster when their cumulative exposure to removal was at a medium level (Fig. S2). At medium exposure, wild pigs in the natural 2 site selected for NDVI more strongly but avoided crops and barren landcover more strongly (Fig. S3). Likewise, at low exposure, wild pigs also avoided barren landcover more strongly, but actually avoided cropland landcover less than in the landfill sites. Pigs also moved faster in the natural 2 site relative to the landfill site when under medium and low exposure (Fig. S3).

4 DISCUSSION

Over the last few decades the ecological and economic impacts of wild pigs have increased substantially across much of their invasive range.[44,45] In response to these impacts, there has been a surge of organized efforts to reduce populations of wild pigs. Throughout North America, trapping is the most widely used approach to control wild pigs,[15] yet there remains a paucity of data on the efficacy of trapping programs and the behavioral response of surviving animals subsequent to removal efforts.[46] Using GPS tracking data, we found limited evidence of substantive shifts in wild pig space use at the home-range level in response to removal efforts. However, we did observe a more nuanced response in the fine-scale movement behavior of wild pigs in response to control efforts, including increased movement speed and a reduction in selection of areas with higher primary productivity (NDVI). Cumulative exposure to the removal (how much an individual has been exposed to removal) seemed to be the best predictor of removal index explored for explaining pig movement. The nuanced response to trapping contrasts with more intrusive forms of removal (aerial gunning, drive hunts, hunting with dogs) where changes in spatial behavior have been observed as a direct response to control efforts.[11,23] Overall, our work provides a better understanding of the impact of removal *via* trapping on pig movement and its implications for management.

4.1 Movement responses

Few individual pigs in the landfill site appeared to modify their home-range size or distance of home ranges to removal areas, either during or following the removal period. While many individuals showed signs of changes in home-range properties, only two individuals had changes that corresponded temporally to the removal period. Vacant niche space created by removals did not elicit changes in the home ranges of adjacent individuals within our monitoring period, even in an area with unnaturally high and concentrated resource availability (*i.e.* the landfill), contrary to previous work.[22] Two factors that may have driven this pattern are (i) the demographic makeup of survivors and (ii) the temporal extent of our monitoring (Fig. 2). Wild pigs are not overtly territorial, yet territorial patterns in space use (mutually exclusive core areas) have been recorded for both males and females.[22,47–49] Across our sites the majority of individuals removed were juveniles, and the density of adult wild pigs did not vary between pre- and post- removal periods. The removal of juveniles may not have influenced the spatial behavior of surrounding individuals if more dominant individuals remained in removal areas, although several adults were also removed from each site. Alternatively, or in conjunction with this effect, it is possible that not enough time elapsed since the removal for individuals to shift their home ranges into newly depopulated areas, as movements and changes in density of wild pigs were monitored for up to 100 days post-control efforts in the landfill site. It is currently unknown for how long removal programs impact local wild pig densities and thus management plans would benefit from a greater understanding of the temporal effectiveness of control programs. While most removal in the landfill site was concentrated over a short window of time, some pigs were also removed before and after this period, which could also influence pig movement behavior.

Despite the general lack of wild pig response to control at the home-range scale in the landfill site, we did observe several notable trends in wild pig movements that suggest individuals likely altered their fine-scale movement behavior in response to the removal of conspecifics. This response appeared to be modulated by the extent of an individual's exposure to the removal risk and also by site (Fig. S3). Increased exposure to risk led to less acute response (weaker avoidance) of specific landcover type including crops, forest, and shrubs. All these landcovers types were strongly underused by pigs not exposed (low) to removal risk while this

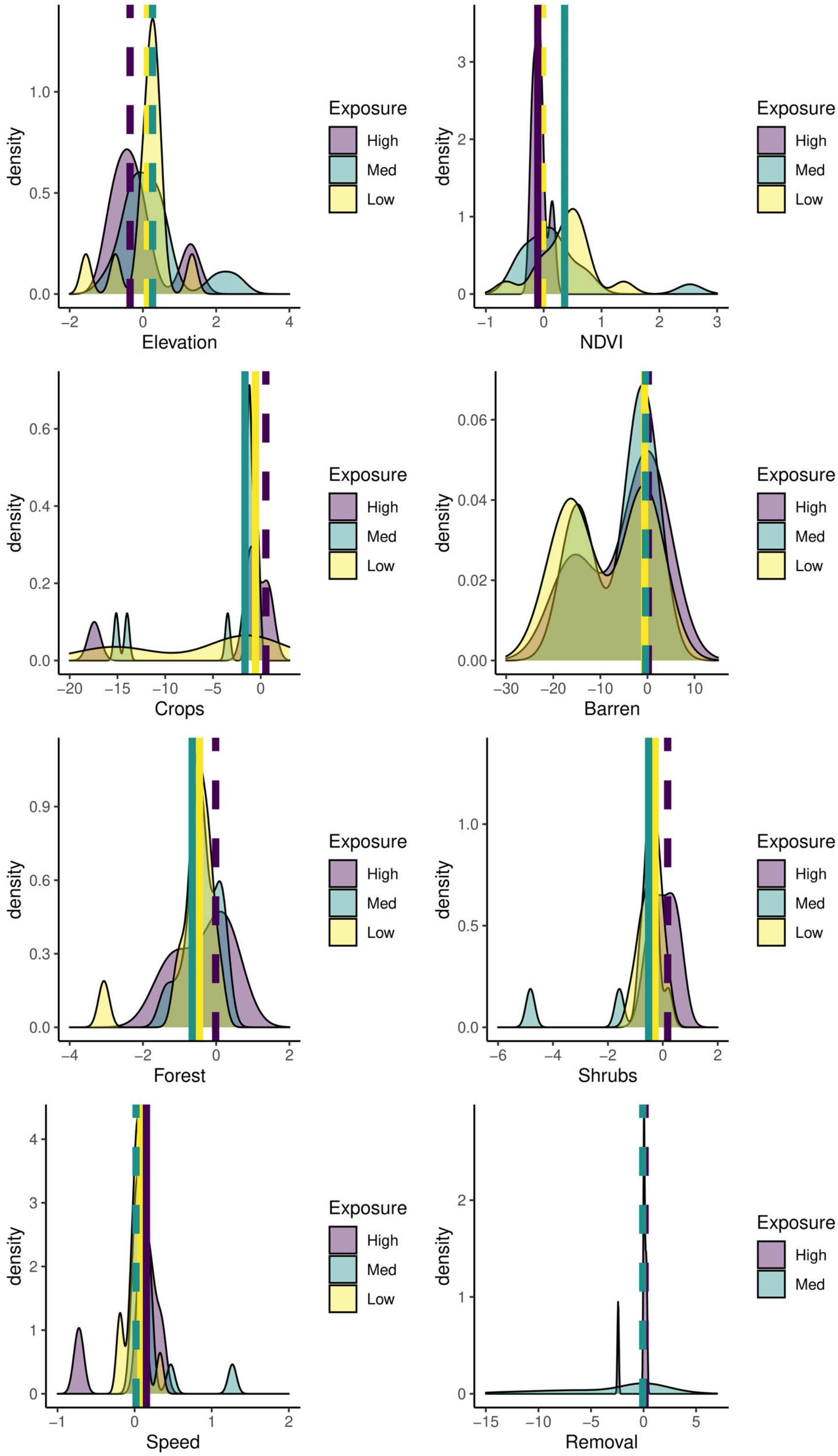

Figure 5. Density plots showing individual variation in individual responses of wild pigs based on a step selection function. Color-coding indicates coefficients for the response based on the cumulative level of exposure of pigs to removal. Matching colored vertical solid lines indicate when a significant population-level response was detected while dashed line indicates not-significant population-level response (see Table 2).

underuse disappeared when exposure was high. We note that the avoidance of crops by wild pigs is peculiar and might be driven by the rarity and type of crops within the SRS. Similarly, the strong selection for productive natural areas (high NDVI) when pigs were not exposed to risk reverted to underuse of these same areas when pigs experienced a high level of exposure to risk. Lastly, increased exposure to the removal increased pig movement rates (speed). All these responses, (less acute selection, reduction in selection of productive areas, and increased movement rates) are common anti-predator behavioral responses displayed by other species,[50,51] indicating that pig responses to trapping may be similar to prey attempting to avoid predation.

Even if some of the movement responses of pigs are similar to antipredator behavioral responses observed elsewhere, the context of these responses is different. For some wild pigs, the removal of conspecifics represents a new experience, more akin to the introduction of a new predator, while for other pigs, the removal represents a risk comparable to an ambush predator. Ambush predation is supposed to be less predictable on the landscape and elicit stronger antipredator responses.[52] This could explain why the individual cumulative exposure of a pig to the removal best predicted its movement. Animals are also typically assumed to be using some level of spatial (location-based) or attribute (landscape characteristics) memory when deciding how to move,[53] but our results do not support this type of memory in pigs response to removal given we found weaker support for models testing for a direct response to the removal (whether current or cumulative). This indicates that pig movement is more strongly influenced by the temporal aspect related to learning about the risk (or the type of risk itself) of being removed, than a direct spatial response to this removal risk. Longer tracking of pigs following the removal period or a shorter removal period would better allow testing of the temporal nature of spatial response. Similarly, comparing the impact of removal periods of different length of times (*i.e.* same number of pigs removed over a couple of days *vs* over a couple of weeks) would better unveil the nuanced behavioral response of pigs to risk.

4.2 Management implications

The spatial response of pigs to trapping programs has implications for the management and removal of this invasive species. Similar to previous work,[24] wild pigs did not evidently shift home range placement but used different habitats within the home range when trapping pressure increased. This shift in usage suggests that removal efforts could vary trap placement through time to increase the likelihood that wild pigs will be exposed. However, wild pigs become more elusive as removal exposure increases,[24,54,55] which may render trap placement immaterial if pigs have learned to associate traps with risk. In such instances, shifting tactics from trapping to alternative control measures may be more effective at achieving management goals.[56,57] Location of home ranges relative to control areas were similar for pre- and post-removal periods which could be informative for those managers trying to mitigate wild pig damage during time periods when imperiled species or environments are particularly susceptible. Given that wild pigs did not shift their spatial behavior post-removal, at least within the first 90 days, localized removals could provide a critical time window for ground nesting birds or species that congregate for breeding to escape predation or environmental damage by wild pigs. Similarly, our data suggest that this may also apply to crop damage where intensive removal efforts immediately prior to planting of crops could reduce crop losses from wild pigs, particularly for crops such as corn and peanuts where losses from wild pigs are most severe shortly after planting.[58]

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SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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