



Original Article

The Population Origins and Expansion of Feral Cats in Australia

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Abstract

The historical literature suggests that in Australia, the domestic cat (*Felis catus*) had a European origin [~200 years before present (ybp)], but it is unclear if cats arrived from across the Asian land bridge contemporaneously with the dingo (4000 ybp), or perhaps immigrated ~40000 ybp in association with Aboriginal settlement from Asia. The origin of cats in Australia is important because the continent has a complex and ancient faunal assemblage that is dominated by endemic rodents and marsupials and lacks the large placental carnivores found on other large continents. Cats are now ubiquitous across the entire Australian continent and have been implicit in the range contraction or extinction of its small to medium sized (<3.5 kg) mammals. We analyzed the population structure of 830 cats using 15 short tandem repeat (STR) genomic markers. Their origin appears to come exclusively from European founders. Feral cats in continental Australia exhibit high genetic diversity in comparison with the low diversity found in populations of feral cats living on islands. The genetic structure is consistent with a rapid westerly expansion from eastern Australia and a limited expansion in coastal Western Australia. Australian cats show modest if any population structure and a close genetic alignment with European feral cats as compared to cats from Asia, the Christmas and Cocos (Keeling) Islands (Indian Ocean), and European wildcats (*F. silvestris silvestris*).

Subject areas: Population structure and phylogeography, Conservation genetics and biodiversity

Key words: *Felis catus*, *Felis silvestris silvestris*, genetic structure, microsatellite, population ecology, wild cat

Unlike commensal species that have been domesticated for agricultural (e.g., cow, sheep) or transport use (camel, horse), cats (*Felis catus*) share a relationship with humans that is largely mutualistic.

The cat probably began its association with humans as a secondary commensal, feeding on rodent pests that fed in agricultural grain stores (Driscoll et al. 2007). The origin of the cat is reported by

Driscoll et al. (2007) to have occurred around 9000 years ago in the Fertile Crescent, which extends from the Mesopotamian plains, along the Mediterranean coast to the Levant (but does not include Egypt). It is the location of some of the earliest settlements of hunter-gatherers in a region rich in wild stocks of 8 major grain species (see Driscoll et al. 2009). The origin of cats on the Australian continent is less well known but it appears that cats never naturally dispersed to Australia, nor has Australia any recent exposure to large placental mammalian predators, such as wolves, bears, or large cats. Australia's only recent mammalian predators were marsupials ranging from the Tasmanian tiger weighing 30 kg (which went extinct in 1936) to the smallest weighing just 9 g (the diminutive Pilbara Ningau, *Ningau timealeyi*; Van Dyck and Strahan 2008). The largest extant predator is a relatively small carnivorous marsupial, the Tasmanian devil (at 6 kg), only found in modern times on the island state of Tasmania, and not on the Australian continent. There are no generalist indigenous mammalian predators found over the entire continent.

A range of introduced predators have become established in Australia, including the dingo that has been present for ~5000 years, originating from East Asia (e.g. New Guinea) from a narrow genetic introduction (Savolainen et al. 2004; Ardalan et al. 2012), and more recent introgression with the wild dog (Savolainen et al. 2004). The red fox (*Vulpes vulpes*) was introduced coinciding with European settlement for sport and to control plagues of mice, black rats and rabbits (*Oryctolagus cuniculus*) in the colonies. The fox has a relatively well documented spread across Australia since its release in 1871, and only recently (>1920s) arrived on the western side of the continent (Dickman 1996a). The timing, locale, and origin of the domestic cat introduction is less precise.

Dating the introduction of feral cats is important because they have caused the decline and extinction of native fauna on islands as well as contributing to a significant impact on ground birds and small native mammals (Dickman 1996b; Risbey et al. 1999; Doherty et al. 2015). Cats have been estimated to consume 70 million animals per day (<http://www.australianwildlife.org/>) and are considered a key contributor to the enormous loss of biodiversity as well as being implicit in the declines of Critical Weight Range (35–5500g) mammals recorded in Australia (Burbidge and McKenzie 1989; Cardillo and Bromham 2001; Woinarski et al. 2014; Doherty et al. 2015).

Australia has experienced a very high rate of decline in its native mammalian assemblage where one-third of all, and 90% of the medium size (0.03–3.5 kg) mammals have suffered either dramatic range contraction or extinction since European settlement (Dickman 1996a; Woinarski et al. 2014, 2015). A number of causes have been proposed to explain the decline in mammals, including competition, disease, altered fire patterns, variability in weather and site fertility and predation by introduced predators, specifically the fox (*Vulpes vulpes*), and the feral cat (*F. catus*) (see; Burbidge and McKenzie, 1989; Morton, 1990; Dickman 1996b; Woinarski et al. 2014). Predators appear to have contributed more than any other causative factor—and to the detriment of conservation programs. A number of Australian arid zone mammal reintroductions have been completely compromised due to direct predation from introduced predators (Christensen and Burrows, 1995; Gibson et al., 1995). Moreover, Christensen and Burrows (1995) proposed that predation by introduced predators (foxes and feral cats) was the single most important factor leading to the modern decline of arid zone mammals (see also Woinarski et al. 2014).

The spread of feral cats in Australia has been comprehensively documented by Abbott (2002, 2008) who showed that the historical record provided no documentary evidence that cats were present in

Australia prior to European settlement (in 1788). Cats are suggested to have spread over the continent from multiple coastal introductions after the 1820s, and by 1890 most of continental Australia had been colonized (Abbott 2002). The historical record suggests an expansion of feral cats over an area of ~7.6 million square kilometers in just 70 years, which would appear to be an extraordinary accomplishment, and unprecedented in invasion ecology (Arim et al. 2006).

There are competing hypotheses in regards to the origin of cats into Australia. These include: cats 1) associated with the arrival of Aboriginal peoples (40 000 years BP), 2) affiliated with the arrival of the dingo (4000 ybp; McKay 1996), 3) transported with Maccassan traders from Indonesia, 4) brought by the early European navigators and settlers (see Abbott 2002). The date of origin seems important to determine because the arrival of the cat onto the Australian mainland “is crucially important in evaluating its role in causing extinctions and declines in the distribution and abundance of native mammal and bird species” (Abbott, 2002, p. 51). The fauna decline has corresponded with the arrival and settlement of Europeans since 200 years ago, and importantly, if the cat was already present on the continent for hundreds, or even a thousand(s) years prior to this event then its implicit involvement in the fauna decline may not be as convincing as other factors that may have played a more important role in the loss of Australia's biodiversity.

Cats are well adapted to Australian conditions as they do not require free water when live prey are available (Newsome 1991). They are also agile, arboreal, and stalk prey. They tend to be selective for live prey, and only choose scavenging when conditions are particularly adverse (Jones and Coman 1981; Read and Bowan 2001). Socially, cats tend to be solitary, with small non-overlapping female home ranges, encompassed by multiple male ranges, which are much larger (Brothers et al. 1985). However, this pattern appears to be resource dependent, and where food is plentiful their densities can reach 700–2000 cats/km² (Liberg and Sandell 1994; Denny et al. 2002). The group-living cats appear to exploit abundant food sources and the social dynamic results in coalescing groups, dependant on human subsidies (Liberg and Sandell 1994; Denny et al. 2002). One such location is rubbish dumps that are ubiquitous features of human settlements associated with towns, mining sites, tourist resorts, and agricultural settlements throughout Australia (Wilson et al. 1994; Denny et al. 2002).

This study, developed from a large sample of cats from mainland Australia, Australian islands, Europe, and Asia ($n = 830$), generated a dataset of population genetic informative markers which were used to examine the association between cats from various source populations to infer the origin, population structure, and potential management strategies for the feral cat of Australia. Specifically, we use genetic information to 1) infer the origin of cats in Australia, 2) examine the population structure of cats on the mainland, and 3) interrogate the local population structure and possible relationship amongst cats from house, stray, and feral origin.

Materials and Methods

Cat samples were collected as ear, liver, or blood samples in conjunction with ongoing feral cat control programs initiated by the Department of Parks and Wildlife (DPaW; Algar and Burrows 2004), landowners, or from tissue (surgical sterilization). Cats were sampled from sites from all states on continental Australia ($N = 500$), Asia ($N = 118$), the Middle-East ($N = 64$), and Europe ($N = 50$); see Figure 1; Table 1). The Australian samples were predominantly from Western Australia ($N = 436$), Queensland ($N = 27$), Northern

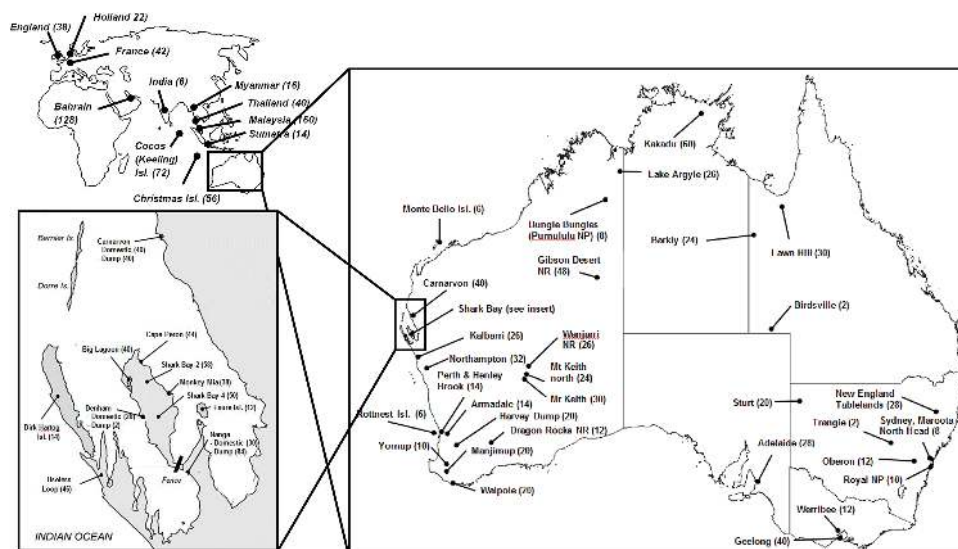


Figure 1. Sampling locations used in this study. *N* indicates the number of cats genotyped at each sampling location.

Territory ($N = 30$), South Australia ($N = 13$), New South Wales ($N = 88$), and Queensland ($N = 27$). Samples ($N = 83$) were also collected from 4 near-shore islands: Faure, Dirk Hartog, Monte Bello, Rottneet and 2 oceanic islands: Christmas and the Cocos (Keeling) Islands (Figure 1).

We refer to 3 categories of cats: house, stray and feral *F. catus*, following Denny et al. (2010). These definitions were fashioned on whether the ecological needs of the cat are provided by humans: entirely (e.g., pet, house cat), to some extent (street, alley, rubbish-tip, farm, or semi-dependent cat), or not at all (bush or feral cat). The categories may not be entirely suitable because cats near urban refuse sites (rubbish dumps etc) may also seek human attention, and as such, these definitions are convenient but unlikely to be obligatory groupings (Izawa and Doi 1993; Denny et al. 2002). The relative contribution of genetic diversity and material flowing from house to stray and the feral population (and back) remains unknown. Pairwise combinations of these groups (e.g., house vs. stray, stray vs. feral, or house vs. stray) were tested to identify differences in allele frequencies using Markov Chain algorithms. Comparisons were then averaged over all loci and tested using a Fisher's exact probability test for significance using GENEPOP 4.3 (Raymond and Rousset 1995).

Amplification and Electrophoresis and Genotyping of the STR Multiplex

Short tandem repeat (STR) loci were selected that were previously used in a large population genetic study of cats (Table 2; Driscoll et al. 2007; Menotti-Raymond et al. 2003, 2005, 2009). PCR amplification was performed with a touchdown PCR protocol and products were fluorescently labeled as described by Boutin-Ganache et al. (2001). Sample electrophoresis was carried out as described previously (Ishida et al. 2006). Genotyping was performed using the software package GENEMARKER (Soft Genetics, Version 1.85). Alleles were assigned to "bins" using the ALLELOGRAM software application (<http://tech.groups.yahoo.com/group/allelogram/files>). The entire sample set was genotyped 2 times by 2 independent investigators in the same laboratory using the same equipment. Genotypic data were initially manipulated and checked for errors using Microsoft EXCEL Descriptive

statistics (number of alleles, observed and expected heterozygosities) were calculated using GENALEX v.6.5b (Peakall and Smouse 2006). All abbreviations and calculations performed using GENALEX are described in the program's documentation (Blyton and Flanagan 2012).

Quantifying Genetic Diversity Population Structure and Demographic History

Genetic variation was measured as mean observed (H_o) and expected heterozygosity (H_e), observed (N_A) and effective number of alleles (N_A) using GENALEX 6.5. Each locus was examined for significant departure from Hardy-Weinberg proportions and linkage disequilibrium using GENEPOP using a subset of 100 randomly chosen feral cats from Australia (with a $Q \geq 0.95$; see STRUCTURE analysis below). MICRO-CHECKER 2.2.3 (Van Oosterhout et al. 2004) was used to examine each locus for evidence of null alleles. We used genetic distance measures (F_{ST}) and model-based clustering to detect and infer population structure. Wright's F -statistics (measured as θ ; Weir and Cockerham 1984) was performed using the program GENALEX 6.5. We identified genetic structure and assigned individuals to their likely population of origin using the program STRUCTURE 2.3.3 (Pritchard et al. 2000). STRUCTURE uses a Bayesian assignment approach to determine the most likely number of inferred populations (K) and the extent of the contribution from each inferred population to each animal's genotype. Analysis of the data was repeated with both, admixture and no admixture models (Pritchard et al. 2000). In addition, the hypothesis that the allele frequencies were or were not correlated, was tested under the admixture model. We also tested whether adding information on the geographic location into the prior probability would alter the results. STRUCTURE analysis was run with simulations from 1 to 10 ($K = 1-10$) inferred populations, using an extended burn-in period of 50 000 iterations with 10^6 iterations of MCMC simulation (repeated 10 times, using a cluster array at <http://www.ivec.org/>). The number of inferred populations (K) most compatible with the data set was estimated using values of delta K (ΔK ; Supplementary Figure S1) following the approach introduced by Evanno et al. (2005), using HARVESTER for STRUCTURE software (Earl and vonHoldt 2012).

Table 1. Sampling information including decimal latitude/longitude, whether the sample was from a domestic, stray, or feral cat and descriptive statistics, including the number of cats sampled (*N*), actual (*N_a*), and effective (*N_e*) number of alleles, observed (*H_o*) and expected (*H_e*) heterozygosity, fixation index (*F* = *HE* - *HO*)/*HE*. Locations from different states in Australia, include Western Australia (WA), New South Wales (NSW), Queensland (QLD), South Australia (SA), and the Northern Territory (NT). NR refers to a Nature Reserve (National Park). Values are given as mean ± SE

Sampling location	Decimal Latitude	Longitude	<i>N</i>	Domestic, stray or feral	No. of alleles (<i>N_a</i>)	Effective No. of alleles (<i>N_e</i>)	Heterozygosity		Fixation index (<i>F</i>)
							Observed (<i>H_o</i>)	Expected (<i>H_e</i>)	
Coastal Western Australian population									
1. Shark Bay (area 2, WA)*	-25.7512	113.5522	29	Feral	6.4±0.7	3.8±0.50	0.60±0.07	0.67±0.05	0.10±0.06
2. Shark Bay (area 4, WA)*	-26.1815	113.6990	25	Feral	5.8±0.6	3.4±0.35	0.61±0.06	0.67±0.04	0.06±0.08
3. Shark Bay, Big Lagoon (WA)*	-25.7421	113.4779	20	Feral	5.9±0.7	3.6±0.47	0.64±0.06	0.67±0.05	0.02±0.06
4. Monkey Mia (township, WA)	-25.7979	113.7061	19	Domestic	2.7±0.5	2.1±0.41	0.30±0.08	0.45±0.10	0.23±0.10
6. Denham (rubbish dump, WA)	-25.9209	113.5644	1	Stray	1.5±0.2	1.5±0.17	0.60±0.13	0.74±0.04	-1.00±0.00
7. Nanga (Township, WA)	-26.2555	113.8050	15	Domestic	5.2±0.5	3.4±0.30	0.66±0.07	0.74±0.04	0.01±0.10
8. Nanga (Rubbish dump, WA)*	-26.2526	113.8110	42	Stray	7.2±0.7	3.9±0.45	0.62±0.05	0.70±0.04	0.10±0.06
9. Peron Peninsula (WA)*	-25.6032	113.4785	22	Feral	5.8±0.6	3.6±0.45	0.65±0.07	0.68±0.05	0.03±0.07
10. Useless Loop (WA)*	-26.1620	113.4127	23	Domestic	5.9±0.6	3.8±0.46	0.59±0.07	0.68±0.05	0.13±0.06
11. Faure Island (WA)	-25.8439	113.8910	6	Feral	1.9±0.2	1.6±0.12	0.39±0.09	0.34±0.06	-0.23±0.12
12. Dirk Hartog Island (WA)	-25.7865	113.0313	7	Feral	3.7±0.5	2.8±0.33	0.59±0.08	0.59±0.07	-0.08±0.07
13. Camarvon (Rubbish dump, WA)*	-24.8847	113.7098	20	Stray	6.4±0.6	4.1±0.48	0.61±0.06	0.71±0.05	0.11±0.07
14. Monte Bello Islands (WA)	-20.4027	115.5770	3	Feral	1.5±0.2	1.4±0.14	0.31±0.10	0.26±0.08	-0.43±0.11
31. Walpole (WA)*	-34.9699	116.7211	20	Feral	6.1±0.5	3.9±0.44	0.64±0.06	0.71±0.03	0.08±0.06
Pan-Australian population									
5. Denham (domestic, WA)	-25.9253	113.5371	13	Domestic	5.5±0.5	3.8±0.37	0.62±0.06	0.74±0.04	0.12±0.07
15. Northampton (WA)*	-28.3341	114.6777	16	Domestic	5.9±0.5	3.8±0.44	0.65±0.07	0.69±0.05	0.03±0.07
16. Kalbarri, Red Bluff (WA)	-27.6803	114.2308	13	Feral	4.9±0.6	3.5±0.48	0.60±0.07	0.65±0.06	0.03±0.07
17. Lake Argyle (WA)*	-16.1220	128.8340	6	Feral	4.3±0.4	2.7±0.32	0.59±0.06	0.62±0.06	-0.07±0.06
18. Gibson desert NR (WA)*	-25.4749	126.0245	24	Feral	7.7±0.7	4.3±0.58	0.65±0.06	0.72±0.04	0.10±0.06
19. Bungle Bungles (WA)	-17.4272	128.4481	4	Feral	3.3±0.3	2.7±0.24	0.67±0.08	0.69±0.07	-0.18±0.07
20. Argyle Diamond Mine (WA)	-16.7232	128.4068	13	Stray	5.0±0.4	3.1±0.31	0.55±0.07	0.63±0.06	0.08±0.07
21. Mt Keith (north of lease, WA)	-27.1853	120.5411	12	Feral	3.9±0.3	3.1±0.28	0.92±0.07	0.71±0.05	-0.01±0.09
22. Mt Keith*	-27.1600	120.5422	15	Stray	5.5±0.5	3.3±0.36	0.62±0.06	0.67±0.04	0.06±0.05
23. Wanjarii NR (WA)*	-27.4261	120.7266	13	Feral	5.5±0.7	3.7±0.52	0.61±0.06	0.68±0.05	0.05±0.06
24. Leonora (rubbish dump, WA)	-28.8904	121.3228	4	Stray	3.0±0.3	2.5±0.24	0.69±0.09	0.65±0.07	-0.27±0.12
25. Perth domestic (WA)	-31.9808	115.9200	7	Domestic	4.5±0.4	3.2±0.41	0.54±0.07	0.66±0.06	0.10±0.09
26. Armadale (rubbish dump, WA)	-32.1378	115.9642	7	Stray	4.3±0.4	3.1±0.35	0.60±0.07	0.65±0.06	-0.01±0.06
27. Rottnest Island (WA)	-32.0021	115.5085	3	Stray	1.8±0.2	1.6±0.14	0.36±0.10	0.38±0.08	-0.17±0.15
28. Canning Dam (WA)	-32.1458	116.1287	4	Feral	2.4±0.3	2.1±0.25	0.63±0.09	0.62±0.08	-0.35±0.07
29. Harvey (rubbish dump, WA)	-33.0925	115.9178	10	Stray	3.4±0.3	2.6±0.28	0.51±0.08	0.57±0.06	0.01±0.10
30. Henley Brook (WA)	-31.7851	116.1119	1	Feral	1.5±0.2	1.5±0.17	0.53±0.13	0.53±0.13	-1.00±0.00
32. Manjimup (rubbish dump, WA)*	-34.2169	116.1238	10	Stray	5.3±0.6	3.5±0.52	0.60±0.06	0.66±0.06	0.04±0.06
33. Yornup rubbish tip (WA)	-34.0342	116.1831	5	Stray	2.4±0.2	2.0±0.16	0.61±0.09	0.58±0.08	-0.38±0.11
34. Dragon Rocks NR (WA)	-32.7789	119.0329	6	Feral	4.6±0.4	3.4±0.34	0.62±0.08	0.71±0.05	0.07±0.09
35. Birdsville (NSW)	-25.8990	139.3453	1	Feral	0.7±0.2	0.7±0.23	0.27±0.12	0.27±0.12	-1.00±0.00
36. Maroota (NSW)	-33.4985	150.9863	1	Feral	1.1±0.2	1.1±0.23	0.40±0.13	0.40±0.13	-1.00±0.00
37. New England Tablelands (NSW)*	-30.4014	151.6520	14	Feral	5.0±0.7	3.2±0.43	0.60±0.08	0.66±0.07	0.00±0.09
38. North Head (NSW)	-33.8195	151.2936	2	Feral	1.3±0.2	1.3±0.23	0.60±0.13	0.60±0.13	-1.00±0.00

Table 1. Continued

Sampling location	Decimal		N	Domestic, stray or feral	No. of alleles (N_A)	Effective No. of alleles (N_E)	Heterozygosity		Fixation index (F)
	Latitude	Longitude					Observed (H_O)	Expected (H_E)	
39. Oberon (NSW)	-33.7173	149.8614	6	Feral	2.8±0.6	2.2±0.43	0.40±0.09	0.44±0.09	-0.06±0.09
40. Royal National Park (NSW)	-34.1180	151.0564	5	Feral	2.2±0.4	1.8±0.34	0.44±0.10	0.42±0.09	-0.20±0.09
41. Surt (NSW)*	-29.1960	141.7162	10	Feral	4.2±0.6	2.9±0.46	0.53±0.08	0.61±0.07	0.09±0.07
42. Sydney (NSW)	-34.1036	151.1166	1	Stray	1.1±0.2	1.1±0.23	0.40±0.13	0.40±0.13	-1.00±0.00
43. Trangie (NSW)	-32.0302	147.9831	1	Feral	1.3±0.2	1.3±0.23	0.53±0.13	0.53±0.13	-1.00±0.00
44. White Cliffs (NSW)*	-30.8458	143.0837	10	Feral	3.9±0.7	2.7±0.49	0.47±0.09	0.53±0.09	0.04±0.08
45. Kakadu (NT)*	-13.0947	132.3907	30	Feral	6.6±0.7	3.9±0.44	0.58±0.06	0.69±0.05	0.14±0.06
46. Barkly (QLD)*	-20.4877	138.4253	12	Feral	5.5±0.6	3.6±0.41	0.60±0.07	0.69±0.05	0.09±0.07
47. Lawn Hill (QLD)*	-18.7025	138.4875	15	Feral	4.7±0.6	2.9±0.45	0.46±0.06	0.60±0.07	0.16±0.07
48. Adelaide (SA)*	-34.8761	138.5249	14	Stray	5.6±0.5	3.6±0.36	0.65±0.07	0.74±0.04	0.05±0.11
49. Geelong (Victoria)*	-38.0995	144.2775	20	Stray	6.6±0.6	3.9±0.51	0.60±0.06	0.69±0.05	0.11±0.05
50. Werribee (Victoria)	-37.9221	144.4458	6	Stray	4.0±0.4	2.9±0.39	0.58±0.08	0.65±0.06	0.01±0.11
Christmas Island									
51. Christmas Island, Australia	-10.4272	105.6747	28	Feral	5.8±0.4	3.5±0.34	0.58±0.05	0.67±0.04	0.12±0.05
Cocos Island									
52. Cocos (Keeling) Islands, Australia	-12.1776	96.8196	18	Feral	3.7±0.3	2.4±0.22	0.42±0.05	0.54±0.03	0.21±0.08
European sampling locations									
53. Birmingham (England, UK)	52.4866	1.8914	19	Stray	7.5±0.7	4.6±0.66	0.58±0.06	0.70±0.06	0.18±0.05
54. France	48.8367	2.3624	21	Stray	7.0±0.6	4.1±0.47	0.64±0.07	0.74±0.04	0.09±0.08
55. Texil Island (Holland)	53.0405	4.8487	11	Stray	1.1±0.2	1.1±0.24	0.47±0.13	0.47±0.13	-1.00±0.00
Asian sampling locations									
56. Inya Lake, Yangon, Myanmar	16.8479	96.1431	8	Stray	4.9±0.6	3.4±0.41	0.64±0.08	0.69±0.06	0.02±0.08
57. India, Gujarat	22.2915	71.1695	3	Stray	3.0±0.2	2.5±0.19	0.68±0.07	0.67±0.04	-0.21±0.10
58. Kuala Lumpur, Malaysia	3.0520	101.6688	43	Stray	6.5±0.9	4.2±0.63	0.57±0.07	0.72±0.06	0.18±0.07
59. Malaysia	3.0520	101.6688	23	Stray	8.4±0.8	5.1±0.58	0.65±0.04	0.79±0.02	0.15±0.04
60. Shah Alam, Selangor, Malaysia	3.0963	101.5180	14	Stray	6.7±0.8	4.1±0.58	0.59±0.07	0.71±0.06	0.16±0.07
61. Medan, Sumatra	3.6011	98.6724	7	Stray	4.3±0.5	3.2±0.46	0.58±0.08	0.67±0.06	0.06±0.09
62. Pattaya, Thailand	—	—	20	Stray	6.6±0.8	3.8±0.48	0.63±0.06	0.69±0.04	0.08±0.05
Middle East sample									
63. Bahrain	—	—	64		9.5±0.6	4.3±0.46	0.62±0.04	0.73±0.03	0.14±0.05
<i>Felis silvestris silvestris</i> (outgroup cats)									
64. <i>Felis silvestris</i> (Israel)	—	—	1		1.6±0.2	1.6±0.19	0.73±0.12	0.73±0.12	-1.00±0.00
65. Scottish wildcat	—	—	21		3.1±0.3	1.9±0.11	0.49±0.06	0.43±0.05	-0.13±0.05
Average					4.4±0.1	2.9±0.06	0.56±0.01	0.62±0.01	-0.06±0.01

* Indicates the 22 sampling localities where reasonable sample sizes were available (>10 cats, excluding domestic cats sampled and those marooned on islands) for use in the analysis of isolation-by-distance.

Table 2. Characteristics of 15 dinucleotide short tandem repeat (STR) loci isolated from the cat, *Felis catus* (*sensu* Menotti-Raymond et al. 2003, 2005, 2009) used in this study including heterozygosity and polymorphic information statistics generated from a subset of 485 feral cats sampled from Australia

STR no. (FCAXXX)	Chromosome	Map position ^a	cM from another STR on same chromosome	Heterozygosity			PIC
				Prev study ^b	Observed	Expected	
018 ^c	X	DA	—	0.71	0.1767	0.5128	0.450
026	D3	11.3	22	0.67	0.5446	0.7593	0.728
058	E2	66.4	55	0.81	0.6204	0.6534	0.589
077	C2	67.1	4.7	0.50	0.5515	0.5905	0.561
088	B3	218.8	—	0.74	0.4000	0.7748	0.749
096	E2	121.4	55	0.22	0.6198	0.6682	0.649
171	A3	146.2	4.7	0.85	0.6644	0.6922	0.639
224	A3	150.9	4.7	0.40	0.2071	0.2425	0.236
232	B4	250.8	—	0.84	0.7394	0.8528	0.835
532	A2	173.8	56 ^d	0.81	0.7409	0.8497	0.836
723	A1	173.2	—	0.57	0.8923	0.8894	0.879
078	D2	214.8	—	0.69	0.6461	0.8107	0.784
124	A2	DA	56 ^d	—	0.7950	0.8919	0.881
369	D3	DA	22	—	0.7336	0.8081	0.786
547	C2	62.4	4.7	—	0.6929	0.7510	0.712

cM, centiMorgans; STR, short tandem repeat/microsatellite; observed (H_o) and expected (H_e) heterozygosity; PIC, polymorphic information content.

^aMenotti-Raymond et al. (2009); ^bHeterozygosity as observed in Egyptian mau; ^csex-linked marker was removed from Bayesian and other analyses; ^dMenotti-Raymond et al. (2003); DA: does not apply because it was not included in the Menotti-Raymond et al. (2009) publication.

The relationship of isolation-by-distance (between genetic and geographical distances) was assessed and implemented using the GENALEX program. Pairwise estimates of F_{ST} (Weir and Cockerham 1984) and Nei's genetic similarity index were calculated in GENALEX. Geographic distances were measured as linear distance in km between the sampling locations and inferred using the Geographic Distance Matrix Generator program (http://biodiversityinformatics.amnh.org/open_source/gdmg/). Pairwise Mantel tests were performed using GENALEX and significance was assessed using 999 permutations. We selected localities where reasonable sample sizes were available (>10 cats) and excluded domestic cats sampled and those marooned on islands. Analyses were performed for pairwise comparisons of 22 Australian mainland locations (see details given in Table 1).

Principal component analysis was performed in PAST 2 software (Hammer et al. 2001) using a correlation matrix. Before the analysis each allele for every locus was labeled as 0, 0.5, or 1 for allele absence, heterozygote or homozygote in a given individual. An individually-based tree phenogram was constructed using NEIGHBOR from the PHYLIP package (Felsenstein 1993) based on an allelesharing, Dps (Bowcock et al. 1994) distance-matrix generated in MSA 4.05 software (Dieringer and Schlötterer 2003) with 1-Dps correction and visualized in FigTree software (Rambaut 2009).

We also considered different approaches to address the question of simple expansion versus an alternative hypothesis, for example, involving expansion aided by human-mediated transport and interbreeding with stray or domestic stocks. To test this within a rigid framework, we modeled if the population was expanding (or declining), using MSVAR (Beaumont 1999) but priors did not converge (data not shown). We also considered Approximate Bayesian Computation (Cornuet et al. 2008), but the alternative to an expansion scenario could not be formulated with sufficient precision.

Data Archiving

In fulfilment of data archiving guidelines (Baker 2013), microsatellite genotypes have been submitted to Dryad (<http://datadryad.org/>).

Results

The Origin of the Cat in Australia

Samples of 830 cats from Australia, Asia and Europe representing 65 sampling locations (Figure 1) were genotyped with a panel of 15 STR markers. Upon performing Holm's (1979) correction for multiple testing there were no statistically significant departures from Hardy-Weinberg equilibrium or statistical evidence for genotypic equilibrium. MICROCHECKER did not detect any evidence for null alleles. Using the Bayesian clustering program STRUCTURE, we identified 6 distinct populations ($K = 6$; Figure 2a; Supplementary Figure S1) corresponding to *F. silvestris silvestris*, Asian, European, 2 island populations (Cocos Keeling/Christmas Islands), and coastal Western Australian population and a pan-Australian cat population ($K = 6$; Figure 2a). When the wild cat sample from Scotland (*F. s. silvestris*; i.e. "out-group") was removed, the greatest delta observed, ($K = 2$), included 2 distinct clusters, corresponding to cats that originated from Europe and another from Asia (Supplementary Figure S2). Australian cats clustered consistently with European cats (average $Q = 0.92$; See averages in Supplementary Table S1 and S2), to slightly varying degrees depending on the sampling location. The data clearly demonstrates the distinctiveness of the island populations from the mainland populations and from each other (Supplementary Figure S2). Analysis of Australian cats alone (excluding the Cocos-Keeling and Christmas Islands populations), showed 2 groups ($K = 2$) within the Australian continent (Figure 2; Supplementary Figure S3). These cats corresponded with sampling locations on the west coast (with the exception of house cats from the township of Denham) and a second population representing the remainder of the continent (with the exception of cats sampled from the far south-west coast at Walpole; population designated 2 in Supplementary Figures S3 and S4). We designate these populations as a "coastal Western Australian population" and a "pan-Australian" cluster (Supplementary Figure S4). Unlike mainland Australian cats, the Cocos-Keeling Island (a territory of Australia, located in the Indian Ocean) cats demonstrate a predominantly

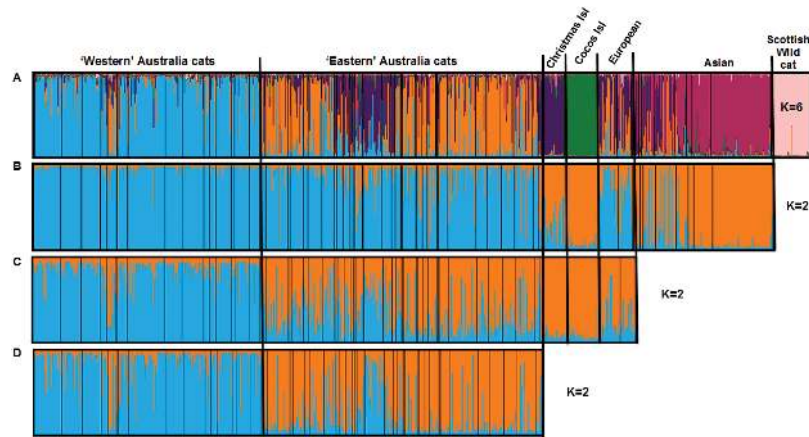


Figure 2. Structure outputs that include all (A) 830 samples in the study, (B) *Felis catus* samples (Scottish wild cat, *F. s. silvestris* samples were excluded), (C) Australian and European cats, including various island populations, and (D) Australian mainland cats (island sampling locations are excluded). Colors are viewable in the online version of the article.

Asian origin (Asian $Q = 95\%$; Supplementary Figure S2), while those on Christmas Island exhibit an admixed European/Asian signature (Asian $Q = 0.72$; European $Q = 0.28$; Supplementary Tables S1 and S2). Malaysian cats also exhibit admixture of Asian and European stock (Figure 2).

PCA analysis confirms the STRUCTURE results. Both the first 2 principal components (PC1-2) explain a substantial percentage (13.91 %) of an observed inter-individual variation (Figure 3) forming 2 highly differentiated clusters of domestic cats from different regions and Scottish wild cats. At the same time, cats from Australia (Figure 2a; blue, orange and purple colors), Europe (purple color), and Christmas Island (purple blue color) form a slightly overlapped cluster with Asian (mauve color) and Cocos Island (green color) specimens supporting the deep separation of the Asian versus European groups and the European ancestry of the Australian cats. West and East Australian cats are grouped in 2 separate clusters based on the first and second principal components. STRUCTURE clusters are supported by an individually based phenogram generated from Dps distances, demonstrating 5 populations, clustering European and mainland Australian cats in a single group, Asian, Cocos Island, Christmas Island, and *F. s. silvestris* populations (Figure 3).

Structure of Australian Cats

Cat samples from the Australian mainland consisted of a single genetic cluster that was most closely associated with cats of a European origin (Figure 2b). After removing Asian and European cats from the analysis, Australian cats form 2 clusters corresponding to a coastal Western Australian population and pan-Australian population (Figure 2c). The western grouping ($Q > 90\%$) was confined predominantly to the Shark Bay area of Western Australia (Supplementary Figures S2–S4; on the coastal, western edge of the Australian continent), and included samples from as far south as Walpole on the south-western coast. These cats had no genetic affinity to any other cats from our sampled locations. Not surprisingly given the large amount of potential (post-European settlement) mixing, there is some variation occurring around Australia. For example, in the Victorian/Kakadu feral cat samples, Asian cats account for 13–14%, whereas in feral populations from Western Australia it is ~only 8%. In general, an Asian influence in Australian feral cats appears to be minimal and overall, the cats from Australia appear to be of European origin. A pattern of isolation-by-distance was found

to be highly significant among Australian feral cats (F_{ST} , $r = 0.434$, $P = 0.001$, Figure 4; Nei's genetic similarity index $r = 0.553$, $P = 0.001$). Furthermore we could not identify different genetic structure within our European samples, and as such we were unable to distinguish if Australian cats originated from Holland or England.

Genetic Relationship Between House, Stray, Feral, and Cats Stranded on Islands

House and stray cats did not demonstrate significantly different allele frequencies (from 2 comparisons). However, true feral cats always demonstrated a significant difference from nearby sampled house/stray individuals based on pairwise comparisons of allele frequencies ($\chi^2 > 50$; $df = 30$; $P < 0.006$ from pairwise comparisons; Table 3). This result might suggest that mixing is common between house and stray animals ($P > 0.07$; Table 3). It also suggests that feral cats generally have little mixing with their house counterparts. Australian feral cats (excluding house cats) exhibited high levels of diversity (average heterozygosity = $67\% \pm 5$; No. of alleles = 7.9 ± 0.7 ; Table 4). Feral cats demonstrated comparable levels of diversity than house cats (across all markers), and island populations showed the lowest levels of genetic diversity. The island cats had between 60 and 80% less diversity than their (feral) mainland counterparts. House-stray cat comparisons showed only a small difference ($<10\%$), generally for measures such as number of alleles and heterozygosity. In general, the house and feral cat populations do not exhibit extensive gene flow, but are relatively high in diversity ($H_o = 71\%$ and 8.1 alleles per locus) and low in differentiation ($F_{ST} = 0.005$). In contrast, island populations exhibit low diversity (heterozygosity of 56%) and not surprisingly, show higher levels of differentiation to mainland cats ($F_{ST} = 0.041$).

Discussion

This study analyzed a large number of cats from a wide geographic distribution to characterize the level of diversity and infer the origin, and spread of feral cats in Australia. Our data conclusively support a European origin of Australian cats, with little evidence of any Asian influence in the current population. Feral cats are distributed over the entire Australian continent and appear to be highly mobile, with persistent gene flow enhancing diversity and limiting population differentiation.

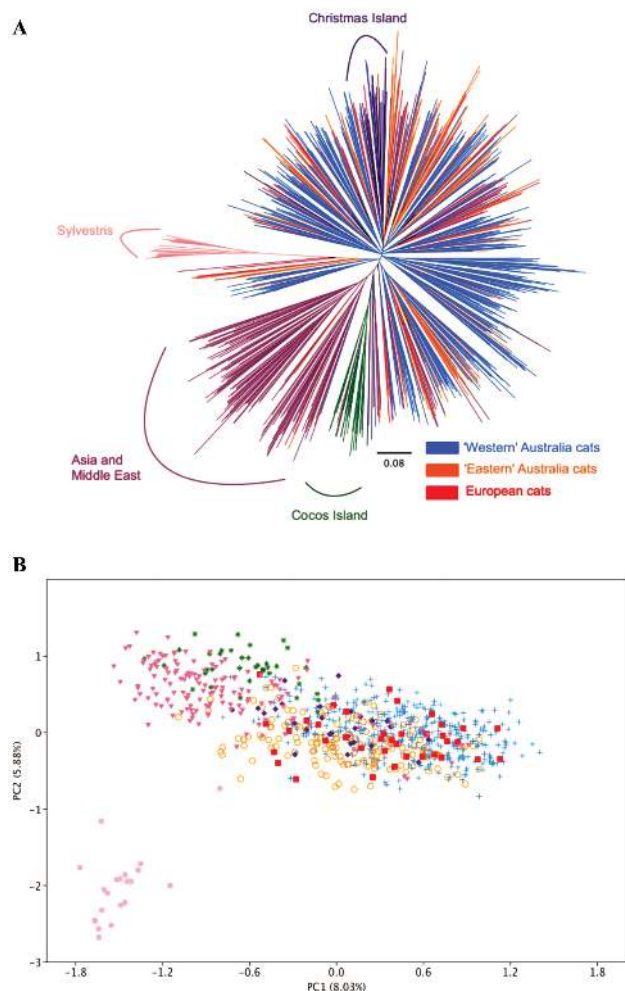


Figure 3. Details of the (A) individual-based tree (phenogram; using Dps-distances, with 1-Dps correction) of 830 domestic, stray, and wild specimens created on the basis of STR profiles showing 4, near “monophyletic” groups—Asia, Cocos (Keeling) Island, Scottish wild cat (*Felis silvestris silvestris*), Christmas Island (Indian Ocean), Dps genetic distance and minimum evolution (neighbor-joining) algorithm and (B) Principal Component Analysis plot based on STR frequencies, confirming a European origin for Australian cats and also the separation of coastal Western Australian population and pan-Australian populations of cats within Australia. Colors are viewable in the online version of the article.

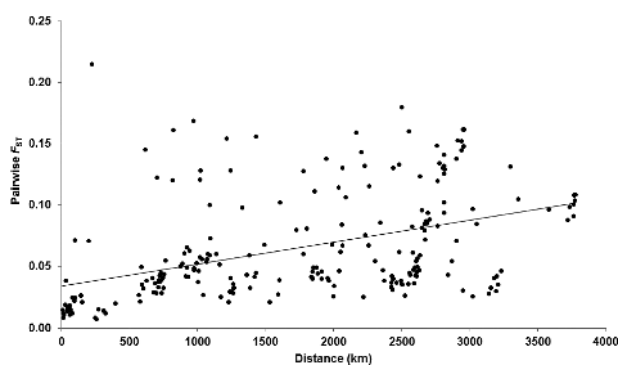


Figure 4. Graph of isolation by distance (IBD) results, where F_{ST} values ($F_{ST}/(1 - F_{ST})$) were regressed upon the linear distance (in km) between pairs of sampling locations of feral cats from the Australian mainland, showing a significant IBD effect (Mantel’s test $P < 0.001$; $r^2 = 0.199$).

The Origin of Cats Sampled in Australia

High levels of genetic variability and gene flow are apparent over the Australian continent. Abbott suggested that cats spread across the mainland quickly. From 2 introduction points (Sydney and Perth), the population of cats appears to have spread over the entire (~7.6 million km²) continent within approximately 70 years (Abbott 2008). The genetic information presented here supports Abbott’s report of the historical record and suggests that the most successful cat population originated from the settlements around Sydney and quickly spread westwards, until approximately longitude 119°E, showing a strong relationship of isolation by distance. Although we are not able to identify other points of introduction of the cat suggested by Abbott (2008), this study shows that the only other successfully remaining population is the one that originated from Perth and Albany. However, its spread eastwards does not appear to be nearly as successful as the western migration by cats released from the eastern seaboard. This finding is useful if we can assume that the migration of cats occurred from the east to the west of the continent, and using Abbott’s paper as a “null-hypothesis”, the genetic structure suggests that the eastern origin, and the westward movement of the cat occurred quickly (~70 years to spread over the entire Australian continent). If we assume a single point of entry (somewhere on the eastern seaboard near Sydney), then this corresponds to a linear distance (to the edge of the cats western range) of 3800 km (2300 miles) in just over 70 years. The sample of house cats in Denham showed a clear pan-Australian origin, so some separation of these cats from the surrounding feral population appears to be evident and supported by our finding of differences between domestic and feral cats from other areas in this study. Although speculative, the Shark Bay population may be the remnant of the original Perth release described by Abbott from around 1830–1840.

The finding of one panmictic breeding pool indicates that there are very high levels of gene flow across the continent. Despite their small size, cats have large continental-sized populations which have been demonstrated in other highly mobile vertebrates (Kyle and Strobeck 2001; Schwartz et al. 2002), including newly introduced invasive species, such as the camel in Australia (Spencer et al. 2012). More commonly, highly structured populations have been identified for several invasive species, including feral cats (Pontier et al. 2005; Hansen et al. 2007), rabbits (Fuller et al. 1997), feral pigs (Hampton et al. 2004; Cowled et al. 2008), rats (Ruscoe et al. 1998; Abdelkrim et al. 2005), and birds (Rollins et al. 2009). This finding is important, as the decline of the Australian native fauna appears to be linked with a recent invasion from cats (~200 years), as opposed to the view that cats entered into Australia with the Macassan traders from Indonesia (1000 years bp).

Introduced populations have generally lower genetic diversity in comparison with their source populations (Dlugosch and Parker 2008). Australian feral cats appear to have maintained high diversity and there are several possible mechanisms that could produce this observed pattern including multiple source populations for Australian cats, sustained supplementation of new individuals associated with European settlement and insufficient sampling of European stock. Cats are distributed continuously throughout the Australian arid zone, which according to Abbott (2002), has an almost total absence of barriers to dispersal and a uniquely unpredictable climate (Norbury et al. 1994). Such variable and resource-poor environments are generally understood to discourage philopatry and encourage dispersal (Norbury et al. 1994; Fuller et al. 1997) which may explain the rapid spread across continental Australia.

Table 3. Comparison of allele frequencies and cats from domestic/stray and feral origin

Population sampled		F_{ST}	P	G_{ST}	P	N	χ^2	d.f.	P
Comparison of domestic and stray cats									
Nanga (town)	Domestic					10	41.80	30	0.0743
Nanga (rubbish dump)	Stray	0.045	0.002	0.023	0.002	40			
Carnarvon (town)	Domestic					16	39.71	30	0.1106
Carnarvon (rubbish dump)	Stray	0.033	0.038	0.100	0.0036	17			
Comparison of domestic/stray and feral cats ^a									
Nanga (town/dump)	Stray					50	52.74	30	0.0063
Shark Bay (general 2)	Feral	0.045	0.001	0.023	0.001	29			
Carnarvon (town/dump)	Stray					33	1000.00	30	0.0000
Gibson Desert Nature Reserve	Feral	0.042	0.001	0.026	0.001	24			
Monkey Mia (town)	Stray					17	55.73	30	0.0029
Shark Bay, Big Lagoon	Feral	0.042	0.012	0.018	0.014	20			
Manjimup (dump)	Stray					10	96.57	30	0.0000
Walpole	Feral	0.066	0.001	0.043	0.001	20			
Useless Loop	Stray					23	81.30	30	0.0000
Dirk Hartog Island	Feral	0.062	0.001	0.035	0.001	7			

N , number of cats sampled; df, degrees of freedom.

^aThe domestic/stray category is the pooled sample of domestic and stray cats (that had allele frequencies not significantly different from each other).

Table 4. Descriptive statistics that summarise levels of genetic diversity within feral, domestic/stray and island cats from Australia including the sample size (N), actual (N_A) and effective (N_E) number of alleles, observed (H_O) and expected (H_E) heterozygosity, fixation Index ($F = HE - HO/HE$)

	N	N_A	N_E	H_O	H_E	F
Feral cats	126.7±3.3	7.9±0.7	3.9±0.5	0.61±0.06	0.67±0.05	0.09±0.05
Domestic/stray	75.7±2.343	8.1±0.7	4.3±0.4	0.61±0.050	0.71±0.04	0.14±0.05
Island cats	15.8±0.1	4.7±0.6	2.7±0.29	0.46±0.06	0.56±0.06	0.15±0.07

Genetically, Australian feral cats conform to theoretical expectation of rapid expansion as there was a highly significant signature of isolation-by-distance. In addition, the number of founders must have been relatively large (e.g., >10) to have retained the levels of diversity observed in all the extant sampling locations (Table 1). Coupled with this presumed rapid expansion, this large founder size would also contribute to the maintenance of diversity observed in all the mainland cat samples (Veale et al. 2015). The high levels of genetic diversity observed are likely to be sustained through the periodic interbreeding and addition of cats sourced from Europe, after their initial introduction, and at multiple locations (Abbott 2002, 2008). This diversity could also be maintained by intermixing with stray, domestic or Asian cats, although the latter options were not strongly supported in this study (see below). The present data cannot rule out alternatives to a natural expansion from a singlepoint, such as human-mediated transport post-introduction as well as supplementation as new settlements were established around Australia.

Are House, Stray and Feral Cats Inter-related and Intermixing?

At a local level and in colonies, cats are generally solitary species, aggressive to immigrants, and that exhibit high inbreeding and low dispersal (Say et al. 2002; Devillard et al. 2003). Contrasting this, females will occupy small non-overlapping home ranges, overlaid by a larger male home range occupied by a dominant male and may form large groups given a steady and plentiful food source (Brothers et al 1985; Denny et al. 2002). House and stray cats from

Western Australia show no genetic differences. Unlike species that are semi-nomadic and utilize vast areas, gene flow between stray and domestic cats appears to be high on a local level and any distinction between house and strays is poorly supported. Additionally, the prevalence of de-sexing is high in Australian pet cats, with estimates in large state or national surveys greater than 90% (Murray and Penridge 1997; Lilit et al. 2006). These compare, for example, to rates of 43% in Teromo, Italy (Slater et al. 2008) or 80% in the USA (Chu et al. 2009), where genetic similarity between stray and feral cats might be expected to be less extreme than found in this study. In contrast, truly feral/wild cats were genetically distinct from the closest house and stray cats sampled.

How Can Genetic Information be Used to Provide Better Information on Managing Cats in Australia?

The data suggest a lack of strong geographic subdivision and that cats on mainland Australia would be difficult to eradicate, as the genetic population is likely to encompass most of the continent, with the exception of the restricted population on the west coast around Shark Bay. This finding also suggests that cats are not influenced by the large range of environmentally limiting factors affecting geographic ranges in many continental-sized species, such as giraffe, elephants, pigs, or ungulates (Van Hooff et al. 2000; Comstock et al. 2002; Brown et al. 2007). The study also suggests that house cats and their conspecifics associated with street, alley, rubbish-dump, farm, or semi-dependent cats show high levels of genetic mixing. Surprisingly, comparisons between them and true bush or feral cats show less genetic similarity.

Unfortunately, this study offers little by way of proposing improvements to the management, and remote chance of eradication, of cats in Australia. Cats may be able to respond and recover from local control efforts through immigration. If so, then control efforts may need to be ongoing and site-specific. Cats appear to have adapted surprisingly quickly to the Australian environment, they are also highly transient, moving quickly over the continent and show genetically high level of diversity.

Supplementary Material

Supplementary material can be found at <http://www.jhered.oxfordjournals.org/>.

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Data Availability

Data deposited at Dryad: <http://dx.doi.org/doi:10.5061/dryad.22834>

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