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### Effects of Ungulate-proof Fencing on Space Use by Wild Pigs

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## RESEARCH ARTICLE

# Effects of ungulate-proof fencing on space use by wild pigs

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## Abstract

Wild pigs (*Sus scrofa*) are a highly adaptable species that have invaded many regions and cause significant damage throughout the world. Ungulate-proof fencing is increasingly used in conjunction with other control techniques to manage wild pig populations. However, little is known about how fencing affects wild pig space use behaviors and whether any changes may be exploited to increase efficacy of control activities. Our goal was to understand how wild pigs altered their space use behaviors in response to newly constructed fencing. Specifically, we examined for changes in space use area (home range and core area), increases in overlap with conspecifics, and shifts in space use as ungulate exclusion fencing was constructed on northern Guam from February 2021 to March 2022. Wild pigs closer to the fence had decreased space use. For every 200 m nearer newly constructed fence, home ranges and core areas decreased approximately 15% and 16%, respectively. When individual wild pigs were enclosed by the fence, those animals increased their home range overlap with conspecifics by approximately 76% compared to wild pigs outside the fence. Wild pigs shifted their home ranges 3 to 9 times more during the first part of fence construction when 68% of the fence was completed compared to all other time

periods, with male wild pigs shifting greater distances than females by 1.15 times. The construction of ungulate fencing led to smaller space use areas of wild pigs on both sides of the fence and intensified use of the area inside the fence by wild pigs contained within (i.e., more overlap). Management activities nearer the fence should account for decreases in home range and core area size to maximize population control efforts (i.e., more densely spaced trap sites). Enclosed wild pigs should be eradicated quickly to minimize damages to sensitive flora and fauna and decrease disease risk from intensified movement behaviors inside the fence.

#### KEYWORDS

fencing, feral swine, Guam, home range overlap, space use, *Sus scrofa*, wildlife damage management

Wild pigs (*Sus scrofa*) are a highly adaptable species that have invaded many regions throughout the world (Barrios-García and Ballari 2012). Their ability to thrive in various environments is due in part to their generalist diet (Ballari and Barrios-García 2013, Keiter and Beasley 2017, Gray et al. 2020) and high reproductive potential (Comer and Mayer 2009, Snow et al. 2020). The presence of wild pigs in introduced and invasive ranges often has detrimental impacts to humans, agriculture, and ecosystems (Mayer 2009b, Barrios-García and Ballari 2012, Strickland et al. 2020). Wild pigs cause damage to the flora and fauna of native ecosystems through direct predation (Diong 1982, Wilcox and Van Vuren 2009, Jolley et al. 2010, McClure et al. 2018) soil disturbances from rooting and wallowing (Sierra 2001, Mayer 2009b), and alteration of plant community structure through dispersal and rooting (Dovrat et al. 2012, Boughton and Boughton 2014). Wild pigs also serve as a reservoir for bacteria, parasites, and viruses that pose a threat to wildlife, domestic livestock, and human health (Seward et al. 2004, Wyckoff et al. 2009, Wehr et al. 2018, Corn and Yabsley 2020). Additionally, wild pigs cause significant damage to agricultural crops, costing billions of dollars annually in the United States alone (Pimentel et al. 2000, Pimentel 2007, Anderson et al. 2016).

To mitigate the negative impacts, managers attempt to control populations of wild pigs to lessen their effects (Keiter and Beasley 2017, Ditchkoff and Bodenchuk 2020). A variety of management tools, including trapping, recreational hunting, agency shooting, Judas pigs, fencing, and in some places, toxicants, are available and recommended depending on goals of wild pig population management (McIlroy and Gifford 1997, Massei et al. 2011, Snow et al. 2017, Ditchkoff and Bodenchuk 2020). Often, an integrated pest management approach that combines multiple techniques to address the population is most effective (McCann and Garcelon 2008, Massei et al. 2011, Cox et al. 2022). However, permanently eliminating an established population of wild pigs from an area remains extremely challenging and may not be accomplished, in part because nearby wild pigs may re-invade (Mayer 2009a, Keiter and Beasley 2017).

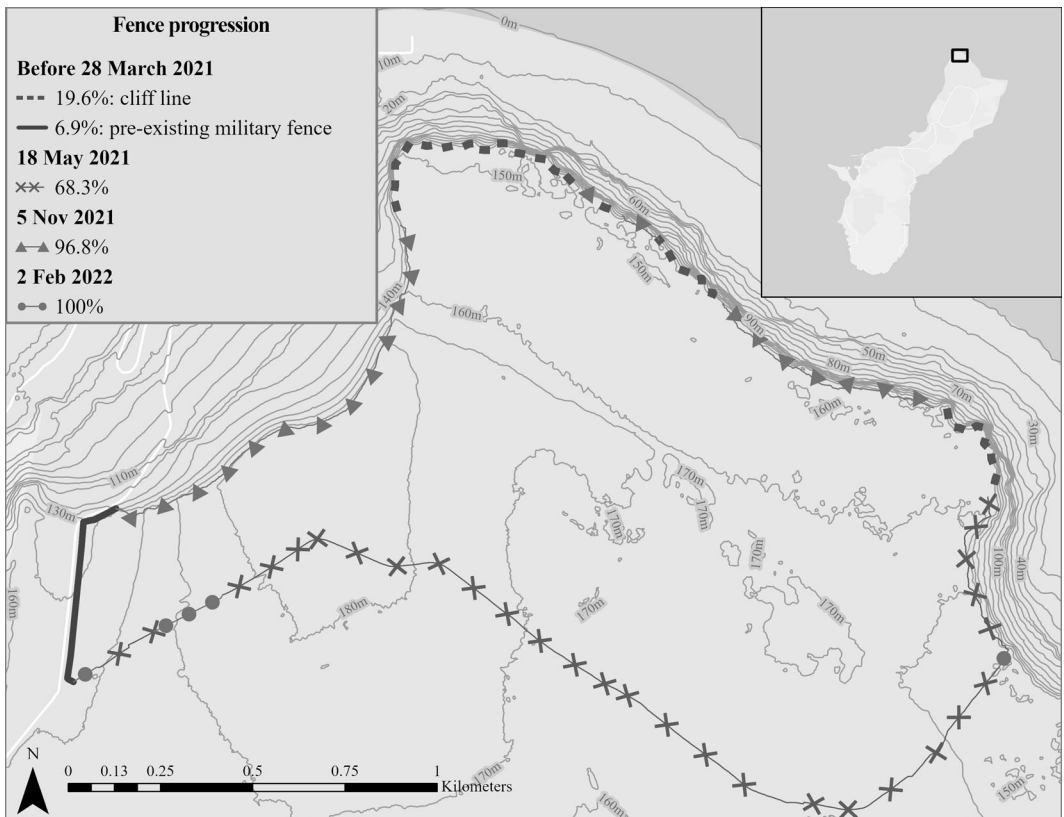
Ungulate-proof fencing is increasingly used in conjunction with other control methods to exclude wild pigs from an area or divide large areas into more manageable, contained units (Barrett et al. 1988, McCann et al. 2004, Garcelon et al. 2005, McCann and Garcelon 2008). Wild pigs must be removed as quickly as possible from the interior of the fence once construction is complete to mitigate possible negative secondary effects within the enclosed areas (Ditchkoff and Bodenchuk 2020). Also, if the fencing is damaged or breached, any incoming wild pigs must be quickly removed before a new population is established. It is currently unknown how fencing affects the movements of wild pigs both inside and outside of the fenced

area. Previous studies have investigated pig movement behaviors in response to environmental conditions (Clontz et al. 2021), trapping (Snow and VerCauteren 2019, Bastille-Rousseau et al. 2020), and varying eradication methods (Campbell et al. 2010, Fischer et al. 2016, Keuling and Massei 2021) as a way to enhance population control activities. Yet no studies have examined how fencing impacts on wild pig behavior could be exploited for similar aims.

Our goal was to understand how wild pigs changed their behaviors relative to construction and completion of a new ungulate exclusion fence on northern Guam. Specifically, we used global positioning system (GPS)-collar data collected from wild pigs to investigate the effect of fencing on home range and core area size, home range overlap, and home range shifts of wild pigs as an exclusion fence was constructed to completion.

## STUDY AREA

The study encompassed 11.4 km<sup>2</sup> and took place from February 2021 to March 2022 on the United States territory of Guam, the largest and southernmost island of the Marianas archipelago. The study site is located on the northernmost section of the island on the United States Marine Corps, Camp Blaz, and includes the Mason Live Fire Training Complex (MLFTRC; latitude, longitude: 13.63714, 144.85338). The MLFTRC was constructed as part of the military buildup for Camp Blaz, and the construction plan included enclosing a 2.37-km<sup>2</sup> area (Figure 1). Before the construction of the firing range, the land was part of United States



**FIGURE 1** Progression of exclusion ungulate fencing on the perimeter of Mason Live Fire Training Range Complex (MLFTRC), Guam, March 2021–February 2022. Service layer credits: Esri, NASA, and other contributors.

Anderson Air Force Base and was primarily used for military operations and munitions storage. The area is a limestone plateau that is defined by steep slopes and cliffs with elevation ranging from 0–194 m. The dominant landscape of the study site is native limestone karst forest with patches of scrub-shrub and grassland. The dominant flora includes native mapunyo (*Aglaia mariannensis*), Pacific banyan (*Ficus prolixa*), langiti (*Ochrosia mariannensis*), screwpines (*Pandanus* spp.), and invasive river tamarind (*Leucaena leucocephala*). Guam has a tropical marine climate and is hot and humid year-round. Average annual temperature is 27.8°C and annual rainfall is 213.3–294.6 cm (Gingerich et al. 2015). There are defined dry and wet seasons from January to June and July to December, respectively. During the study, average temperature was 28.3°C and total rainfall was 56.7 cm and 196.9 cm in dry and wet seasons, respectively.

Dominant fauna of the area includes the invasive brown tree snake (*Boiga irregularis*), wild pig (*Sus scrofa*), and Philippine deer (*Rusa marianna*). Wild pigs in Guam originated from domestic pigs brought to the island by Spanish colonizers in the late seventeenth century (Intoh 1986). Since that time, wild pigs have dispersed throughout the island and have been reported in high densities in some areas (Conry 1989). The native limestone karst forests contain many of Guam's native and endemic plant and animal species, some of which are protected or endangered. These forests evolved without the presence of large ungulates; therefore, the removal of invasive ungulates from these forests could aid in forest regeneration and restoration and promote increases to native wildlife populations (Kessler 2002).

## METHODS

### Fence installation and wild pig collaring

Construction on the exclusion fence began in late March 2021 (Figure 1). The exclusion fence consisted of a mixture of 2 fence types, all meant to be a barrier to invasive ungulate movements. Most of the ungulate-proof fence was constructed of 2.4-m-tall, chain link security fencing (3,762.8 m or 45.7% of entire perimeter). Prior to the decision to enclose the MLFTRC, 569.3 m (6.9% of entire perimeter) of this security fence was already installed on the perimeter from previous military construction. The second type of exclusion fence was composed of a 1.1-m-tall, galvanized hog panel fence with an additional 1.1 m of poly-netting secured above panels, with both materials attached to embedded t-posts (2,839.4 m or 34.5% of entire perimeter fence). In areas in the northern section of MLFTRC that consisted of cliff lines and steep slopes, the cliff line was considered a barrier to ungulate movements (1,625.0 m or 19.6% of entire perimeter). Exclusion fencing was not constructed along these cliff sections. We measured the length of fence in May 2021 and November 2021 when the fence was 68.3% and 95.8% completed, respectively. By February 2022 the area was fully enclosed. We created a fence treatment variable, which we referred to as fence progression, using the start and end dates of construction along with the 2 dates where we measured fence construction. The fence progression variable therefore corresponded to the completion of the fence (i.e., pre-fence construction, 68%, 96%, and 100%; Table S1, available in Supporting Information) and is correlated with time (i.e., date) of construction.

We captured wild pigs using corral traps baited with whole-kernel corn from February 2021 to December 2021. We placed traps in locations with signs of obvious wild pig activity (e.g., rooting, wallowing, feces, trails). We focused on deploying traps throughout the study area (i.e., within the perimeter of the exclusion fence, despite the fence not being fully constructed) in locations where we could haul traps. We considered wild pigs that were sexually mature with an estimated approximate mass >27 kg to be adults. We attempted to collar only 1–2 adult wild pigs per social group to minimize dependence among animals collared. In cases where 2 wild pigs were collared from the same captured group, 1 was a female and 1 was a male. We redeployed functional collars when pigs slipped them or died.

Once captured, we chemically immobilized adult pigs in traps using butorphanol-azaperone-medetomidine (BAM™) at target dosage of approximately 0.02 mL/kg (Ellis et al. 2019) via intramuscular injection. We released

non-target animals from traps once target animals were fully immobilized. We fitted target animals with uniquely identifiable ear tags (Allflex Two Piece Cattle Tags, Allflex USA, Dallas, TX, USA) and GPS collars (VERTEX Plus-2 Collar, VECTRONIC Aerospace GmbH, Berlin, Germany). We programmed collars to collect and store locations every 15 minutes and emit a very high frequency (VHF) signal from 0700 to 1900 local time. We monitored vital signs while the animals were immobilized, and regulated body temperatures, when necessary, with the use of ice packs, water, and shade. We reversed the chemical immobilants with atipamezole and naltrexone and monitored animals until they were fully ambulatory.

Overall, we monitored 43 adult pigs between February 2021 and March 2022. Three collars were never recovered from the field and 4 collars collected <20 days of valid data. We excluded all 7 from analyses. Therefore, we used GPS collar data from 36 individual pigs ( $n = 17$  females, 19 males) for a total of 8,775.4 collar days (range = 23.0–396.6 days).

We monitored wild pigs before, during, and after fence construction. We removed GPS collar data from the first 3 days after collaring to account for any behaviors associated with trapping and anesthesia effects. Additionally, we removed any potentially erroneous locations acquired with <4 satellites and with dilution of precision >10. Finally, because some wild pigs we collared appeared to be in the same social groups, we accounted for this potential pseudoreplication by grouping wild pigs into sounders when their home range overlap was >80% following methods from Snow and VerCauteren (2019). We conducted all data preparation, analysis, and modeling using Program R and RStudio (R Core Team 2020, R Studio Team 2020).

## Movement response variables

We estimated space use areas of collared pigs using utilization distributions (UDs). To estimate UD, we used a movement-based kernel density estimator (MKDE) from the package *adehabitatHR* (Calenge 2023) that accounted for serial autocorrelation of relocations (Benhamou and Cornelis 2010, Benhamou 2011). We considered fixes  $\leq 12$  m apart to be inactive and selected an upper limit of 45 minutes between fixes that were considered active. We defined the grid for an individual using 30-m cells and extents based on their minimum and maximum coordinates. We considered the 50% and 95% UD to be core areas and home ranges, respectively. We constructed UD for each of the 4 fence progressions described above. For each of 2 partially constructed fence progressions, we estimated UD using 4 weeks of locational data that consisted of 2 weeks of locations before and after the date associated with the fence progression measurements. We estimated UD pre- and post-construction by using 4 weeks of locational data, leading up to the start date and immediately following the completion date, respectively. We excluded any wild pigs monitored for <14 days during a 4-week fence progression period in UD estimation for that period (Table S1). Additionally, we chose to estimate seasonal space use metrics to contribute to the understanding of wild pig ecology. We constructed UD for both dry and wet seasons and included all wild pigs monitored >42 days during each season. This criterion resulted in a total of 31 wild pigs ( $n = 14$  females, 17 males) included in seasonal space use estimation.

To examine how construction of fencing affected shared space use, we calculated the average inter-individual (individual to every other individual) overlap for each wild pig at each fence progression. Specifically, we estimated kernel overlap of the 95% UD (i.e., home range) using the UD overlap index (UDO) in *adehabitatHR* (Calenge 2023). We used the same MKDE model and parameters as described above for home range estimation, with the exception of grid extent, which was adjusted to include the space use of all animals during the respective fence progression.

To examine whether the construction of the fence triggered any shifts in home ranges, we calculated a metric of home range shifts using a segmentation method for multivariate time series developed by Patin et al. (2020). This method identifies breakpoints in the relocations of wild pigs that correspond to rapid changes in mean location or rapid changes in variation of mean location, indicating shifts between home ranges. The breakpoints result in

stationary periods called segments, which then can be further distinguished into distinct stationary periods (i.e., differing home ranges), also referred to as states. Specifically, we used the `segclust2D` package to identify those breakpoints and the distances shifted between states, or home ranges, for each wild pig amongst the fence progression periods (Patin et al. 2020). To segment data in a computationally efficient manner, we randomly subsampled a single GPS relocation during each quarter of each day (i.e., 0001–0600, 0601–1200, 1201–1800, 1801–0000 hours). We set the segment length parameter, or the minimum duration of a state before and after a shift, to  $\geq 21$  days to ensure the model identified home range shifts rather than fine-scale behavior changes. We set the maximum number of states (i.e., 21-day segments) to 16 because it accommodated a shift occurring almost every 21 days on the longest deployed collars (max. deployment = 396 days) and limited the potential for oversegmentation that may occur when the given maximum number of states is too large. We visually inspected the Lavielle's criterium likelihood curve for each segmentation to confirm the optimal number of segments was identified (Lavielle 2005). Lastly, we summed the total number of shifts and averaged the distance shifted between home ranges during each fence progression period for every individual.

## Data analysis

We used 4 explanatory variables related to the exclusion fence to evaluate their effects on wild pig movements. First, we used fence progression described above. Second, we calculated the distance of home range centroid to the nearest part of the completed fence for each pig during each fence progression period. Third, we identified if each pig was effectively enclosed within the fence (i.e., fenced or unfenced) during each fence progression period. We termed this enclosure status and considered individuals enclosed in the fence if their home range centroid was located inside the fenced area or  $>75\%$  of their home range was inside the fenced area. Finally, we calculated the proportion of the home range perimeter that was bounded by the fence (i.e., proportion of estimated home range boundary within 25-m buffer of the fence).

Along with fence-related variables, we included 2 other variables in our analyses as explanatory variables that may have influenced movement responses: sex and season. Seasons in our study were defined by wet and dry periods; therefore, we used average daily precipitation (in cm) collected from Anderson AFB weather station as a covariate (station ID GHCND:GQC00914025, National Climatic Center; <https://www.ncdc.noaa.gov>). Prior to analyses, we estimated the Pearson's correlation coefficient for all explanatory variables. We considered variables where  $|r| > 0.5$  to be highly correlated and we did not include them in the same model. For *a priori* models containing highly correlated variables, we chose to retain the variable that made most sense biologically. We used generalized linear mixed models (GLMM) to quantify the effects of fencing and other covariates on each response variable.

We conducted separate model selections for each of the 5 response variables: home range area, core area, home range overlap, number of home range shifts, and distance between shifts. First, we determined the random effects structure by comparing 2 null models. The first model included individual wild pig as a random effect to account for repeated observations. The second model included individual wild pig nested within group to account for non-independence of individuals from the same social group. We used Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) to compare null models (Burnham and Anderson 2002). Only 2 individuals were in the same social group and the addition of the nested random effect did not improve any of our null models (i.e.,  $\Delta AIC_c > 2$ ). Therefore, we did not include social groupings as a random effect in our models.

We then generated 22 biologically relevant *a priori* models for each response variable, including interaction effects and the null model described above (Table S2, available in Supporting Information). We used GLMMs with gamma distributions and log links for response variables of home range size, core area size, and average shifting distance because they were continuous and right skewed. We used GLMMs with beta distributions and logit links



for home range overlap estimates because the proportion values were bounded between 0 and 1. Lastly, we used GLMMs with Poisson distributions with a log link for total shifts because it was non-negative, count data. We conducted all modeling analyses in Program R glmmTMB (Brooks et al. 2017).

To rank models within each model set, we used  $AIC_c$  and models within  $\Delta AIC_c > 2$  of the lowest ranked model were considered top competing models (Anderson and Burnham 2002, Burnham and Anderson 2004). From the set of top competing models, we considered our best model as the one with the lowest  $AIC_c$  and most parsimonious (fewest parameters; Anderson and Burnham 2002). To assess goodness of fit, we used package DHARMA (Hartig 2022) to test for significance of residual patterns and dispersion. We tested goodness of fit by estimating the trigamma conditional and marginal coefficients ( $R^2_{GLMMc}$  and  $R^2_{GLMMm}$ ) in program R, package MuMIn (Bartoń 2023) for all models except the beta regression models. For the beta models, we estimated the delta conditional and marginal coefficients. Lastly, we developed predictive graphs of significant relationships and 95% confidence intervals from the best models using ggeffects (Lüdtke 2018).

## RESULTS

### Space use

The average home range size for female wild pigs during the dry and wet season was 0.345 km<sup>2</sup> (SE = 0.051) and 0.278 km<sup>2</sup> (SE = 0.056), respectively. Male wild pigs had an average home range size of 0.735 km<sup>2</sup> (SE = 0.076) and 0.823 km<sup>2</sup> (SE = 0.167) in dry and wet seasons.

There were 3 competing top models for estimating home range size. The best fitting model included distance to fence, sex, and precipitation (Table 1). This model indicated that for approximately every 200 m nearer to the fence, home ranges shrunk by approximately 15% (Table 2; Figure 2). Also, on average male wild pigs had 88% larger home ranges than females. Although inclusion of precipitation in the model improved model fit, the data did not support an influence of precipitation on home range size ( $P = 0.924$ ). The other 2 models considered competing top models for estimating home range size both included distance to fence,

**TABLE 1** Highest ranked models from a generalized linear mixed model describing home range size, core area size, home range overlap, total home range shifts, and average distance shifted for wild pigs in Guam, March 2021–March 2022, with Akaike's Information Criterion ( $AIC_c$ ),  $\Delta AIC_c$ , log-likelihood (LL), and parameters ( $K$ ) used in model selection.

Model		$AIC_c$	$\Delta AIC_c$	LL	$K$
Home range size	~Sex + precipitation + distance to fence + fence progression	-67.72	0.00	44.06	9
	~Sex + precipitation + distance to fence + fence progression + enclosure status	-67.11	0.61	45.04	10
	~Sex + precipitation + distance to fence	-66.76	0.96	39.92	6
Core area size	~Sex + precipitation + distance to fence	-378.18	0.00	195.63	6
	~Distance to fence	-376.59	1.59	192.54	4
Home range overlap	~Sex + precipitation + enclosure status	-224.44	0.00	118.76	6
	~Sex + precipitation + enclosure status + proportion buffer	-223.80	0.65	119.53	7
	~Enclosure status	-222.62	1.82	115.56	4
Total home range shifts	~Fence progression	190.96	0.00	-90.10	5
Average distance shifted	~Sex	-25.26	0.00	17.12	4



**TABLE 2** The coefficient estimates or incidence rate ratios, 95% confidence intervals, and *P*-values for fixed effects and marginal ( $R^2_{\text{GLMMm}}$ ) and conditional ( $R^2_{\text{GLMMc}}$ ) coefficient estimates in the best generalized linear mixed models for home range size, core area size, home range overlap, total shifts, and average distance shifted for wild pigs in Guam, March 2021–March 2022. Asterisks indicate  $P < 0.05$ .

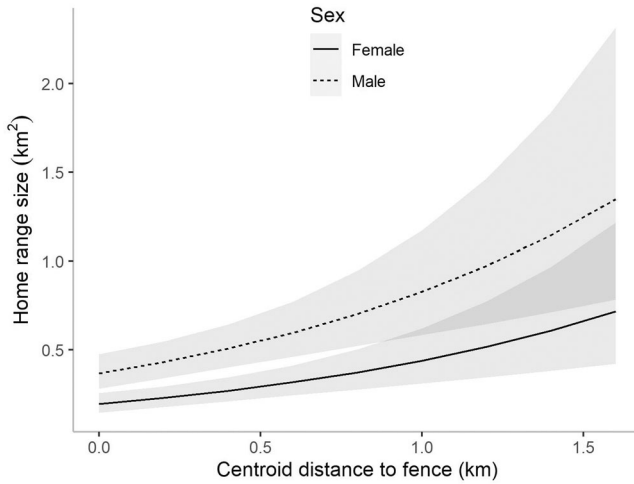
Response variable	Predictor	Estimate	95% CI	<i>P</i>	Observations	$R^2_{\text{GLMMm}}/R^2_{\text{GLMMc}}$ <sup>a</sup>
Home range size					85	0.329/0.754
	Intercept	0.19	0.13–0.28	<0.001*		
	Sex (male)	1.88	1.35–2.63	<0.001*		
	Distance to fence	2.26	1.55–3.28	<0.001*		
Core area size	Precipitation	1.03	0.61–1.71	0.924		
					85	0.110/0.729
	Intercept	0.04	0.03–0.05	<0.001*		
Home range overlap	Distance to fence	2.37	1.59–3.54	<0.001*		
					85	0.129/0.488
Total shifts	Intercept	0.14	0.10–0.18	<0.001*		
	Enclosure status (unfenced)	0.54	0.34–0.85	0.008*		
					84	0.227/0.298
	Intercept	0.34	0.17–0.68	0.002*		
Average distance shifted	Fence progression (68%)	4.68	2.28–9.58	<0.001*		
	Fence progression (96%)	1.64	0.70–3.84	0.251		
	Fence progression (100%)	0.46	0.10–2.19	0.332		
Average distance shifted					46	0.148/0.841
	Intercept	0.18	0.11–0.29	<0.001*		
	Sex (male)	2.15	1.12–4.13	0.022*		

<sup>a</sup>The trigamma  $R^2_{\text{GLMMm}}$  and  $R^2_{\text{GLMMc}}$  coefficients are estimated for home range size, core area size, total shifts, and average distance shifted, whereas the delta  $R^2_{\text{GLMMm}}$  and  $R^2_{\text{GLMMc}}$  coefficients are estimated for home range overlap.

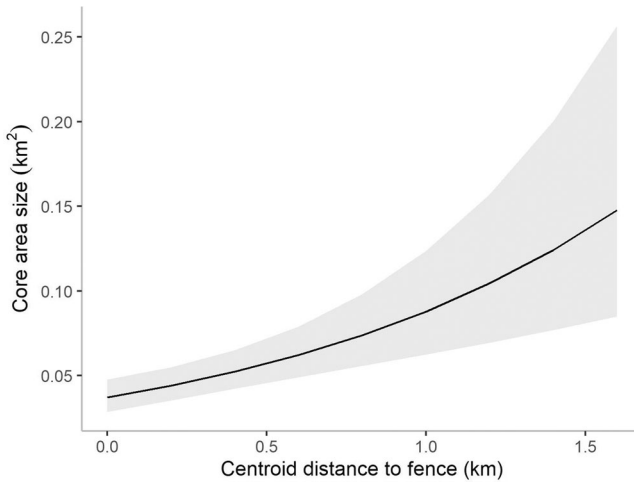
sex, precipitation, and fence progression, and one of these top models included pig enclosure status. Both top competing models showed home range size decreased by approximately 30% and 48% during 68% and 96% fence progressions, respectively, compared to pre-fencing (Table S3, available in Supporting Information). However, home range sizes did not differ between pre-fence and 100% fence progression ( $P \geq 0.117$ ). In a top competing model, including enclosure status improved the model fit, but there was no evidence for an influence on home range size ( $P = 0.158$ ).

Average core area size for female wild pigs during dry and wet seasons was 0.062 km<sup>2</sup> (SE = 0.009) and 0.051 km<sup>2</sup> (SE = 0.010). Male wild pigs had an average core area size of 0.109 km<sup>2</sup> (SE = 0.011) and 0.118 km<sup>2</sup> (SE = 0.021) during dry and wet seasons.

The best fitting model for estimating core area size included only distance to fence (Table 1). The model showed that for approximately every 200 m nearer the fence, core areas shrunk 16% (Table 2; Figure 3). A competing top model for estimating core area size included distance to fence, sex, and precipitation. On average, male wild pigs had 62% greater core area sizes than female wild pigs in the top competing model



**FIGURE 2** Predicted estimates of home range size with 95% prediction intervals for distance to the fence from the home range centroid as identified in the best generalized linear mixed model for wild pigs in northern Guam, March 2021–March 2022.

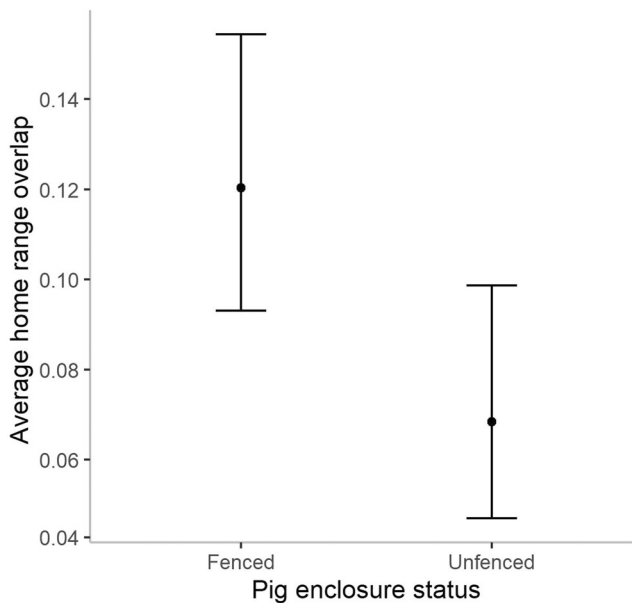


**FIGURE 3** Predicted estimates of core area size with 95% prediction intervals for distance to the fence from the home range centroid as identified in the best generalized linear mixed model for wild pigs in northern Guam, March 2021–March 2022.

(Table S3). The addition of precipitation improved model fit, but there was no evidence for an effect on core area size ( $P = 0.359$ ).

### Home range overlap

We found 60.6% of possible pairs of wild pigs in the dry season had overlap between their overall home ranges, of which the UDOI averaged 0.134 (SE = 0.008). In the wet season, 62.7% of possible pairs of wild pigs had overlap between their home ranges and the UDOI between them averaged 0.107 (SE = 0.010).



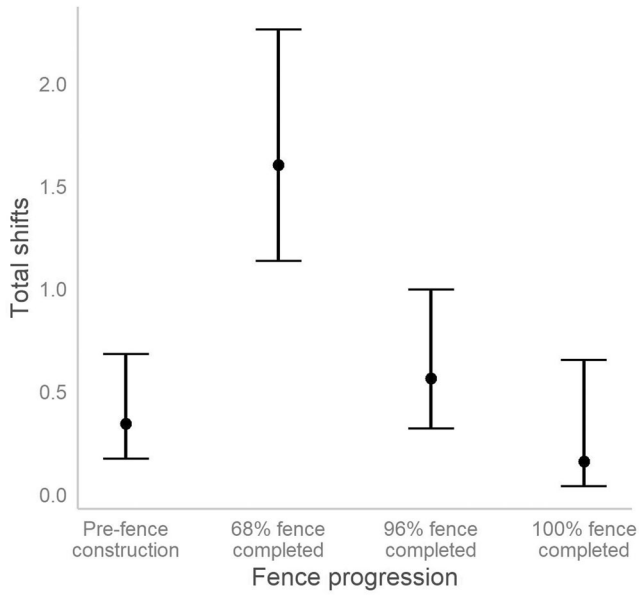
**FIGURE 4** Predicted estimates of average home range overlap with 95% prediction intervals for fenced and unfenced wild pigs in northern Guam, March 2021–March 2022. Fenced pigs are effectively enclosed or contained by ungulate-proof fencing, whereas unfenced describes pigs that are unconfined by fencing. Note the y-axis begins at 0.04.

Home range overlap was best modeled by pig enclosure status (Table 1). On average, wild pigs inside the fence enclosure had approximately 76% greater home range overlap than wild pigs outside the fence (Table 2; Figure 4). We identified 2 competing top models, and both included the addition of sex and precipitation in the model. One of these models also included the addition of proportion of home range bordered by the fence. Both top competing models showed a 15% decrease in conspecific overlap with every 0.2-cm increase of precipitation (Table S3). The addition of sex and proportion of home range bordered by the fence variables improved model fit for competing models, but there was no evidence for effects on home range overlap ( $P \geq 0.212$  and  $P = 0.198$ , respectively).

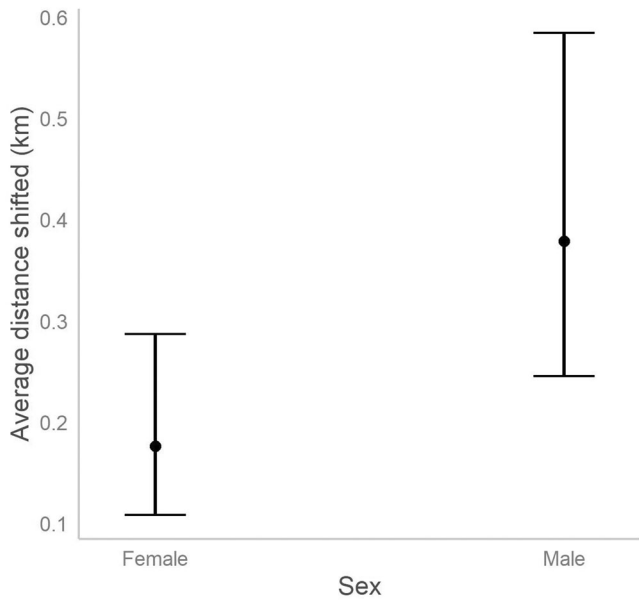
## Home range shifts

Twenty-six wild pigs were collared through >1 fence progression. Segmentation method estimated 75 total shifts for 35 individuals (range of shifts = 0–14). The average distance shifted between states was 303.7 m (SE = 41.5 m). Home range shifts were best modeled by fence progression (Table 1). On average, wild pigs were approximately 3–9 times more likely to shift their space use during the fence progression period when 68% of the fence was completed compared to all other fence progression periods (Table 2; Figure 5). All other periods had similar amounts of shifts. There were no competing top models (Table S2).

Finally, the best model for estimating average distance shifted between home range included the variable sex (Table 2; Figure 6). On average, male wild pigs shifted their home ranges 1.15 times greater distances than females. Model selection did not reveal any top competing models (Table S2).



**FIGURE 5** Predicted estimates of number of home range shifts with 95% prediction intervals for temporal periods indicating fence progression as identified in the best generalized linear mixed model for wild pigs in northern Guam, March 2021–March 2022.



**FIGURE 6** Predicted estimates of average distance shifted between states with 95% prediction intervals for male and female wild pigs in northern Guam, March 2021–March 2022. Note the y-axis begins at 0.1.

## DISCUSSION

Wild pigs living near a newly constructed exclusion fence will alter their behaviors to have smaller home ranges and core areas, and when enclosed by the fence will have increased overlap with other wild pigs. This is not surprising considering a fence confines the normal movements of wild pigs (Hone and Atkinson 1983, Reidy et al. 2008), but the results have some important implications for population control of wild pigs enclosed in a fenced area, and for native flora and fauna within the enclosure.

First, our results indicated the closer to the fence, the smaller the home range and core area size for all wild pigs, regardless of pig enclosure status. This suggests space movements were inhibited by fencing and supports other studies that demonstrated restricted pig movements beyond certain fencing structures (Hone and Atkinson 1983, Reidy et al. 2008, Lavelle et al. 2011, Laguna et al. 2022). Management and control techniques often exploit space use patterns of wild pigs for effective implementation; thus, control actions executed in conjunction with fencing should adjust strategies to plan for changes to wild pig space use closer to the fence. For example, Snow and VerCauteren (2019) and McRae et al. (2020) showed that visitation to bait sites by wild pigs were dependent on home range distance to the site, where probability of visit decreased with increasing distance to the bait site. Additionally, wild pigs are more likely to visit a bait site when sites are within their home range (McRae et al. 2020). To present an opportunity for all pigs to visit bait sites and ultimately be exposed to management actions (e.g., removal), bait sites should account for reduced space use near fencing.

Second, we determined fenced wild pigs have higher degrees of home range overlap than unfenced wild pigs. This increased home range overlap could result in overexploitation of resources, increased damage to habitat, and altered space use of native wildlife inhabiting the same enclosed areas. Management plans often first confine wild pigs in areas of conservation concern using fencing and then implement an eradication effort throughout the enclosed area (Barrett et al. 1988, Garcelon et al. 2005, McCann and Garcelon 2008, Ramsey et al. 2009, Cox et al. 2022). Intensified use of resources and increased interactions in these sensitive areas may be counterproductive for the overall goals of management, especially if eradication occurs over an extended period.

Additionally, increased home range overlap of enclosed wild pig populations may alter disease dynamics. An important metric describing disease transmission is contact rate (or association rate). Both Pepin et al. (2016) and Podgórski et al. (2018) demonstrated that association rates were dependent on distance between home ranges, where decreased distance between home ranges led to increased associations between pigs. Studies of other species have shown that home range overlap and contact rates are positively correlated (Robert et al. 2012, Vander Wal et al. 2013, Sanchez and Hudgens 2015). This is particularly concerning because fences are rarely 100% effective, especially relative to containing wild pigs (Reidy et al. 2008, Laguna et al. 2022). Wild pigs infected with a disease, such as African swine fever, could pose an increased risk to nearby wild pig populations, swine livestock, and humans.

Overall, our home range and core area estimates were considerably smaller than most reported estimates for wild pig populations (Gray et al. 2020), though other studies have noted smaller space use areas of insular wild pig populations (Baber and Coblenz 1986, Coblenz and Baber 1987, McIlroy 1989, Schlichting et al. 2016). Specifically, Baber and Coblenz (1986) reported similar small space use areas of wild pigs on Santa Catalina Island. Like Santa Catalina Island, Guam's geologic origin is volcanic and consists of very rugged terrain. The limestone karst forest is composed of jagged rocks, uneven terrain, and steep cliffs. It is possible the rugged topography naturally limits wild pig movements, resulting in smaller home ranges and core areas.

Some limitations to our findings exist. First, this study took place on northern Guam, which may represent other locations where wild pigs exist to lesser degrees (e.g., differences in climate or topography). Ungulate-proof fencing, though, is increasingly being used for wild pig management, including in Guam and other Pacific Islands (e.g., Hawaii; Kessler 2011, Massei et al. 2011, Wittenmyer and Quitazol 2014, Hess et al. 2020, Cox et al. 2022); therefore, we expect our results will be beneficial to protection of insular ecosystems. Also, the wild pigs in Guam have considerably

smaller space use than other mainland locations (Gray et al. 2020). Intersections or fragmentation by the fence of these smaller space use areas likely represent a disturbance to a significant portion of the overall range in comparison to populations with larger space use areas. Second, we did not have a control area; thus, it is difficult to fully parse out effects from season and fence progression. In particular, the differences seen in total number of shifts through fence progression could be intertwined with a seasonal effect. Despite these limitations, no other studies have evaluated the impact of fencing on enclosed wild pig movements to the authors' knowledge. Our results may provide guidance and insight for management in non-insular ecosystems with fencing. Lastly, we recommend that future studies evaluate whether daily movement activities of wild pigs are altered relative to a more fine-scale evaluation of fence construction (i.e., immediately pre- and post-fence intersection of a home range).

## MANAGEMENT IMPLICATIONS

Overall, understanding pig movement behaviors in response to fencing can provide important information for developing more effective and sustainable management and control strategies for wild pig populations, while also minimizing negative impacts on the native ecosystems. Our findings suggest that managers applying control efforts including trapping may need to decrease spacing between trap sites closer to fences to maximize population control activities. Additionally, once a fence has been constructed, contained wild pigs may need to be removed quickly to minimize damages to native flora and fauna, and minimize risk of disease spread. Lastly, we recommend managers using fencing for wild pig population control consider and plan for all potential consequences from altered pig space use as part of their integrated wild pig management strategy, especially if the fencing is used to control an emerging disease because it may increase disease spread within contain areas.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## ETHICS STATEMENT

All study procedures were approved by the United States Department of Agriculture, National Wildlife Research Center, Institutional Animal Care and Use Committee (QA-3312).

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## **SUPPORTING INFORMATION**

Additional supporting material may be found in the online version of this article at the publisher's website.

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1 **SUPPORTING INFORMATION**

2 19 April 2024

3 Koriakin et al. 2024. Effects of ungulate-proof fencing on space use of wild pigs. Journal of  
4 Wildlife Management.

5 **Table S1.** Sample size with average and median days monitored for wild pigs during each 4-  
6 week fence progression used for space use analyses, Guam, March 2021-March 2022.

Fence progression	Sample size	Average (days)	Median (days)
Pre-fence construction	24	23.1	24
68% fence completed	28	27.6	28
95% fence completed	22	27.1	28
100% fence completed	11	24.6	28

7

8 **Table S2.** All models from generalized linear mixed model describing home range size, core  
9 area size, home range overlap, total home range shifts, and average distance shifted for wild pigs  
10 with parameters (K), Akaike's information criterion (AIC<sub>c</sub>, Burnham and Anderson 2002),  
11  $\Delta$ AIC<sub>c</sub>, and log-likelihood (LL) used in model selection, Guam, March 2021-March 2022.

Response	Fixed effects	K	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	LL
Home range size	~Sex + precipitation + distance to fence + fence progression	9	-67.7	0.0	44.1
	~Sex + precipitation + distance to fence + enclosure status + fence progression	10	-67.1	0.6	45.0
	~Sex + precipitation + distance to fence	6	-66.8	1.0	39.9
	~Sex + precipitation + distance to fence + enclosure status	7	-65.3	2.5	40.4
	~Precipitation + distance to fence + sex x fence progression	12	-60.6	7.1	44.5
	~Sex + precipitation + proportion buffer	6	-60.3	7.4	36.7
	~Distance to fence	4	-60.1	7.6	34.3
	~Precipitation + enclosure status + distance to fence + fence progression x sex	13	-59.8	7.9	45.5
	~Sex + precipitation + proportion buffer + enclosure status	7	-59.8	8.0	37.6
	~Sex + precipitation + enclosure status + fence progression	9	-59.3	8.4	39.9
	~Sex + precipitation + fence progression	8	-57.1	10.6	37.5
	~Sex + precipitation + enclosure status x fence progression	12	-55.5	12.2	41.9
	~Proportion buffer	4	-54.9	12.8	31.7
	~Sex	4	-53.8	14.0	31.1
	~Sex + precipitation + enclosure status	6	-52.2	15.5	32.6
	~Sex + precipitation	5	-51.9	15.8	31.3
	~Precipitation + enclosure status + sex x fence progression	12	-51.6	16.1	40.0
	~Precipitation + sex x fence progression	11	-49.5	18.2	37.5
	~Enclosure status	4	-49.0	18.7	28.8
	~Null	3	-47.4	20.3	26.8
~Fence progression	6	-46.9	20.8	30.0	
~Precipitation	4	-45.8	21.9	27.2	
Core area size	~Sex + precipitation + distance to fence	6	-378.2	0.0	195.6
	~Distance to fence	4	-376.6	1.6	192.5
	~Sex + precipitation + distance to fence + enclosure status	7	-376.0	2.2	195.7

	~Sex + precipitation + distance to fence + fence progression	9	-373.9	4.2	197.2
	~Sex + precipitation + distance to fence + enclosure status + fence progression	10	-371.4	6.8	197.2
	~Sex + precipitation + proportion buffer	6	-370.5	7.7	191.8
	~Proportion buffer	4	-368.5	9.7	188.5
	~Sex + precipitation + proportion buffer + enclosure status	7	-368.2	10.0	191.8
	~Precipitation + distance to fence + sex x fence progression	12	-368.1	10.1	198.2
	~Sex + precipitation + fence progression	8	-366.0	12.1	192.0
	~Sex	4	-365.7	12.5	187.1
	~Precipitation + enclosure status + distance to fence + fence progression x sex	13	-365.3	12.9	198.2
	~Sex + precipitation + enclosure status + fence progression	9	-363.6	14.6	192.0
	~Sex + precipitation	5	-363.5	14.7	187.1
	~Fence progression	6	-363.1	15.1	188.1
	~Null	3	-362.4	15.7	184.4
	~Sex + precipitation + enclosure status	6	-361.2	17.0	187.1
	~Precipitation + sex x fence progression	11	-360.4	17.7	193.0
	~Enclosure status	4	-360.4	17.8	184.5
	~Precipitation	4	-360.2	17.9	184.4
	~Sex + precipitation + enclosure status x fence progression	12	-360.2	17.9	194.3
	~Precipitation + enclosure status + sex x fence progression	12	-357.9	20.3	193.1
Home range overlap	~Sex + precipitation + enclosure status	6	-224.4	0.0	118.8
	~Sex + precipitation + proportion buffer + enclosure status	7	-223.8	0.6	119.6
	~Enclosure status	4	-222.6	1.8	115.6
	~Sex + precipitation + distance to fence + enclosure status	7	-222.1	2.4	118.8
	~Sex + precipitation + enclosure status + fence progression	9	-221.9	2.5	121.2
	~Sex + precip	5	-221.7	2.8	116.2
	~Sex + precipitation + enclosure status x fence progression	12	-221.6	2.8	125.0
	~Precipitation + enclosure status + sex x fence progression	12	-220.8	3.6	124.6
	~Precipitation	4	-220.7	3.8	114.6
	~Sex + precipitation + proportion buffer	6	-220.0	4.4	116.5
	~Sex + precipitation + distance to fence	6	-219.9	4.6	116.5
	~Fence progression	6	-219.7	4.8	116.4

	~Sex + precipitation + fence progression	8	-219.7	4.8	118.8
	~Sex + precipitation + distance to fence + enclosure status + fence progression	10	-219.5	4.9	121.2
	~Sex	4	-219.1	5.4	113.8
	~Precipitation + enclosure status + distance to fence + fence progression x sex	13	-218.3	6.1	124.7
	~Precipitation + sex x fence progression	11	-218.2	6.3	121.9
	~Null	3	-218.2	6.3	112.2
	~Sex + precipitation + distance to fence + fence progression	9	-218.1	6.4	119.2
	~Proportion buffer	4	-217.0	7.4	112.8
	~Precipitation + distance to fence + sex x fence progression	12	-217.0	7.5	122.6
	~Distance to fence	4	-216.1	8.3	112.3
Total shifts	~Fence progression	5	191.0	0.0	-90.1
	~Sex + precipitation + fence progression	7	194.9	4.0	-89.7
	~Sex + precipitation + enclosure status x fence progression	11	196.4	5.4	-85.4
	~Sex + precipitation + enclosure status + fence progression	8	196.6	5.7	-89.4
	~Sex + precipitation + distance to fence + fence progression	8	197.1	6.1	-89.6
	~Sex + precipitation + distance to fence + enclosure status + fence progression	9	199.0	8.0	-89.3
	~Precipitation + sex x fence progression	10	202.1	11.1	-89.5
	~Precipitation + enclosure status + sex x fence progression	11	204.1	13.1	-89.2
	~Precipitation + distance to fence + sex x fence progression	11	204.3	13.4	-89.3
	~Precipitation + enclosure status + distance to fence + fence progression x sex	12	206.5	15.6	-89.1
	~Sex + precipitation + proportion buffer	5	209.9	19.0	-99.6
	~Sex + precipitation + proportion buffer + enclosure status	6	211.8	20.9	-99.4
	~Precipitation	3	213.5	22.5	-103.6
	~Sex + precipitation	4	214.9	24.0	-103.2
	~Sex + precipitation + distance to fence	5	216.9	25.9	-103.1
	~Sex + precipitation + enclosure status	5	216.9	26.0	-103.1
	~Sex + precipitation + distance to fence + enclosure status	6	219.0	28.1	-103.0
	~Proportion buffer	3	222.1	31.2	-107.9
	~Null	2	222.6	31.7	-109.2
	~Distance to fence	3	223.5	32.5	-108.6
	~Sex	3	224.2	33.2	-108.9
	~Enclosure status	3	224.5	33.5	-109.1



Average distance shifted	~Sex	4	-25.3	0.0	17.1
	~Sex + precipitation	5	-22.9	2.3	17.2
	~Null	3	-22.9	2.4	14.7
	~Sex + precipitation + fence progression	8	-22.8	2.5	21.3
	~Enclosure status	4	-22.3	3.0	15.6
	~Fence progression	6	-22.3	3.0	18.2
	~Sex + precipitation + enclosure status	6	-21.0	4.2	17.6
	~Proportion buffer	4	-21.0	4.3	15.0
	~Precipitation	4	-20.7	4.5	14.9
	~Distance to fence	4	-20.6	4.7	14.8
	~Sex + precipitation + proportion buffer	6	-20.4	4.8	17.3
	~Sex + precipitation + distance to fence	6	-20.3	5.0	17.2
	~Sex + precipitation + enclosure status + fence progression	9	-19.9	5.4	21.4
	~Sex + precipitation + distance to fence + fence progression	9	-19.7	5.5	21.4
	~Sex + precipitation + proportion buffer + enclosure status	7	-18.5	6.7	17.7
	~Sex + precipitation + distance to fence + enclosure status	7	-18.4	6.9	17.6
	~Precipitation + sex x fence progression	11	-16.9	8.4	23.3
	~Sex + precipitation + distance to fence + enclosure status + fence progression	10	-16.6	8.6	21.5
	~Precipitation + enclosure status + sex x fence progression	12	-13.2	12.0	23.3
	~Precipitation + distance to fence + sex x fence progression	12	-13.2	12.1	23.3
	~Precipitation + enclosure status + distance to fence + fence progression x sex	13	-9.3	15.9	23.3
	~Sex + precipitation + enclosure status x fence progression <sup>1</sup>	12	Na	Na	Na

<sup>1</sup>Model resulted in warnings of overfitting and did not produce valid results.

13 **Table S3.** The coefficient estimates, 95% confidence intervals, and p-values for fixed effects and  
 14 marginal ( $R^2_{GLMMm}$ ) and conditional ( $R^2_{GLMMc}$ ) estimates in the top competing generalized linear  
 15 mixed models for home range size, core area size, and home range overlap estimates for wild  
 16 pigs, Guam, March 2021-March 2022.

<i>Response variable</i>	Observations		$R^2_{GLMMm}/ R^2_{GLMMc}$ <sup>a</sup>	
	Predictor	Estimate	95% CI	<i>P</i>
<i>Home range size</i>	85		0.356/0.799	
	Intercept	0.11	0.07 - 0.19	< <b>0.001</b>
	Sex (male)	1.82	1.30 - 2.55	< <b>0.001</b>
	Distance to fence	2.12	1.42 - 3.17	< <b>0.001</b>
	Precipitation	7.01	1.73 - 28.44	<b>0.006</b>
	Fence progression (68%)	0.70	0.50 - 0.99	<b>0.044</b>
	Fence progression (96%)	0.51	0.31 - 0.82	<b>0.005</b>
	Fence progression (100%)	1.30	0.94 - 1.81	0.117
<i>Home range size</i>	85		0.365/0.812	
	Intercept	0.11	0.07 - 0.19	< <b>0.001</b>
	Sex (male)	1.72	1.21 - 2.43	<b>0.002</b>
	Distance to fence	1.97	1.31 - 2.96	<b>0.001</b>
	Precipitation	7.74	1.96 - 30.65	<b>0.004</b>
	Fence progression (68%)	0.67	0.47 - 0.94	<b>0.021</b>
	Fence progression (96%)	0.48	0.31 - 0.77	<b>0.002</b>
	Fence progression (100%)	1.29	0.93 - 1.79	0.123
	Enclosure status (unfenced)	1.20	0.93 - 1.53	0.158
<i>Core area size</i>	85		0.243/0.716	
	Intercept	0.03	0.02 - 0.04	< <b>0.001</b>
	Sex (male)	1.62	1.11 - 2.37	<b>0.013</b>
	Distance to fence	2.42	1.62 - 3.63	< <b>0.001</b>
	Precipitation	1.31	0.74 - 2.34	0.359
<i>Home range overlap</i>	85		0.217/0.558	
	Intercept	0.24	0.14 - 0.38	< <b>0.001</b>
	Sex (male)	0.74	0.47 - 1.18	0.212
	Precipitation	0.36	0.15 - 0.86	<b>0.022</b>
	Enclosure status (unfenced)	0.57	0.36 - 0.92	<b>0.020</b>
<i>Home range overlap</i>	85		0.241/0.550	
	Intercept	0.25	0.15 - 0.42	< <b>0.001</b>
	Sex (male)	0.76	0.49 - 1.20	0.247
	Precipitation	0.37	0.15 - 0.91	<b>0.030</b>

Enclosure status (unfenced)	0.54	0.34 - 0.86	<b>0.010</b>
Proportion buffer	0.35	0.07 - 1.73	0.198

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<sup>a</sup>The trigamma  $R^2_{GLMMm}$  and  $R^2_{GLMMc}$  coefficients are estimated for home range size, core area size, total shifts, and average distance shifted whereas the delta  $R^2_{GLMMm}$  and  $R^2_{GLMMc}$  coefficients are estimated for home range overlap.