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6-10-2022

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Titus, Chelsea L.; Bowden, Courtney F.; Smyser, Timothy J.; Webb, Stephen L.; and Beasley, James C., "Genomic tools reveal complex social organization of an invasive large mammal (*Sus scrofa*)" (2022). *USDA Wildlife Services - Staff Publications*. 2610.
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Genomic tools reveal complex social organization of an invasive large mammal (*Sus scrofa*)

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Received: 8 November 2021 / Accepted: 16 May 2022 / Published online: 10 June 2022
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Abstract A comprehensive understanding of sociality in wildlife is vital to optimizing conservation and management efforts. However, sociality is complicated, especially for widely distributed species that exhibit substantive behavioral plasticity. Invasive wild pigs (*Sus scrofa*), often representing hybrids of European wild boar and domestic pigs, are among the most adaptable and widely distributed large mammals. The social structure of wild pigs is believed to be similar to European wild boar, consisting of matriarchal groups (sounders) and solitary males. However, wild pig social structure is understudied and largely limited to visual observations. Using a hierarchical approach, we incorporated genomic tools to describe wild pig social group composition in two disparate ecoregions within their invaded range in

North America. The most common social unit was sounders, which are characterized as the association of two or more breeding-aged wild pigs with or without dependent offspring. In addition to sounders, pseudo-solitary females and male-dominated bachelor groups were observed at a greater frequency than previously reported. Though primarily composed of close female kin, some sounders included unrelated females. Bachelor groups were predominantly composed of young, dispersal-aged males and almost always included only close kin. Collectively, our study suggests social organization of wild pigs in their invaded range is similar to that observed among wild boar but is complex, dynamic, and likely variable across invaded habitats.

Keywords Genetics · Invasive mammal · Relatedness · Social groups · *Sus scrofa*

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-022-02840-4>.

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Introduction

Sociality is the tendency for individuals to live within a group and exhibit coordinated behavioral patterns, conveying both benefits and costs to group members (Silk 2007; Prox and Farine 2020). Benefits of sociality may include “safety in numbers,” increased access to resources, or increased offspring survival (Krause et al. 2002; Silk 2007). On the other hand, group members may compete for mating opportunities (Cafazzo et al. 2016), be at greater risk of disease

transmission (Moore et al. 1988), or be more visible to predators (Krause and Godin, 1995) – all of which can influence their individual fitness (Krause et al. 2002; Silk 2007; Prox and Farine 2020). Thus, social structures persist in a species when the benefits of intraspecific interactions outweigh the costs (Krause et al. 2002; Silk 2007).

Social structures can be as varied as the animals that display them, with differences observed even within a taxon. Among mammals, social structures encompass subsocial species (i.e., primarily living alone, except briefly for mating or rearing offspring; jaguar – *Panthera onca*; Cavalcanti and Gese, 2009), parasocial species (i.e., primarily living in a group cooperatively; African lion – *Panthera leo*; Dickinson and Koenig 2018), and species with complex eusocial societies (i.e., hive or colonial cooperation, majority of colony members forgo reproduction to collectively care for and assist the minority reproductive caste; Damaraland mole-rats – *Crytomys damarensis*; Nowak et al. 2010, Dickinson and Koenig 2018). Among social species, group organization and composition are important life history traits that drive interspecific interactions, and ultimately conservation and management decisions. However, costs and benefits associated with group membership can be dynamic across both space and time, contributing to greater diversity in social organization across a species' range (Gehrt and Fox 2004). For example, Connor et al. (2001) reported temporary individual-based fission–fusion in male groupings of Indian Ocean bottlenose dolphins (*Tursiops aduncus*), an aggregation not described in other populations of this species. Similarly, density-dependent variability in the social organization of red foxes (*Vulpes vulpes*) has been reported, in which typically monogamous breeding pairs recruit related and unrelated individuals to share parental care when population densities are high (Macdonald 1979). Alternatively, caribou (*Rangifer tarandus*) displayed different rates of fission and fusion among social groups before and during peak rutting seasons (Body et al. 2015). Describing social organization of a species becomes further complicated when the species is found globally in both domestic and free-living populations and in native and introduced ranges.

Sus scrofa, which includes domestic pigs, wild boar, and invasive wild pigs (hereafter referred to as “wild pigs;”; Keiter et al. 2016), are one of the most

widely distributed species globally, with populations of wild boar or wild pigs occurring on all continents except Antarctica (Barrios-Garcia and Ballari 2012; Lewis et al. 2019). As they are classified under the same taxon, many of the behavioral patterns observed among European wild boar (*Sus scrofa* spp.) in their native range are believed to be reflected in wild pigs among invaded ranges. The social organization of European wild boar is complex, but social units are generally characterized as matriarchal social groups (referred to as sounders) or solitary males that only temporarily associate with sounders to mate (Dardaillon 1988; Kaminski et al. 2005; Iacolina et al. 2009; Poteaux et al. 2009; Podgórski et al. 2014a, b; Battocchio et al. 2017; Beasley et al. 2018). Dardaillon (1988) documented a third social unit comprised of males believed to be young, dispersing individuals transitioning to solitary, breeding-aged adults, which has since been observed in other populations. Most studies have reported that sounders are typically composed of several closely related females and their offspring; however, genetic determinations of relatedness within social groups have often yielded conflicting reports (Dardaillon 1988; Poteaux et al. 2009; Podgórski et al. 2014a, b; Battocchio et al. 2017). For example, Iacolina et al. (2009) found that wild boar social groups in Italy consisted mostly of unrelated females and their offspring. Podgórski et al. (2014a, b) found that social groups in Poland were comprised of one or more females and their offspring, whose home ranges overlapped with those of neighboring relatives. Similarly, adult female Japanese wild boar (*Sus scrofa leucomystax*) were found to occasionally group together but were typically either solitary or with their current litter of offspring (Nakatani and Ono 1994).

Within North America, wild pigs are a destructive invasive species with free-ranging populations long-established on the continent. Swine were first introduced as livestock in 1539 and subsequently established widespread feral populations. Feral populations of domestic pigs later hybridized with escaped European wild boar introduced for sport hunting (Mayer and Beasley 2018; Mayer et al. 2020). As a result, contemporary wild pig populations generally represent extensive admixture of wild boar and domestic pig lineages (Keiter et al. 2016; Smyser et al. 2020). Throughout the United States of America (USA), broad variability in the hybridization of

domestic versus wild lineages has been observed both within and among wild pig populations (Smyser et al. 2020). With humans artificially selecting different phenotypic traits from specialized domestic lineages and natural selection of adaptive traits in hybridized wild populations, the extent to which wild pig social organization differs from that of native populations of European wild boar is difficult to predict and has not been well described in the literature (Spencer et al. 2005). Within the USA, wild pigs are presumed to reflect the social organization of European wild boar and sounders are assumed to be primarily composed of closely related females and their dependent offspring. Observational studies of wild pigs in the USA have demonstrated that sounders vary in size and composition (Mayer and Brisbin 2009; Poteaux et al. 2009; Beasley et al. 2018; Gaskamp et al. 2021), ranging from a single female with offspring to groups with over 30 pigs; however, sounders composed of 3–9 individuals have typically been reported. The underlying factors contributing to variance in sounder size are largely unexplored, although some studies have suggested water availability may influence group size in wild pigs (Gabor et al. 1999; Gaskamp et al. 2021). It is worth noting that these reports are often limited to behavioral observations and lack robust genetic assessment (Gabor et al. 1999; Mayer and Brisbin 2009; Delgado-Acevedo et al. 2010). As with European wild boar, previous studies have observed male social groups within wild pig populations; however, the frequency of occurrence, composition, and dynamics of these male coalitions is relatively unknown and are thought to be temporary associations (Gabor et al. 1999; Mayer and Brisbin 2009).

A detailed description of the relatedness and demographic composition of wild pig social units (inclusive of solitary pigs and pig social groups) is important for understanding the broader population dynamics of this taxon. Little work has been done on wild pig social organization outside of the arid region in their USA range (Beasley et al. 2018); additional research is needed to elucidate how the size and familial composition of social groups may vary with differences in resource distribution, genetic lineage, and other factors. Among published studies, few have used genomic tools to investigate previously held assumptions of the relatedness displayed in social groups. However, the incorporation of genomics would provide the resolution to investigate the

complexity of variation in group composition across different ecosystems. Using samples collected across two disparate ecoregions within the invaded range in the USA, our study aims to describe the composition of invasive wild pig social groups and social organization within the two datasets. Our study is the first to utilize robust genomic tools to understand invasive wild pig social group composition, as well as the first to investigate relatedness among male wild pig social groups.

Study areas

We captured wild pigs for this study across two regions of the USA that have had established wild pig populations for hundreds of years. Wild pigs were abundant in both study areas, but the landscapes differed considerably in habitat composition, land use, and genetic composition of founding populations.

South Carolina

Wild pigs were captured on the Savannah River Site (SRS) near Aiken, South Carolina, USA from 2012 to 2019 as part of ongoing population control and research efforts (Supplementary Fig. 1). The SRS is an 802.67 km² restricted access site managed by the USA Department of Energy (DOE). Originally constructed for nuclear weapons manufacturing, the industrial footprint of SRS comprises a small portion of the landscape, with >90% of the site representing natural habitats including upland pine (*Pinus spp.*), cypress-tupelo (*Taxodium distichum*-*Nyssa aquaticus*) or oak-hickory (*Quercus spp.*-*Ulmus spp.*) bottomland hardwood, shrub/herbaceous areas (*Myrica cerifera*, *Ilex spp.*, *Vaccinium corymbosum*), and upland/mixed forests (*Quercus spp.*, *Pinus spp.*; Imm and McLeod 2005). The climate is generally warm and humid, with average monthly temperatures ranging from 15.4–33.4 °C, average monthly relative humidity ranging from 63 to 80%, and average annual precipitation of approximately 1,200 mm (Imm and McLeod 2005). The wild pig population predates the acquisition of SRS by the USA DOE in the 1950s. Individuals within the population are characterized as hybrids between Western heritage breeds and wild boar, however there is considerable variation in the extent of European wild boar ancestry

among individuals (Mayer et al. 2020; Smyser et al. 2020). Since the establishment of the SRS, wild pigs have been extensively controlled to minimize damages through a combination of trapping, opportunistic shooting, and hunting with dogs (Mayer et al. 2020). Despite being managed since SRS's establishment, the wild pig population has expanded substantially over the past several decades (Mayer et al. 2020). Wild pigs are now abundant and widely distributed throughout SRS, with an estimated abundance of > 5,000 individuals as of 2017 (Keiter et al. 2017).

Oklahoma

Wild pigs were captured from 2010 to 2017 in south-central Oklahoma (Carter and Love counties) as a component of ongoing research and control efforts at the Noble Research Institute's (NRI) Coffey Ranch (10.17 km²), Oswalt Road Ranch (20.77 km²), and Red River Ranch (13.39 km²), in addition to the Strate Ranch (3.90 km²), Hoffman Ranch 99.35 km²), and Ljungdahl Ranch (2.33 km²; Supplementary Fig. 2). These ranches were all grazed by cattle and found in the Cross Timbers and Prairies regions of Oklahoma and incorporate a mix of oak (*Quercus spp.*), elm (*Ulmus spp.*), and hickory (*Carya spp.*) forest and prairie habitat predominately of big and little bluestem (*Andropogon gerardii* and *Schizachyrium scoparium*, respectively), switchgrass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*), as well as agricultural areas and rangelands (Boyer et al. 2020; Gaskamp et al. 2021; Haydett et al. 2021). Red River Ranch also managed 150 ha of pecan trees (*Carya illinoensis*) for production, which included native groves and improved orchards (Boyer et al. 2020). Long-term monthly average precipitation ranges from 47.75 to 133.6 mm, totaling 990.85 mm on average annually (Oklahoma Climatological Survey; accessed 31 March 2022). Monthly temperature averages 16.89 °C annually, and ranges from 5.0 to 28.17 °C across months (Oklahoma Climatological Survey; accessed 31 March 2022). Relative humidity averages 69% annually with monthly averages that range from 65 to 73% (Oklahoma Climatological Survey; accessed 31 March 2022). Wild pigs are widely distributed and abundant the across the Cross Timbers and Prairies regions and have been intensively controlled since 2010 (using various methods;

Stevens 2010; VerCauteren et al. 2020; Gaskamp et al. 2021).

Methods

Field sampling

We collected samples from wild pigs that were captured as part of other research and control efforts, with detailed descriptions of capture and handling procedures described previously (e.g., Gaskamp et al. 2016, 2018, 2021, Keiter et al. 2017, Haydett et al. 2021, Yang et al. 2021). Briefly, at NRI we captured wild pigs from 2010 to 2017 using drop nets, corral traps, and suspended metal traps, and captured wild pigs at SRS from 2012 to 2019 with drop traps and/or corral traps. We set and monitored corral traps at SRS primarily via cellular cameras to identify and target entire social groups or solitary males, or large corral traps set with trip wires that were baited and set by experienced trappers to capture entire social groups. For NRI, we similarly targeted social groups using dual compartment corral traps with tripwires to trigger either a single spring or saloon style gate, suspended metal traps triggered using remotely controlled traps, or drop nets targeting groups that we triggered with a line-of-sight remote control (Gaskamp et al. 2021). Individuals were included in the study that were live captured and released as part of other ongoing research projects as well as lethally sampled as part of control and management activities. At time of capture, we recorded weight, sex, and age based on tooth rupture (0–0.5 year [piglet], 0.5–1 year [juvenile], 1–1.5 years [yearling], 1.5–3 years [sub-adult], and > 3 years [adult], Matschke 1967 or weight estimates recorded in the field when tooth rupture was unavailable). Furthermore, hair (NRI) and/or tissue (SRS, NRI) was also collected for genotyping. Tissue samples were stored in vials with 99.5% ethanol at –70 °C or dry vials at –18 °C and hair samples were stored in paper coin envelopes at –18 °C.

We assigned individuals captured at the same time/location to a social group if at least one breeding-age individual (e.g., yearling, subadult, or adult) was included in the trapping event. For four social groups caught on the SRS, we also used telemetry or remote camera imagery to validate group membership. We used the sex ratio to categorize social groups

as either sounders (i.e., female dominant groups or groups with an equal sex ratio) or bachelor groups (i.e., male dominant groups). We used other social unit descriptors (pseudo-solitary females and pseudo-solitary males) to classify breeding-aged individuals that were captured with extraneous group members (e.g., offspring, suitor males) and are essentially not a stable social group. We included all samples of individuals collected at each study site to determine population structure to adjust genomic pairwise relatedness; however, we only used samples of individuals captured as social groups (including pseudo-solitary individuals) to determine degrees of relatedness within groups. Because they were captured with other individuals (offspring and/or suitors), degrees of relatedness were also assigned to dyads (pairs) of pseudo-solitary individuals.

Laboratory analyses

Following extraction of DNA with MagMax DNA extraction kit (Thermo Fisher Scientific), we genotyped samples using GeneSeek's Genomic Profiler for Porcine biallelic single nucleotide polymorphism (SNP loci) array (GeneSeek, a Neogen Company, Lincoln, Nebraska) developed with Illumina (San Diego, California) bead array chemistry (Ramos et al. 2009). We mapped SNP loci to the Sscrofa11.1 reference genome assembly (Warr et al. 2020) and filtered genotypes to remove unmapped or non-autosomal SNP loci, with 62,128 loci available for analysis. We then implemented quality control measures using PLINK 1.9 (Purcell and Chang 2015) to remove loci with call rates < 0.99 , with minor allele frequencies < 0.05 , or in linkage disequilibrium (window size = 50 loci, step size = 5 loci, $r^2 > 0.5$). Following loci filtering, samples were pruned if their call rate was < 0.95 .

Statistical analyses

For each study area, we estimated coefficients of relatedness (r) for all sampled pigs using the methods described in Conomos et al. (2015, 2016). Specifically, through an iterative process executed in program R (version 4.1.3; R Core Team 2021), samples were classified as unrelated or related using pairwise kinship coefficients and ancestry divergence (SNPRelate package; Zheng et al. 2012). We then

used PC-AiR to conduct a principal component analysis (PCA) on the subset of unrelated samples (GENESIS package; Gogarten et al. 2019). Finally, using PC-Relate (GENESIS package; Gogarten et al. 2019) we adjusted pairwise estimates of kinship using the ancestry representative principal components (PC) to account for any potential population structure. The number of PC to be retained was determined by (1) eigenvalues and associated scree plots and (2) self-kinship based on the expectation that values should be distributed around one (Simeone et al. 2011). Adjusted pairwise kinship coefficients were scaled by two to obtain coefficients of relatedness (r).

To characterize relatedness within wild pig social groups, we evaluated r values calculated for all dyads sampled within a given social group (Supplementary Fig. 3) and respectively assigned degrees of familial relationship for each pair (up to third-degree relatives as delineated in Manichaikul et al. (2010)). Specifically, we considered dyads with $r \geq 0.707$ as monozygotic twins, $0.354 \leq r \leq 0.707$ as first-degree relatives (parent-offspring and full, non-monozygotic siblings), $0.177 \leq r \leq 0.354$ as second-degree relatives (grandparent-grandoffspring, avuncular, double-cousins, and half-siblings), and $0.088 \leq r \leq 0.177$ as third-degree relatives (first-cousins, great-grandparent-great-grandoffspring, grand-avuncular, and half-avuncular; Manichaikul et al. 2010). More distant relationships ($r \leq 0.088$) could not be confidently classified as previous work that combined genetic estimates of relatedness with pedigrees demonstrated increasingly smaller expected ranges of relatedness values and greater inconsistency in identifying true degrees of relatedness (Ramstetter et al. 2017). Following classification, we assembled relatedness networks for each social group.

For each study area, we then identified the following demographic composition for each group: group size, sex ratio, age composition, degree of relatedness composition, and mean group genomic relatedness. Given that wild pigs can reproduce year-round throughout much of their invaded range (Chinn, unpublished data), breeding-aged males (hereafter referred to as suitor males) are often captured with female-dominated social groups but are not actual group members. Accordingly, unrelated suitor males were identified as breeding-aged males that shared a pairwise relatedness of less than 0.088 with all other members of the group they were captured

with. Further, because sounders often are numerically dominated by juveniles due to the high reproductive capacity of this species, genomic relatedness values within groups can be highly dependent upon the occurrence and number of offspring present at the time of sampling. Therefore, to account for these factors and establish a comprehensive understanding of socio-genomic relationships within groups, we applied the following hierarchical approach in the analysis of our data: (1) all group membership included, (2) nonbreeding-aged individuals excluded (i.e., piglets and juveniles), and (3) nonbreeding-aged individuals and suitor males excluded.

Results

Savannah river site

After retaining 16,656 SNP loci and 5 PCs for estimation of relatedness (Supplementary Fig. 4), pairwise relatedness coefficients were calculated for 969 individuals on SRS. The average relatedness across all wild pigs caught on SRS was $r=0.012$. We assigned 299 of the 969 genotyped individuals and an additional 4 individuals that were not genotyped to 77 social groups for demographic analyses. The remaining individuals were excluded due to capture as solitary individuals, incomplete social groups (i.e., only piglets and/or juveniles were captured), or missing age or other necessary capture information. For relatedness analyses, we excluded the four non-genotyped individuals. Overall, we found sounders were the most common group type across all analysis hierarchies; however, bachelor groups remained present in all hierarchies (Supplementary Fig. 7).

All group members included

The first hierarchy of analysis included all 303 individuals assigned to 77 social groups for demographic analysis and 299 individuals assigned to 76 groups for the genomic relatedness analysis. Based on demographic analysis, most social groups were classified as sounders (81.8%; Supplementary Fig. 7). Average group size (n) was 3.7 individuals (Table 1), and groups were typically composed of only breeding-aged (i.e., yearling or older; 51.9%; Fig. 1), first-degree relatives (27.3%; Fig. 2). However, 14.3% of

all kin-based groups included at least one unrelated group member. Sounders had an average of 3.7 individuals and an average group r of 0.318 (Table 1). Sounders were most commonly composed of only breeding-aged (50.8%; Fig. 1), first-degree relatives (25.4%; Fig. 2). Groups consisting of only unrelated individuals made up 9.1% of all sounders (Fig. 2). Interestingly, it was not uncommon for sounders to include at least one completely unrelated group member (15.9%). The remaining 18.2% of social groups were bachelor groups (Supplementary Fig. 7) and on average consisted of 4.5 individuals. The average group r for bachelor groups was 0.342 (Table 1). Bachelor groups were also typically composed of only breeding-aged (57.1%; Fig. 1), first-degree relatives (35.7%; Fig. 2). Unlike sounders, bachelor groups were unlikely to be composed of only unrelated individuals (7.1%; Fig. 2), nor include an unrelated group member when groups were comprised of kin.

Nonbreeding-aged group members excluded

Under the second hierarchy, 32.5% of social groups were excluded because they classified as pseudo-solitary individuals (Supplementary Fig. 7); therefore, 144 individuals assigned to 53 groups were retained for the demographic analysis and 137 individuals assigned to 52 groups were retained for the relatedness analysis. When compared to the first hierarchy of analysis, the average group size decreased to 2.1 individuals and average group r decreased to 0.318 (Table 1). Groups of only first-degree (34.6%; Fig. 2), female (57.1%; Supplementary Fig. 7) relatives were the most common group composition. The average sounder size was 2.7 individuals and the average sounder relatedness was 0.315 (Table 1). Sounders composed of only first-degree relatives remained the most common group relatedness composition (34.1%; Fig. 2). However, 20.5% of sounders included at least one unrelated group member and unrelated group members also frequently formed sounders (17.3%; Fig. 2). Bachelor groups accounted for 10.4% of the dataset analyzed under the second hierarchy (Supplementary Fig. 7). As observed with sounders, the average group relatedness and average group size for bachelor groups decreased (Table 1). Similarly, groups of only first-degree relatives remained the most common group relatedness composition (37.5%;

Table 1 Descriptive statistics under three hierarchies of analysis for wild pig (*Sus scrofa*) social groups (female dominated, male majority, pseudo-solitary female, and pseudo-solitary male) observed at the Savannah River Site (SRS), South Carolina, USA and Nobel Research Institution (NRI), Oklahoma, USA

Group type	Count ^a		Min n ^b		Average n ^c		Max n ^d		Min r ^e		Average r ^f		Max r ^g	
	SRS	NRI	SRS	NRI	SRS	NRI	SRS	NRI	SRS	NRI	SRS	NRI	SRS	NRI
<i>First hierarchy: All group members</i>														
Sounders	63 (263)	8 (32)	2	2	3.7	4.0	12	12	0.003	-0.071	0.318	0.163	0.863	0.592
Bachelor Groups	14 (63)	7 (41)	2	3	4.5	5.9	16	9	-0.015	0.145	0.342	0.295	0.558	0.498
All	77 (299)	15 (73)	2	2	3.9	4.9	16	12	-0.015	-0.071	0.323	0.225	0.863	0.592
<i>Second hierarchy: offspring excluded</i>														
Sounders	44 (118)	6 (17)	2	2	2.7	2.8	6	6	0.003	-0.086	0.315	0.161	0.863	0.498
Bachelor Groups	8 (19)	5 (16)	2	3	2.4	3.2	5	4	-0.015	0.068	0.338	0.359	0.558	0.621
Pseudo-solitary Female	23 (23)	2 (2)												
Pseudo-solitary Male	2 (2)	0 (0)												
All	77 (162)	13 (35)	1	1	2.1	2.7	6	6	-0.015	-0.086	0.318	0.251	0.863	0.621
<i>Third hierarchy: offspring, suitors excluded</i>														
Sounders	42 (109)	5 (15)	2	2	2.6	3.0	5	6	0.015	-0.086	0.345	0.203	0.863	0.498
Bachelor Groups	8 (19)	4 (13)	2	3	2.4	3.3	5	4	-0.015	0.068	0.338	0.415	0.558	0.621
Pseudo-solitary Female	25 (25)	4 (4)												
Pseudo-solitary Male	2 (2)	0 (0)												
All	77 (155)	13 (32)	1	1	2.0	2.5	5	6	-0.015	-0.086	0.344	0.297	0.863	0.621

^aTotal number of groups with the total number of individuals in parentheses in relatedness analysis

^cAverage group size

^dMaximum group size

^eMinimum group relatedness

^fAverage group relatedness

^gMaximum group relatedness

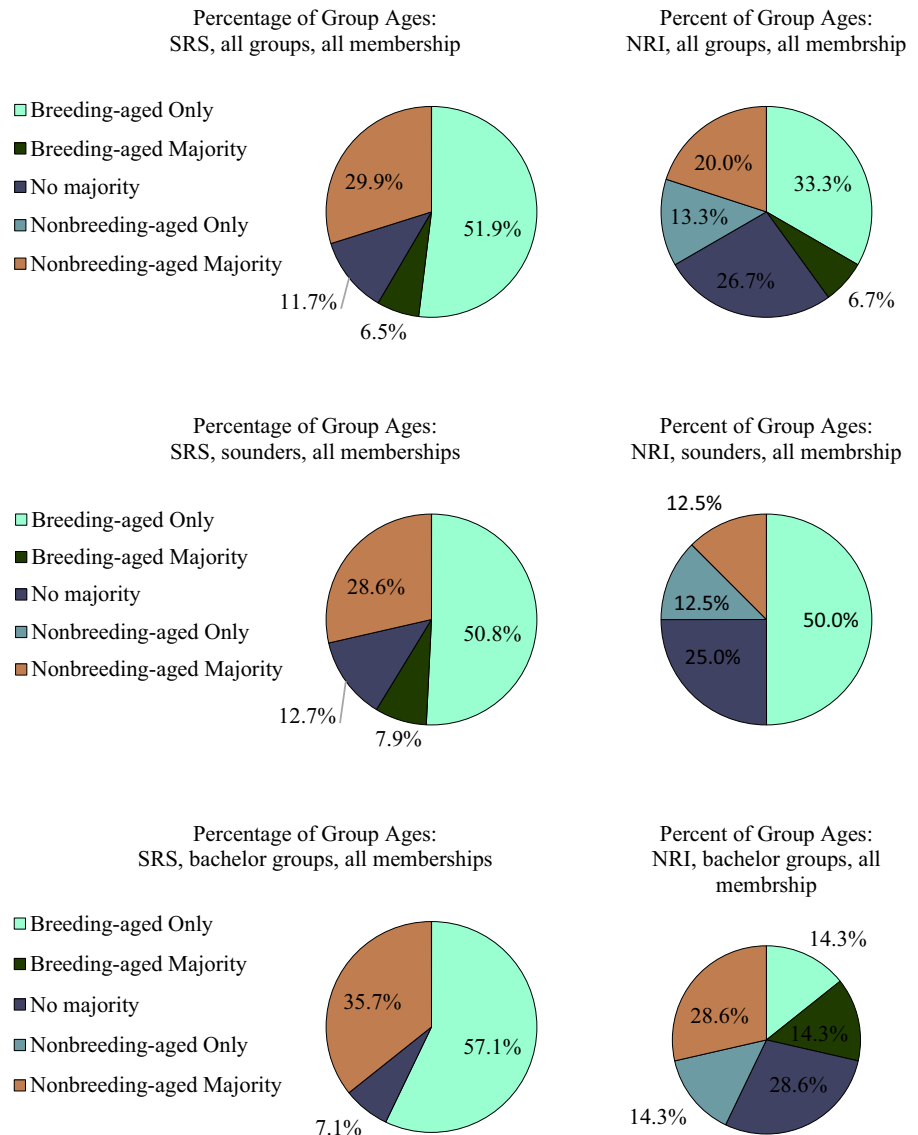
Fig. 2). None of the kin-based bachelor groups included a completely unrelated group member.

Nonbreeding-aged and unrelated male group members excluded

Similar to the second hierarchy, 35.1% of social groups were pseudo-solitary individuals and removed from consideration (Supplementary Fig. 7). Subsequently, the third hierarchy of analysis included 133 group members assigned to 50 groups for demographic analysis and 128 group members assigned to 50 groups for relatedness analysis. Compared to the first hierarchy of analysis, the average group size decreased to 2.0 individuals but the average group *r* increased to 0.344 (Table 1). The majority of groups were composed of only first-degree relatives (38.0%; Fig. 2); however, 4.0% of groups included a completely unrelated group member. The average sounder

group size was 2.6 and average group relatedness was 0.345 (Table 1). Sounders consisting of only first-degree relatives were the most common group demographic under the third hierarchy (38.1%; Fig. 2); however, two of the sounders still retained at least one unrelated group member. Interestingly, one sounder consisted of an unrelated female captured with a male and female that were first-degree relatives (Fig. 3). Bachelor groups accounted for 10.4% of the dataset (Supplementary Fig. 7). The average bachelor group size and average group *r* did not change from the second hierarchy of analysis to the third (Table 1). Bachelor groups consisting of only first-degree relatives remained the most common relatedness composition (37.5%; Fig. 2), although one bachelor group was a pair of unrelated yearling males. Another bachelor group was composed of a subadult female with four subadult males that displayed variable degrees of relatedness (Fig. 3).

Fig. 1 Percentage of majority age classes of groups at the Savannah River Site (SRS) (left) and Noble Research Institute (NRI) (right) under the first hierarchy (all group members) with all groups (top), sounders (middle), and bachelor groups (bottom). The majority age classes displayed in groups are shown as proportions of the total dataset for each study area



Noble research institute

With 6,735 SNP loci and 4 PCs retained (Supplementary Fig. 5), adjusted pairwise relatedness coefficients were calculated for 403 individuals from southcentral Oklahoma. The average relatedness across all wild pigs sampled in NRI was $r=0.022$. We assigned 383 of the 403 individuals to 44 social groups. The remaining 20 individuals were captured alone and excluded from analysis. Furthermore, 31 social groups (310 individuals) were excluded due to incomplete social groups (i.e., only piglets and/or juveniles were captured) and/or individuals that

were missing age or other necessary capture information. It is worth mentioning that among the excluded social groups, many were very large (Supplementary Table 1). Sounders were the most common group type under all hierarchies of analysis (Supplementary Fig. 7). As with SRS, bachelor groups were present under all hierarchies of analysis (Supplementary Fig. 7).

All group members included

The first hierarchy of analysis considered all 13 social groups and their 73 group members for both

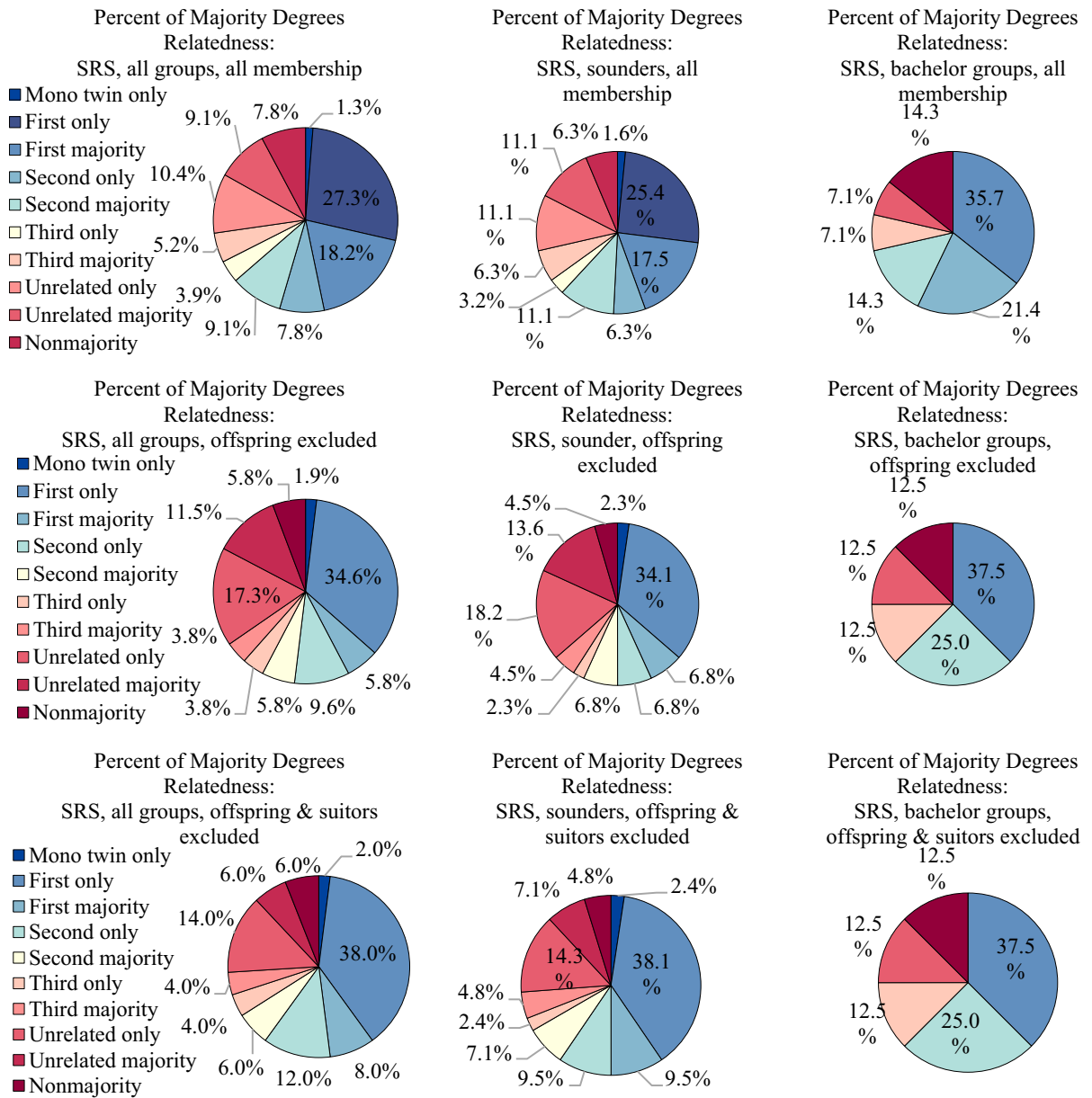


Fig. 2 Percentage of majority degrees relatedness of groups at the Savannah River Site (SRS) with all group membership (top), proposed offspring excluded (middle), and proposed

offspring and potential suitor males excluded (bottom). The majority degree of relatedness displayed in groups are shown as proportions of the total dataset

demographic and relatedness analyses. The average group size was 4.9 individuals and the average group relatedness was 0.197 (Table 1). Southcentral Oklahoma groups were typically composed of only breeding-aged individuals or did not display an age majority (33.3 and 26.7%, respectively; Fig. 1). The most common group relatedness composition were

groups that displayed a majority of unrelated dyads (26.7%; Fig. 4). However, groups of either only first-degree relatives or only unrelated individuals were not uncommon (20.0 and 20.0%, respectively; Fig. 4). Five groups that included relatives also had an unrelated group member (33.3%). Sounders were slightly more common than bachelor groups (53.3

SRS Relatedness Network of Group 99 and 161

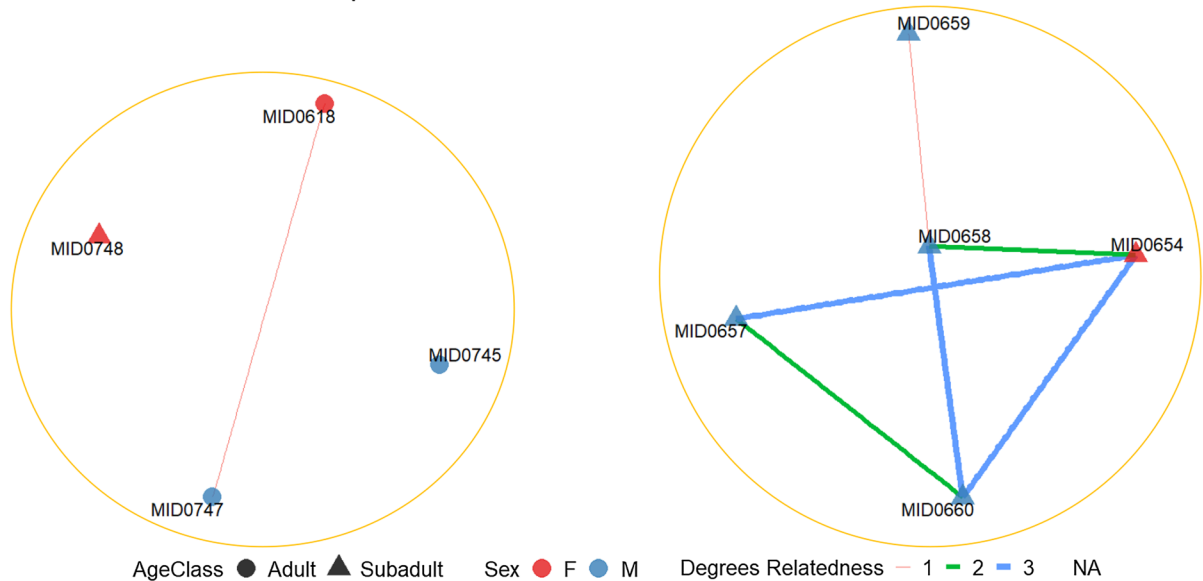


Fig. 3 Plot of relatedness network of Savannah River Site (SRS) social group 99 (left) and 161 (right). Each individual in the group is represented by a plot point. Age class of an individual is indicated by point symbol, sex of an individual

is indicated by point color, and degree of relatedness for each dyad is represented by the line connecting the pair. If the dyad was classified as unrelated (NA), then points were not connected

and 46.7%, respectively; Supplementary Fig. 7). The average sounder size was 4.0 individuals and the average group relatedness was 0.163 (Table 1). Half of all sounders were composed of only breeding-aged individuals (Fig. 1). Interestingly, most sounders were composed of only unrelated individuals (37.5%; Fig. 4); however, sounders that included kin were unlikely to also include a completely unrelated group member. The average group size and group r of bachelor groups were slightly larger than sounders (Table 1). Bachelor groups were typically composed of a majority of nonbreeding-aged individuals or did not display an age majority (28.6 and 28.6%, respectively; Fig. 1). Groups of either first-degree relatives, a majority of first-degree dyads, or a majority of unrelated dyads were the most common group relatedness composition (28.6, 28.6 and 28.6%, respectively; Fig. 4).

Nonbreeding-aged group members excluded

The second hierarchy of analysis excluded 15.4% of social groups identified as pseudo-solitary (Supplementary Fig. 7), retaining 33 individuals assigned to 11 social groups for demographic and relatedness

analyses. The average group size greatly decreased from the first hierarchy of analysis, but the average group r was slightly higher (Table 1) and groups were commonly composed of only first-degree relatives (36.4%; Fig. 4). Sounders were more common than bachelor groups (46.2 and 38.5%, respectively; Supplementary Fig. 7). The average sounders size was 2.8 individuals and average group relatedness was 0.161 (Table 1). As with the first hierarchy of analysis, sounders of only unrelated individuals remained most common (33.3%; Fig. 4); however, sounders with relatives never included an unrelated group member. Bachelor groups had an average group size of 3.2 individuals and average group relatedness of 0.359 (Table 1). Unlike sounders, bachelor groups composed of only first-degree relatives were most common (60.0%; Fig. 4).

Nonbreeding-aged and unrelated male group members excluded

Under the third hierarchy of analysis, 30.8% of social groups were determined to be pseudo-solitary and excluded from consideration (Supplementary Fig. 7); therefore, 28 individuals assigned to nine social

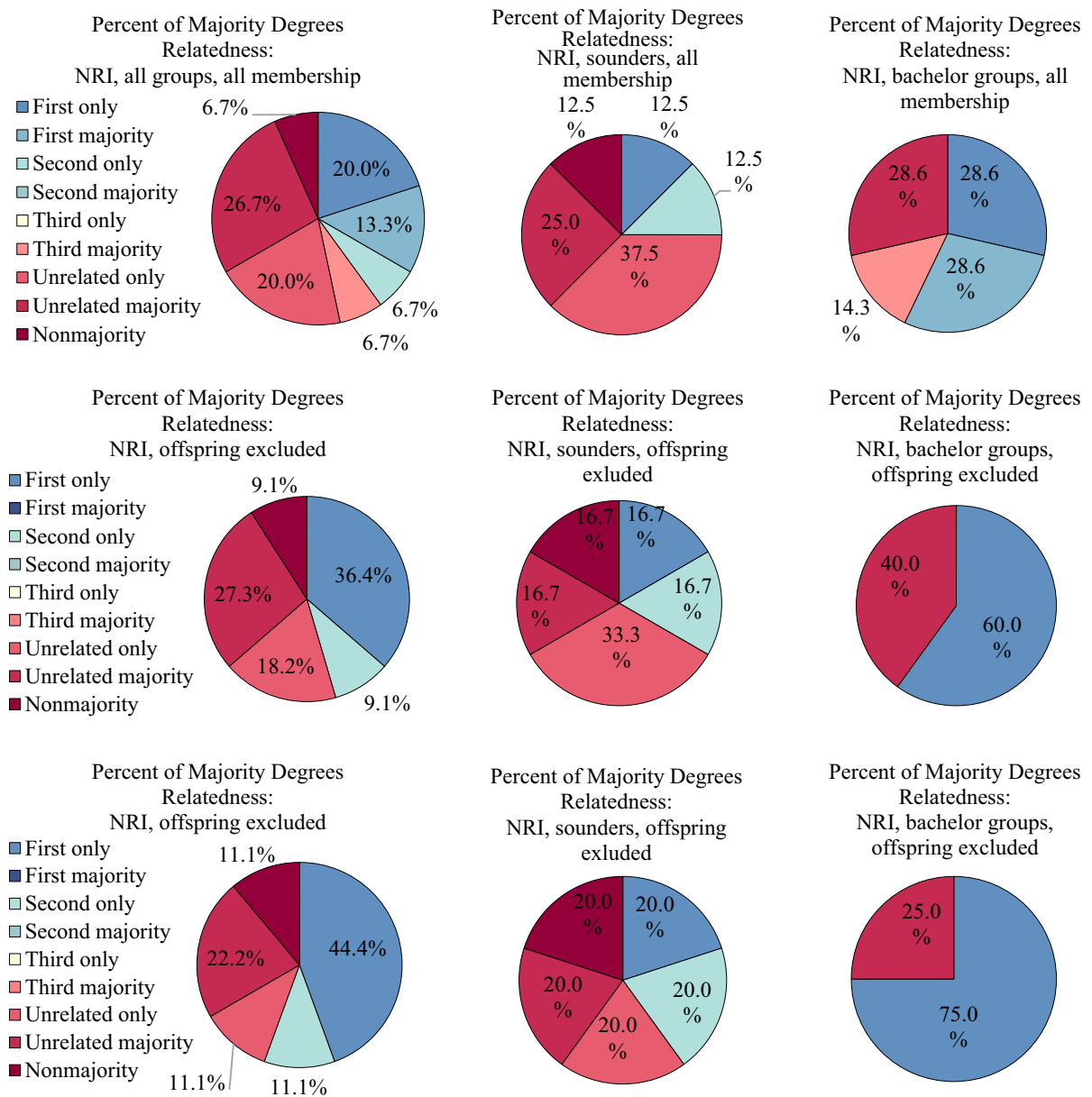


Fig. 4 Percentage of majority degrees relatedness of groups at Noble Research Institute (NRI) with all group membership (top), proposed offspring excluded (middle), and proposed

offspring and potential suitor males excluded (bottom). The majority degree of relatedness displayed in groups are shown as proportions of the total dataset

groups were retained for demographic and relatedness analyses. In comparison to the first hierarchy of analysis, the average group size decreased to 2.5 individuals and average group *r* increased to 0.297 (Table 1). As with the second hierarchy of analysis, groups were typically composed of only first-degree relatives (44.4%; Fig. 4). The sounders that persisted

under the third hierarchy accounted for 38.5% of the dataset (Supplementary Fig. 7), had an average group size of 3.0 individuals, and average group relatedness of 0.203 (Table 1). Sounders of only first-degree relatives, only second-degree relatives, only unrelated group members, a majority of unrelated dyads, and no relatedness majority composition were

all equally represented (20.0% each, respectively; Fig. 4). Although some sounders were comprised of only unrelated individuals, none of the sounders that displayed kin relationships incorporated a completely unrelated group member. Interestingly, one sounder included adult male relatives (Fig. 5). This group displayed variable relatedness among its members, and was composed of two adult males, two subadult females, and two yearling females. Bachelor groups comprised 30.8% of the dataset (Supplementary Fig. 7). When compared to the first hierarchy of analysis, the average bachelor group size decreased to 3.3 individuals and average group relatedness greatly increased to 0.415 (Table 1).

Discussion

Despite their widespread distribution and extensive ecological and economic impacts, the social organization of invasive wild pigs has been understudied and largely limited to observational behavioral data (Fernández-Llario et al. 1996; Hampton et al. 2004; Rosell et al. 2004). Using robust genomic tools, our results revealed that previously held assumptions of familial associations within invasive wild pig sounders were generally correct; however, these assumptions did not fully capture the diversity in group composition observed within the study populations. Across both geographic areas sampled, wild pig social units consisted of sounders, pseudo-solitary females, bachelor groups, and solitary males. Aside from solitary males, sounders were the most common social group observed across our two study sites. Although adult females in these groups were often close kin

NRI Relatedness Network Group 20

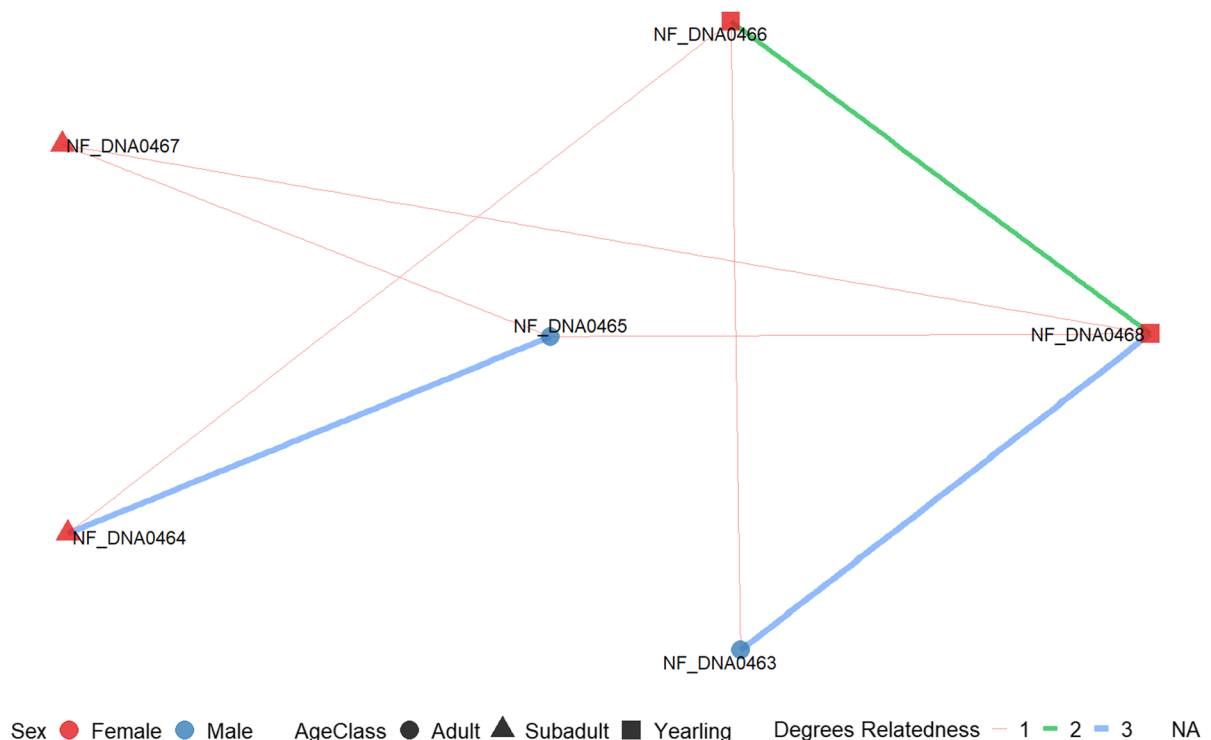


Fig. 5 Plot of relatedness network of Noble Research Institute (NRI) social group 20. Each individual in the group is represented by a plot point. Age class of an individual is indicated by point symbol, sex of an individual is indicated by point

color, and degree of relatedness for each dyad is represented by the line connecting the pair. If the dyad was classified as unrelated (NA), then points were not connected

(first-degree relatives), many of these groups also included an unrelated breeding-aged female – counter to previous assumptions. In southcentral Oklahoma, we observed a dichotomy in sounder organization in which some sounders were comprised of only unrelated individuals whereas those sounders that included relatives did not include unrelated group members. Even though there were many sounders of only unrelated females, kin-only sounders were still more common in southcentral Oklahoma. This tendency for females to form sounders with close kin has also been reported in European wild boar across their native range. Conversely, few studies have found that these groups will recruit unrelated females; behavior that was observed among the SRS sounders (Kaminski et al. 2005; Iacolina et al. 2009; Podgórski et al. 2014b). We also found that many adult females were captured with only their offspring or unrelated breeding-aged males, suggesting the size and composition of sounders are dynamic and variable within populations. Though they occurred less frequently, bachelor groups were prevalent in both populations and primarily comprised of young, related individuals. Though our study can only describe social groups at the time of their capture, we have demonstrated invasive wild pigs display more complex and diverse social organization than previously believed.

Similar to wild boar (Iacolina et al. 2009; Podgórski et al. 2014a, b), matriarchal sounders were the most common social unit observed across both study sites. Sounders were highly variable in size depending on the number of offspring present, ranging from 2 to 45 individuals. The largest group captured at SRS had 16 individuals and average SRS group size was approximately four individuals before offspring and suitors were excluded. When these individuals were excluded, social groups at SRS were typically composed of two breeding-aged relatives. The largest group captured in southcentral Oklahoma was 45 individuals; however, this group, as well as many other large social groups at this location, could not be included in our dataset because age and/or sex was not recorded at time of collection. In fact, >40% of the excluded groups captured in southcentral Oklahoma had over 10 individuals, and approximately 10% had over 20. Within their native range, average group size for European wild boar generally ranges from 4 to 9 individuals, depending on the location (Dardaillon 1988; Poteaux et al. 2009; Podgórski

et al. 2014a, b; Battocchio et al. 2017), although studies do not always explicitly state whether offspring are included in these calculations. Thus, while groups at SRS were generally smaller than those reported for European wild boar, sounders in southcentral Oklahoma were more comparable in size to groups within the native range of this species. Studies of wild pigs in Texas and Oklahoma also have reported large social groups (>5 individuals; Gabor et al. 1999; Wehr et al. 2018; Gaskamp et al. 2021). The propensity for invasive wild pigs to form smaller groups in the Southeastern USA compared to more arid regions of the USA may be due to differences in resource distributions, management strategies, or genetic lineages. Productive bottomland swamps are abundant and widely distributed throughout much of the Southeastern USA and have a strong influence on wild pig movements and population dynamics (Keiter et al. 2017; Clontz et al. 2021). Furthermore, wild pigs on the SRS are intensively managed to reduce collisions with vehicles and minimize other damages (Beasley et al. 2014), and individuals within the SRS generally have lower wild boar ancestry than those individuals encountered in the NRI population (Smyser et al. 2020). More in-depth studies are needed to better understand how ancestry, management strategies, and landscape attributes, as well as other biotic and abiotic factors, may influence sounder sizes among invasive populations.

Interestingly, our data revealed wild pig group members are not always closely related to each other and may include unrelated individuals. Sounders at SRS were most commonly composed of only first-degree relatives; however, nearly half of all SRS sounders displayed variable relatedness. Many groups included group members that were first-degree relatives to some and distantly related or unrelated to others (Fig. 3). Furthermore, 4.8% of SRS kin sounders included an unrelated breeding-aged female. Telemetry data collected from these groups as part of complementary studies (Beasley et al. 2021; Clontz et al. 2021) confirmed these unrelated individuals were established group members as opposed to simply temporary associates. Some populations of European wild boar also exhibit tolerance of unrelated females within sounders, but this tolerance is not shared uniformly across their range (Iacolina et al. 2009; Podgórski et al. 2014a, b). Conversely, southcentral Oklahoma sounders typically displayed greater

variability in patterns of relatedness among group members (Fig. 5).

Despite the variability in relatedness exhibited among southcentral Oklahoma sounders, kin-based sounders were not likely to include a completely unrelated individual. Some studies on European wild boar have suggested frequent hunting or population control efforts may disrupt the social structure of sounders and facilitate the collective association of unrelated individuals (Poteaux et al. 2009; Podgórski et al. 2014a). Though our two study sites both implement control strategies, the sites differ in the frequency and type of removal efforts. In particular, the majority of wild pigs removed from the SRS are captured in box traps or small corral traps, methods that often result in partial removal of sounders, whereas whole-sounder removal efforts are more common at NRI (Gaskamp et al. 2021). The disruption of social units at SRS due to partial removal of sounders may facilitate the integration of unrelated members within social groups in this study site and other areas that employ similar management strategies. Indeed, a study to assess the movement ecology of translocated wild pigs found that the majority of translocated sows integrated within a new (unrelated) sounder within 1–2 months following translocation (Smith et al. 2022).

It may be that the genetic ‘snapshot’ provided by our dataset fails to represent the full breadth of familial associations within sounders. McIlraith (2021) described fission–fusion dynamics among sounders within four southern USA populations as group members coalesced and separated over time. Further, wild pigs captured together, and subsequently collared, tended to associate with one another more than individuals distributed between sounders. However, even collared pigs from the same captured sounder exhibited irregular separation periods. Future research is needed to combine relatedness with movement data to better understand fission–fusion dynamics and social structure. Although wild pigs throughout much of their invasive range in North America reproduce year-round, mating often peaks in late winter following a pulse in mast availability (Chinn unpublished data). The seasonality of reproduction may result in variable group size and composition across seasons, particularly for populations at the northern extent of the species’ range. Thus, subsequent studies of wild pig and wild boar social groups should incorporate broader environmental factors to elucidate their effects on

group size, formation, and recruitment. Landscape features also may influence the structure of sounders. Past studies have suggested habitat quality and access to resources could affect the size of sounders and the recruitment of an unrelated individual (Delgado et al. 2008; Gaskamp et al. 2021). Differences in landscape features between southcentral Oklahoma and SRS may account for the different relatedness compositions between the two sites. The SRS is generally wetter and more humid than southcentral Oklahoma and encompasses a mixture of upland and bottomland woodlands. However, determining the influence of habitat differences between the two sites was outside the scope of this study due to the disparity in sample sizes. Future studies should further investigate if differences in resource availability and/or removal pressure can account for the disparity in sounder relatedness between locations.

In addition to sounders, we observed individual adult females, who were captured with either dependent offspring, suitor males, or both in southcentral Oklahoma and SRS. These individuals are thought to be temporary associations as suitor males are not likely to remain with a female for more than a week or two and offspring often disperse as older juveniles or yearlings. Among these pseudo-solitary groups, some included offspring that were a few weeks old. These females may be temporarily separated from their sounder for parturition (Gabor et al. 1999; Mayer et al. 2020). This secretive behavior has been observed in studies of European wild boar (Dardaillon 1988; Kaminski et al. 2005; Poteaux et al. 2009). Indeed, we were able to confirm from camera data that some of these females had been in association with an uncaptured female prior to parturition (Clontz et al. 2021). However, other pseudo-solitary groups included offspring that were several months old, suggesting not all of these groups were temporary disassociations from larger groups during parturition. Gabor et al. (1999) demonstrated that female dispersal does occur, though rare. There remains a strong possibility that social organization for wild pig females may include both sounder and pseudo-solitary females, although the fission–fusion dynamics of wild pig social groups remains largely unknown. We are limited by our sampling strategy and can only describe the social organization of these individuals at the time of capture when no camera is available. Even so, through use of genomic data we can

highlight the complexity of sounder composition and diversity in female social units with greater resolution than described in past studies.

Though not as common as sounders, our study also revealed male majority groups (i.e., bachelor groups) are relatively common, and primarily composed of small, breeding-aged kin. Past studies have described bachelor groups as being rare (e.g., Gabor et al. 1999). However, these studies, as well as ours, largely targeted sounders or solitary adult males as part of ongoing research and management, and thus male-dominated groups undoubtedly occur more frequently than reported herein or in the prior literature due to biases in sampling strategies. Although typically composed of only closely related males, a few bachelor groups in our study included a related female and one group included an unrelated female. Unlike sounders, bachelor groups were highly unlikely to include an unrelated group member, and none were composed of only unrelated individuals. Similar male coalitions have been observed in other species. Most notably in African lions, male crèche mates will take over and defend female prides (Packer and Pusey 1982). Male groups have also been observed in some raccoon (*Procyon lotor*) populations in which males of varying age have been observed traveling and denning in the same tree (Gehrt and Fox 2004). Though uncommon in African elephants (*Loxodonta africana*), Asian elephants (*Elephas maximus*) frequently display bachelor herds that sometimes include females and are not dependent on relatedness of its members (Schneck 1991; Ahlering et al. 2011). Unlike raccoons and Asian elephants, wild pig bachelor groups in our study seem to be intolerant of unrelated individuals. However, the lack of capture groups composed of large, breeding-aged males suggests that bachelor groups are unlikely to be as cooperative as male African lion coalitions and are likely transitioning to become independent and solitary. Bachelor groups in European wild boar have been reported to be littermates that disperse from their natal groups for a short period before transitioning to become solitary (Dardaillon 1988). Wild boar females were also observed to disperse with their male litter mates on rare occasions (Kaminski et al. 2005). However, the behavior and frequency of bachelor coalitions in both wild pigs and European wild boar is understudied.

Collectively, our study suggests wild pig social organization is complex, dynamic, and likely variable

across the species' introduced range. Wild pig social organization seems to mirror European wild boar in that they both are largely composed of matriarchal groups and tolerance of unrelated individuals varies by population. In addition to matriarchally dominated sounders and solitary males, pseudo-solitary females and bachelor coalitions were relatively common and should be included in future investigations of wild pig social organization. Interestingly, we found that sounders in southcentral Oklahoma, the drier and less humid study site, were less likely to include unrelated group members but were more likely to have groups composed of only unrelated individuals. It is unclear whether this observation was due to differences in resource distribution between sites or differences in culling strategies resulting in greater disruption of sounder composition at the SRS or an artifact of the dichotomous sample sizes between SRS and southcentral Oklahoma. Thus, future research is needed to individually elucidate the impacts of resource distribution and management strategies on wild pig and wild boar social dynamics, as these data could have direct implications to the development of more efficient management strategies for this destructive species. Further studies also are needed to better understand the dynamics and stability of associations of group members, as well as the frequency of pseudo-solitary females and male groups in wild pig populations.

Acknowledgements Funding for this research was provided by the U.S. Department of Energy under Award No. DE-EM0005228 to the University of Georgia Research Foundation, the Warnell School of Forestry and Natural Resources, the United States Department of Agriculture – Animal and Plant Inspection Services – Wildlife Services – National Wildlife Research Center, the United States Department of Agriculture – Animal and Plant Inspection Services – National Feral Swine Damage Management Program, and the Noble Research Institute, LLC. We also thank USFS personnel and contractors for their assistance in collecting samples, as well as the numerous field assistants and other researchers that contributed to this research, particularly A. Mangan, A. Piaggio, S. Chinn, L. Clontz, C. Kupferman, P. Schlichting, D. Keiter, J. Gaskamp, C. Ellis, D. Warren, S. Peper, A. Wilson-Fallon, K. Haydett, H. Tiffen, K. Boyer, Z. Johnson, K. Klement, F. Motal, M. Proctor, and K. Gee.

Authors contribution JCB, SLW and TJS contributed to the study conceptualization, provided resources, and acquired funding for the study. CFB, CLT, JCB and TJS developed the study methodology; CFB, JCB, SLW and TJS collected data; CFB, CLT and TJS ran analyses and visualized the results.

CLT wrote the first draft of the manuscript and CFB, JCB, SLW and TJS reviewed, edited, and made intellectual contributions to subsequent revisions of the manuscript.

Data availability Supporting data and R code for this study will be uploaded on the Dryad Digital Repository upon acceptance. Materials will be provided upon request during the review process.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

- Ahlering MA, Hedges S, Johnson A et al (2011) Genetic diversity, social structure, and conservation value of the elephants of the Nakai Plateau, Lao PDR, based on non-invasive sampling. *Conserv Genet* 12:413–422. <https://doi.org/10.1007/s10592-010-0148-y>
- Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biol Invasions* 14:2283–2300. <https://doi.org/10.1007/s10530-012-0229-6>
- Battocchio D, Iacolina L, Canu A, Mori E (2017) How much does it cost to look like a pig in a wild boar group? *Behav Proc* 138:123–126. <https://doi.org/10.1016/j.beproc.2017.03.001>
- Beasley JC, Grazia TE, Johns PE, Mayer JJ (2014) Habitats associated with vehicle collisions with wild pigs. *Wildl Res* 40:654. <https://doi.org/10.1071/WR13061>
- Beasley JC, Ditchkoff SS, Mayer JJ et al (2018) Research priorities for managing invasive wild pigs in North America: Research Priorities for Wild Pigs. *J Wildl Manage* 82:674–681. <https://doi.org/10.1002/jwmg.21436>
- Beasley JC, Clontz LM, Rakowski A et al (2021) Evaluation of a warfarin bait for controlling invasive wild pigs (*Sus scrofa*). *Pest Manag Sci*. <https://doi.org/10.1002/ps.6351>
- Body G, Weladji RB, Holand Ø, Nieminen M (2015) Fission-fusion group dynamics in reindeer reveal an increase of cohesiveness at the beginning of the peak rut. *Acta Ethol* 18:101–110. <https://doi.org/10.1007/s10211-014-0190-8>
- Boyer KS, Fairbanks WS, Rohla C, Webb SL (2020) Surficial soil damage by wild pigs (*Sus scrofa*) decreases pecan harvest efficiency. *Crop Prot* 128:104992. <https://doi.org/10.1016/j.cropro.2019.104992>
- Burn mesonet summary. *Oklahoma Climatological survey* | *BURN Mesonet Summary*. https://www.climate.ok.gov/index.php/climate/county_climate_mesonet_summary/love/BURN_stnsum.html (Accessed 31 March 2022)
- Cafazzo S, Lazzaroni M, Marshall-Pescini S (2016) Dominance relationships in a family pack of captive arctic wolves (*Canis lupus arctos*): the influence of competition for food, age and sex. *PeerJ* 4:e2707. <https://doi.org/10.7717/peerj.2707>
- Cavalcanti SMC, Gese EM (2009) Spatial Ecology and Social Interactions of Jaguars (*Panthera Onca*) in the Southern Pantanal, Brazil. *J Mammal* 90:935–945. <https://doi.org/10.1644/08-MAMM-A-188.1>
- Clontz LM, Pepin KM, VerCauteren KC, Beasley JC (2021) Behavioral state resource selection in invasive wild pigs in the Southeastern United States. *Sci Rep* 11:6924. <https://doi.org/10.1038/s41598-021-86363-3>
- Connor RC, Heithaus MR, Barre LM (2001) Complex social structure, alliance stability and mating access in a bottlenose dolphin ‘super-alliance.’ *Proc R Soc Lond B* 268:263–267. <https://doi.org/10.1098/rspb.2000.1357>
- Conomos MP, Miller MB, Thornton TA (2015) Robust inference of population structure for ancestry prediction and correction of stratification in the presence of relatedness. *Genet Epidemiol* 39:276–293. <https://doi.org/10.1002/gepi.21896>
- Conomos MP, Reiner AP, Weir BS, Thornton TA (2016) Model-free estimation of recent genetic relatedness. *Am J Hum Genet* 98:127–148. <https://doi.org/10.1016/j.ajhg.2015.11.022>
- Dardaillon M (1988) Wild boar social groupings and their seasonal changes in the Camargue, southern France. *Z Säugetierkunde* 53:22–30
- Delgado R, Fernández-Llario P, Azevedo M et al (2008) Paternity assessment in free-ranging wild boar (*Sus scrofa*) – Are littermates full-sibs? *Mamm Biol* 73:169–176. <https://doi.org/10.1016/j.mambio.2007.07.008>
- Delgado-Acevedo J, Zamorano A, DeYoung RW et al (2010) Promiscuous mating in feral pigs (*Sus scrofa*) from Texas, USA. *Wildl Res* 37:539–546
- Dickinson J, Koenig W (2018) Animal social behaviour. *Encyclopedia Britannica*
- Fernández-Llario P, Carranza J, Hidalgo de Trucios SJ (1996) Social organization of the wild boar (*Sus scrofa*) in Doñana National Park. *Miscelánea Zoológica* 19:9–18
- Gabor TM, Hellgren EC, Van Den Bussche RA, Silvy NJ (1999) Demography, sociospatial behaviour and genetics of feral pigs (*Sus scrofa*) in a semi-arid environment. *J Zool* 247:311–322
- Gaskamp JA, Gee KL, Campbell TA et al (2016) Pseudorabies virus and *brucella abortus* from an expanding wild pig (*Sus scrofa*) population in southern Oklahoma, USA. *J Wildl Dis* 52:383–386. <https://doi.org/10.7589/2015-08-218>
- Gaskamp JA, Gee KL, Campbell TA et al (2018) Damage caused to rangelands by wild pig rooting activity is mitigated with intensive trapping. *Cogent Environ Sci*. <https://doi.org/10.1080/23311843.2018.1540080>
- Gaskamp JA, Gee KL, Campbell TA et al (2021) Effectiveness and efficiency of corral traps, drop nets and suspended traps for capturing wild pigs (*Sus scrofa*). *Animals* 11:1565. <https://doi.org/10.3390/ani11061565>
- Gehrt SD, Fox LB (2004) Spatial patterns and dynamic interactions among raccoons in eastern Kansas. *Southwest Nat* 49:116–121
- Gogarten SM, Sofer T, Chen H, Yu C, Brody JA, Thornton TA, Rice KM, Conomos MP (2019) Genetic association testing using the GENESIS R/Bioconductor package. *Bioinformatics* 35:5346–5348. <https://doi.org/10.1093/bioinformatics/btz567>
- Hampton J, Pluske JR, Spencer PBS (2004) A preliminary genetic study of the social biology of feral pigs in

- south-western Australia and the implications for management. *Wildl Res* 31:375–381
- Haydett KM, Peper ST, Reinoso Webb C et al (2021) Prevalence of neospora caninum exposure in Wild Pigs (*Sus scrofa*) from Oklahoma with implications of testing method on detection. *Animals* 11:2487. <https://doi.org/10.3390/ani11092487>
- Iacolina L, Scandura M, Bongi P, Apollonio M (2009) Nonkin associations in wild boar *Sus scrofa*. *J Mammal* 90:666–674. <https://doi.org/10.1644/08-MAMM-A-074R1.1>
- Imm DW, McLeod KW (2005) *Plant Communities. Ecology and management of a forested landscape: fifty years on the Savannah river site.* Island Press, Washington, DC, USA, pp 106–161
- Kaminski G, Brandt S, Baubet E, Baudoin C (2005) Life-history patterns in female wild boars (*Sus scrofa*): mother-daughter postweaning associations. *Can J Zool* 83:474–480. <https://doi.org/10.1139/z05-019>
- Keiter DA, Mayer JJ, Beasley JC (2016) What is in a “common” name? A call for consistent terminology for non-native *Sus scrofa*: Terminology for *Sus scrofa*. *Wildl Soc Bull* 40:384–387. <https://doi.org/10.1002/wsb.649>
- Keiter DA, Davis AJ, Rhodes OE et al (2017) Effects of scale of movement, detection probability, and true population density on common methods of estimating population density. *Sci Rep*. <https://doi.org/10.1038/s41598-017-09746-5>
- Krause J, Krause P of FB and EJ, Ruxton GD, et al (2002) *Living in Groups.* Oxford University Press, Oxford
- Krause J, Godin J-GJ (1995) Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. *Anim Behav* 50:465–473. <https://doi.org/10.1006/anbe.1995.0260>
- Lewis JS, Corn JL, Mayer JJ et al (2019) Historical, current, and potential population size estimates of invasive wild pigs (*Sus scrofa*) in the United States. *Biol Invasions* 21:2373–2384. <https://doi.org/10.1007/s10530-019-01983-1>
- Macdonald DW (1979) ‘Helpers’ in fox society. *Nature* 282:69–71. <https://doi.org/10.1038/282069a0>
- Manichaikul A, Mychaleckyj JC, Rich SS et al (2010) Robust relationship inference in genome-wide association studies. *Bioinformatics* 26:2867–2873
- Matschke GH (1967) Aging European wild hogs by dentition. *J Wildl Manag* 31:109–113. <https://doi.org/10.2307/3798365>
- Mayer JJ, Beasley JC (2018) Chapter 11: Wild Pigs. In: *Ecology and management of terrestrial vertebrate invasive species in the United States.* CRC Press
- Mayer JJ, Brisbin IL (2009) Wild pigs: biology, damage, control techniques, and management. Savannah River National Library, Savannah River Site
- Mayer JJ, Beasley JC, Boughton RK, Ditchkoff SS (2020) Wild Pigs in Southeastern North America. In: *Invasive Wild Pigs in North America: Ecology, Impacts, and Management.* CRC Press, pp 369–402
- McIlraith J (2021) Social structure and cohesiveness Of GPS tracked wild pigs in the southeastern United States. Master of Science Thesis, University of Western Ontario
- Oklahoma Climatological Survey. Monthly climate normals by County. http://climate.ok.gov/index.php/climate/climate_normals_by_county/local_data (Accessed 31 March 2022)
- Moore J, Simberloff D, Freehling M (1988) Relationships between bobwhite quail social-group size and intestinal helminth parasitism. *Am Nat* 131:22–32. <https://doi.org/10.1086/284771>
- Nakatani J, Ono Y (1994) Social groupings of Japanese wild boar *Sus scrofa leucomystax* and their changes in the Rokko mountains. *J Mamm Soc Japan* 19:45–55
- Nowak MA, Tarnita CE, Wilson EO (2010) The evolution of eusociality. *Nature* 466:1057–1062. <https://doi.org/10.1038/nature09205>
- Packer C, Pusey AE (1982) Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* 296:740–742. <https://doi.org/10.1038/296740a0>
- Podgórski T, Lusseau D, Scandura M et al (2014a) Long-lasting, kin-directed female interactions in a spatially structured wild boar social network. *PLoS ONE* 9:e99875. <https://doi.org/10.1371/journal.pone.0099875>
- Podgórski T, Scandura M, Jędrzejewska B (2014b) Next of kin next door - philopatry and socio-genetic population structure in wild boar. *J Zool* 294:190–197. <https://doi.org/10.1111/jzo.12167>
- Poteaux C, Baubet E, Kaminski G et al (2009) Socio-genetic structure and mating system of a wild boar population. *J Zool* 278:116–125. <https://doi.org/10.1111/j.1469-7998.2009.00553.x>
- Prox L, Farine D (2020) A framework for conceptualizing dimensions of social organization in mammals. *Ecol Evol* 10:791–807. <https://doi.org/10.1002/ece3.5936>
- Purcell S, Chang C (2015) PLINK. Version 1.9 URL www.cog-genomics.org/plink/1.9
- Ramos AM, Crooijmans RPMA, Affara NA et al (2009) Design of a high density SNP genotyping assay in the pig using SNPs identified and characterized by next generation sequencing technology. *PLoS ONE* 4:e6524. <https://doi.org/10.1371/journal.pone.0006524>
- Ramstetter MD, Dyer TD, Lehman DM et al (2017) Benchmarking relatedness inference methods with genome-wide data from thousands of relatives. *Genetics* 207:75–82. <https://doi.org/10.1534/genetics.117.1122>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rosell C, Navàs F, Romero S, de Dalmases I (2004) Activity patterns and social organization of wild boar (*Sus scrofa*, L.) in a wetland environment: preliminary data on the effects of shooting individuals. *Galemys* 16:157–166
- Schneck M (1991) *Elephants: gentle giants of Africa and Asia.* Gramercy, New York
- Silk JB (2007) The adaptive value of sociality in mammalian groups. *Phil Trans R Soc B* 362:539–559. <https://doi.org/10.1098/rstb.2006.1994>
- Simeone R, Misztal I, Aguilar I, Legarra A (2011) Evaluation of the utility of diagonal elements of the genomic relationship matrix as a diagnostic tool to detect mislabelled genotyped animals in a broiler chicken population. *J Am*

- Breed Genet 128:386–393. <https://doi.org/10.1111/j.1439-0388.2011.00926.x>
- Smith JS, Sweeney S, Miller R, Schlichting P, Beasley JC (2022) Habitat quality influences trade-offs in animal movement along the exploration-exploitation continuum. 18 March 2022, Preprint available at Research Square. <https://doi.org/10.21203/rs.3.rs-1466681/v1>
- Smyser TJ, Tabak MA, Sloomaker C et al (2020) Mixed ancestry from wild and domestic lineages contributes to the rapid expansion of invasive feral swine. *Mol Ecol* 29:1103–1119. <https://doi.org/10.1111/mec.15392>
- Spencer PBS, Lapidge SJ, Hampton JO et al (2005) The socio-genetic structure of a controlled feral pig population. *Wild Res* 32:297–304. <https://doi.org/10.1071/WR04076>
- Stevens RL (2010) *The feral hog in Oklahoma*. Samuel Roberts Noble Foundation, Ardmore, Okla
- VerCauteren KC, Beasley JC, Ditchkoff SS et al (2020) *Invasive wild pigs in north america: ecology, impacts, and management*. CRC Press, Cambridge
- Warr A, Affara N, Aken B et al (2020) An improved pig reference genome sequence to enable pig genetics and genomics research. *GigaScience* 9:1–14. <https://doi.org/10.1093/gigascience/giaa051>
- Wehr NH, Hess SC, Litton CM (2018) Biology and Impacts of Pacific Islands Invasive Species. 14. *Sus scrofa*, the Feral Pig (Artiodactyla: Suidae) <sup>. *Pac Sci* 72:177–198. <https://doi.org/10.2984/72.2.1>
- Yang A, Schlichting P, Wight B et al (2021) Effects of social structure and management on risk of disease establishment in wild pigs. *J Anim Ecol* 90:820–833
- Zheng X, Levine D, Shen J et al (2012) A high-performance computing toolset for relatedness and principal component analysis of SNP data. *Bioinformatics* 28:3326–3328. <https://doi.org/10.1093/bioinformatics/bts606>

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