Original Article

Factors Affecting Bait Site Visitation: Area of Influence of Baits

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ABSTRACT Baiting is a fundamental strategy for the global management of wild pigs (*Sus scrofa*); however, little information exists on how anthropogenic bait affects wild pig movements on a landscape. We investigated factors that are important in determining the spatial area of attraction for wild pigs to bait ('area of influence' of a bait site) using data from Global Positioning System (GPS) collars and locations of bait sites. We monitored movements of wild pigs in 2 distinct study areas in the United States from February to September 2016 and used locational data using GPS collars to analyze the influence of habitat quality (dependent on site), home range size, number of bait sites in the home range, distance to a bait site, and sex in relation to movement in time and space. We determined the average area of influence by calculating the area of a circle with the radius as the average maximum distance travelled by wild pigs to reach a bait site. The average area of influence for our bait sites was 6.7 km² (or a radius of approximately 1.5 km), suggesting a bait spacing of approximately 1.5 km would be adequate to capture visitation by most wild pigs and a spacing of 3 km could allow substantial visitation while minimizing redundant effort depending on the spatial structure of the populations. Eighty percent of wild pigs first visited bait sites within 8.9 days after bait deployment; and they visited earlier when their home range size was larger. As the number of bait sites in an individual's home range increased, individual pigs visited more bait sites, and the probability of a visit increased dramatically up to approximately 5 bait sites and much less thereafter. Wild pigs travelled farther distances to visit bait sites in lower quality habitat. Our results support the hypothesis that habitat quality can mediate the efficacy of baiting programs for wildlife by influencing their movement patterns and motivation to use anthropogenic resources. Our results suggest wild pigs will travel extensively within their home range to visit bait sites, and that in lower quality habitat, most animals will find bait sites more quickly. Determining the area of influence of bait sites can increase the efficacy of planning and monitoring management programs. Our study provides new information to help managers plan baiting designs to attract the greatest number of pigs. © 2020 The Wildlife Society.

KEY WORDS baiting, invasive species, South Carolina, supplemental feeding, *Sus scrofa*, Texas, wild pigs, wildlife management.

Provisioning of anthropogenic food resources to wildlife species has the ability to fundamentally alter their demographic processes, physiology, behavior, relationships with predators and prey, and population dynamics (Oro et al. 2013). One of the primary ways that human resource subsidies can alter ecosystem processes is through their influence on animal movement behaviors, with important consequences for predator–prey interactions (Godbois

et al. 2004, Harju et al. 2018), intra- and interspecific disease transmission (Sorenson et al. 2014, Murray et al. 2016), and spatial distribution of animals (Prange et al. 2004, Newsome et al. 2013). Thus, understanding the influence of human resources on animal movement behavior is also often critical to implementing management and conservation practices, particularly in light of increasing anthropogenic effects on the environment.

One common form of resource provisioning to wildlife is through the practice of baiting, either for recreational, management, or research purposes. For example, Wilkins et al. (1999) estimated that wildlife baiting used >130 million kg of corn each year in Texas, USA. Attractants and baits are often used to increase animal detection probabilities to allow estimation of population densities of wildlife (Gerber et al. 2010, Keiter et al. 2017) and targeted control of invasive species (West et al. 2009). By their nature, baits are designed to attract animals to a specific location, which can artificially inflate the estimated population density of animals in an area. Lack of accounting for the response of animals to bait can lead to biases in population estimates (Ivan et al. 2013). Therefore, it is necessary to understand the spatial scale at which baits influence animal behavior (i.e., the area of influence; Davis et al. 2017). Without accurate knowledge of the area influenced by baits, abundance estimates from nongrid designs cannot be converted to density accurately, diminishing our ability to quantify management efficacy. Davis et al. (2016) demonstrated how a removal model (Zippin 1958) could be used to assess the effect of management actions using only management data. However, evaluation can only take place when it is known that the same area is being affected by repeated management actions. Thus, understanding the area of influence is important for developing practical methods of assessing management programs that use bait-based techniques.

When planning trapping or toxicant campaigns for invasive species management, understanding the area of influence of bait also provides insight into how many bait sites are required for effective coverage of a management area and how long the bait should be set in a given location. Prior studies have found home range size, study site, weather, sex, previous experiences with baits sites, and the animal's instinctive behavior toward bait sites are additional factors affecting the probability of animals visiting a bait site (Saunders et al. 1993, Lavelle et al. 2017). The combination of these factors will affect how influential bait sites are and thus the efficacy of management programs, but there are few studies that examine this (Davis et al. 2017). Identifying and quantifying factors that affect bait-site visitation probability is necessary to improve preparation and response to disease outbreaks (i.e., planning the fastest and most effective removal strategies) and develop more efficient strategies for implementing damage reduction programs (Davis et al. 2017).

Invasive wild pigs (*Sus scrofa*) are a wildlife species often managed in conjunction with use of baiting. Wild pigs negatively affect agriculture, natural resources, and personal property throughout the world (Tisdell 1982, Barrios-Garcia and Ballari 2012, Bevins et al. 2014, Keiter and Beasley 2017); thus, they are routinely subject to population control (Bengsen et al. 2014, Bevins et al. 2014). In particular, wild pigs cause extensive damage to many agricultural crops, costing billions of dollars annually around the world (Pimental 2007, Cai et al. 2008, Anderson et al. 2016). Wild pigs are also reservoirs for animal and plant pathogens, capable of infecting livestock, wildlife, and humans; some of these pathogens—including viruses, parasites, and bacteria—are fatal to both animals and humans (Bengsen et al. 2014, Miller et al. 2017). Techniques to control wild pigs include ground or aerial shooting, hunting, fencing, snares, trapping, and toxicants, which have been and continue to be developed in New Zealand, Australia, and United States (Campbell and Long 2009, Shapiro et al. 2016, Snow et al. 2017, Poché et al. 2018). Several methods of pig damage control require use of baits that can range from pungent and colored meat to flavored and scented syrups to plant-based bait for optimal attraction (Lapidge et al. 2004). The effectiveness of an attractant depends on the motivation of wild pigs to seek out bait in addition to variables such as the proximity of bait and other environmental or habitat conditions. This motivation can be affected by food availability during various seasons, social behaviors, and physiological senses such as smell, hearing, sight, and taste (Lavelle et al. 2017). Both management and monitoring of invasive wild pigs often depend on baiting programs; therefore, it is imperative to understand relationships between bait placement and wild pig movement ecology to facilitate improved use of resources and meet project objectives.

We sought to understand factors that determine the area of influence of bait explicitly through use of Global Positioning System (GPS) collar data collected from wild pigs in 2 different regions (TX and SC, USA) within the United States. Our objectives were to directly measure and compare the area of influence of bait across 3 disparate sites and determine visitation frequency and time to bait detection by wild pigs with multiple bait piles deployed. We examined how ecological factors (e.g., sex, home range size, study site) and baiting practices (e.g., no. of bait sites per home range, spacing) influenced 1) the probability of a bait site being visited, 2) the amount of time until an animal first visited a bait site, and 3) movement patterns of animals with regard to baited locations. Understanding these relationships will provide guidance on monitoring and management strategies that use attractant to enhance detection.

STUDY AREA

We conducted trials in 2 sites in South Carolina on the Savannah River Site (SRS), an approximately 800-km² property managed by the U.S. Department of Energy located in the coastal plain and bordering the Savannah River. The SRS was composed of 68% pine (*Pinus* spp.) forest and 22% bottomland vegetation communities consisting of swamp and hardwood forests (Imm and McLeod 2005).

During the trial period (Feb to Sep 2016) average temperature was 16.84° C, ranging from −1.1 to 37.8° C, and precipitation averaged 2.3 mm/day, ranging from 0.0 to 59.4 mm (National Climatic Data Center). One site was placed adjacent to an unfenced municipal facility, the Three Rivers Landfill, hereafter the "landfill" site. The forest vegetation community surrounding the landfill was dominated by mature bottomland hardwood. The second site included a mix of upland pine and bottomland hardwood vegetation communities, hereafter referred to as the "mixed" site. Wild pigs regularly utilized the Three Rivers Landfill, and the landfill site had greater densities than the mixed site. We consider the landfill site to be higher quality for pigs than the mixed site because of abundant food resources for pigs and pig selection for bottomland hardwood on the SRS (Beasley et al. 2014).

We conducted trials in Texas on Joint Base San Antonio, Camp Bullis (112.9 km^2), Texas. This property was located in the Edwards Plateau and Blackland Prairie ecoregions of Texas and consisted of rolling hills with rocky soils and limestone outcrops with vegetation characterized by a matrix of oak (*Quercus* spp.), cedar (*Juniperus* spp.), woodland, and grasslands (Bailey 1980, 1998). The average daily temperature during January–July, 2016 was 21.19° C, ranging from −8.3 to 37.2° C, and precipitation averaged 2.9 mm/day, ranging from 0.0 to 73.7 mm (National Climatic Data Center).

METHODS

Global Positioning System Collaring
We captured wild pigs in South Carolina between November 2015 and February 2016 using corral traps baited with whole kernel corn. We anesthetized wild pigs with a dart rifle (X-Caliber; Pneu-Dart Inc., Williamsburg, PA, USA) using a combination of Telazol® (4.4 mg/kg; MWI Veterinary Supply, Boise, ID, USA) and xylazine (2.2 mg/kg; Wildlife Pharmaceuticals Inc., Fort Collins, CO, USA). We tagged pigs with individually numbered ear tags (Y-Tex medium cattle tags; Y-Tex, Cody, WY, USA), and affixed GPS collars to adult females (>50 kg) and large males (~100 kg or greater) throughout the study area. We programmed collars (Lotek Globalstar or LiteTrack store-on-board collar [Lotek Wireless Inc., Newmarket, ON, Canada]) to take a location every 1 or 4 hours, respectively. We programmed drop-off mechanisms to release the collars following a 6-month deployment time, after which we collected the collars and retrieved full location data sets. Factory specifications provided by the collar manufacturer estimated locational error for all collars to be 5–10 m under ideal conditions. Limited testing of these collars in closed canopy forest including truthing of locations with a Garmin GPSMAP 64st (Garmin Ltd., Olathe, KS, USA) had an error of ≤ ±23 m (SE = 2.37, $n = 168$). The University of Georgia's Institutional Animal Care and Use Committee approved all capture and handling procedures (IACUC approval # A2015 05-004-Y3-A5).

We trapped wild pigs in Texas during 15 January–20 June 2016 (see Lavelle et al. 2018 for more details) using corral

and box traps baited with whole kernel corn. We placed and relocated traps to generate an even distribution of collared wild pigs throughout the study area (≤2 wild pigs/family group and ≤4 wild pigs/trapping location). We chemically immobilized wild pigs using a mixture of 3.3 mg/kg Telazol® and 1.5 mg/kg xylazine delivered via intramuscular injection and affixed adult wild pigs (i.e., ≥45 kg) with GPS satellite transmitting collars (VERTEX PLUS-2 Collar; VECTRONIC Aerospace GmbH, Berlin, Germany) equipped with ultra-high frequency (UHF) proximity sensors. We also applied ear tags (Allflex A Cattle Tags; Allflex USA Inc., Dallas, TX, USA) with unique IDs. After handling was complete, we reversed the xylazine with 0.2 mg/kg of yohimbine hydrochloride delivered via intramuscular injection (Sweitzer et al. 1997). We immediately released captured wild pigs without collars. We programmed GPS collars to collect and store locations every 15 minutes and transmit every sixth location via Iridium satellite to allow real-time monitoring. We programmed drop-off mechanisms to release the collars on 15 August 2016, after which we collected the collars and retrieved full location data sets. We assessed locational error of GPS collars to be ≤ ±5.0 m (SE = 0.16) throughout the study area using $n = 2,840$ fix locations truthed with a Trimble GEOXH 2008 (Trimble Navigation, Sunnyvale, CA, USA). The Texas A&M University-Kingsville's Institutional Animal Care and Use Committee (2015-08-20) and National Wildlife Research Center (U.S. Department of Agriculture—Animal and Plant Health Inspection Service—Wildlife Services—National Wildlife Research Center, QA-2263) approved the capture and handling procedures.

Baiting Design and Techniques
At the SRS, we used cameras (Reconyx Hyperfire HC500, white-flash and infra-red; RECONYX, Inc., Holmen, WI, USA) to confirm bait visitation. We created a grid of 42 and 56 cameras spaced 750 m apart at the landfill and mixed sites, respectively (Fig. 1). These sites were independent of the trapping sites and not active concurrently. After a prebaiting period lasting 21 days, we placed cameras within 75 m of grid locations for 10 days; we moved locations that fell within the landfill to the closest vegetated area. We initially baited all cameras with 23 kg of dry corn approximately 2–3 m from the camera and rebaited with an additional 11.5 kg after 5 days. We programmed cameras to take a burst of 3 photos with 3 minutes between bursts and used these photos to identify GPS-collared wild pigs. Cameras were active for 10 days. We set camera arrays on 2 different occasions with roughly 5 months between surveys.

We generated 61 spatially balanced and random baiting sites for Camp Bullis in the Texas study area using the Spatially Balanced Points tool in ArcGIS (ESRI, Redland, CA, USA). We separated all points by ≥660 m to reduce any nonindependence among bait sites. We prebaited each of the 61 sites for 1–6 days to ascertain the presence of pigs. Prebaiting consisted of deploying 11.3 kg of whole kernel corn in a pile on the ground and refreshing this
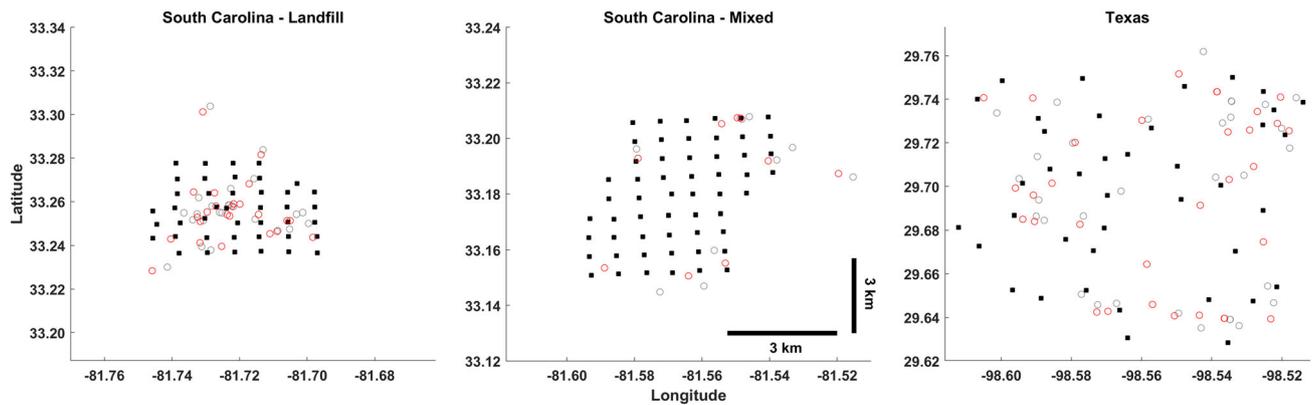
Figure 1. Location of bait sites (filled squares) and wild pigs (open circles) in the 3 study sites, February to September 2016, South Carolina and Texas, USA. All plots are on the same scale (shown in the lower right of the middle plot; X-axes are 10 km wide, Y-axes are 17 km wide). Grey circles represent the centroids of wild pig home ranges prior to baiting. Red circles represent the centroids during baiting (10 days in SC, 30 days in TX).

corn daily if needed. We monitored sites with cameras (Reconyx-PC900; RECONYX, Inc.). After the prebaiting period, we selected 41 sites with the most consistent and largest visitation by wild pigs and discontinued baiting the other sites. We deployed UHF-emitting stationary ID tags (VECTRONIC Aerospace GmbH) placed within 5 m of the bait station that measured encounters with collared wild pigs if those animals approached within approximately 25 m at each site. The GPS collars logged these encounters as proximity events and included the date and time of each event. We maintained bait at bait sites where cameras were active for 12–29 days, refreshing bait daily with whole-kernel corn and peanut paste following the methods outlined in Lavelle et al. (2018).

We split GPS collar data for all sites into 2 periods to test how wild pig spatial behavior varied before baiting and while bait was present on the landscape. The monitoring period prior to baiting was 21 days in South Carolina and 28 days in Texas. The baiting period was 10 days in South Carolina and 30 days in Texas. We conducted the first set of trials (prebait period + baiting period) at the landfill from 19 February to 21 March 2016 and the second set from 13 August to 9 September 2016. Trial dates for the mixed site were 18 March–18 April 2016 and 19 August–19 September 2016. Trial dates for the Texas field site were 1 June–30 July 2016.

Data Organization

We created minimum convex polygon home ranges for wild pigs during the prebait period using Geospatial Modeling Environment (Version 0.6.0.0; Spatial Ecology LLC, http://www.spatialecology.com/gme/index.htm), and calculated home range centroids in ArcGIS 10.1 (ESRI 2011). We then determined the distance from the home range centroid to all bait sites during prebaiting and baiting periods using the Proximity toolbox in ArcGIS, creating a distance matrix for each individual. We buffered prebaiting home ranges by 100 m, and determined the number of bait sites within the buffered home range. We buffered prebaiting home ranges to account for potential home range shifts after bait was placed on the landscape; that is, if a bait

site is close (<100 m) to the prebait home range it is likely it would be visited by wild pigs. We examined camera images and determined the time it took for each collared pig to first visit a bait site.

Statistical Analysis

We analyzed data with generalized linear mixed models using the 'fitglme' function in the Statistics Toolbox from Matlab (Version R2016b; The Mathworks Inc., Natick, MA, USA). We considered 4 response variables: 1) the time in days it took pigs to visit their first bait (count data modeled as a Poisson distribution with a log link; now referred to as "time to visit"); 2) the number of different bait sites an individual pig visited (count data modeled with a Poisson distribution and log link; now referred to as "number visited"); 3) given that an individual pig visited ≥1 bait site, the maximum distance to a bait site it visited relative to the centroid of its prebait home range (continuous, positive data modeled with a gamma distribution and log link; now referred to as "max. dist."); and 4) the probability that a pig visited ≥1 bait site (binary data modeled with a binomial distribution and logit link; now referred to as "probability of visit"). For each of these responses we analyzed the effects of 1) ecological factors including pig sex, study site, and home range size, and 2) baiting practices including number of bait sites in the home range and distance between home range centroid and nearest bait. Distance to the nearest bait, number of bait sites in the home range, and home range size (as independent variables) were metrics based on movement data prior to the start of baiting. In South Carolina, each site had 2 separate baiting sessions for which we assessed the area of influence (2 months apart), and thus we sampled some pigs twice. To account for repeated measures on some pigs, we included individual pig as a random effect in all models. A descriptive summary of these data is presented in Table 1.

We examined all possible model combinations of the 5 independent variables, including 2-way interactions (Tables S1–S4, available online in Supporting Information), and present results for models with the lowest Akaike Information Criterion values (AIC; Tables 2–5). Although

Table 1. Mean values, standard errors (SE), and population sizes (n) of factors affecting movement characteristics of wild pigs that did or did not visit a bait site, February to September 2016, South Carolina and Texas, USA.

Location	Factor	No visit			Visit		
		$\bar{x}$	SE	n	$\bar{x}$	SE	n
South Carolina—Landfill	Home range size (km^2)	2.0	0.3	4	3.1	1.1	20
	Distance between home range centroid and nearest bait	456.7	161.4	4	410.2	133.3	20
	No. of bait sites in home range	2.5	1.2	4	5.0	0.6	20
South Carolina—Mixed	Home range size (km^2)	7.5	0	1	16.2	6.5	8
	Distance between home range centroid and nearest bait	429.9	0	1	591.3	245.3	8
	No. of bait sites in home range	7.0	0	1	11.4	3.0	8
Texas	Home range size (km^2)	3.8	1.1	2	5.2	0.7	30
	Distance between home range centroid and nearest bait	697.4	124.9	2	751.0	62.3	30
	No. of bait sites in home range	1.0	0.0	2	2.8	0.3	30

Table 2. Beta estimates, standard errors (SE), degrees of freedom (DF), and P-values for factors affecting "time to visit" for wild pigs, February to September 2016, South Carolina and Texas, USA.

Predictor	Coefficient	SE	DF	P
Intercept	1.291	0.184	50	<0.001
Distance between home range centroid and nearest bait	6.85E-04	2.37E-04	50	0.006
Sex [Male]	0.147	0.189	50	0.44
No. of bait sites in home range	0.058	0.035	50	0.11
Home range size (km^2)	−0.062	0.024	50	0.01

Table 3. Beta estimates, standard errors (SE), degrees of freedom (DF), and P-values for factors affecting "number visited" for wild pigs, February to September 2016, South Carolina and Texas, USA.

Predictor	Coefficient	SE	DF	P
Intercept	0.357	0.200	55	0.008
Sex [Male]	−0.735	0.421	55	0.090
No. of bait sites in home range	0.076	0.025	55	0.004
Study site [Mixed]	0.407	0.374	55	0.280
Study site [TX]	−0.032	0.262	55	0.810
Sex [Male] × Study site [Mixed]	−0.232	0.648	55	0.720
Sex [Male] × Study site [TX]	1.484	0.484	55	0.003

models within 2 AIC of the top model were considered competitive (Burnham and Anderson 2002), we were interested in inference of all parameters; thus, we conducted AIC selection as a means of excluding parameters that were likely to be uninformative and used the top model for our inferences. We estimated the area of influence for baiting

Table 4. Beta estimates, standard errors (SE), degrees of freedom (DF), and P-values for factors affecting "max. dist." for wild pigs, February to September 2016, South Carolina and Texas, USA.

Predictor	Coefficient	SE	DF	P
Intercept	0.271	0.205	50	0.19
Sex [Female]	−0.149	0.126	50	0.24
No. of bait sites in home range	0.049	0.036	50	0.18
Study site [Mixed]	−1.122	0.268	50	1.14E-04
Study site [TX]	0.547	0.310	50	0.08
No. of bait sites in home range × Study site [Mixed]	0.137	0.044	50	0.003
No. of bait sites in home range × Study site [TX]	−0.045	0.038	50	0.24

sites in each study site as a circle with a radius equal to the average of the maximum distance pigs were observed travelling to visit a bait site.

RESULTS

We collared 17 individuals (14 F, 3 M) for the first survey at the landfill in South Carolina, and had 5 individuals (3 F, 2 M) with collars on for the second survey at the landfill. We collared 9 individuals (4 F, 5 M) for the first survey at the mixed site in South Carolina, and had 2 individuals (1 F, 1 M) with collars on for the second survey at the mixed site. In Texas, we collared 32 individuals (13 F, 19 M). Wild pigs first visited a bait site as early as 1 day or as late as 20 days following placement but 80% of pigs visited before 8.9 days and most frequently they visited at 5 days for the first time (Fig. 2). They visited between 0 and 7 bait sites with 80% visiting 5 or fewer different bait sites and most often they only visited 2 different bait sites (Fig. 3). Finally, most frequently, wild pigs traveled a maximum distance of 1.5 km to a bait site with 80% travelling up to 7.9 km (Fig. 4) and 2 outliers (not shown on Fig. 4) having home range centroids at approximately 20 km from a bait site they visited. For pigs that visited a given bait site, the average number of visits to the same bait site was 2.05 (range = 1–7).

The model with the lowest AIC score for the "time to visit" included distance between the home range centroid and nearest bait, sex, number of bait sites in the home range, and home range size. As we expected, we found that pigs with home range centroids located closer to bait visited the bait earlier (Table 2). There was no difference between males and females in time to visitation (Table 2). On average, pigs visited a bait site as early as 2.6 days at a

Table 5. Beta estimates, standard errors (SE), degrees of freedom (DF), and P-values for factors affecting "probability of visit" for wild pigs, February to September 2016, South Carolina and Texas, USA.

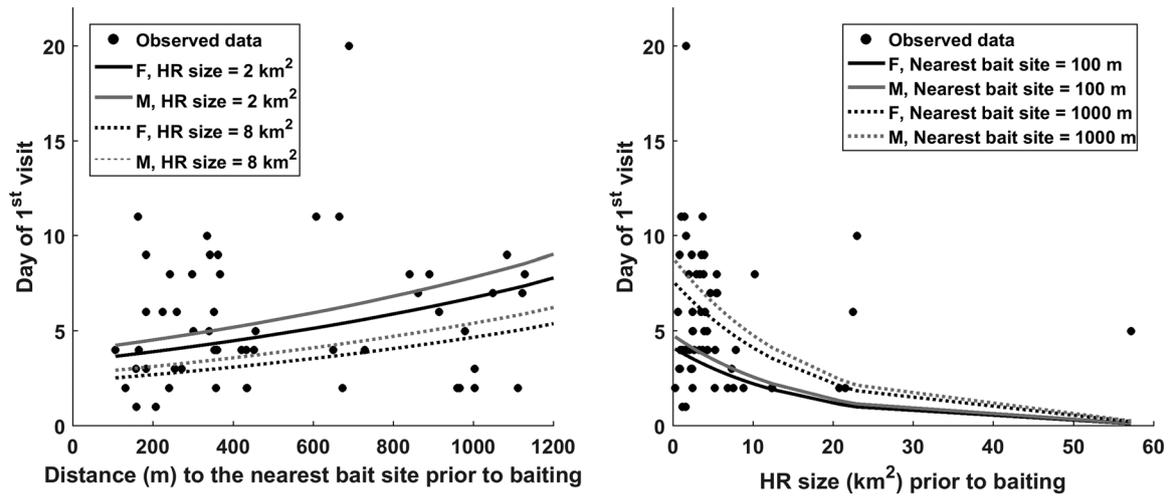| Predictor	Coefficient	SE	DF	P
Intercept	−0.088	0.961	57	0.93
Sex [Male]	−1.532	1.087	57	0.16
Number of bait sites in home range	0.589	0.297	57	0.05
Study site [Mixed]	−0.947	1.455	57	0.52
Study site [TX]	2.27	1.179	57	0.06

Figure 2. Factors affecting "time to visit" for wild pigs, February to September 2016, South Carolina and Texas, USA. The best model included distance between the home range (HR) centroid and the nearest bait, home range size, sex, and number of bait sites in the home range. The best model did not include any interaction terms. Left: Relationship between the earliest day that pigs visit bait sites and distance to the nearest bait. Right: Relationship between the earliest day that pigs visit bait sites and home range (HR) size. Raw data for each pig are the filled black points. Lines are predictions from the best model made at the covariate values indicated in the legend and X-axes, and the number of bait sites in the prebaiting home range was fixed at 1 for prediction (i.e., predictions represent visitation timing for conditions with a single bait site in the prebaiting home range). F—female, M—male.

distance of 100 m and a larger home range size, or as late as 8.5 days with a distance of 1,200 m and a smaller home range size (Fig. 2). We also found pigs with larger home range sizes visited bait sites earlier (Table 2; Fig. 2).

On average, pigs had 5.8 bait sites (range = 1–27 bait sites) within their home range (Fig. 3). The model with the lowest AIC score for the "number visited" included number of bait sites in the home range, study site, sex, and the interaction between sex and study site. As expected, pigs visited more bait sites with more bait sites in their home range (Table 3). On average, pigs with 5 bait sites in their

home range visited 2 bait sites, and pigs with 10 bait sites in their home range visited 3 bait sites, showing that bait site visitation does not increase at the same rate as availability (Fig. 3). Thus, overall the number of bait sites visited remained low despite large increases in the number of available bait sites. In Texas, males visited more bait sites than females, although this pattern did not hold for the South Carolina mixed site (Table 3). On average, male pigs visited 3 bait sites at the Texas site compared with an average of 2.3 bait sites visited for the remaining 5 sex–site combos (Fig. 3).
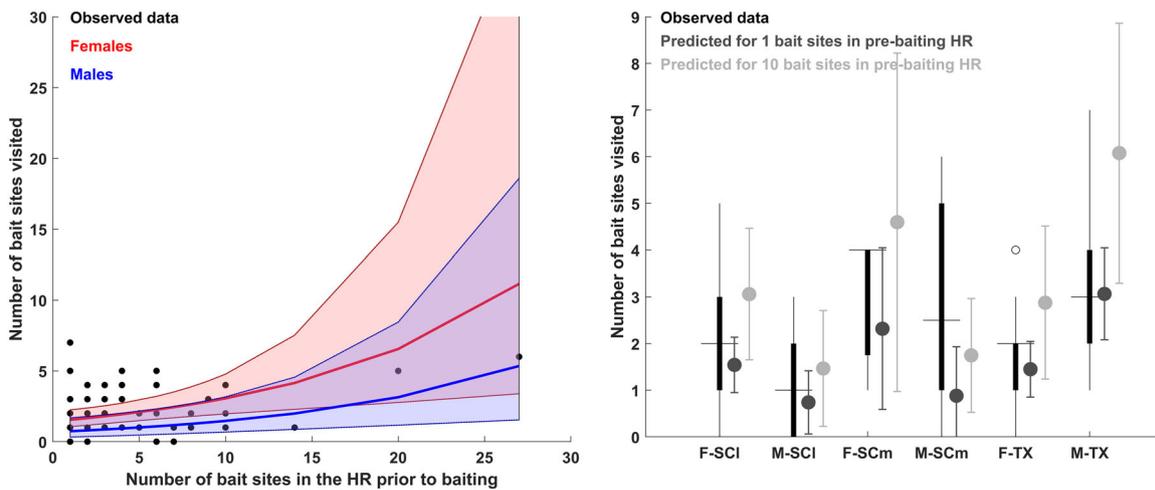

Figure 3. Factors affecting the "number visited" for wild pigs, February to September 2016, South Carolina and Texas, USA. The best model included the number of bait sites in the home range, sex, study site, and an interaction between sex and study site. Left: Lines are predictions from the best model made at the covariate values indicated in the legend (male—blue, female—red) and X-axes, and the site values from the raw data. Shading indicated 95% prediction intervals. Right: The predicted number of different bait sites visited by different sexes in different sites. The raw data are shown as black box plots (horizontal lines are the median number of bait sites visited). Solid circles are the predicted average number of bait sites visited for 2 different values of the number of bait sites in the prebaiting home range (HR): 1 (dark grey) or 10 (light grey). Error bars are 95% prediction intervals. Females in South Carolina landfill (F-SCl), males in South Carolina landfill (M-SCl), females in South Carolina mixed (F-SCm), males in South Carolina mixed (M-SCm), females in Texas (F-TX), males in Texas (M-TX).
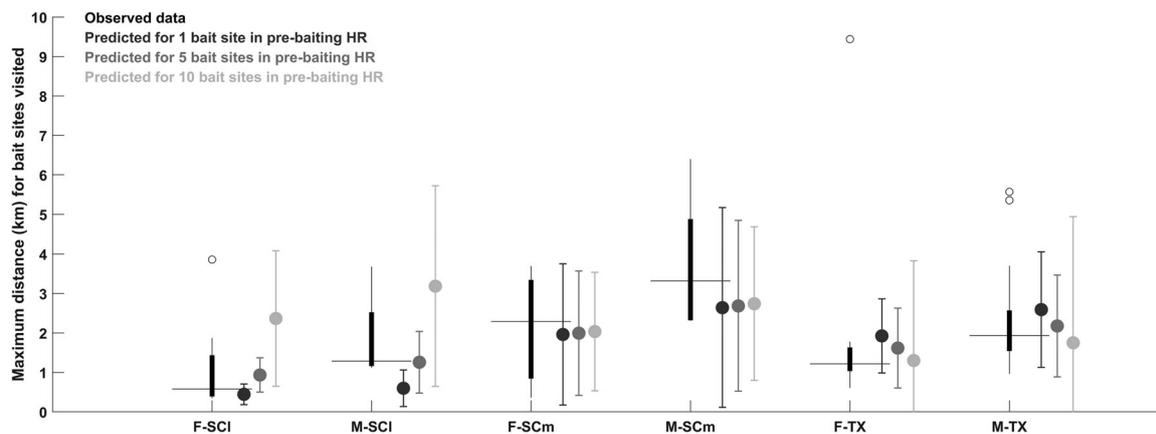
Figure 4. Factors affecting "max. dist." for wild pigs, February to September 2016, South Carolina and Texas, USA. The best model included number of bait sites in the home range, sex, study site, and an interaction between study site and number of bait sites in the home range. The raw data are shown as black box plots (horizontal lines are the median value for the maximum distance of bait sites visited). Solid circles are the predicted average maximum distance (km) of bait sites visited by pigs for 3 different values of number of bait sites in the prebaiting home range (HR): 1 (dark grey), 5 (medium grey), or 10 (light grey). Error bars are 95% prediction intervals. Females in South Carolina landfill (F-SCl), males in South Carolina landfill (M-SCl), females in South Carolina mixed (F-SCm), males in South Carolina mixed (M-SCm), females in Texas (F-TX), males in Texas (M-TX).

The average maximum distance traveled to a bait site from the home range centroid was 0.9 km at the South Carolina landfill site, 2.8 km at the South Carolina mixed site, and 1.5 km at the Texas site (Fig. 4). The model with the lowest AIC score for the "max. dist." included sex and the interaction between study site and number of bait sites in the home range (Table 4). The mixed site in South Carolina, with fewer food resources, produced the greatest average maximum distance for bait sites visited for both females and males. In the landfill site where food resources were plentiful, pigs traveled 2.5–3 km on average to bait only when there were numerous baits in their home range (e.g., 10 baits), otherwise they only traveled <1 km.
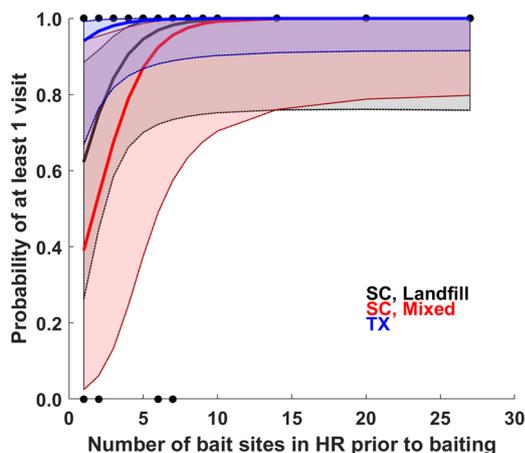
The model with the lowest AIC score for the "probability of visit" contained number of bait sites in the home range, sex, and study site. The model predicted that the probability of visiting a bait site increased with the number of bait sites in the home range (although the evidence was weak; Table 5, Fig. 5). For the South Carolina mixed site, the probability of visiting a bait site increased, on average, 6.7% for every additional bait site in the prebait home range. An average 4.2% increase in the South Carolina landfill site and 0.7% increase in the Texas site was also observed. However, at values beyond 10 bait sites in the home range, there was no further increase in probability of a visit for any of the 3 sites (Fig. 5). There was also a trend of greater visit probability in the Texas site relative to the sites in South Carolina (Table 5). The Texas site had the largest initial probability of a visit at around 94% for one bait site, whereas the South Carolina mixed and landfill sites began with approximately a 39% and 62% probability of a visit with one bait site, respectively (Fig. 5).

For our area of influence calculation, the median maximum distance traveled to a bait site or the radius, across all sites was 1.46 km ± 3.70 km. There were site differences in maximum distances moved. The radius was 0.92 km ± 1.02 km in the landfill site, 2.81 km ± 1.78 km in the mixed site, and 1.57 km ± 4.79 km in the Texas site. With these radii, our areas of influence were overall 6.7 km^2 ± 16.97 km^2, 2.64 km^2 ± 3.76 km^2 in the landfill site, 24.98 km^2 ± 17.57 km^2 in the mixed site, and 7.75 km^2 ± 47.81 km^2 in the Texas site.

DISCUSSION

Pigs in our study traveled up to 1.46 km, on average, to reach a bait site but this distance depended on habitat; at sites with better pig habitat or more plentiful food resources (i.e., TX and SC landfill), pigs traveled shorter distances to reach a bait site. Our results are similar to Wang and Grimm (2007), who discovered common shrews (*Sorex araneus*) continuously altered their home ranges to

Figure 5. Factors affecting the "probability of visit" for wild pigs, February to September 2016, South Carolina and Texas, USA. The best model included number of bait sites in the home range (HR), sex, and study site. There were no interactions in the best model. The raw data are shown as black points. Lines are predictions from the best model made for the 3 different sites (South Carolina, mixed—red, South Carolina, landfill—black, Texas—blue) at values on the X-axes, and fixing the sex to males (females showed a similar average pattern with slightly more uncertainty). Shading indicated 95% prediction intervals.

acquire enough food and left the area when they discovered low levels of resources. Thus, animals with sufficient resources may not travel as far to a bait site in comparison with animals with inadequate resources. Similarly, previous research suggests that wild pigs are more difficult to trap using bait during times when food resources are abundant (West et al. 2009). Thus, in higher quality habitats or during times when food resources are abundant, greater visitation success could be achieved by placing bait sites closer together. This agrees with our findings that with a larger home range size and a shorter distance from the home range centroid to the nearest bait site, pigs tended to visit the bait site sooner. This is somewhat counterintuitive because an animal with a smaller home range will generally be closer to a given bait site than an animal with a large home range. Therefore, this result suggests that habitat quality may have a significant mediated effect on the efficacy of baiting programs. With insufficient resources, wild pigs will travel farther to reach food, increasing their home range size. We suggest that these wild pigs will have greater need, and therefore drive, to find resources; thus, they will visit a bait site sooner than a wild pig with an abundance of food resources.

We found that the probability of a visit increased asymptotically with each additional bait site until a threshold of 10 bait sites in the home range was reached, and that we reached >0.9 probability of a visit with 5 bait sites in the home range. Knowing this level of bait saturation, managers can optimize baiting programs to reduce allocation of time and money while maintaining an equal probability of wild pig visitation. This may be particularly useful for population control practices that aim to remove the largest proportion of wild pigs in the shortest amount of time in attempt to drastically reduce the population or protect certain commodities during critical times of year.

One of the primary questions addressed with this study was to measure the maximum distance traveled to reach a bait site; on average, the maximum distance traveled by wild pigs to reach bait sites was 1.46 km ± 3.70 km. As such, the area of influence for our bait sites was 6.7 km^2. Davis et al. (2017) reported an average area of influence of 8.6 km^2 (± 0.4 km^2, $n = 3$) for corral traps in Texas during the summer, which is slightly larger than the area of influence from our Texas study area (7.75 km^2) but within the range of our findings. These differences, although not considerable, may be due to the variation in site or habitat and season between our studies as well as the small sample size and use of indirect measures to calculate the area in the Davis et al. (2017) study. From our area of influence calculations, by placing bait sites approximately 3 km apart (i.e., radii of 1.5 km), management programs should have success with attracting most wild pigs in a target site, assuming similar conditions. These results are similar to a recent study that suggested placing bait sites within 1–1.25 km of where wild pigs are centrally located to ensure consistent visitation to the bait site (i.e., ≥0.50 daily visitation probability) that would be most useful for population control activities, such as trapping or toxic baiting (Snow

and VerCauteren 2019). In poor quality habitat where animal home ranges are larger, as in our mixed area, bait sites can be spaced farther apart with a similar likelihood of being visited by wild pigs.

Our study sites differed in the number of bait sites, time of year the trials took place, length of the prebaiting and baiting periods, average temperature and precipitation, vegetation, and terrain. Although we observed significant differences at the site level, some relationships applied more generally, thus providing direction for the development of future studies. In particular, we found males were quicker to detect bait than females, which may relate to the general trend of males having larger home range sizes than females. As the number of bait sites in the home range increases, pigs visited a smaller proportion of the total baits present, suggesting there are diminishing returns at greater bait densities. In the future, it might be useful to understand factors that determine selection of specific bait sites to further optimize baiting design. For example, why are some bait sites selected over others in their home range?

We only had data from 3 sites in 2 states and found site-level effects, but incorporating data from other regions could help to identify additional factors that affect bait visitation or alter the area of influence. By introducing data from other regions, future work could also quantify the relationship between habitat quality and baiting outcomes. Understanding these relationships more broadly will allow for more effective baiting designs catered to the specific area of baiting. Adkins and Harveson (2007) analyzed 7 different habitats in Texas, looking at how the proportion of total visits by wild pigs differed between them. Integrating these animal resource-selection patterns and previously established relationships (e.g., the positive relationship between precipitation and wild pig density [Ilse and Hellgren 1995, Gabor et al. 1999, Harveson et al. 2000, Adkins and Harveson 2007, Lewis et al. 2017]) could aid in the design and implementation of a study of the influence of habitat quality on animal movement behavior.

Although the findings in this study inform the distances that wild pigs are attracted to bait sites, it does not inform the effectiveness of subsequent population control. Developers of toxic baits for wild pigs have ensured that toxic baits are palatable to wild pigs, and that most wild pigs will consume lethal doses once expose to the baits (Snow et al. 2016, 2019). In particular, 2 types of orally delivered toxic baits are under development in the United States (i.e., sodium nitrite and warfarin) and have been shown to be 95–100% lethal for wild pigs in pens (Snow et al. 2017, Poché et al. 2019). Additionally, the potential efficacy for free-ranging wild pigs was estimated at 91–100% of wild pigs that lived near the bait sites (Poché et al. 2018, Snow et al. 2019). A recently developed model using data from Snow et al. (2019) and the current study predicted that this high level of visitation could be very efficient for reducing wild pig populations substantially (by 80%), but that other methods might need to be applied alongside toxic baiting to improve cost-effectiveness when the objective is to reduce the population further (by 99%) because costs increase

dramatically when bait stations need to be located near 99% of wild pigs in the population (Pepin et al. 2020).

Variability in area of influence values is not unexpected because movement varies across time and space, even for individuals within a species (Singh et al. 2012). Generally, animal movement in space and time depends on food accessibility, the existence of other animals, reproductive condition, sex, physical durability, and memory (Morales et al. 2010). Given these possibilities, landscape and climate of the site including water access, food availability before baiting, previous interactions with baiting and traps, group and individual social behavior, endurance, and reproductive period may have played a role in determining how far wild pigs traveled to a bait site and affected the estimated area of influence. Even though various conditions influenced estimates of the area of attraction, we found some consistencies that might be useful more broadly for management programs.

MANAGEMENT IMPLICATIONS

An improved understanding of how wildlife baiting may affect animal movement is necessary because of the wide-ranging influence of anthropogenic food resources on wildlife populations (Oro et al. 2013) and implications of these effects for management and conservation. From our results, we suggest baiting within 1.46 km of suspected pig activity (the radius for the average area of influence 6.7 km²), equating to bait sites approximately 3 km apart to attract wild pigs effectively under similar conditions. Placing more bait sites in the home range will increase the likelihood of attracting wild pigs sooner in areas with better pig habitat, but only up to a threshold number of baits that is >5 but <10. The same holds true for individuals with a larger home range size that are closer to a bait site. Future work could explore selection by wild pigs of specific bait sites and evaluating the relationship between habitat quality and baiting outcomes. Subsequent efforts to study the best ways to attract wild pigs to traps or toxicants will decrease the damage to resources and spread of disease caused by this invasive species.

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LITERATURE CITED

Adkins, R. N., and L. A. Harveson. 2007. Demographic and spatial characteristics of feral hogs in the Chihuahuan Desert, Texas. Human–Wildlife Conflicts 1:152–160.

Anderson, A., C. Slootmaker, E. Harper, J. Holderieath, and S. A. Shwiff. 2016. Economic estimates of feral swine damage and control in 11 US states. Crop Protection 89:89–94.

Bailey, R. G. 1980. Description of the ecoregions of the United States. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.

Bailey, R. G. 1998. Ecoregions: the ecosystem geography of the oceans and continents. Second edition. Springer-Verlag, New York, New York, USA.

Barrios-Garcia, M. N., and S. A. Ballari. 2012. Impact of wild boar (Sus scrofa) in its introduced and native range: a review. Biological Invasions 14:2283–2300.

Beasley, J. C., T. E. Grazia, P. E. Johns, and J. J. Mayer. 2014. Habitats associated with vehicle collisions with wild pigs. Wildlife Research 40:654–660.

Bengsen, A. J., M. N. Gentle, J. L. Mitchell, H. E. Pearson, and G. R. Saunders. 2014. Impacts and management of wild pigs Sus scrofa in Australia. Mammal Review 44:135–147.

Bevins, S. N., K. Pedersen, M. W. Lutman, T. Gidlewski, and T. J. Deliberto. 2014. Consequences associated with the recent range expansion of nonnative feral swine. BioScience 64:291–299.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cai, J., Z. Jiang, Y. Zeng, C. Li, and B. D. Bravery. 2008. Factors affecting crop damage by wild boar and methods of mitigation in a giant panda reserve. European Journal of Wildlife Research 54:723–728.

Campbell, T. A., and D. B. Long. 2009. Feral swine damage and damage management in forested ecosystems. Forest Ecology and Management 257:2319–2326.

Davis, A. J., M. B. Hooten, R. S. Miller, M. L. Farnsworth, J. Lewis, M. Moxcey, and K. M. Pepin. 2016. Inferring invasive species abundance using removal data from management actions. Ecological Applications 26:2339–2346.

Davis, A. J., B. Leland, M. Bodenchuk, K. C. VerCauteren, and K. M. Pepin. 2017. Estimating population density for disease risk assessment: the importance of understanding the area of influence of traps using wild pigs as an example. Preventive Veterinary Medicine 141:33–37.

ESRI. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, California, USA.

Gabor, T. M., E. C. Hellgren, R. A. Van Den Bussche, and N. J. Silvy. 1999. Demography, sociospatial behaviour and genetics of feral pigs (Sus scrofa) in a semi-arid environment. Journal of Zoology 247:311–322.

Gerber, B., S. M. Karpanty, C. Crawford, M. Kotschwar, and J. Randrianantenaina. 2010. An assessment of carnivore relative abundance and density in the eastern rainforests of Madagascar using remotely triggered camera traps. Oryx 44:219–222.

Godbois, I. A., L. M. Conner, and R. J. Warren. 2004. Space-use patterns of bobcats relative to supplemental feeding of northern bobwhites. Journal of Wildlife Management 68:514–518.

Harju, S. M., C. V. Olson, J. E. Hess, and B. Bedrosian. 2018. Common raven movement and space use: influence of anthropogenic subsidies within greater sage-grouse nesting habitat. Ecosphere 9:e02348.

Harveson, L. A., M. E. Tewes, N. J. Silvy, and J. Rutledge. 2000. Prey use by mountain lions in southern Texas. Southwestern Naturalist 45:472–476.

Ilse, L. M., and E. C. Hellgren. 1995. Spatial use and group dynamics of sympatric collared peccaries and feral hogs in southern Texas. Journal of Mammalogy 76:993–1002.

Imm, D. W., and K. W. McLeod. 2005. Plant communities. Pages 106–161 in J. C. Kilgo and J. I. Blake, editors. Ecology and management of a forested landscape: fifty years on the Savannah River Site. Island Press, Washington, D.C., USA.

Ivan, J. S., G. C. White, and T. M. Shenk. 2013. Using simulation to compare methods for estimating density from capture–recapture data. Ecology 94:817–826.

Keiter, D. A., and J. C. Beasley. 2017. Hog heaven? Challenges of managing introduced wild pigs in natural areas. Natural Areas Journal 37:6–16.

Keiter, D. A., A. J. Davis, O. E. Rhodes, F. L. Cunningham, J. C. Kilgo, K. M. Pepin, and J. C. Beasley. 2017. Effects of scale of movement,

detection probability, and true population density on common methods of estimating population density. Scientific Reports 7:9446.

Lapidge, S. J., B. D. Cowled, and M. Smith. 2004. Ecology, genetics and socio-biology: practical tools in the design of target-specific feral pig baits and baiting procedures. Proceedings of the Vertebrate Pest Conference 21:317–322.

Lavelle, M. J., N. P. Snow, J. W. Fischer, J. M. Halseth, E. H. VanNatta, and K. C. VerCauteren. 2017. Attractants for wild pigs: current use, availability, needs, and future potential. Journal of Wildlife Research 63:86.

Lavelle, M. J., N. P. Snow, J. M. Halseth, E. H. VanNatta, H. N. Sanders, and K. C. VerCauteren. 2018. Evaluation of movement behaviors to inform toxic baiting strategies for invasive wild pigs (*Sus scrofa*). Pest Management Science 74:2504–2510.

Lewis, J. S., M. L. Farnsworth, C. L. Burdett, D. M. Theobald, M. Gray, and R. S. Miller. 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. Scientific Reports 7:44152.

Miller, R. S., S. J. Sweeney, C. Slootmaker, D. A. Grear, P. A. Salvo, D. Kiser, and S. A. Shwiff. 2017. Cross-species transmission potential between wild pigs, livestock, poultry, wildlife, and humans: implications for disease risk management in North America. Scientific Reports 7:7821.

Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2289–2301.

Murray, M. H., D. J. Becker, R. J. Hall, and S. M. Hernandez. 2016. Wildlife health and supplemental feeding: a review and management recommendations. Biological Conservation 204:163–174.

National Climatic Data Center. Station USC00380072 in Aiken, SC and USW00012921 in San Antonio, TX. https://www.ncdc.noaa.gov/cdo-web/. Accessed 19 Feb 2020.

Newsome, T. M., G. Ballard, C. R. Dickman, P. J. S. Fleming, and R. van de Ven. 2013. Home range, activity and sociality of a top predator, the dingo: a test of the resource dispersion hypothesis. Ecography 36:914–925.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514.

Pepin, K. M., N. P. Snow, and K. C. VerCauteren. 2020. Optimal bait density for delivery of acute toxicants to vertebrate pests. Journal of Pest Science. https://doi.org/10.1007/s10340-020-01196-9

Pimental, D. 2007. Environmental and economic costs of vertebrate species invasions into the United States. Pages 2–8 *in* G. W. Witmer, W. C. Pitt, and K. A. Fagerstone, editors. Managing vertebrate invasive species: proceedings of an international symposium. U.S. Department of Agriculture—Animal and Plant Health Inspection Service—Wildlife Services—National Wildlife Research Center, Fort Collins, Colorado, USA. https://www.aphis.usda.gov/wildlife_damage/nwrc/symposia/invasive_symposium/nwrc_TOC_index.shtml. Accessed 12 Feb 2020.

Poché, R. M., N. Davis, D. M. Poché, G. A. Franckowiak, B. Tseveenjav, D. A. Hartman, and L. Polyakova. 2019. Development of a low-dose warfarin bait for controlling feral hogs. Crop Protection 120:134–140.

Poché, R. M., D. Poché, G. Franckowiak, D. J. Somers, L. N. Briley, B. Tseveenjav, and L. Polyakova. 2018. Field evaluation of low-dose warfarin baits to control wild pigs (*Sus scrofa*) in north Texas. PLoS ONE 13:e0206070.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. Journal of Mammalogy 85:483–490.

Saunders, G., B. Kay, and H. Nicol. 1993. Factors affecting bait uptake and trapping success for feral pigs (*Sus scrofa*) in Kosciusko National Park. Wildlife Research 20:653–665.

Shapiro, L., C. Eason, C. Bunt, S. Hix, P. Aylett, and D. MacMorran. 2016. Efficacy of encapsulated sodium nitrite as a new tool for feral pig management. Journal of Pest Science 89:489–495.

Singh, N. J., L. Börger, H. Dettki, N. Bunnefeld, and G. Ericsson. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecological Applications 22:2007–2020.

Snow, N. P., J. A. Foster, J. C. Kinsey, S. T. Humphrys, L. D. Stapes, D. G. Hewitt, and K. C. VerCauteren. 2017. Development of toxic bait to control invasive wild pigs and reduce damage. Wildlife Society Bulletin 41:256–263.

Snow, N. P., J. M. Halseth, M. J. Lavelle, T. E. Hanson, C. R. Blass, J. A. Foster, S. T. Humphrys, L. D. Staples, D. G. Hewitt, and K. C. VerCauteren. 2016. Bait preference of free-ranging feral swine for delivery of a novel toxicant. PLoS ONE 11:e0146712.

Snow, N. P., M. J. Lavelle, J. M. Halseth, M. P. Glow, E. H. VanNatta, A. J. Davis, K. M. Pepin, L. D. Staples, and K. C. VerCauteren. 2019. Exposure of a population of invasive wild pigs to simulated toxic bait containing biomarker: implications for population reduction. Pest Management Science 75:1140–1149.

Snow, N. P., and K. C. VerCauteren. 2019. Movement responses inform effectiveness and consequences of baiting wild pigs for population control. Crop Protection 124:104835.

Sorenson, A., F. M. van Beest, and R. K. Brook. 2014. Impacts of wildlife baiting and supplemental feeding on infectious disease transmission risk: a synthesis of knowledge. Preventive Veterinary Medicine 113:356–363.

Sweitzer, R. A., G. S. Ghneim, I. A. Gardner, D. V. Vuren, B. J. Gonzales, and W. M. Boyce. 1997. Immobilization and physiological parameters associated with chemical restraint of wild pigs with Telazol® and xylazine hydrochloride. Journal of Wildlife Diseases 33:198–205.

Tisdell, C. A. 1982. Wild pigs: environmental pest or economic resource? Pergamon Press, Ruschcutters Bay, New South Wales, Australia.

Wang, M., and V. Grimm. 2007. Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex araneus*. Ecological Modelling 205:397–409.

West, B. C., A. L. Cooper, and J. B. Armstrong. 2009. Managing wild pigs: a technical guide. Human–Wildlife Interactions Monograph 1.

Wilkins, N., R. D. Brown, and D. W. Steinbach. 1999. Reducing risks to wildlife from corn contaminated with aflatoxins. Department of Wildlife and Fisheries, Texas A&M University, Annual Report (1997–1998), College Station, USA.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82–90.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's web-site. This includes a document with all the models for each response variable and their corresponding AIC and ΔAIC values.