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Johanna Delgado-Acevedo
Texas A&M University-Kingsville

Randy W. DeYoung
Texas A&M University-Kingsville, randall.deyoung@tamuk.edu

Tyler A. Campbell
United States Department of Agriculture, tcampbell@eastfoundation.net

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Effects of local-scale removals on feral swine populations in southern Texas

Johanna Delgado-Acevedo[a], Randy W. DeYoung[a] and Tyler A. Campbell[b*]

[a] *Caesar Kleberg Wildlife Research Institute, MSC 218, Texas A&M University-Kingsville, Kingsville, TX 78363, USA;* [b] *United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Florida Field Station, 2820 East University Avenue, Gainesville, FL, 32641, USA*

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Feral swine (*Sus scrofa*) are one of the most threatening mammalian pest species in North America owing to the damage they cause to natural habitats and agroecosystems, and the risk of disease transmission they pose to wildlife, livestock, and humans. The long-term (> 1 year) effects of lethal control efforts on feral swine populations at local scales are largely unknown. Using a panel of molecular markers, we assessed the effects of lethal control efforts on selected populations of feral swine in southern Texas. We collected tissue samples from two sites during removal campaigns, extracted and amplified DNA, and assessed population structure, genetic clustering, and immigration. We removed 145 individuals (9.7 swine per km^2) at one site and 204 individuals (6.6 swine per km^2) at another site. Fixation indices, Bayesian clustering, and assignment tests based on allele frequencies all produced similar results, indicating little or no differentiation among removals at either site. Localized feral swine removals aimed at reducing damage had no long-term impact on population parameters. Removals occurred at sites in which the swine groups were contiguous with neighboring feral swine family units and groups. This may have resulted in immigration of adjacent, but not genetically distinct, feral swine onto sites following the initial removals. To achieve long-term reduction of damage by feral swine populations, additional information is needed to enable genetic populations and corresponding management units to be defined.

Keywords: damage; helicopter; lethal; pest control; *Sus scrofa*; trapping

1. Introduction

Feral swine (*Sus scrofa*) are one of the most threatening mammalian pest species in North America, because of their damage to natural habitats and agroecosystems, and the risk of disease transmission risks they pose to wildlife, livestock, and humans (Barrios-Garcia and Ballari 2012). In the United States, feral swine damage control methods include a suite of lethal and non-lethal methods such as exclusion fencing, hunting, aerial gunning, harvesting using trained dogs, trapping, and snaring (Campbell and Long 2009). Vertebrate pest managers recommend an integrated combination of control techniques applied to reduce damage caused by feral swine (Campbell and Long 2009). Unfortunately, these methods have not universally reduced long-term (>1 year) feral swine population abundance and growth rate, and related damage to resources. These shortcomings are likely the result of immigration and compensatory responses in feral swine recruitment (Hanson et al. 2009), as well as resource and support constraints (Campbell and Long 2009). In addition, the scale at which management is commonly applied may not be adequate to achieve long-term population effects, although this is poorly understood.

Texas has the largest feral swine population in the United States, with an estimated 2 million animals (Mapston 2004). The United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services program (USDA-WS) is the lead federal agency charged with managing human–wildlife conflicts, including the management of invasive feral swine. Accordingly, USDA-WS feral swine management efforts have been extensive in Texas, where feral swine damage control occurs on > 2870 km^2 of public land and $> 73{,}000$ km^2 of private land annually (R. Sramek, USDA-WS Texas, pers. comm.). Although the total area where feral swine damage control occurs annually is extensive, most lethal control efforts are directed at relatively small, non-contiguous landholdings. For instance, during 2008–2009 the average size of a private landholding in southern Texas where the USDA-WS applied lethal control methods was < 19 km^2 (R. Sramek, USDA-WS Texas, pers. comm.). The effects of lethal control efforts on feral swine populations at local scales such as this are unknown; few studies have evaluated the effects of such control on feral swine population variables in the United States (e.g. see Hanson et al. 2009; Sparklin et al. 2009; Ditchkoff et al. 2012) and none has

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*Corresponding author. Email: tyler.a.campbell@aphis.usda.gov used genetic methods. Such data are needed to develop and implement effective management strategies for invasive feral swine throughout their expanding range.

We used a panel of molecular markers to assess the effects of lethal control efforts on selected populations of feral swine in southern Texas. The markers would enable us to assess the impact of swine removal on overall genetic diversity, immigration (from outside the study sites), and whether removal unequally targeted genetically similar individuals (i.e. “trap-happy” or “trap-shy” family groups or relatives). Decreases in genetic diversity due to the loss of unique or uncommon alleles, lack of evidence of replacement through immigration, and lack of evidence of specificity in removal would be evidence of the success of short term removal. Our additional aims were to evaluate the effect of multiple feral swine removals on population structure and composition, genetic clustering, and immigration. Given the localized scale on which lethal control was applied, which was typical for many feral swine damage management scenarios in southern Texas, we hypothesized that localized removals would have little long-term impact on feral swine population variables (Cowled et al. 2006).

2. Materials and methods

2.1. Sample collection

We collected tissue samples from two sites in southern Texas. One site occurred on 15 km^2 of private property in Kleberg County (27º27′N, 97º53′W). This site was a semi-arid rangeland dominated by Honey Mesquite (*Prosopis glandulosa*) and Huisache (*Acacia farnesiana*) embedded in an agricultural matrix with Sorghum (*Sorghum bicolor*) and Cotton (*Gossypium* sp.) crops. Another site occurred on 31 km^2 of private property in San Patricio County (28°06′N, 97°22′W). That site was also a semi-arid rangeland with vegetation characteristic of the Texas Gulf Prairies and South Texas Plains Ecoregions (Griffith et al. 2004). Previous research found feral swine populations at these sites to be genetically differentiated (Delgado-Acevedo 2010).

At each site, we collected samples from feral swine removed during routine management activities intended to reduce damage. Feral swine were trapped using box traps (2.5 m × 1.2 m × 1 m) baited with fermented corn (Long and Campbell 2012). Additional animals were removed following aerial shooting (Campbell et al. 2010): helicopters with one pilot and one gunner flew multiple transects over the study site and killed all feral swine observed. During the first removal at the Kleberg County site, we trapped feral swine from July–September 2005, and for the second removal we trapped feral swine during April 2007. At the San Patricio County site, we conducted three removals. The first removal occurred during June 2006 and used trapping and aerial gunning techniques. The second removal occurred from November–December 2007 and used trapping techniques. The third removal occurred from May–June 2008 and used trapping and aerial gunning techniques. We recorded UTM coordinates of capture or kill site, and sex and age of feral swine removed. We also collected muscle tissue from all feral swine removed and stored samples at −20°C or in ethanol. We followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research throughout (Sikes et al. 2011).

2.2. DNA extraction and amplification

We extracted DNA from tissue samples using a commercial kit (Qiagen DNeasy, Qiagen Genomics, Bothell, Washington state, USA). We used 13 fluorescent-tagged polymorphic DNA microsatellite markers from Set XI (the diversity panel), developed by the US Swine Genome Coordination Program (http://www.animalgenome.org/swine/) to genotype the samples (Hampton et al. 2004). We loaded samples onto an ABI 3130 automated DNA sequencer (Applied Biosystems, Foster City, California, USA) for separation and detection. We binned and assigned alleles, and constructed multilocus genotypes using the GeneMapper software (Applied Biosystems).

2.3. Data analysis

We estimated allele frequencies and allelic richness (El Mousadik and Petit 1996), and evaluated departures from Hardy–Weinberg equilibrium using program FSTAT (Goudet et al. 2002). We assessed significance of departure from Hardy–Weinberg expectations by 1000 randomizations of alleles among individuals and corrected for multiple comparisons using a Bonferroni procedure (Rice 1989). If removals adversely affected the population, then the expected and observed heterozygosity in the population may differ due to the loss of rare alleles by population reduction or the introduction of new alleles from immigrants. We assessed differences in expected and observed heterozygosity per locus among removals within each site (i.e. Kleberg County and San Patricio County) using a Wilcoxon rank test (Wilcoxon 1945).

We assessed the effect of control efforts on population structure and composition within each site using three different methods: fixation statistics (genetic structure based on F_{ST} and F_{IS}; Wright 1943), Bayesian clustering (Structure 2.2; Pritchard et al. 2000), and assignment tests (GeneClass 2; Piry et al. 2004).

We quantified population structure among the removal events at both sites by computing an overall F_{ST} value (Weir and Cockerham 1984), which measures the differentiation of subpopulations relative to the total sample, as an index of population structure (Wright 1943). If the post-control populations comprised immigrants from outside the local population, we expected differences in F_{ST} among individuals collected in subsequent removals. We constructed 95% confidence intervals for overall F_{ST} by bootstrapping over loci.

If the post-removal population includes immigrants from peripheral or genetically differentiated populations, the resulting substructuring should be reflected in an increase in the inbreeding coefficient (F_{IS}) as new samples are added. We calculated F_{IS} (Weir and Cockerham 1984) and its standard error using bootstrapping, by serial pooling of samples. We estimated F_{IS} for the first removal, added samples from the second removal, and calculated F_{IS} on the pooled sample, and so on for all removals. This analysis was aimed at detecting departures from equilibrium values caused by the grouping of genetically different subpopulations (Wahlund effect; Wahlund 1928). An increase in F_{IS} as samples from successive removals are pooled indicates the pooling of two genetically differentiated populations. We completed the F_{ST} and F_{ST} analyses using the program FSTAT.

To investigate whether samples collected at each site during removals represent distinct genetic clusters, we used a Bayesian clustering algorithm implemented in program Structure 2.2 (Pritchard et al. 2000). The presence of unique genetic clusters in samples collected during subsequent removals would be evidence for immigration into the area from outside the local population. The algorithm groups individuals into genetic clusters (K) that minimize Hardy–Weinberg and linkage disequilibrium (Pritchard et al. 2000). We analyzed data for each site separately, using a burn-in of 150,000 repetitions to minimize the effect of the starting configuration, followed by 250,000 repetitions of data collection. We used the admixture model and assumed allele frequencies were correlated. For each site, we considered samples collected during the first removal as a cluster of known origin and attempted to assign individuals collected in subsequent removals as unknowns. We modelled from $K = 1$ to $K = 2$ and $K = 1$ to $K = 3$ genetic clusters for Kleberg County and San Patricio County sites, respectively. We conducted 10 independent repetitions for each value of K to ensure consistency of the results. We calculated the log posterior probability to estimate the number of populations (Pritchard et al. 2000).

To determine whether immigrants from outside the local population were present after a removal, we performed an assignment test. Genetic assignment tests use genetic data to assign (or exclude) individuals or groups of individuals to populations. We performed assignment tests using program GeneClass 2 (Piry et al. 2004), which employs a Monte Carlo resampling approach (Paetkau et al. 2004) to calculate the probability that an individual belongs to a given population. The principle behind the resampling method is to estimate the distribution of genotype likelihoods in a reference population sample and then compare the likelihood computed for individuals of unknown origin. The resampling simulates individuals through the creation of multilocus gametes to preserve the pattern of linkage disequilibrium in recent immigrants (Paetkau et al. 2004). Similarly to previous Bayesian clustering analyses, we considered individuals taken in the first removal as a known population, while individuals taken in subsequent removals were treated as of unknown origin. We used Bayesian assignment criterion (Rannala and Mountain 1997) to estimate assignment probabilities based on 10,000 simulated individuals with a Type I error rate of 0.01.

3. Results

We removed 145 individuals (9.7 swine per km^2) at the Kleberg County site, of which 102 were adults and 43 were juveniles (Table 1). Each locus was in Hardy–Weinberg equilibrium in the total sample (Table 2). There was no difference in the expected and observed heterozygosity between removals ($Z = 0.366$, $P > 0.05$; Table 2).

Table 1. Number of feral swine (*Sus scrofa*) sampled during lethal removals at two southern Texas sites from 2005 to 2008. The number of females and males (F/M) is given for each age class.

Site	Removal	Adults	Juveniles	Total
Kleberg County	1	50 (19/31)	13 (10/3)	63
	2	52 (20/32)	30 (10/20)	82
San Patricio County	1	57 (32/25)	51 (25/26)	108
	2	31 (13/18)	16 (8/8)	47
	3	49 (35/14)	0	49

Table 2. Observed (H_{OBS}) and expected (H_{EXP}) heterozygosity for each removal at each of 13 microsatellite DNA loci amplified in feral swine (*Sus scrofa*) populations from the Kleberg County site in southern Texas from 2005 to 2007. All loci conform to Hardy–Weinberg expectations.

	Removal			
	1		2	
Marker	H_{OBS}	H_{EXP}	H_{OBS}	H_{EXP}
S0002	0.595	0.606	0.788	0.674
S0026	0.386	0.424	0.395	0.413
S0068	0.870	0.847	0.712	0.861
S0090	0.300	0.265	0.329	0.290
S0155	0.698	0.698	0.855	0.784
S0226	0.685	0.718	0.671	0.723
SW122	0.704	0.670	0.772	0.698
SW240	0.704	0.735	0.660	0.722
SW632	0.684	0.679	0.625	0.699
SW857	0.629	0.658	0.357	0.646
SW911	0.556	0.512	0.526	0.551
SW936	0.764	0.800	0.818	0.765
SW951	0.418	0.484	0.487	0.450

Table 3. Observed (H_{OBS}) and expected (H_{EXP}) heterozygosity for each removal at each of 13 microsatellite DNA loci amplified in feral swine (*Sus scrofa*) populations from the San Patricio County site in southern Texas from 2006 to 2008. All loci conform to Hardy–Weinberg expectations.

	Removal					
	1		2		3	
Marker	H_{OBS}	H_{EXP}	H_{OBS}	H_{EXP}	H_{OBS}	H_{EXP}
S0002	0.614	0.607	0.511	0.496	0.655	0.626
S0026	0.729	0.711	0.872	0.720	0.587	0.695
S0068	0.587	0.638	0.711	0.564	0.578	0.631
S0090	0.490	0.594	0.775	0.648	0.671	0.585
S0155	0.770	0.763	0.638	0.741	0.771	0.801
S0226	0.783	0.798	0.864	0.801	0.761	0.791
SW122	0.804	0.810	0.787	0.833	0.826	0.811
SW240	0.670	0.740	0.787	0.725	0.747	0.720
SW632	0.618	0.633	0.609	0.609	0.591	0.618
SW857	0.238	0.273	0.370	0.443	0.422	0.392
SW911	0.645	0.625	0.553	0.564	0.604	0.550
SW936	0.804	0.767	0.804	0.773	0.772	0.712
SW951	0.224	0.231	0.234	0.262	0.290	0.280

We removed 204 individuals (6.6 swine per km^2) at the San Patricio County site, of which 137 were adults and 67 were juveniles (Table 1). Each locus was in Hardy–Weinberg equilibrium in the total sample (Table 3), and we detected no difference in the expected and observed heterozygosity among removals ($Z = 0.274$, $P > 0.05$; Table 3).

Fixation statistics revealed that feral swine removed within each site (i.e. Kleberg County and San Patricio County) were genetically similar. Pairwise F_{ST} estimates for removals at the Kleberg County site did not differ from 0.0 (Table 4). We detected a slight differentiation between removal 1 and removal 3 and between removal 2 and removal 3 at the San Patricio County site. The values were statistically different from 0.0 but very low, consistent with a large local population that is distributed continuously (Table 4).

The F_{IS} increased slightly from removal 1 to removal 2 by 0.02 at the Kleberg County site (Table 5). Positive and increased values of F_{IS} suggest a slight increase of homozygosity. At the San Patricio County site, F_{IS} decreased from removal 1 to removal 2 and to removal 3 by 0.067 and 0.034, respectively, and from removal 2 to removal 3 by 0.049 (Table 5). The pooled F_{IS} at the San Patricio site in subsequent removals showed no difference, or a decrease in F_{IS}, indicating an increase in heterozygotes. Despite minor changes in F_{IS}, none of the values were different from 0.0, providing no evidence for the Wahlund effect.

The Bayesian clustering analyses produced maximal values of estimated model log-likelihood (LnP(D)) assuming $K = 1$ genetic cluster at each site (Table 6). At the Kleberg County site, LnP(D) values decreased and became more variable among runs, assuming $K = 2$ genetic clusters; the proportion of individuals in each cluster were distributed evenly (50 : 50) among clusters for $K = 2$. Data from the San Patricio site displayed a maximum value for LnP(D) at $K = 3$ genetic cluster. The LnP(D) for $K = 2$ and $K = 3$ increased and became more variable among runs (Table 6), and individuals were distributed evenly among clusters assuming $K > 1$ genetic cluster.

The assignment tests revealed no evidence for first-generation immigrants at either site. All individuals were unambiguously assigned to the initial population (e.g., individuals collected in the first removal). Overall, we conclude that the fixation statistics, Bayesian clustering, and assignment test results support a single genetic cluster at each site.

4. Discussion

Consistent with our hypothesis, localized feral swine removals aimed at reducing damage had no long-term (> 1 year) impact on population variables, including structure and composition, genetic clustering, and immigration. Our observations were similar to findings from research conducted in southwestern Queensland, Australia where aerial gunning was performed and population genetics were compared over two years (Cowled et al. 2006). In the Australian study, researchers found that feral swine removed during the second year were not genetically differentiated as compared to feral swine that occupied the area during the previous year (Cowled et al. 2006). Our results mirrored these findings and indicated no differentiation among removals at either site, though differences between the Australian study and our study were apparent. First, in Australia, removals were conducted over 4430 km^2, whereas our removals occurred on

Table 4. Pairwise F_{ST} (± 95% confidence intervals) for feral swine (*Sus scrofa*) samples collected during successive lethal removals in Kleberg and San Patricio counties in Texas from 2005 to 2008. The estimates are based on data from 13 DNA microsatellite markers.

	Kleberg County site		San Patricio County site		
	Removal 1	Removal 2	Removal 1	Removal 2	Removal 3
Removal 1	0	0.0022 (−0.004–0.009)	0	0.005 (0.000–0.010)	0.009 (0.003–0.015)
Removal 2		0		0	0.014 (0.003–0.026)
Removal 3					0

Table 5. Estimates of F_{IS} (with standard error) derived from pooling of feral swine (*Sus scrofa*) samples collected during successive lethal removals in Kleberg and San Patricio counties in Texas from 2005 to 2008. The F_{IS} estimates are based on data from 13 DNA microsatellite loci.

Removal	Kleberg County site	San Patricio County site
1	0.013 (−0.063–0.089)	0.026 (−0.041–0.093)
2	0.034 (−0.126–0.194)	−0.041 (−0.089–0.011)
3		−0.008 (−0.092–0.016)
1 + 2		0.008 (−0.052–0.068)
2 + 3		–0.012 (−0.071–0.048)
All individuals	0.024 (–0.076–0.124)	0.007 (−0.022–0.036)

sites ≤ 31 km^2 (Cowled et al. 2006). Second, in Australia, overall feral swine removal density was 0.07 swine per km^2 (Cowled et al. 2006), whereas our overall feral swine removal densities were 9.7 and 6.6 swine per km^2 for the Kleberg County and San Patricio County sites, respectively. Despite differences in scale and density, feral swine populations in southwestern Queensland and southern Texas responded similarly to lethal control efforts.

There are several explanations for why our removals did not alter feral swine populations. First, our removals occurred at sites with a contiguous distribution to neighboring family units and groups of feral swine. This, in turn, may have resulted in immigration of adjacent, but not genetically distinct, feral swine onto sites following initial removals (Hanson et al. 2009). Stated another way, the genetic population may have occurred on a scale greater than the one at which our removals were carried out (Cowled et al. 2006). Second, our initial removals may have missed a number of feral swine, with animals killed during subsequent removals occurring at sites through reproductive processes, rather than through immigration. For example, researchers in west-central Georgia, USA found compensatory reproduction within a feral swine population that was intensively managed through lethal techniques (Hanson et al. 2009). This process may have resulted in populations that were genetically similar across removals. Lastly (and related to the second point), our removals may not have been conducted with sufficient duration and intensity to achieve population impacts. Our removals were conducted similarly to many feral swine removal programs with limited resources that occur within established populations in the United States. Such programs often have the goal of reducing feral swine damage in the short-term and not necessarily altering populations in the long-term. Specifically, our removals were short in duration (≤ 3 months) and were intermittent. It is possible that, if continuous and more intensive effort were applied to removing feral swine, population impacts could be obtained, though others challenge whether this is possible on a sustained basis given limited resources (Ditchkoff et al. 2012).

Table 6. Statistical support for the number of discrete genetic clusters in feral swine (*Sus scrofa*) sampled during removals at two sites in southern Texas from 2005 to2008.[a]

Site	K[b]	LnP(D)	Log P(K/X)	Var[LnP(D)]
Kleberg County	1	−3649	~1.0	13.413
	2	−3664	~0.0	21.022
San Patricio County	1	−7942	~1.0	8.944
	2	−7785	~0.0	29.611
	3	−7699	~0.0	18.662

[a] The posterior probability is derived from a Bayesian clustering algorithm implemented in program Structure 2.2 (Pritchard et al. 2000).

[b] Number of genetic clusters (K) assumed, and the estimated model log-likelihood (LnP(D)), log probability of the data given the number of clusters (Log P(K/X)), and the variance in repeat scores of the estimated model log-likelihood (Var[LnP(D)]) for each K provided.

To achieve feral swine population and damage reduction in the long term, information is needed aimed at defining genetic populations and corresponding management units (Cowled et al. 2006). Our data and data from Cowled et al. (2006) suggest that management units should be > 31 km^2 in southern Texas and > 4400 km^2 in southwestern Queensland. Using available feral swine damage control methods in the United States, this would likely necessitate the formulation of cooperatives of multiple landowners with common management goals. However, if new tools – such as bait-delivered toxicants that can be applied over expansive areas – were registered for use in the United States (Lapidge et al. 2012), then the formulation of large cooperatives would be less important. Another approach is to target removal efforts during periods of resource scarcity when feral swine are concentrated near water or other resources (Cowled et al. 2006). In arid and semi-arid environments, artificial water sources could be manipulated to concentrate feral swine during removal campaigns and increase removal effectiveness. This proposal needs to be explored experimentally by controlling artificial water availability and comparing the effectiveness of control activities with and without water available.

Our data emphasize the need to identify terrain features affecting movements and dispersal. This information is critical to long-term control of feral swine damage. Future research should evaluate landscape features that facilitate or impede movement and dispersal of feral swine.

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