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Seasonal variation in space use and territoriality in a large mammal (*Sus scrofa*)

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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 between 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). Among sexes, home range size did not vary seasonally, and males exhibited larger home ranges compared to females ($M = 10.36 \pm 0.79 \text{ km}^2 (\pm \text{SE})$, $F = 3.21 \pm 0.16 \text{ km}^2$). Strength of overlap varied by season with wild pig home ranges overlapping more during the dry season. Males interacted with a greater number of individuals of both sexes, compared to females, and exhibited greater strength of overlap during the dry season. 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. Our framework can be used to understand patterns of space use and territoriality in populations, which has important implications in understanding intraspecific interactions and population processes, such as how pathogens and parasites might spread within and among populations.

Variation in spatial interactions among animals can identify the selective pressures that shape spatial behavior. The relationship between the spatial organization of a species and dynamic interactions among individuals is expected to vary based on both behavioral and environmental factors. Differences between males and females in spatial behavior are related to differing reproductive strategies and spatial requirements allometrically scaling with body size^{1–3}, which can influence home range size⁴ and habitat use⁵. Seasonal changes in behavioral and environmental influences can also modify spatial behavior and influence overlap and association of conspecifics^{4,6–8}. Spatial overlap of individuals influences intraspecific interactions, which can drive population processes, such as disease transmission⁹, survival^{10,11}, competition¹², and reproduction¹³. Despite the growing evidence that spatial relationships affect a diverse range of socio-ecological processes¹⁴, variation in spatial overlap patterns between sexes and seasons is poorly understood for many species and is dependent on the individual's spatial organization. Identifying factors that influence heterogeneity in spatial overlap can improve management and conservation decisions by understanding important time periods for disease transmission¹⁵, intraspecific competition¹², and management actions¹⁶.

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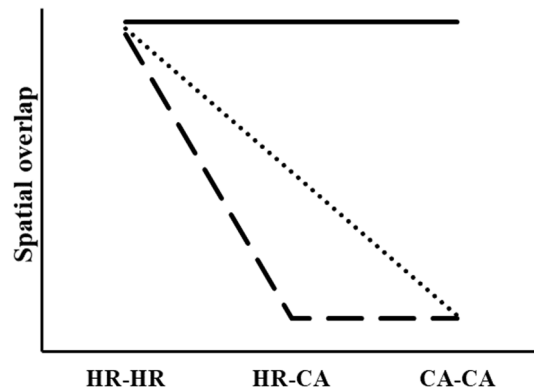


Figure 1. Predicted relationships evaluating territoriality among animals based on spatial overlap in home ranges (HR) and core areas (CA). Interactions can occur between two individual's home ranges (HR–HR), between one individual's home range and another individual's core area (HR–CA), or between two 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)].

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^{17–20}. 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^{19,20} and they are often approximated by estimating core areas (i.e., areas of high probability of use within an animal's home range^{21–23}). 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^{24–26}. 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 Burt¹⁷ and Schoener¹⁸, territorial species overlap in their home ranges but have exclusive core areas and thus home ranges do not overlap core areas between neighboring individuals (Figs. 1, 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^{23,24,26–28} (Figs. 1, 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^{29–32}. Seasonal wild pig home ranges can vary inversely with forage availability and other landscape features^{33–40}, which could influence spatial overlap^{41,42} and territorial patterns^{12,42,43}. Although territorial patterns have been predicted for wild pigs⁴⁴, 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^{27,45,46}. This pattern, however, is not detected in other systems^{35,47,48} and the role of territoriality in wild pig social structure is unclear. Males are reported to be less territorial than females (but see Ref.³⁵), with males exhibiting larger home ranges that overlap with both sexes⁴⁹. 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 and seasons. We expected that males would (1) exhibit larger home ranges, (2) exhibit increased space-use overlap compared to females^{49,50} and (3) interact with a greater number of conspecifics within their home ranges. 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^{51,52}, 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 of home ranges and core areas and how overlap varied

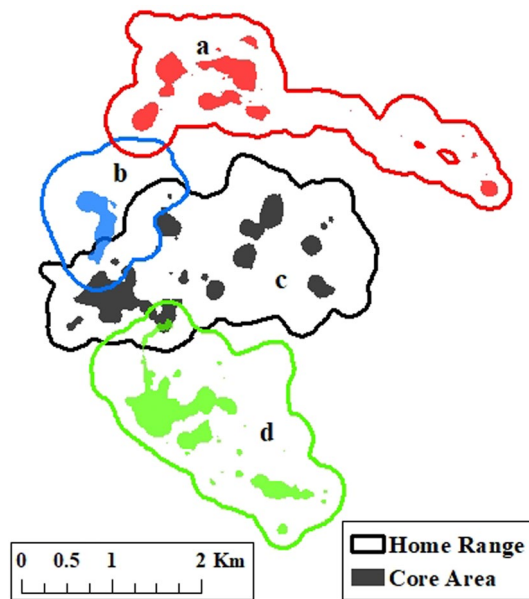


Figure 2. Home range (HR) and core area (CA) overlap of 4 female wild pigs at Buck Island Ranch, FL, during the Dry 2017 season. As an example, overlap of home ranges (HR–HR) occurs between 3 pairs of individuals (a–b, b–c, and c–d), overlap of home ranges and core areas (HR–CA) occurred between two pairs (b–c and c–d), and core area overlap (CA–CA) occurred between one pair (c–d). Figure was created in ArcMap 10.1.

Season	Sex	n	Home range				Core area			
			Ave	S.E	Min	Max	Ave	S.E	Min	Max
Wet	F	25	3.54	0.28	1.26	6.80	0.49	0.05	0.11	0.93
	M	18	10.16	1.26	1.61	22.97	1.27	0.17	0.08	2.81
Dry	F	18	3.59	0.32	1.22	6.67	0.50	0.05	0.17	1.02
	M	19	10.66	1.05	4.70	23.25	1.20	0.13	0.35	2.48

Table 1. Average (Ave.) seasonal home range and core area sizes (km²) for wild pigs at Buck Island Ranch, FL. Home range information was provided for all wet and dry seasons. Home range information was divided by sex (F: female, M: male) with sample size (n), standard error (S.E.), minimum values (Min.), and maximum values (Max.) included.

by sex and season. 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 multiple years, with the number of monitored individuals and sex ratio varying by season and sampling period (Tables 1 and 2). Following predictions in objectives one and two, males and females differed in home range size with females having smaller home ranges than males in wet and dry seasons (Table 1). The highest ranked model for estimating home range size included sex and it accounted for 95% of model weight with no other models within $\Delta 2$ AIC (Supplementary Table S1a). For space-use overlap of home ranges, the highest ranked model included the covariates season and sex, with the top two models accounting for 77% of model weight (Supplementary Table S1b). Space-use overlap (Ave. \pm SE) was greater during the dry season compared to the wet season (Fig. 3a.) and lowest for interactions among females (Dry = 0.010 ± 0.033 , Wet = 0.098 ± 0.025), intermediate for interactions among males (Dry = 0.230 ± 0.041 , Wet = 0.174 ± 0.052), and greatest for female-male interactions (Dry = 0.264 ± 0.065 , Wet = 0.190 ± 0.048 ; Supplementary Fig. S1). For degree, the highest ranked model included sex (Supplementary Table S1c), and males overlapped with more individuals in both seasons, compared to females (Table 2, Fig. 3b). Season was also included in a competitive model with greater overlap during the dry season (Supplementary Table S1c). For analyses of both home range size and space-use overlap, including year as a random effect did not improve model fit and it was excluded from all models with fixed effects (Supplementary Table S1).

	Wet 2015		Dry 2016		Wet 2016		Dry 2017		Wet 2017	
	F	M	F	M	F	M	F	M	F	M
a. HR–HR										
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										
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										
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

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).

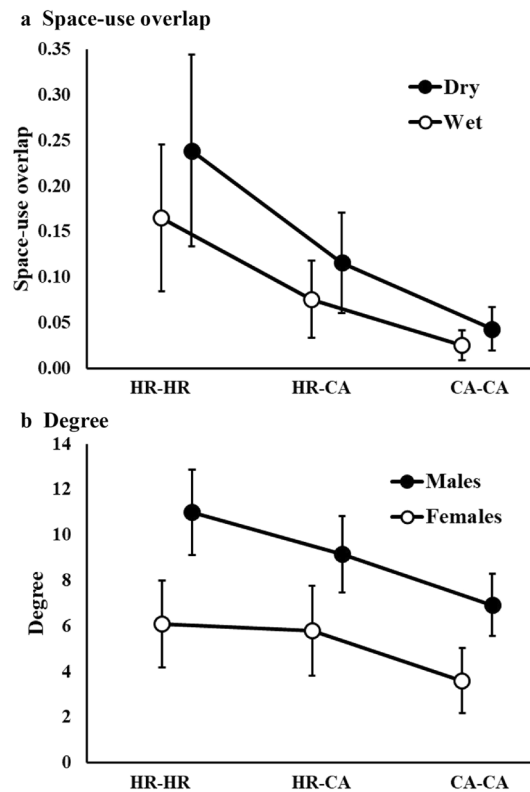


Figure 3. Space-use overlap (measured by utilization distribution of overlap index (UDO); (a) and degree (number of individuals overlapped; (b) estimates with associated 95% confidence intervals for wild pigs at Buck Island Ranch, FL. Space-use overlap estimates come from all seasons while degree represents the Dry 2016 season which contained the greatest number of monitored individuals. 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. Space use overlap was estimated for dry (Dry) and wet (Wet) seasons. Degree values were estimated for male (M) and female (F) wild pigs.

Wild pigs exhibited territorial behavior, which was consistent with our predictions for objective three (Figs. 1 and 3a). The highest ranked models for space-use overlap of HRHR–HRCA interactions included the variables level (HR–HR, HR–CA), season (Wet or Dry), the interaction between level and season, and sex. The top models accounted for 99% of the model weight (Table 3a). The highest ranked models for HRCA–CACA interactions included the variables level (HR–CA or CA–CA interactions), season (Wet or Dry), and the interaction between level and season. Sex was not included as a covariate in models within $\Delta 2$ AIC (Table 3b). Space-use overlap (Ave. \pm SE) 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), and overlap was greater in the dry than wet season across home range levels (Fig. 3a). Space-use overlap was lowest for interactions among females, intermediate for male–male interactions, and greatest for female–male interactions. For both HRHR–HRCA and HRCA–CACA analyses of space-use overlap, including year as a random effect did not improve model fit and it was excluded from all models with fixed effects (Table 3a,b).

Further, the metric “degree”, also indicated that wild pigs exhibited territorial behavior. Models that included level, sex of the individual, season, and the interaction of sex and level were the most supported (Table 3c,d). 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,d, Fig. 3b and Supplementary Fig. S2). Males consistently overlapped with a greater number of individuals than females (Table 2, Fig. 3b. and Supplementary Fig. S2). Wild pigs overlapped more conspecifics during the dry than wet season in both analyses and season was included in models within $\Delta 2$ AIC (Table 3c,d). The highest ranked models for HRHR–CACA and HRCA–CACA analyses accounted for 84% and 96% of model weight respectively.

Discussion

Heterogeneity in wild pig spatial behavior identified several factors that shape overlap of individuals and territorial patterns. Consistent with our predictions and previous research, males exhibited greater home range size and interacted with more conspecifics than females likely due to allometric requirements or to maximize reproductive potential^{1–3}. 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}. This could influence important ecological processes, such as genetic structuring of populations and transmission of pathogens^{55,56}. The role of sex in structuring spatial overlap was more nuanced when evaluating the strength of home range overlap. Space-use overlap of female home ranges was consistently lower than female–male and male–male overlap. It was common for male home ranges to completely overlap one or more female home ranges and males overlapped extensively. Female’s expression of territoriality was more robust than males, and the overlap patterns presented here support the hypothesis that females exhibit greater territoriality with neighboring females compared to associated males or between males^{50,57}.

The influence of seasonality on wild pig spatial patterns varied depending on how space use was evaluated. Home range size did not vary seasonally in this system. Landscape structure^{33,39,58} and the presence of agriculture⁵⁹ can influence seasonal space use by wild pigs but these factors were not present in this study, potentially limiting seasonal effects. High population density can also influence spatial patterns and potentially limit seasonal variation in home range size⁶⁰, although changes in density have not elicited expansion or shifting of wild pig home ranges in other systems⁶¹. Although home range size did not vary seasonally, our results suggest that the strength and number interactions were greater during dry seasons. Wild pigs often forage on grasses and below the soil surface by rooting during the dry season, and utilization of these abundant but lower quality resources can mitigate the reductions in productivity⁵¹. Changes in foraging strategy may result in shifts in space-use within the home range⁴⁰ and a reduction in territoriality^{41,62}. Although environmental and social factors likely influenced how seasonal effects were expressed in spatial overlap, territorial patterns were consistently detected from the spatial behavior of wild pigs.

Territoriality exists on a continuum and is influenced by the species’ social structure and ecological conditions^{17,19,20}. In our system, core areas were not exclusive, where home ranges of neighboring wild pigs overlapped conspecific core-areas, indicating wild pigs do not conform to some traditional definitions of territoriality^{17,18}. Similar to recent work on wild pig territoriality⁴³, core areas of neighboring individuals also overlapped based on the 80% cumulative probability isopleth selected for this study. We selected this cumulative probability isopleth to retain a similar proportion of the home range within the core area across individuals. It is challenging to monitor all neighboring social groups and the unknown influence of unmonitored conspecifics, as well as variation in the spatial distribution of monitored individuals, led us to evaluate overlap at predetermined isopleths. Where all neighboring groups are monitored, analysis of overlap at varying isopleth levels could identify a threshold where core area exclusivity is consistently expressed. Exclusive use of areas is likely maintained by indirect communication^{27,63,64} and limited direct interactions^{43,50,57,65}. Interactions within shared space may also be limited due to temporal partitioning via avoidance, site specific dominance, or priority of access to resources¹⁹. Evaluating how wild pigs interact in both time and space, particularly under contrasting resource availability could identify how spatial behavior varies with ecological conditions.

The conceptual framework that we presented (Fig. 1) suggests that spatial overlap patterns can be used to evaluate territoriality in species without overt territorial behavior and non-exclusive core areas. However, there are several considerations about our study that suggest further work is needed to understand the role of territoriality in wild pig social structure. 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 resources⁶². 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 pigs^{19,43}. Further, spatial interactions and territorial patterns could be evaluated in relation to important resources, such as mast producing

	K	AIC	Δ AIC	w_i	Dev
a. UDOI: HRHR–HRCA					
(1 Dyad) + Level + Season	5	– 2077.35	–	0.53	1043.71
(1 Dyad) + Level + Season + (Level \times Season)	6	– 2075.92	1.43	0.26	1044.01
(1 Dyad) + Level + Sex + Season	7	– 2075.43	1.92	0.20	1044.78
(1 Dyad) + Level + Sex + Season + (Level \times Sex \times Season)	14	– 2065.31	12.04	0.00	1046.89
(1 Dyad) + Sex + Level	6	– 2064.47	12.88	0.00	1038.28
(1 Dyad) + Level	4	– 2064.25	13.09	0.00	1036.15
(1 Dyad) + Level + Sex + (Level \times Sex)	8	– 2060.87	16.48	0.00	1038.52
(1 Dyad) + Season	4	– 2002.05	75.30	0.00	1005.05
(1 Dyad) + Sex + Season	6	– 2000.18	77.16	0.00	1006.14
(1 Dyad) + Sex + Season + (Sex \times Season)	8	– 1998.16	79.19	0.00	1007.16
(1 Dyad) + Sex	5	– 1991.35	85.99	0.00	1000.71
(1 Dyad)	3	– 1991.15	86.20	0.00	998.59
(1 Dyad) + (1 Year)	4	– 1989.14	88.21	0.00	998.59
Intercept-only	2	– 1551.06	526.29	0.00	777.54
(1 Year)	3	– 1546.80	530.55	0.00	776.41
b. UDOI: HRCA–CACA					
(1 Dyad) + Level + Season	5	– 1289.16	–	0.45	649.65
(1 Dyad) + Level + Season + (Level \times Season)	6	– 1287.55	1.61	0.20	649.88
(1 Dyad) + Level	4	– 1286.87	2.29	0.14	647.48
(1 Dyad) + Level + Sex + Season	7	– 1286.61	2.55	0.13	650.44
(1 Dyad) + Level + Sex	6	– 1285.17	3.99	0.06	648.69
(1 Dyad) + Level + Sex + (Level \times Sex)	8	– 1283.11	6.05	0.02	649.73
(1 Dyad) + Level + Sex + Season + (Level \times Sex \times Season)	14	– 1277.25	11.91	0.00	653.15
(1 Dyad) + Season	4	– 1253.95	35.21	0.00	631.02
(1 Dyad)	3	– 1252.29	36.87	0.00	629.17
(1 Dyad) + Sex + Season	6	– 1251.44	37.73	0.00	631.82
(1 Dyad) + Sex	5	– 1250.59	38.57	0.00	630.37
(1 Dyad) + (1 Year)	4	– 1250.25	38.91	0.00	629.17
(1 Dyad) + Sex + Season + (Sex \times Season)	8	– 1249.71	39.45	0.00	633.03
Intercept-only	2	– 1092.45	196.71	0.00	548.24
(1 Year)	3	– 1090.42	198.74	0	548.24
c. Degree: HRHR–HRCA					
(1 ID) + (1 SP) + Level + Sex	6	695.30	–	0.45	– 341.37
(1 ID) + (1 SP) + Level + Sex + Season	7	696.55	1.25	0.24	– 340.90
(1 ID) + (1 SP) + Level + Sex + (Level \times Sex)	7	697.49	2.18	0.15	– 341.37
(1 ID) + (1 SP) + Sex	5	698.97	3.66	0.07	– 344.29
(1 ID) + (1 SP) + Sex + Season	6	700.19	4.89	0.04	– 343.82
(1 ID) + (1 SP) + Sex + Season + (Sex \times Season)	7	701.80	6.49	0.02	– 343.52
(1 ID) + (1 SP) + Level	5	702.57	7.26	0.01	– 346.09
(1 ID) + (1 SP) + Level + Season	6	703.69	8.39	0.01	– 345.57
(1 ID) + (1 SP) + Level + Sex + Season + (Level \times Sex \times Season)	11	704.11	8.81	0.01	– 340.15
(1 ID) + (1 SP) + Level + Season + (Level \times Season)	7	705.23	9.93	0.00	– 345.24
(1 ID) + (1 SP)	4	706.26	10.96	0.00	– 349.00
(1 ID) + (1 SP) + Season	5	707.35	12.05	0.00	– 348.48
(1 ID)	3	741.46	46.16	0.00	– 367.65
(1 SP)	3	756.12	60.82	0.00	– 374.98
Intercept-only	2	766.09	70.79	0.00	– 381.01
d. HRCA–CACA					
(1 ID) + (1 SP) + Level + Sex	6	653.17	–	0.40	– 320.31
(1 ID) + (1 SP) + Level + Sex + Season	7	653.47	0.30	0.34	– 319.36
(1 ID) + (1 SP) + Level + Sex + (Level \times Sex)	7	654.37	1.20	0.22	– 319.81
(1 ID) + (1 SP) + Level	5	660.74	7.57	0.01	– 325.17
(1 ID) + (1 SP) + Level + Season	6	660.84	7.67	0.01	– 324.14
(1 ID) + (1 SP) + Level + Sex + Season + (Level \times Sex \times Season)	11	660.90	7.73	0.01	– 318.55
(1 ID) + (1 SP) + Level + Season + (Level \times Season)	7	662.43	9.26	0.00	– 323.84
Continued					

	K	AIC	Δ AIC	w_i	Dev
(IID) + (1 SP) + Sex + Season	6	669.65	16.48	0.00	– 328.55
(IID) + (1 SP) + Sex + Season + (Sex \times Season)	7	671.63	18.46	0.00	– 328.44
(IID) + (1 SP)	4	676.96	23.79	0.00	– 334.35
(IID) + (1 SP) + Season	5	677.04	23.87	0.00	– 333.32
(IID) + (1 SP) + Sex	4	692.98	39.81	0.00	– 342.36
(1 ID)	3	714.55	61.38	0.00	– 354.20
(1 SP)	3	717.57	64.40	0.00	– 355.71
Intercept-only	2	813.62	160.45	0.00	– 404.77

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). Random effects include the two individuals that are interacting (Dyad) or the individual (ID) and the year (Year) or the sampling period (e.g. Wet 2015, SP). 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 as fixed effects. 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).

trees, supplemental feeders, or at water locations where 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^{50,66} affecting both livestock and humans^{67,68}. 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 animals⁴³.

Study areas

Our work was conducted at Archbold’s—Buck Island Ranch (27° 10' N, 81° 2' W, elevation 6–12 m), located in a biologically diverse area of central Florida⁶⁹. The study area (4250 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 bahia-grass (*Paspalum notatum*) and native C4 grasses. Average temperatures range from 26 °C in July to 13 °C in January⁷⁰. Rainfall averages 1365 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 (2.5 m deep \times 1.25 m wide \times 1.5 m high) and corral traps (5 m 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 Xylazine 100 mg/ml (Akorn Inc. Lake Forest, Illinois, USA) mixed following the recommendations of established dosages (Telazol, 4.40 mg/kg; Xylazine, 2.5 mg/kg)^{71–73}. 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 min. Wild pig capture and handling procedures were administered under approved University of Florida Animal Care and Use Committee protocols (#201408495 and #201808495) and all methods were performed in accordance with the relevant guidelines and regulations. The study complies with ARRIVE guidelines.

Space use and animal interactions. We estimated home ranges and core areas using the Brownian bridge movement model⁷⁴ (BBMM) in the package “mkde”⁷⁵ in program R⁷⁶. Home ranges were estimated using a 99.999% cumulative probability and core areas were estimated using an 80% cumulative probability. An 80% cumulative probability was selected so that approximately 25% of the home range was conserved in the core area (following Sawyer and Kauffman⁷⁷; Fig. 2). A minimum of six weeks of GPS data were required for an individual to be included in analyses and if more than one adult female was collared within the same social group, the individual with the greater number of locations was included in analyses. Spatial data were available for 3 wet and 2 dry seasons (Wet 2015, Dry 2016, Wet 2016, Dry 2017, Wet 2017), which we refer to as sampling periods to avoid confusion when wet and dry seasons are combined in analyses.

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^{78,79}. 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^{54,78–80}. 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 index⁸¹ (UDOI), 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^{82,83}.

For objectives one and two, we quantified the effects of sex and season on wild pig home range size and spatial overlap using generalized linear mixed-effect models regression models⁸⁴ and AIC model selection⁸⁵. We analyzed home range size using a Gamma distribution because home range size was non-normal and right skewed. We accounted for yearly variation and repeated observations of individuals by including year and individual as random effects (Year and ID, Supplementary Table S1a). We analyzed space-use overlap (UDOI) of home ranges for each interacting dyad (pair of individuals), using a log normal distribution. In models, random effects included the dyadic interaction and the year (Dyad and Year, Supplementary Table S1b). Finally, we evaluated degree using a negative binomial distribution because counts were over dispersed. We accounted for repeated measures by specifying individuals as a random effect (ID, Supplementary Table S1c). Because the number of monitored wild pigs varied among sampling periods (Table 2), we also controlled for differences in the maximum number of potential interactions by including sampling period (e.g. Wet 2015) as a random effect (SP, Supplementary Table S1c). For all analyses, fixed effects included sex of the individual or sexes within the dyad [female–female (F–F), female–male (F–M), or male–male (M–M)], season (Wet or Dry), and the interaction of sex and season (Supplementary Table S1). We generated 8 a priori models including an intercept only null model and combinations of random and fixed effects (Supplementary Table S1).

To evaluate patterns of territoriality, 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 per sampling period, we estimated UDOI values from each interaction level (HR–HR, HR–CA, and CA–CA). Variation in UDOI was evaluated using a log normal distribution. In models, random effects included the dyadic interaction and the year. Fixed effects included the space use level, sexes within the dyad, season, and all two-way and three-way interaction terms (Table 3a,b). We also calculated degree per individual for each space use level and evaluated degree with a negative binomial distribution because counts were overdispersed. Random effects included individual animal and the sampling period. Fixed effects included space use level, sex, season, and all two-way and three-way interaction terms (Table 3c,d). For both UDOI and degree, 15 a priori models were identified that included an intercept-only model (i.e., model without any covariates) and all combinations of level, sex, season, and interaction terms (Table 3). We ranked models using Akaike Information Criterion⁸⁶ and validated each model by graphically examining the residuals and inspecting the QQ-plot. All analyses were conducted in R version 3.5.2⁷⁶ using package “lme4”⁸⁴.

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Author contributions

P.E.S. and J.S.L. conceived the study. P.E.S. wrote the manuscript with input from J.S.L., R.K.B., K.C.V., and R.S.M. Field work study design was developed by J.S.L., R.K.B., and R.S.M and R.K.B., W.A. and B.W. carried out fieldwork. 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 authors edited and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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