

The sociogenetic structure of a controlled feral pig population

Peter B. S. Spencer^{A,C}, Steve J. Lapidge^B, Jordan O. Hampton^A and John R. Pluske^A

^ASchool of Veterinary and Biomedical Sciences, Murdoch University, Murdoch, WA 6150 Australia.

^BPest Animal Control Cooperative Research Centre, GPO Box 284, Canberra, ACT 2601, Australia and Queensland Department of Natural Resources and Mines, PO Box 318, Toowoomba, Qld 4350, Australia.

^CCorresponding author. Email: P.Spencer@murdoch.edu.au

Abstract. In Australia, the feral pig (*Sus scrofa*) is a significant vertebrate pest that has an impact on agricultural production, public health and ecosystem integrity. Although feral pigs are controlled throughout much of their range, little is known about the impact that these control programs have had on the social biology, structure and the dispersal of pigs. To begin to address this, we collected demographic data and genetic samples from 123 feral pigs culled during a regional aerial shooting program over 33 pastoral properties in the semi-arid rangelands of southern Queensland, Australia. Sampling was carried out after two years of extensive control efforts (aerial 1080-baiting) and the samples therefore represented a controlled, persecuted population with a bias towards young animals. The analysis of 13 microsatellite loci suggested that females will accept multiple matings, females form loose mobs that appear to be highly dynamic social groups, and males will travel large distances between mobs. These data indicate that feral pigs in this population had a high level of social contact and form a single open population with no evidence of genetic (population) structuring. Such information may be important to integrate into management strategies, particularly the development of contingency plans regarding the spread of wildlife diseases.

Introduction

The management of overabundant and invasive species is complex (see Olsen 1998 and Braysher and Saunders 2003) and made all the more challenging because of the difficulty in obtaining information about the population structure, social behaviour and spatial dynamics of the species of concern (Caughley and Sinclair 1994; Zenger *et al.* 2003; Hampton *et al.* 2004a, 2004b). Determining these factors is further compromised because, by definition of being invasive, these species are also usually highly productive (e.g. high rates of reproduction, reduced generation time, longevity) and have high dispersal rates, genetic variability and phenotypic plasticity. They are usually tolerant of a wide range of conditions (e.g. habitat generalists, polyphagous), gregarious and, importantly, lack any natural control. As a result, they are highly adaptive to their new environments (Agrawal 2001).

Understanding both the dispersal patterns and social interaction of individuals is an important element of pest animal management. Until recently, kinship and mate choice were often inferred primarily from behavioural observations and, in the absence of other data, adult males and females that associated closely were assumed to have been mating and any resultant young were their descendants (Barrett 1978). However, with the recent advances in genetic technology, complementary approaches that utilise the available genetic, behavioural and demographic information are becoming increasingly relevant to understanding population

dynamics (e.g. Sugg *et al.* 1996; Gabor *et al.* 1999; Sunnucks 2000; Hampton *et al.* 2004a, 2004b). Despite the obvious benefits, such an approach has received little attention with respect to the management of vertebrate pests, particularly mammalian species (although see Taylor *et al.* 2000; Hampton *et al.* 2004a, 2004b). In Australia, the feral pig (*Sus scrofa*) is one such mammalian pest (Caley 1997; Long 2003), and we use this species to illustrate the potential advantages of a multidisciplinary approach.

The feral pig is arguably one of Australia's most serious vertebrate pests in that it has a direct impact on agricultural production, on biodiversity and ecosystem integrity, and on human health (Choquenot *et al.* 1996; Crooks 2002; Hone 2002). This large, cryptic species is found across large areas of Australia, where its ecology, impacts and management have been widely documented (e.g. Giles 1980; Pech and Hone 1988; Hone 1990, 2002; Dexter 1999). From a public health point of view, feral pigs also have the ability to act as sylvatic reservoirs or vectors for several animal diseases, both endemic (leptospirosis, brucellosis, Ross River fever) and exotic (e.g. foot and mouth disease (FMD), Japanese encephalitis, surra, pseudorabies) in Australia (Pech and McIroy 1990; Wilson and Choquenot 1996; Dexter 2003).

Behaviourally, mating can occur throughout the year. Males reach sexual maturity at 15–24 months (~25 kg) and sows at 7–12 months (~25–30 kg). Average litter size is 5–6 and under favourable conditions sows can produce two weaned litters every 12–15 months (Choquenot *et al.* 1996).

Although groups of more than 100 individuals can aggregate during drought in northern Australia (Hone 1990), group size is generally <10 pigs (Choquenot *et al.* 1996). These groups usually comprise familial (matrilinal) assemblages (see Gabor *et al.* 1999); however, boars are less gregarious than sows, spending much of their time either alone or in small batchelor groups (Giles 1980; Choquenot *et al.* 1996). A recent genetic study of the social biology of feral pigs in south-western Australia suggested that they exhibit a mildly polygynous mating system (Hampton *et al.* 2004b). Findings from that study also revealed that boars with the highest reproductive success were large individuals (>90 kg) and were significantly heavier than non-breeding boars.

Hampton *et al.* (2004b) also showed a positive correlation between boar weight and distance moved to mate, where large boars (>100 kg) were more likely to disperse over large distances (>30 km) to secure paternity, in agreement with the results obtained by Caley (1997) from mark-recapture work in the wet tropics of northern Australia. It was also found in that study that the percentage of parents captured (37% of fathers and 52% of mothers) indicated that the trapping program used to sample the pigs had failed to capture a large proportion of the breeding population, particularly boars, and that trapping may preferentially remove sows, as previously suggested by Choquenot *et al.* (1993). The result also reinforced the suggestion by Saunders and Kay (1991) that larger, more 'sexually motivated' boars disperse further in search of breeding opportunities. These 'rogue' animals are the greatest concern for spreading directly transmitted diseases over large areas (see Saunders *et al.* 2002).

In this paper, we use 13 polymorphic microsatellite markers to describe the genetic structure and mating strategies of a persecuted, free-ranging, feral pig population. We

use these data, together with the corresponding demographic information, to make inferences about the likely impact of a control exercise on the social behaviour and the dispersal of these pigs. We also discuss the potential implications of these outcomes for wildlife management programs in general, particularly those involving mammalian pests.

Materials and methods

Population and demographic information

This study was conducted during February 2003 on 33 pastoral properties comprising 4430 km² near the town of Cunnamulla (Noorama area), in Queensland, Australia (28°29'S, 146°16'E). This feral pig population was assumed to be an 'open' (non-fenced) population. Prior to our study, this region was subjected to at least two years of intensive feral pig control, mainly through aerial baiting with 1080 (sodium monofluoroacetate) baits (see Mitchell 1998).

Feral pigs were shot by a trained marksman (Department of Primary Industries, Queensland), and their GPS location recorded. Ground crews located and sampled the pigs within 2 h of their being shot. A 1-cm³ piece of liver was collected from each animal and stored in 100% ethanol for genetic analysis. The weight, sex and reproductive condition were recorded for each pig. Feral pigs were considered to be sexually mature once they had reached 25 kg (Choquenot *et al.* 1996).

Laboratory techniques

We generated complete genotypes for 122 feral pigs (55 adults, 67 juveniles) using 13 polymorphic microsatellite loci (Table 1) following protocols described in Hampton *et al.* (2004a, 2004b). DNA fragments were separated on an ABI 377 automatic sequencer and sized by corunning a size standard (TAMRA-350; Applied Biosystems, Melbourne). DNA fragments were scored manually with the aid of Genescan (Applied Biosystems, Melbourne).

Genetic data analysis

Data were initially manipulated using a program (available from <http://oscar.gen.tcd.ie/~sdepark/ms-toolkit/index.php>) that checked for errors, created input files for 'F-stat' and calculated some basic statis-

Table 1. Characteristics of the 13 microsatellite loci amplified in 55 adult feral pigs in the Noorama study

Summary statistics shown include the chromosomal position of each marker, multiplex group (*sensu* Hampton *et al.* 2004a, 2004b), actual (N_A) and effective (N_E) number of alleles, observed (H_O), and Nei's (1978) unbiased (H_E) estimate of heterozygosity and hierarchical F -statistics of Weir and Cockerham (1984)

Marker ^A	Chromosomal location	Multiplex group	N_A	N_E	H_O	H_E	$F (F_{IT})$	$\theta (F_{ST})$	$f (F_{IS})$
SW936	Chr. 15	3	6	3.6	0.833	0.724	-0.030	0.097	-0.141
S0026	Chr. 16	1	4	3.6	0.765	0.725	-0.071	0.029	-0.103
SW240	Chr. 02	3	4	3.5	0.706	0.711	0.094	0.047	0.148
SW951	Chr. 10	1	2	2.0	0.333	0.500	0.272	0.080	0.209
S0155	Chr. 01	3	6	5.6	0.765	0.822	0.008	0.093	0.112
SW632	Chr. 07	3	5	3.6	0.813	0.719	0.017	0.127	-0.017
S0002	Chr. 03	1	4	2.9	0.765	0.657	-0.048	0.086	0.146
S0068	Chr. 13	2	5	2.3	0.556	0.568	0.002	0.020	-0.019
SW122	Chr. 06	2	5	2.0	0.546	0.508	-0.040	0.076	-0.126
SW911	Chr. 09	2	5	2.6	0.500	0.619	0.141	0.184	-0.053
S0090	Chr. 12	4	6	2.1	0.429	0.518	-0.092	0.038	-0.134
SW857	Chr. 14	1	5	2.5	0.722	0.602	0.097	0.104	-0.008
S0226	Chr. 02	4	6	2.9	0.889	0.659	-0.079	0.108	-0.209
Mean \pm s.d.			4.62 \pm 1.19	3.0 \pm 0.99	0.662 \pm 0.172	0.641 \pm 0.099	-0.002 \pm 0.024	0.085 \pm 0.012	-0.095 \pm 0.023

^ADetails for these markers can be found at <http://www.genome.iastate.edu/pig>.

tics (including number of alleles, observed and expected heterozygosities). Descriptive statistics were also generated using 'Popgene' (Version 1.31; available from <http://www.ualberta.ca/~fyeh/index.htm>). The level of genetic differentiation among groups of pigs was determined by using Fisher's exact tests for genetic differentiation (hierarchical statistics) (F_{IS} , F_{ST} and F_{IT} , denoted as f , θ/R_{ST} and F respectively) and relatedness (R) was estimated using 'F-stat' (Goudet 2001) or 'RELATEDNESS 5.0' (Queller and Goodnight 1989). Where appropriate, the standard deviation was estimated by jack-knifing.

We utilised a full Bayesian assignment approach to identify the genetic structure of the population using 'Structure' (Version 2.0; Pritchard *et al.* 2000). The clustering procedure followed methods described in Spencer and Hampton (2005), with the outcomes based on simulations from one to ten ($K = 1-10$) inferred populations, using a burn-in period of 50 000 iterations with 1 000 000 iterations of a Markov Chain simulation (Pritchard *et al.* 2000).

Relatedness (R) was estimated for all pair-wise combinations of the 122 individuals by using the program 'RELATEDNESS 5.0' (Queller and Goodnight 1989). Standard errors for average relatedness values were generated by jack-knifing using all loci. Allele frequencies for this analysis were estimated by using 40 randomly selected adult individuals from the population with equal representation of both sexes.

All adult pigs were considered as potential parents, even when they were not found in the same mob. Evidence of multiple paternity in litters from individual sows was inferred by the presence of three or more paternal alleles (after the maternal allele was identified) at any one locus for all the young in the same litter. In determining multiple paternity, a single litter was either collected *in utero* or defined by the presence of a sow with at least three young from the same age cohort (these could be identified by having similar weights, generally within 1 kg). Alternatively, multiple paternity could not be inferred if there were only two paternal alleles at any locus.

Paternity (and maternity) inference was conducted using CERVUS software (Marshall *et al.* 1998). Paternity assignment using likelihood techniques was determined at an 80% (relaxed) confidence threshold. Marshall *et al.* (1998) suggested that 80% confidence in paternity is more accurate than can be achieved using direct observation, and better than can be achieved using exclusionary approaches because the degree of confidence in non-excluded males is unknown in the exclusion technique. Paternity was inferred from the log-likelihood ratios based on the genotypes of the offspring, candidate sire, and dam.

Confidence levels are determined through simulation (10 000 iterations) and defined by the statistic delta (Δ ; the difference between the log-likelihood ratio scores of the two most likely candidates). Input parameters for the CERVUS software have important effects on the resulting paternity assignments. The 'error rate' parameter (0.05 in our study) of the simulation program allows an estimate of scoring error to be included in the calculations. Allowing for error prevents exclusion of true paternal candidates attributable to errors causing single-locus mismatches, while potentially including (erroneously) sires that would otherwise be excluded. As the number of sampled loci increases, this error estimator becomes more important owing to the increased probability of mis-scoring or mutation. Another important simulation parameter for this dataset is the proportion of males sampled. The exact proportion of potential animals sampled in the population is an extremely difficult (if not impossible) parameter to estimate. However, a sampling rate of 0.7 (70% of the potential animals sampled in the population) was assumed, based on estimates of feral pig trapping capture rates (Choquenot *et al.* 1993; Saunders *et al.* 1993) and comparative studies using genetic approaches (Vernesi *et al.* 2003; Hampton *et al.* 2004b). Failure to identify a parent was due to all candidates being excluded, and not the inability to discriminate between related individuals. Reproductive success of females and males was defined as the mean number of young produced per individual pig. All values are shown as mean \pm standard error unless otherwise stated.

Results

Genetic diversity and population structure of feral pigs

We generated genotypes for 122 (95% of all individuals shot) feral pigs at 13 microsatellite loci. Of the pigs sampled, 55 were adults (34 ♀ and 21 ♂) (Table 1; Fig. 1) and 67 were juvenile animals of non-breeding age (28 ♂, 31 ♀ and 8 fetuses). On the basis of GPS locations, most pigs (97.5%) were aggregated into 14 discrete social groups, and only three solitary boars (weighing 27, 83 and 95 kg) were detected (Table 2). The mean adult group size was 4.1 ± 0.8 (mode = 3) adults weighing between 25 and 95 kg (Fig. 1).

Seventy-two different alleles (mean = 4.6 ± 1.2 alleles per locus) were detected at the 13 loci, and all loci were highly polymorphic (Table 1). We found no evidence of allele frequencies deviating from Hardy-Weinberg expectations. The expected heterozygosity (H_E) estimates at each locus were between 0.500 and 0.822, with a mean H_E of 0.64 ± 0.10 . Similarly, H_E estimates in the 14 mobs discriminated were between 0.53 and 0.73 (Table 2), with a mean of 0.65 ± 0.06 , and a mean number of alleles (N_A) of 2.82 ± 0.81 .

The level of inbreeding in these pig groups was low (hierarchical analysis, $f = -0.095$), and θ -values revealed a similarly low level of genetic differentiation among the groups (mean $\theta = 0.085$ and $R_{ST} = 0.083$). No evidence of genetic structure was detected in the Noorama population with a single inferred population ($K = 1$), suggesting that the mobs/groups, as such, are simply small, dynamic associations of pigs that represent a much larger social unit over the study area.

Group relatedness

The relatedness of adult pigs within mobs showed that the mobs generally comprised related individuals. Levels of relatedness within each mob were generally in the order of first-cousin relatives ($R > 0.125$; Table 2). There were nine mobs (of the 12, as two consisted of single individuals) where relatedness was greater than 0.125. Some mobs,

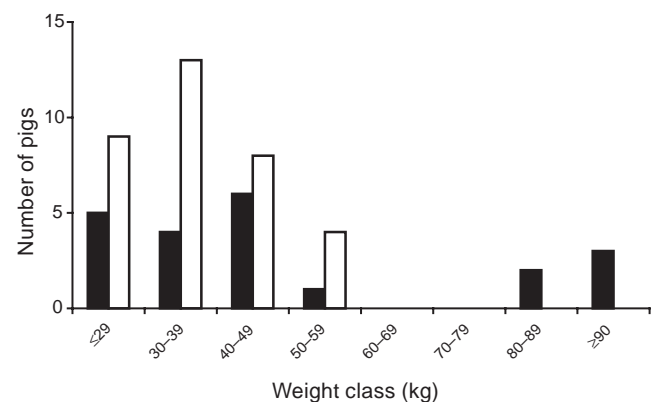


Fig. 1. Number of adult boars (solid bars) and sows (open bars) in each weight class (kg) collected in the Noorama population.

Table 2. Descriptive statistics for each of 14 social groups of feral pigs sampled in the Noorama population, including measures for the three solitary boars for comparison

Measures include the number of adult animals (n), actual number of alleles (N_A), observed heterozygosity (H_O), and Nei's (1978) unbiased (H_E) estimate of heterozygosity, and average relatedness (R) for within each social group

Social group no.	n	N_A	H_O	H_E	R
1	8	3.46 ± 1.13	0.631 ± 0.048	0.557 ± 0.046	0.205 ± 0.028
2	4	2.85 ± 0.90	0.577 ± 0.069	0.602 ± 0.050	0.136 ± 0.035
3	3	3.08 ± 0.76	0.641 ± 0.077	0.667 ± 0.050	0.142 ± 0.023
4	3	2.69 ± 0.75	0.872 ± 0.054	0.656 ± 0.032	0.204 ± 0.039
5	1	1.62 ± 0.51	0.615 ± 0.135	0.615 ± 0.140	–
6	2	2.62 ± 0.96	0.615 ± 0.095	0.667 ± 0.080	0.144 ± 0.039
7	2	2.08 ± 0.76	0.462 ± 0.098	0.526 ± 0.090	0.079 ± 0.032
8	10	4.00 ± 1.08	0.709 ± 0.041	0.662 ± 0.034	0.172 ± 0.034
9	7	4.38 ± 0.77	0.778 ± 0.044	0.722 ± 0.028	0.002 ± 0.026
10	2	2.46 ± 0.78	0.769 ± 0.083	0.654 ± 0.072	0.362 ± 0.115
11	1	1.69 ± 0.48	0.692 ± 0.128	0.692 ± 0.133	–
12	3	3.00 ± 1.08	0.641 ± 0.078	0.703 ± 0.046	0.112 ± 0.061
13	3	2.38 ± 0.77	0.795 ± 0.065	0.605 ± 0.059	0.531 ± 0.140
14	3	2.69 ± 0.63	0.795 ± 0.065	0.621 ± 0.062	0.410 ± 0.083
Solitary boars	3	3.23 ± 0.83	0.692 ± 0.074	0.728 ± 0.033	0.124 ± 0.022

however, showed low relatedness to the other groups (e.g. Mob 9: Table 2). There was no significant relationship found between pair-wise comparisons of the relatedness among mobs and the linear distance between each pair ($F_{1,90} = 0.878$, $R^2 = 0.033$, $P = 0.357$).

Parentage

We identified that 23 adult pigs (10♂, 13♀) did not contribute to the parentage of any of the 67 progeny genotyped in this study. In terms of the mother, it tended to be the older age cohorts (with young weighing >25 kg) and those with young weighing <5 kg (Fig. 2) that were most readily identified. The mother was identified for less than 10% of the young that weighed between 6 and 25 kg (Fig. 2). In contrast, the young for whom the father was not identified were generally distributed across all age cohorts (Fig. 2).

Maternity and maternal sociobiology

We were able to assign maternity to 61 (91%) of the 67 young from Noorama. Of these, 65.7% (44 of 67) were identified as being part of a social mob, and the remaining 7 (10.4%) had mothers that were not present in their group.

Ten litters displayed at least three paternal alleles (once the maternal contribution was removed), which indicates that multiple paternity occurred in many sows. Although we were unable to determine what proportion of each litter was from multiple fathers (there were rarely more than three young in the same age-cohort), our data indicate that some sows will accept multiple sires in a large proportion (77%) of the litters. Of these litters, three of the five had no known adult boar associated with the group, suggesting that males were travelling amongst mobs to secure paternity (see below). Not surprisingly, females were generally found close to their

progeny (mean distance = 10.0 km), particularly younger piglets, but these young were found further away as they reached sexual maturity (Fig. 3).

Paternity and male sociobiology

We were far less successful at identifying fathers, with only 37 young (55%) having a father identified in the sampled population of boars. Of these 37 young, 14 (21% of all young) were found in the same mob as their father. In all, 34% ($n = 23$) of all the young did not have their paternal boar associated with the mob. Boars who fathered young were found, on average, to be 42.0 ± 6.1 km from their progeny. We were unable to identify fathers for 45% ($n = 30$) of young.

The reproductive success of the boars that could be identified showed that by far the most successful fathers in the studied population were those that ranged in bodyweight

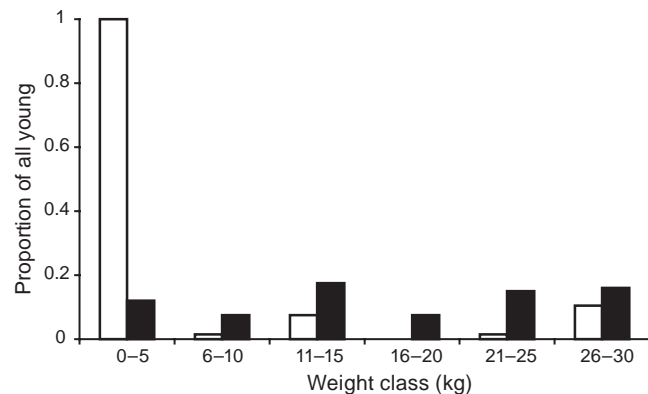


Fig. 2. The proportion of young in different weight cohorts in which either the mother (open bars) or father (solid bars) was identified in the sampled Noorama population of feral pigs. Mothers were identified for all young weighing less than 5 kg.

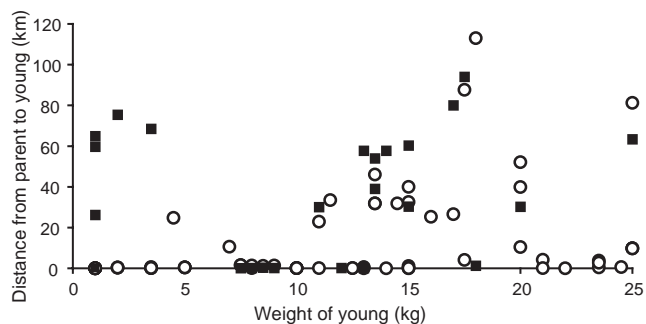


Fig. 3. The relationship between the weight of a young (kg) and the distance they were found from either their mother (open circles) or father (solid squares).

between 40 and 49 kg (Fig. 4; Table 3). We also found that relatively small boars (<40 kg) were fathering young, and that large boars (>90 kg) contributed a relatively small number of young ($n = 3$) to the Noorama population. However, this result may simply reflect the actual (small?) numbers of large boars present as a consequence of selectively targeting large boars. Only one large boar (90 kg) was associated with a mob, and although only a small number of large boars was recovered, the solitary or lone boars subsequently identified (~100 kg) fathered very few of the progeny sampled at Noorama.

Discussion

There are relatively few studies that specifically address the social organisation in groups of wild pigs in detail, such as their group structure (although see Vernesi *et al.* 2003; Hampton *et al.* 2004a), mating systems and the genetic relatedness between individuals (Hampton *et al.* 2004b). While recognising that our study was only for one, albeit relatively large, area (>10000 km²), we believe that some of the long-held beliefs regarding the social biology of feral pigs need to be revisited. First, it seems that some groups of feral pigs exist as highly dynamic units, exhibiting fission–fusion dynamics similar to those identified in the behavioural study

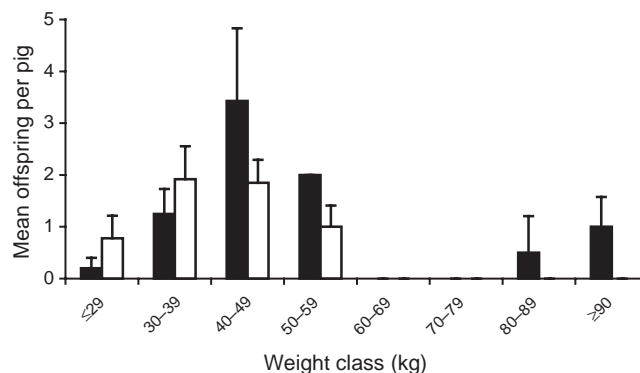


Fig. 4. The reproductive success, measured in terms of the mean number of offspring per adult pig, based on the weight cohort of boars (solid bars) and sows (open bars).

of Gabor *et al.* (1999). This assertion was suggested by the lack of any relationship between levels of relatedness and geographic distance and by the lack of any detectable genetic structure in the Noorama population. Mobs of pigs in the Noorama population tended to comprise matriarchal assemblages (highly related individuals, particularly sows). Some Noorama boars also travelled large distances (mean = 42 km) to secure paternity, although it cannot be excluded that they may have also moved for other reasons, such as searching for food or harassment by people. Finally, although few large boars may have been present in the disturbed pig population studied (large boars are believed to monopolise sows with concomitant high reproductive success: Choquenot *et al.* 1996), the few large boars that were present seem to have contributed little to the overall paternity within the Noorama population.

The genetic variation (diversity) within the Noorama population ($H_E = 0.64$) was similar to that in other feral pig populations in Australia and Papua New Guinea (ranges of H_E and N_A for five feral pig populations were between 0.447–0.803 and 2.97–5.54, respectively: our unpublished data), and to that observed for different pig breeds in Asia, North America and Europe (Martinez *et al.* 2000; Vernesi

Table 3. Reproductive success of boars in different weight cohorts from Noorama

n , the number of boars in each weight cohort. Reproductive success is given as (1) the absolute number of progeny and (2) the number of litters from each boar

Boar Weight (kg)	n	% of males sampled	No. of progeny	% of total progeny	No. of litters	% of all litters
≤ 29	1	1.8	1	1.5	1	2.1
30–39	3	5.4	4	6.0	3	6.3
40–49	8	14.3	18	27.0	13	27.1
50–59	3	5.4	4	6.0	3	6.3
60–69	0	0.0	0	0.0	0	0.0
70–79	1	1.8	3	4.5	3	6.3
80–89	2	3.6	4	6.0	3	6.3
≥ 90	1	1.8	3	4.5	3	6.3
No identified father			30			

et al. 2003). This indicates that our techniques were applicable even though we were deliberately studying a controlled, persecuted population.

The average group size of 4.1 pigs per mob for feral pigs at Noorama was also within the range reported in other studies (e.g. 3.9 pigs per group: Choquenot *et al.* 1996; Gabor *et al.* 1999). There are several advantages for members of a population resulting from low group size (e.g. reduced competition for resources), but males may have to move farther to find receptive females. This, in turn, is likely to influence social interaction, mob composition, and the dispersal of feral pigs, as suggested by the apparent lack of genetic structure in the Noorama population. This contention is consistent with findings that suggest that home ranges of feral pigs will increase in response to lowered population densities in order to maintain social contact rates (Saunders and Kay 1991). In terms of genetic structure, Spencer and Woolnough (2004) recently showed that a single *genetic* feral pig population can occupy a very large area, some greater than 16 000 km² (mean area = 5792 ± 2675 km²), which would suggest that movement from within a population is likely.

Our demonstration of multiple paternity in some Noorama sows is a first for wild suids, although multiple copulations have been observed in behavioural studies between several boars and a single sow in the wild (Barrett 1978). Hampton *et al.* (2004b) detected no multiple paternity from 182 adult and 172 juvenile pigs in south-western Australia. Such behaviour is likely to increase the genetic diversity among mobs, especially where females have synchronised oestrous cycles. Because many males appeared to visit the oestrous sows in the present study, social interaction/contact between groups is also likely to be higher than that which may occur where the mobs are more discrete (e.g. Hampton *et al.* 2004b). The demonstration of multiple paternity, an apparent lack of dominance by the few large boars present (see below), together with what seems essentially to be a homogeneous pool of successful fathers, may explain the apparent absence of any relationship between 'relatedness' and the corresponding geographic distance between some of the related pigs sampled.

In the Noorama area, mobs consisted of matrilineal assemblages with relatively high levels of intermob relatedness. In contrast to several other studies (e.g. Boitani *et al.* 1994; Vernesi *et al.* 2003), feral pigs in our population do not appear to form 'consistent and stable units', although such a finding may be the result of control operations for pigs in our study population, and the likely concomitant reduced competition for food and space. The lack of any inferred population structure (as defined by θ and structure) or significant relationship between genetic relatedness and geographic distance suggests that feral pigs at Noorama are organised into related, but dynamic and highly mobile, assemblages, such as has been found from studies elsewhere in the world (Barrett 1978; Boitani *et al.* 1994). That is, mob-members

show a fission–fusion society (Holekamp *et al.* 1997), whereby groups (or subgroups) exchange constituent individuals (see Gabor *et al.* 1999). Such a group structure implies that dispersal is likely to occur over most of the available habitat or, at least, some pigs travel relatively large distances to mate. This finding has implications for exotic disease contingencies.

The use of genetic analyses and demographic data during our study also enabled the identification of some aspects of the social biology of feral pigs that could not be obtained from visual observations alone. Boars that fathered young were not always associated with the mob that contained their young. Such boars were often found to have moved considerable distances to secure paternity (i.e. they were found, on average, 42 km away). Such movements would need to be accounted for in management strategies for feral pigs.

Similarly, it has been assumed that large (e.g. >80 kg) solitary boars have a higher level of reproductive success than do small, supposedly subordinate, males, such as was identified in south-western Australia (Hampton *et al.* 2004b). However, our study of the Noorama population indicates that this is not necessarily always the case, and that younger boars are quite capable of securing paternity in the absence, or reduced abundance, of large boars. For example, one single large boar (>90 kg) in our study contributed a relatively small number of young ($n = 3$), and the other large solitary boars identified (~100 kg) did not father any of the progeny collected from the Noorama population. One caveat is, however, that we were only able to identify the fathers of 55% of the young, so it is possible that other large boars, which avoided both the poison baits and the sampling by aerial shooting, were present in the population but were not seen or had only recently been harvested. Sampling difficulties are not unusual in studies of this nature, and it is rare for the total population to be genotyped (e.g. Spencer *et al.* 1998; Vigilant *et al.* 2001; Morrison *et al.* 2002). Difficulties can arise from several factors, including: (1) the animal being killed before the tissue-sampling period; (2) individuals being present but not sampled during the collection period; (3) some animals moving temporarily or permanently outside the study area; (4) mother not being identified; or (5) simply natural attrition before they could be sampled, and (6) insufficient young being collected to enable absolute determination of paternity.

At present, a lack of real understanding of contact rates, both within and between pig groups, hampers the development of exotic disease models, and the development of exotic disease contingency plans involving feral pigs (see Pech and Hone 1988; Choquenot *et al.* 1996). One implication is that suboptimal control efforts directed towards key susceptible hosts during an exotic disease emergency may actually result in the increased spread of hosts, and, therefore, the disease. The absolute contact rates between individual pigs need to be quantified and require urgent study,

and genetic technologies like those described here will not be able to answer such questions. Although single-host models suggest that some diseases (e.g. FMD) are unlikely to persist below a threshold density of less than 0.5 pigs km⁻² (Dexter 2003), the effect of control operations in populations of feral pigs and in multihost systems (the norm for Australia) is far from clear (e.g. as documented in seal populations by Swinton *et al.* (1998)). While recognising that genotyping really allows only retrospective inference with respect to successful sexual contacts (i.e. only those resulting in conception) and dispersal events, and that social interaction and dispersal rates are likely to be greater than those indicated from genetic analysis alone, we nevertheless believe that the multidisciplinary approach we suggest will provide additional, and otherwise unobtainable, information for the management of wildlife and wildlife diseases. Our data suggest that, under some circumstances, there may be sufficient genetic mixing of individuals in even highly controlled populations that some directly transmitted diseases may well persist (e.g. feral pigs and FMD). In the absence of other data, the precautionary principle would dictate that, where appropriate, these considerations should be included in the development of wildlife management programs. Our suggested multidisciplinary approach may also help with gaining further understanding of the contact and dispersal rates within many other animal populations.

Acknowledgments

We thank M. Derrick, C. Hunter, J. Farrell, M. Wingett, R. Cobon and J. Kennedy (MI Helicopters) for assisting in organisation and collection of samples. L. E. Twigg, three reviewers and the editor made valuable comments on earlier versions. We are also grateful for the USA Department of Agriculture support from the USA Pig Genome Coordination Project (M. Rothschild). This research was supported by the Noorama Bestprac Group, the Australian Government National Feral Animal Control Program, Murdoch University, Macquarie Bank and the WA Department of Conservation and Land Management. This project was approved by the Queensland Department of Natural Resources and Mines Pest Animal Ethics Committee.

References

- Agrawal, A. A. (2001). Phenotypic plasticity and the interactions and evolution of species. *Science* **294**, 321–326. doi:10.1126/science.1060701
- Barrett, R. H. (1978). The feral hog on the Dye Creek Ranch, California. *Hilgardia* **46**, 283–355.
- Boitani, L., Mattei, L., Nonis, D., and Corsi, F. (1994). Spatial and activity patterns of wild boars in Tuscany, Italy. *Journal of Mammalogy* **75**, 600–612.
- Braysher, M., and Saunders, G. (2003). PESTPLAN – a guide for setting priorities and developing a management plan for pest animals. Bureau of Rural Sciences, Canberra.
- Caley, P. (1997). Movements, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. *Wildlife Research* **24**, 77–87. doi:10.1071/WR94075
- Caughley, G., and Sinclair, A. R. (Eds.) (1994). 'Wildlife Ecology and Management.' (Blackwell Science: Cambridge.)
- Choquenot, D., Kilgour, R. J., and Lukins, B. S. (1993). An evaluation of feral pig trapping. *Wildlife Research* **20**, 15–22.
- Choquenot, D., McIlroy, J. C., and Korn, T. (Eds) (1996). 'Managing Vertebrate Pests: Feral Pigs.' (Bureau of Resource Sciences: Canberra.)
- Crooks, J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers *Oikos* **97**, 153–166. doi:10.1034/j.1600-0706.2002.970201.x
- Dexter, N. (1999). The influence of pasture distribution, temperature and sex on home range size of feral pigs in a semi-arid environment. *Wildlife Research* **26**, 755–762.
- Dexter, N. (2003). Stochastic models of foot and mouth disease in feral pigs in the Australian semi-arid rangelands. *Journal of Applied Ecology* **40**, 239–306.
- Gabor, T. M., Hellgren, E. C., Van den Bussche, R. A., and Silvy, N. J. (1999). Demography, sociospatial behaviour and genetics of feral pigs in a semi-arid environment. *Journal of Zoology* **247**, 311–322. doi:10.1017/S0952836999003039
- Giles, J. R. (1980). The ecology of feral pigs in western New South Wales. Ph.D. Thesis, University of Sydney.
- Goudet, J. (2001). FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from <http://www.unil.ch/izea/software/fstat.html>.
- Hampton, J. O., Spencer, P. B. S., Alpers, D. L., Twigg, L. E., Woolnough, A. P., Doust, J., Higgs, T., and Pluske, J. (2004a). Molecular techniques, wildlife management and the importance of genetic population structure and dispersal: a case study with feral pigs. *Journal of Applied Ecology* **41**, 735–743. doi:10.1111/j.0021-8901.2004.00936.x
- Hampton, J. O., Pluske, J. R., and Spencer, P. B. S. (2004b). A preliminary genetic study of the social biology of feral pigs in southwestern Australia and the implication for management. *Wildlife Research* **31**, 375–381. doi:10.1071/WR03099
- Holekamp, K. E., Cooper, S. M., and Katona, C. I. (1997). Patterns of association among female spotted hyenas (*Crocuta crocuta*). *Journal of Mammalogy* **78**, 55–64.
- Hone, J. (1990). Note on seasonal changes in population density of feral pigs in three tropical habitats. *Wildlife Research* **17**, 131–134.
- Hone, J. (2002). Feral pigs in Namadgi National Park, Australia: dynamics, impacts and management. *Biological Conservation* **105**, 231–242. doi:10.1016/S0006-3207(01)00185-9
- Long, J. L. (2003). 'Introduced Mammals of the World: Their History, Distribution and Influence.' (CSIRO Publishing: Melbourne.)
- Marshall, T. C., Slate, J., Kruuk, L. E. B., and Pemberton, J. M. (1998). Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7**, 639–655. doi:10.1046/j.1365-294x.1998.00374.x
- Martinez, A. M., Delgado, J. V., Rodero, A., and Vega-Pla, J. L. (2000). Genetic structure of the Iberian pig breed using microsatellites. *Animal Genetics* **31**, 295–301. doi:10.1046/j.1365-2052.2000.00645.x
- Mitchell, J. (1998). The effectiveness of aerial baiting for control of feral pigs (*Sus scrofa*) in north Queensland. *Wildlife Research* **25**, 297–303. doi:10.1071/WR97009
- Morrison, S. F., Keogh, J. S., and Scott, I. A. W. (2002). Molecular determination of paternity in a natural population of the multiply mating polygynous lizard *Eulamprus haetwolei*. *Molecular Ecology* **11**, 535–545. doi:10.1046/j.0962-1083.2002.01450.x
- Nei, M. (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89**, 583–590.

- Olsen, P. (1998). 'Australia's Pest Animals. New Solutions to Old Problems.' (Bureau of Resource Sciences: Canberra.)
- Pech, R. P., and Hone, J. (1988). A model of the dynamics and control of an outbreak of foot-and mouth disease in feral pigs in Australia. *Journal of Applied Ecology* **25**, 63–77.
- Pech, R. P., and McIlroy, J. C. (1990). A model of the velocity of advance of foot-and-mouth disease in feral pigs. *Journal of Applied Ecology* **27**, 635–650.
- Pritchard, J. K., Steffens, M., and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959.
- Queller, D. C., and Goodnight, K. F. (1989). Estimating relatedness using genetic markers. *Evolution* **43**, 258–275.
- Saunders, G., and Kay, B. (1991). Movements of feral pigs (*Sus scrofa*) at Sunny Corner, New South Wales. *Wildlife Research* **18**, 49–61.
- Saunders, G., Kay, B., and Nicol, H. (1993). Factors affecting bait uptake and trapping success for feral pigs (*Sus scrofa*) in Kosciuszko National Park. *Wildlife Research* **20**, 653–665.
- Saunders, G., Bunn, C., Eggleston, C., Garner, G., and Henzell, R. (2002). 'AUSVETPLAN, Wild Animal Management Manual – Strategic and Operational Guidelines.' (Agriculture and Resource Management Council of Australia and New Zealand.)
- Spencer, P. B. S., and Hampton, J. (2005). Illegal translocation and genetic structure of feral pigs in Western Australia. *The Journal of Wildlife Management* **69**, 377–384.
- Spencer, P. B. S., and Woolnough, A. P. (2004). Size should matter: distribution and genetic considerations for pest animal management. *Ecosystem Management and Restoration* **5**, 231–233. doi:10.1111/j.1442-8903.2004.209-9.x
- Spencer, P. B. S., Horsup, A., and Marsh, H. (1998). Enhancement of reproductive success in a social rock-wallaby, *Petrogale assimilis* (Macropodidae) as revealed by microsatellite markers. *Behavioural Ecology and Sociobiology* **43**, 1–9. doi:10.1007/s002650050460
- Sugg, D. W., Chesser, R. K., Dobson, F. S., and Hoogland, J. L. (1996). Population genetics meets behavioural ecology. *Trends in Ecology & Evolution* **11**, 338–342. doi:10.1016/0169-5347(96)20050-3
- Sunnucks, P. (2000). Efficient genetic markers for population biology. *Trends in Ecology & Evolution* **15**, 199–203. doi:10.1016/S0169-5347(00)01825-5
- Swinton, J., Harwood, J., Grenfell, B. T., and Gilligan, C. A. (1998). Persistence thresholds for phocine distemper virus infections in harbour seal *Phoca vitulina* metapopulations. *Journal of Animal Ecology* **67**, 54–68. doi:10.1046/j.1365-2656.1998.00176.x
- Taylor, A. C., Cowan, P. E., Fricke, B. L., and Cooper, D. W. (2000). Genetic analysis of the mating system of the brushtail possum (*Trichosurus vulpecula*) in New Zealand farmland. *Molecular Ecology* **9**, 869–879. doi:10.1046/j.1365-294x.2000.00941.x
- Vernesi, C., Crestanello, B., Pecchoili, E., Tartari, D., Caramelli, D., Hauffe, H., and Bertorelle, G. (2003). The genetic impact of demographic decline and reintroduction in the wild boar (*Sus scrofa*): a microsatellite analysis. *Molecular Ecology* **12**, 585–595. doi:10.1046/j.1365-294X.2003.01763.x
- Vigilant, L., Hofreiter, M., Siedel, H., and Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 12890–12895. doi:10.1073/pnas.231320498
- Weir, B. S., and Cockerham, C. C. (1984). Estimating *F*-statistics for the analysis of population structure. *Evolution* **38**, 1358–1370.
- Wilson, D., and Choquenot, D. (1996). Review of feral pigs and exotic disease preparedness. Bureau of Resource Sciences, Canberra.
- Zenger, K. R., Eldridge, M. D. B., and Cooper, D. W. (2003). Intraspecific variation, sex-biased dispersal and phylogeography of the eastern grey kangaroo (*Macropus giganteus*). *Heredity* **91**, 153–162. doi:10.1038/sj.hdy.6800293

Manuscript received 8 September 2004, accepted 24 May 2005