

Seasonal Variation in Space Use and Territoriality in an Invasive Large Mammal (*Sus Scrofa*)

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Abstract

An individual's spatial behavior is shaped by social and environmental factors and provides critical information about population processes to inform conservation and management actions. Heterogeneity in spatial overlap among conspecifics can be evaluated using estimates of home ranges and core areas and used to understand factors influencing space use and territoriality. To understand and test predictions about spatial behavior in an invasive large mammal, the wild pig (*Sus scrofa*), we examined variation in space use between sexes and seasons. We predicted that if animals were territorial that there would be a reduction in space-use overlap when comparing overlap of home ranges (HR-HR), to home ranges and core areas (HR-CA), and in-turn to core areas (CA-CA). Home ranges and core areas were estimated for 54 wild pigs at Buck Island Ranch, FL from GPS telemetry data. Overlap indices were calculated to estimate the strength (space-use overlap) and number of potential interactions within three wet seasons (June-October) and two dry seasons (December-April). Across all seasons, males exhibited larger home ranges compared to females (M = 10.36 ± 0.79 km² (\pm SE), F = 3.21 ± 0.16 km²) and interacted with a greater number of individuals than females. Home range size and strength of interactions did not vary between wet and dry seasons. Consistent with our predictions, wild pigs appeared to exhibit territorial behavior, where strength of overlap decreased when comparing HR-HR to HR-CA and HR-CA to CA-CA. Strength of overlap varied by sex, which was lowest between females, intermediate between females and males, and greatest between males. Our framework can be used to understand patterns of space use and territoriality in populations, which has important implications in understanding population processes and how pathogens and parasites might spread within and among populations.

Introduction

Spatial behavior through time can be characterized by an individual's home range and territory. Home ranges are selected by animals to maximize their survival and reproduction, with territories traditionally defined as a reduced portion of the home range that is actively defended or exclusively used^{1,2,3,4}. Spatial overlap of individuals influences intraspecific interactions, which can drive population processes such as disease transmission⁵, survival^{6,7}, competition⁸, and reproduction⁹. The relationship between the spatial organization of a species and dynamic interaction among individuals is expected to vary based on both behavioral and environmental factors.

Variation in spatial interactions among animals can identify the selective pressures that shape spatial behavior. Differences between males and females in spatial behavior are related to differing reproductive strategies and spatial requirements allometrically scaling with body size^{10,11,12}, which can influence home range size¹³ and habitat use¹⁴. Seasonal changes in behavioral and environmental influences can also modify spatial behavior and influence overlap and association of conspecifics^{13,15,16,17}. Isolating factors that influence heterogeneity in spatial overlap can improve management and conservation decisions by identifying important time periods for disease transmission¹⁹, intraspecific competition⁸, and management actions¹⁹. Despite the growing evidence that spatial relationships affect a diverse

range of socio-ecological processes²⁰, variation in spatial overlap patterns between sexes and seasons is poorly understood for many species and is dependent on the individual's spatial organization.

Territorial behavior can increase an individual's fitness by excluding conspecifics from areas containing limiting resources, including food, cover, and mates. There is considerable variation, however, in how territories are defined and interpreted^{3,4} and they are often approximated by estimating core areas (i.e., areas of high probability of use within an animal's home range^{21,22,23}). Although the identification of core areas can be subjective, territoriality can be identified by examining overlap between adjacent individual's home range and core areas^{24,25,26}. Non-territorial species are expected to overlap with conspecifics at random which would result in overlap with a similar number of individuals in home ranges and core areas (Fig. 1). Conversely, territorial behavior creates spatial heterogeneity in the number and strength of conspecific interactions, leading to reduced overlap of core areas compared to home ranges (Fig. 1). In the paradigm proposed by Burt (1943)¹ and Schoener (1968)², territorial species overlap in their home ranges but have exclusive core areas and thus home ranges do not overlap core areas between neighboring individuals (Fig. 1; Fig. 2). Other studies have defined territoriality as occurring when core areas are mutually exclusive between animals, but home ranges overlap with core areas of adjacent individuals^{24,27,26,23,28} (Fig. 1; Fig. 2). It is predicted that if animals are territorial that there will be a reduction in spatial overlap when comparing overlap of home ranges (HR-HR), home ranges and core areas (HR-CA), and core areas (CA-CA) (Fig. 1). If animals are not territorial and spatial overlap among individuals is random, then it would be predicted that overlap would be similar when comparing HR-HR, HR-CA, and CA-CA (Fig. 1). Spatial overlap patterns could be used to quantify territoriality in many species and across a range of different social structures, but this approach could be particularly useful for species that exhibit heterogeneity in space use yet lack conspicuous territorial behaviors or exclusive core areas.

Wild pigs, *Sus scrofa*, are a large-bodied, gregarious species with an expansive native and invasive range, ecological role as an ecosystem engineer, and complex socio-spatial behavior^{29,30,31,32}. Seasonal wild pig home ranges can vary inversely with forage availability^{33,34,35,36,37,38}, which could influence spatial overlap^{39,40} and territorial patterns^{8,40}. Although territorial patterns have been predicted for wild pigs⁴¹, previous studies have provided conflicting evidence. Female groups are argued to be territorial with other female groups where groups overlap in their home ranges, but exhibit mutually exclusive core areas^{27,42,43}. This pattern, however, is not detected in other systems^{35,44,45}, and the role of territoriality in wild pig social structure is unclear. Males are reported to be less territorial than females (but see Boitani et al.1994³⁵), with males exhibiting larger home ranges that overlap with both sexes⁴⁶. How home range size, spatial overlap, and territoriality vary across seasons has not been widely evaluated for wild pigs and it is unclear how different behavioral and environmental factors influence space-use overlap.

Here we examined variation in the spatial behavior of wild pigs and used this information to understand patterns of territoriality. Our first objective was to examine variation in home range size and spatial overlap between sexes within a single season. We expected that males would 1) exhibit larger home

ranges, 2) interact with a greater number of conspecifics within their home ranges, and 3) exhibit increased intra-sexual space-use overlap compared to females^{46,47}. Our second objective was to evaluate how home range size and space-use overlap varied seasonally. Assuming forage availability to be lower during the dry season than the wet season^{48,49}, we predicted that home range size and space-use overlap would be greater during dry seasons because animals would use larger areas to acquire sufficient resources³⁸. Conversely, if resources are more concentrated and limiting during the dry season, then wild pigs might exhibit less space-use overlap during this season. Our third objective was to use measures of spatial overlap to evaluate territoriality in wild pigs among years and between wet and dry seasons. If wild pigs exhibited territoriality, we expected that spatial overlap among individuals would be greatest for home range to home range (HR-HR) interactions, reduced for home range to core area (HR-CA) interactions, and lowest for core area to core area (CA-CA) interactions (Fig. 1). We predicted that males and females would differ in their spatial overlap, with females exhibiting more exclusive core areas. Territoriality was expected to be strongest during the dry season as resources are assumed to be more limiting.

Results

Spatial data from 54 individuals was used to create 80 seasonal wild pig home ranges across 5 seasons, with the number of monitored individuals and sex ratio varying by season (Table 1). Following predictions, males and females differed in home range size and space use metrics within seasons (Table 1). Females had smaller home ranges than males in all seasons (Table 1; $p < 0.001$), but home ranges did not differ in size seasonally within sexes (Table 1; Female: $p = 0.86$, Male: $p = 0.99$). Between males and females, degree did not differ in any season (p -values ranged from 0.12–0.89), although males overlapped with a greater number of individuals than females in all seasons (Table 2). Similarly, interacting males exhibited greater UDOI values than interacting females in all seasons except the Wet 2017 season (Figs. 3a and S1) where one dyad of females overlapped extensively in their home ranges (UDOI = 0.567). Interactions among males did not differ from interactions among females in any season (p values ranged from = 0.17–0.61). Across all seasons, space-use overlap of interacting male home ranges averaged 0.212 (± 0.045 S.E.) and interacting female home ranges averaged 0.099 (± 0.029). We did not detect differences in UDOI between seasons when evaluating HR-HR interactions of all individuals ($p = 0.21$).

Table 1

Average (Ave.) seasonal home range and core area sizes (km²) for wild pigs at Buck Island Ranch, FL. Home range information was divided by sex (F:female, M:male) and season (wet or dry) with sample size (n), standard error (S.E.), minimum values (Min.), and maximum values (Max.).

Season	Sex	n	Home Range				Core Area			
			Ave.	S.E.	Min.	Max.	Ave.	S.E.	Min.	Max.
Wet 2015	F	6	3.54	0.43	1.94	6.67	0.54	0.06	0.27	1.02
	M	6	10.71	1.33	4.75	23.25	1.22	0.17	0.35	2.48
Dry 2016	F	10	3.67	0.50	1.22	5.77	0.44	0.07	0.17	0.71
	M	13	10.55	1.83	4.70	14.51	1.14	0.19	0.56	1.71
Wet 2016	F	11	3.38	0.65	1.26	5.65	0.41	0.06	0.17	0.53
	M	6	9.32	1.59	2.97	13.15	1.06	0.21	0.35	1.67
Dry 2017	F	8	3.51	0.51	1.85	6.80	0.48	0.09	0.11	0.93
	M	6	10.23	1.87	2.45	14.96	1.38	0.29	0.54	2.28
Wet 2017	F	8	3.71	0.25	2.47	4.56	0.57	0.06	0.31	0.87
	M	6	10.93	3.14	1.61	22.97	1.36	0.40	0.08	2.81

Table 2

Seasonal estimates of degree (number of animals an individual overlapped with in space use) for female (F) and male (M) wild pigs at Buck Island Ranch, Florida. We estimated degree among home ranges (HR-HR), between home ranges and the individual's core area (HR-CA), and among core areas (CA-CA). Degree information includes standard error (S.E.), minimum values (Min.), and maximum values (Max).

a. HR-HR	Wet 2015		Dry 2016		Wet 2016		Dry 2017		Wet 2017	
	F	M	F	M	F	M	F	M	F	M
Average	5.00	7.17	6.10	11.00	4.73	6.67	3.13	4.83	2.50	3.00
S.E.	0.84	0.79	0.97	0.93	0.84	1.15	0.64	1.11	0.38	0.52
Min.	2	4	2	5	1	3	1	1	1	1
Max.	7	9	12	15	9	10	6	8	4	4
b. HR-CA	Wet 2015		Dry 2016		Wet 2016		Dry 2017		Wet 2017	
	F	M	F	M	F	M	F	M	F	M
Average	4.60	6.17	5.80	9.15	3.27	5.33	2.88	4.83	2.00	2.17
SE	0.93	0.83	1.01	0.99	0.56	1.12	0.67	1.11	0.27	0.60
Min	1	4	2	5	1	1	1	1	1	0
Max	6	9	12	14	6	9	6	8	3	4
c. CA-CA	Wet 2015		Dry 2016		Wet 2016		Dry 2017		Wet 2017	
	F	M	F	M	F	M	F	M	F	M
Average	2.60	4.17	3.60	6.92	2.45	4.17	2.38	4.50	0.75	1.33
SE	0.68	0.83	0.73	0.90	0.31	0.70	0.65	1.20	0.25	0.33
Min	0	1	1	3	1	1	0	0	0	0
Max	4	7	9	14	4	6	5	8	2	2

Wild pigs exhibited territoriality behavior, which was consistent with our predictions (Fig. 1 and Fig. 3a). The top model included the variable "level" (HR-HR, HR-CA, or CA-CA interactions) for both comparisons, and these top models accounted for the majority of model weights (Table 3a and 3b). Space-use overlap was greatest for HR-HR interactions (0.207 ± 0.035), intermediate for HR-CA interactions (0.098 ± 0.018) and lowest for CA-CA interactions (0.036 ± 0.008). Along with level, the sex of the individuals within the interacting dyad was included in the second ranked model for both comparisons (Table 3a and 3b). F-F interactions had the lowest space-use overlap values with similar overlap values for F-M interactions and M-M interactions. These trends hold true for UDOI across seasons except for Wet 2017 where overlap was generally low except for one dyad of females (UDOI = 0.567) resulting in greater F-F estimates of overlap

(Figure S1). Seasonal effects were not included in any top models and exhibited minimal model weight (Table 3a and 3b).

Table 3

Results of generalized mixed-effects linear-regression models evaluating variation in spatial overlap of wild pigs at Buck Island Ranch, FL. Spatial overlap was measured by utilization distribution of overlap index (UDOI, a. and b.) and degree (c. and d.). Models include sex (Sex), level (home range-home range (HR-HR), home range - core area (HR-CA), and core area - core area (CA-CA) overlap, and season. For UDOI, sex indicates the sex of the two interacting individuals (two females, female and male, and two males). For degree, sex is the sex of the individual used to determine degree. Model output includes the number of parameters (K), AIC values, Δ AIC values, AIC weights (w_i), and residual deviance (Dev.).

a. UDOI: HRHR-HRCA	K	AIC	ΔAIC	w_i	Dev.
Level	4	278.76	0.00	0.65	-135.34
Sex + Level	6	281.12	2.36	0.20	-134.47
Level + Season	8	283.06	4.30	0.08	-133.37
Level + Sex + (Level \times Sex)	8	283.72	4.96	0.05	-133.70
Level + Sex + Season	10	286.18	7.41	0.02	-132.84
Level + Season + (Level \times Season)	12	287.80	9.04	0.01	-131.55
null	3	312.65	33.88	0.00	-153.30
Sex	5	314.98	36.22	0.00	-152.42
Season	7	316.91	38.14	0.00	-151.33
Sex + Season	9	320.00	41.24	0.00	-150.80
Level + Sex + Season + (Level \times Sex \times Season)	32	325.50	46.74	0.00	-128.25
Sex + Season + (Sex \times Season)	17	335.39	56.63	0.00	-150.00
b. UDOI: HRCA-CACA	K	AIC	ΔAIC	w_i	Dev.
Level	4	-263.18	0.00	0.62	135.63
Sex + Level	6	-261.08	2.10	0.22	136.63
Level + Sex + (Level \times Sex)	8	-259.10	4.08	0.08	137.71
Level + Season	8	-258.61	4.56	0.06	137.47
Level + Sex + Season	10	-255.75	7.42	0.02	138.12
Level + Season + (Level \times Season)	12	-254.69	8.48	0.01	139.70
null	3	-234.41	28.76	0.00	120.23
Sex	5	-232.33	30.84	0.00	121.23
Season	7	-229.89	33.29	0.00	122.07
Sex + Season + (Sex \times Season)	9	-227.05	36.13	0.00	122.72

a. UDOI: HRHR-HRCA	K	AIC	ΔAIC	w_i	Dev.
Level + Sex + Season + (Level×Sex×Season)	32	-215.95	47.22	0.00	142.47
Sex + Season + (Sex×Season)	17	-211.53	51.65	0.00	123.46
c. Degree: HRHR-HRCA	K	AIC	ΔAIC	w_i	Dev.
Level + Sex + Season	9	693.70	0.00	0.85	-337.24
Sex + Season	8	697.28	3.58	0.14	-340.16
Sex + Season + (Sex×Season)	12	704.85	11.15	0.00	-339.35
Level + Season	8	706.57	12.87	0.00	-344.80
Season	7	710.18	16.48	0.00	-347.72
Level + Season + (Level×Season)	12	714.31	20.61	0.00	-344.08
Level + Sex + Season + (Level×Sex×Season)	22	722.23	28.53	0.00	-335.37
Sex + Level	5	728.00	34.30	0.00	-358.80
Level + Sex + (Level×Sex)	6	730.16	36.46	0.00	-358.80
Sex	4	731.70	37.99	0.00	-361.72
Level	4	738.97	45.27	0.00	-365.36
null	3	742.69	48.99	0.00	-368.27
d. Degree: HRCA-CACA	K	AIC	ΔAIC	w_i	Dev.
Level + Sex + Season	9	647.62	0.00	0.99	-314.20
Level + Season	8	661.24	13.61	0.01	-322.14
Sex + Season	8	663.74	16.11	0.00	-323.38
Level + Season + (Level×Season)	12	667.33	19.70	0.00	-320.59
Sex + Season + (Sex×Season)	12	672.05	24.43	0.00	-322.95
Sex + Season + (Sex×Season)	22	674.49	26.87	0.00	-311.50
Season	7	677.38	29.76	0.00	-331.32
Sex + Level	5	681.14	33.52	0.00	-335.37
Level + Sex + (Level×Sex)	6	682.31	34.69	0.00	-334.88
Level	4	692.60	44.98	0.00	-342.17
Sex	4	697.37	49.75	0.00	-344.56
null	3	708.86	61.24	0.00	-351.35

We also detected territorial patterns in degree which were explained by a three-way interaction between level, sex of the individual, and season (Table 3c and 3d). Degree was greatest for HR-HR interactions (5.77 ± 0.24), intermediate for HR-CA interactions (4.89 ± 0.22) and lowest for CA-CA interactions (3.49 ± 0.18 ; Table 3c and 3d, Fig. 3b and Figure S2). Males consistently overlapped with a greater number of individuals than females in all seasons (Table 2, Fig. 3b and Figure S2). Season was also included in the top model with beta coefficients positively correlated with the number of individuals monitored, suggesting that seasonal effects were at least partially due to differences in sampling intensity.

Discussion

Consistent with our predictions, wild pigs exhibited territoriality congruent with proposed patterns of strength and number of interactions. Female's expression of territoriality was more robust than males, with less space-use overlap between females in both home ranges and in core areas. This decreased strength of overlap by females compared to males supports that females appear to exhibit greater territoriality with neighboring females compared to associated males^{47,50} (Pepin et al. 2016; Podgórski et al. 2018). In addition, these same patterns suggest that males exhibit the greater potential to interact with conspecifics, which could influence important ecological processes, such as genetic structuring of populations and transmission of pathogens^{51,52} (Weber et al. 2013; Vander Waal 2016). Differences in the number of indirect interactions between males and females are likely due to differences in home range size, as individuals with larger home ranges are more likely to overlap with a greater number of neighboring animals^{53,54} (Harless et al. 2009; Lewis et al. 2017a), and in this study males exhibited larger home ranges than females.

Territoriality exists on a continuum and is influenced by the species' social structure and ecological conditions^{1,3,4} (Burt 1943; Kaufman 1984; Maher and Lott 1995). In our system, core areas were often not completely exclusive, where home ranges of neighboring wild pigs overlapped conspecific core-areas, indicating wild pigs do not conform to some traditional definitions of territoriality^{1,2} (Burt 1943; Schoener 1968). Exclusive use of areas is likely maintained by indirect communication^{27,55,56} (Gabor et al. 1999; Mendl et al. 2002; Marsh et al. 2011) and limited direct interactions^{47,50,57} (Mayer 2009; Pepin et al. 2016; Podgórski et al. 2018). Interactions within shared space may also be limited due to temporal partitioning via avoidance, site specific dominance, or priority of access to resources³ (Kaufman 1983). Evaluating how wild pigs interact in both time and space, particularly under contrasting resource availability could identify how spatial behavior varies with ecological conditions.

Although males and females exhibited varying sized home ranges and spatial behavior, seasonal variation in home range size and spatial overlap were not detected in wild pigs in this study. The absence of seasonal differences in spatial overlap may reflect more consistent forage availability in subtropical climates, which can stabilize spatial segregation patterns³⁹ (McLoughlin et al. 2000). Conversely, wild

pigs are often foraging below the soil surface by rooting, and utilization of these sub-surface resources may mitigate the reductions in above ground productivity during the dry season⁴⁸ (Singh and Yadava 1974). Additionally, while wild pigs at Buck Island have a birth pulse in the dry season (R. Boughton, unpublished data), breeding occurs year-round, and the reduction in female space use associated with parturition⁵⁸ (Kurz and Marchinton 1972) did not influence seasonal patterns. Other factors such as elevation^{33,59} (Singer 1981; D'Andrea et al. 2014) and the presence of agriculture⁶⁰ (Keuling et al. 2008) can influence seasonal space use by wild pigs but these factors were not present in this study, potentially limiting seasonal changes influencing space-use. Although environmental or behavioral factors may have eliminated the need for seasonal changes in spatial overlap, territorial patterns were consistently detected from the spatial behavior of wild pigs.

The conceptual framework that we presented (Fig. 1) could be used to evaluate species in other systems to understand patterns of space use and territoriality among animals. However, there are several considerations about our study and for future work. Wild pigs can form long-lasting social relationships³⁰ (Podgórski et al 2014), yet seasonal variation in the number and spatial arrangement of monitored wild pigs precluded us from evaluating territorial relationships of adjacent individuals through time. The presence of territoriality within wild pig populations suggests that the sharing of core areas between neighbors is limited and they may contain important and/or limiting resources⁶¹ (Maher and Lott 2000). Comparing habitat characteristics in core areas and shared home range space could identify limiting resources and improve our understanding of how resources shape territorial patterns in wild pigs³ (Kaufman 1983). Further, spatial interactions and territorial patterns could be evaluated in relation to important resources, such as mast producing trees, supplemental feeders, or at water locations where discrete temporal sharing of space likely occurs. Evaluation of how shared space is segregated temporally would identify the mechanisms maintaining territorial patterns of space use and inform transmission of pathogens^{47,62} (Lavelle et al. 2014; Pepin et al. 2016) affecting both livestock and humans^{63,64} (Gortázar et al. 2007; Miller et al. 2017). Ultimately, better understanding patterns of territoriality and space use between animals can inform management and conservation plans aimed at understanding social interactions, disease dynamics, and movement patterns of animals.

STUDY AREAS

Our work was conducted at Archbold's - Buck Island Ranch (27°10'N, 81°21'W, elevation 6–12 m), located in a biologically diverse area of central Florida⁶⁵ (Abrahamson et al. 1984). The study area (4,250 hectare) contains over 600 ephemeral wetlands and an extensive network of drainage ditches. Common tree species on the ranch include live oak (*Quercus virginiana*) and cabbage palm (*Sabal palmetto*) which are interspersed within extensive areas of bahiagrass (*Paspalum notatum*) and native C4 grasses. Average temperatures range from 26°C in July to 13°C in January⁶⁶ (Boughton and Boughton 2014). Rainfall averages 1,365 mm per year with more than 60% of precipitation occurring between June and September. There are two biologically distinct seasons based on temperature and rainfall, a dry (December – April) and wet (June – October) season.

Methods

Animal capture

Wild pigs were captured between May 2015 and May 2017 using open-topped box traps (2.5m deep *1.25m wide * 1.5m high) and corral traps (16ft diameter), both with drop doors. Traps were pre-baited for 10–14 days with soured corn. After capture, adult wild pigs were immobilized using Telazol® 50 mg/ml (Zoetis, Parsippany, New Jersey, USA) and AnaSed® 100mg/ml (Akorn Inc. Lake Forest, Illinois, USA) mixed following the recommendations of established TZX dosages (TZ, 4.40 mg/kg; X, 2.5 mg/kg^{67,68,69} (Ko et al. 1993; Gabor et al. 1997; Sweitzer et al.1997). During anesthesia wild pigs were measured, sexed, physiological samples taken for other studies and fitted with one of three global positioning system (GPS) collars (3300L Lotek Wireless Inc., Newmarket, Ontario, Canada; CatLog Gen 2 GPS, Perthold Engineering LLC, Dallas, Texas, USA 75243; or igot-U, Mobile Action Technology, Inc., Taiwan) that were programmed to record a location every 30 minutes. Wild pig capture and handling procedures were approved by and conducted in compliance with the with University of Florida Animal Care and Use Committee protocols (#201408495 and #201808495) and with Animal Research: Reporting In Vivo Experiments (ARRIVE) guidelines.

Space Use and Animal Interactions

We estimated home ranges and core areas using the Brownian bridge movement model⁷⁰ (BBMM), Horne et al. 2007) in the package “mkde”⁷¹ (Tracey 2014) in program R⁷² (R Development Core Team 2018). Home ranges were estimated using a 99.999% cumulative probability and core areas were estimated using an 80% cumulative probability (following Sawyer and Kauffman 2011⁷³; Fig. 2). A minimum of six weeks of GPS data were required for an individual to be included in analyses. Spatial data were available for 5 seasons (Wet 2015, Dry 2016, Wet 2016, Dry 2017, Wet 2017).

Overlap in space use was used to evaluate indirect interactions among individuals, which can be highly correlated with direct interactions (physical contact between individuals) and represents the potential for animals to interact^{74,75} (Vander Wal et al. 2014, Schauber et al. 2015). Spatial overlap is a useful metric to evaluate potential interactions when GPS data is available at different time periods among animals and when it is unclear what distance between concurrent GPS locations should be used to define an interaction^{54,74,75,76} (Robert et al. 2012; Vander Wal et al. 2014; Schauber et al. 2015; Lewis et al. 2017a). We estimated two overlap metrics that measure the strength (space-use overlap) and number (degree) of potential interactions. Space-use overlap among animals was estimated using the utilization distribution overlap index⁷⁷ (UDOI, Fieberg and Kochanny 2005), which is a normalized index ranging from 0, when there is no overlap, to > 1 if non-uniform utilization distributions exhibit a high degree of overlap. Degree measured the number of potential interactions by summing the number of animals an individual spatially overlapped with^{78,79} (Newman 2003; Wey et al. 2008).

Sex ratios and the number of individuals collared varied among seasons. Therefore, we evaluated variation in home range size and degree between males and females within seasons using t-tests. To evaluate differences in intra-sexual interactions, we compared UDOI values for all male-male and female-female home range interactions using t-tests. Seasonal patterns in home range size and space-use overlap of home ranges were evaluated using ANOVAs. Home range sizes were evaluated separately for males and females and UDOI values were pooled across sexes. We applied a Bonferroni correction to all results to minimize the risk of Type I error.

To evaluate patterns of territoriality, we used generalized mixed-effects regression models⁸⁰ (Bates et al. 2014) and AIC model selection⁸¹ (Burnham and Anderson 2002) to identify predictors of space-use overlap and degree. Specifically, we evaluated what factors were important predictors of overlap by comparing home range to home range interactions (HR-HR) with home range to core area interactions (HR-CA), as well as HR-CA interactions with core area to core area (CA-CA) interactions. For each interacting dyad (pair of individuals) per season, we estimated UDOI values from each interaction level (HR-HR, HR-CA, and CA-CA). Variation in UDOI was evaluated with a Gamma distribution because estimates were nonnegative and right-skewed. In models, random effects included the dyadic interaction, and fixed effects included the space use level, sexes within the dyad (female-female (F-F), female-male (F-M), or male-male (M-M)), season, and the interaction between level and sex. We calculated degree within seasons per individual for each space use level. Random effects included individual animal, and fixed effects included space use level, sex, season, the interaction between level and sex, and the three-way interaction between level, sex, and season. A negative binomial distribution was used to model degree because counts were overdispersed. For both UDOI and degree, 12 *a priori* models were identified that included the null model and all combinations of level, sex, season, and two interaction terms (Table 3). We ranked models using Akaike Information Criterion⁸² (Akaike 1973). We validated each model by graphically examining the residuals and inspecting the QQ-plot^{83,84} (Wilk and Gnanadesikan 1968, Zuur et al. 2009). All analyses were conducted in R version 3.5.2⁷² (R Core Team 2018) using package “lme4”⁸⁰ (Bates et al. 2014).

Declarations

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AUTHOR CONTRIBUTIONS

P.E.S. and J.S.L. conceived the study. P.E.S. wrote the paper with input from J.S.L., R.K.B., K.C.V., and R.S.M. R.K.B., W.A. and B.W. carried out fieldwork and P.E.S. analyzed the data with input from J.S.L. and R.S.M. R.S.M. and J.S.L. secured funding. All author(s) edited and approved the final manuscript.

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Figures

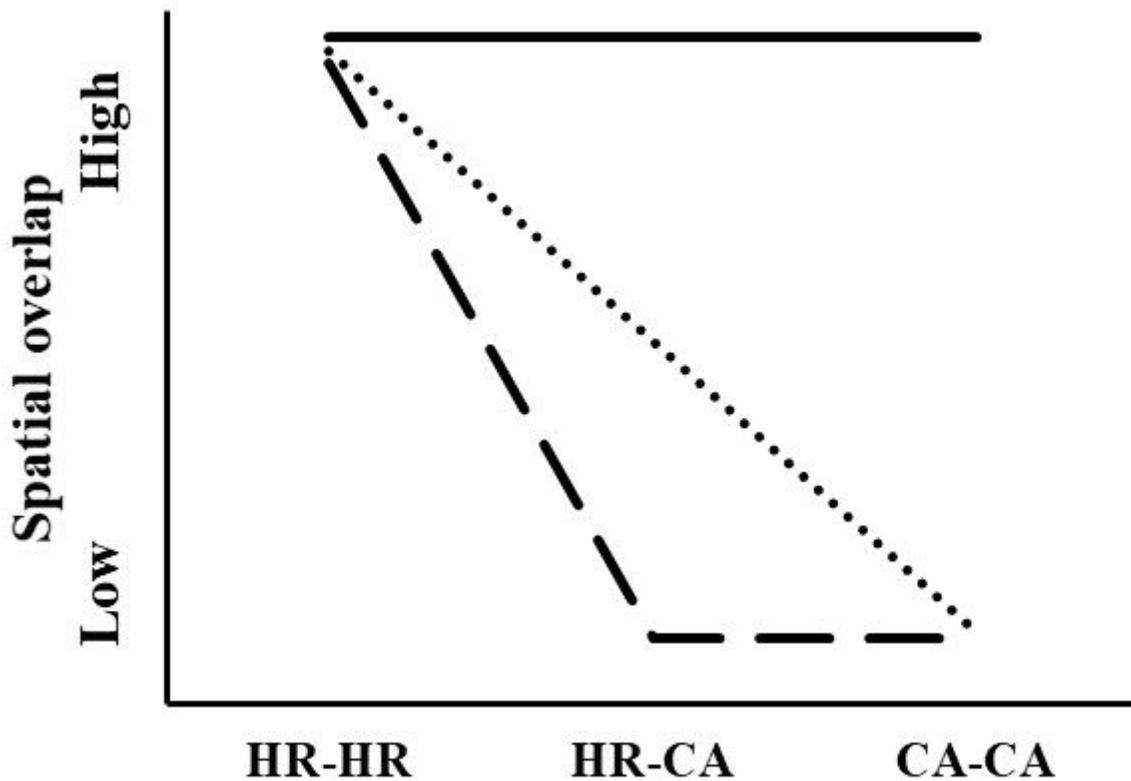


Figure 1

Predicted relationships evaluating territoriality among animals based on spatial overlap in home ranges (HR) and core areas (CA). Interactions can occur between two individual's home ranges (HR-HR), between one individual's home range and another individual's core area (HR-CA), or between two individual's core areas (CA-CA). If animals are not territorial, spatial overlap is expected to be the same across HR-HR, HR-CA, and CA-CA comparisons (solid line). If animals are territorial, it is expected that spatial overlap will decrease between HR-HR and HR-CA comparisons (dashed line; consistent with Burt (1943) and Schoener (1968)) or among HR-HR, HR-CA, and CA-CA comparisons (dotted line; consistent with Gabor et al. (1999), Darden and Dabelsteen (200), and Pierro et al. (2008)).

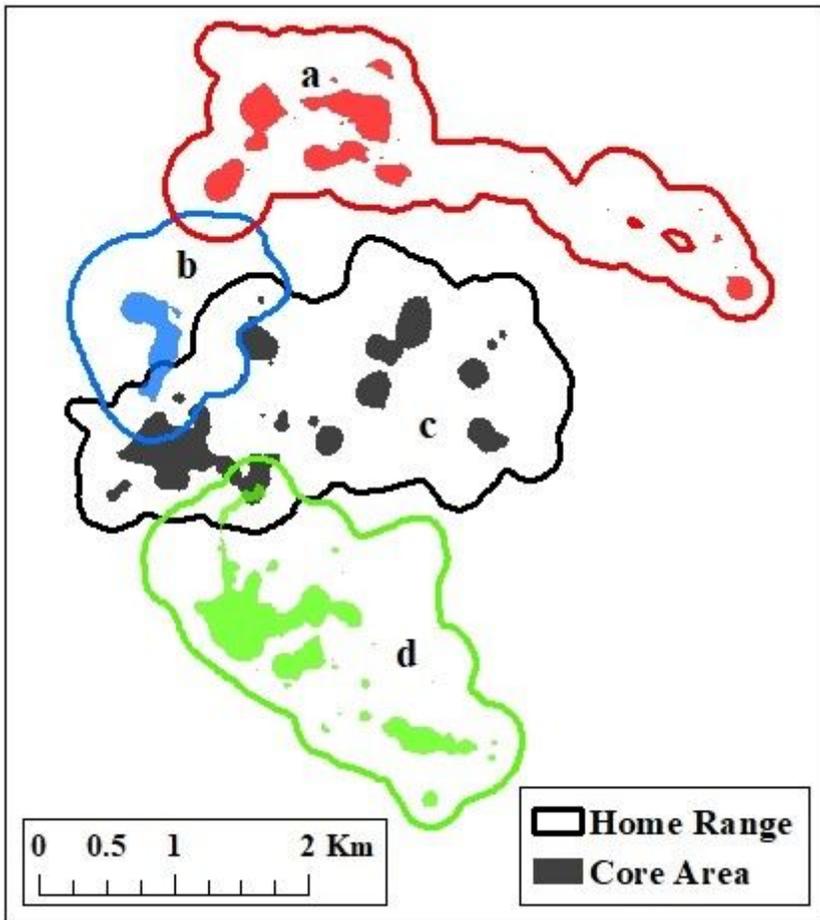
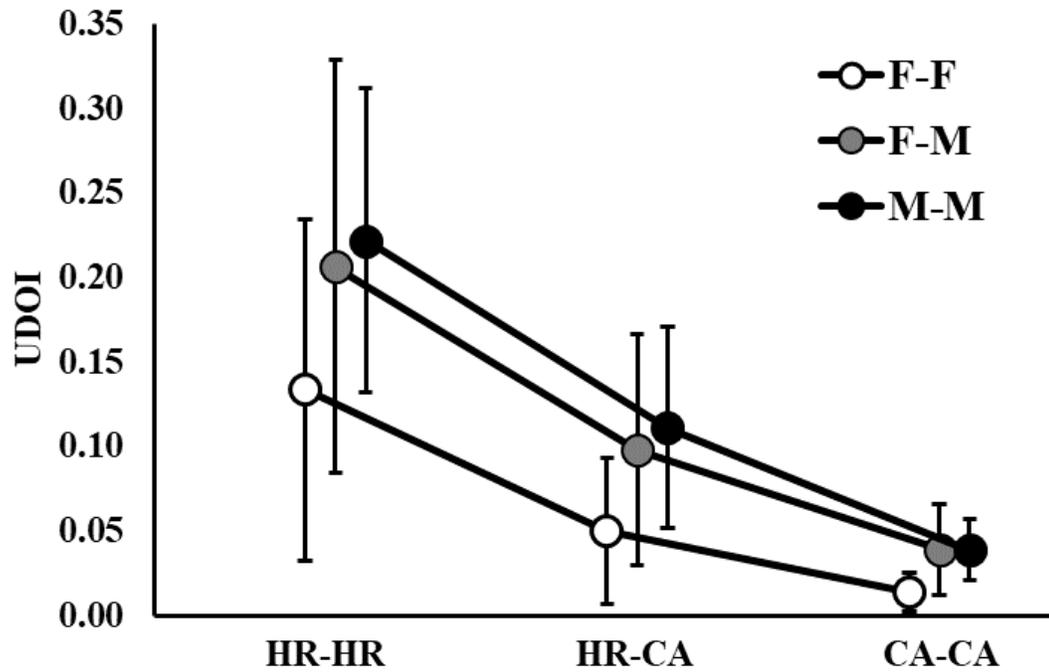


Figure 2

Home range (HR) and core area (CA) overlap of 4 female wild pigs at Buck Island Ranch, FL, during the Dry 2017 season. As an example, overlap of home ranges (HR-HR) occurs between 3 pairs of individuals (a-b, b-c, and c-d), overlap of home ranges and core areas (HR-CA) occurred between two pairs (b-c and c-d), and core area overlap (CA-CA) occurred between one pair (c-d). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

a. Space-use overlap



b. Degree

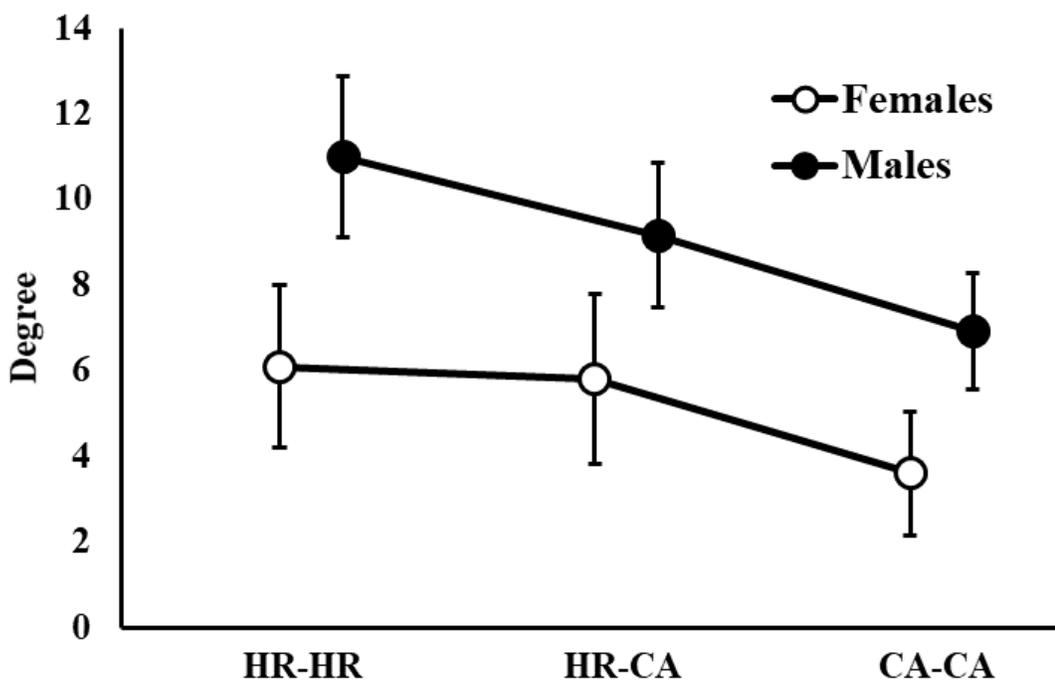


Figure 3

Space-use overlap (measured by utilization distribution of overlap index (UDOI)); a) and degree (number of individuals overlapped); b) estimates with associated 95% confidence intervals for wild pigs at Buck Island Ranch, FL in the Dry 2016 season. Estimates were created for home range to home range (HR-HR), home range to core area (HR-CA) and core area to core area (CA-CA) overlap. UDOI was estimated for

male-male (MM), female-male (FM), and female-female (FF) interactions. Degree values were estimated for male (M) and female (F) wild pigs.

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