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RESEARCH ARTICLE

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Abstract

Faunas of oceanic islands have a high proportion of endemic species which contribute to the uniqueness of island communities. Island species are particularly naïve and vulnerable to alien predators, such as cats (*Felis catus*). On large, inhabited islands, where the complete eradication of feral cat populations is not considered feasible, control represents the best management option to lower their detrimental effects on native fauna. The first objective of our study was to investigate population genetics of feral cats of Réunion Island. The second objective was to understand the space use of feral cats established near the breeding colonies of the two endemic and endangered seabirds of Réunion Island, the Barau's Petrel (*Pterodroma baraui*) and the Mascarene Petrel (*Pseudobulweria aterrima*). We evaluated genetic diversity, population structure and gene flow amongst six groups of feral cats located at a maximum of 10 km from known petrel colonies. We also analysed the behaviour and space use of one of these feral cat groups using camera-trap data and Spatially Explicit Capture-Recapture (SECR) models. Genetic analyses revealed that feral cats were structured in three genetic clusters explained mostly by the island topography. Two clusters were observed at five sampled sites, suggesting high connectivity amongst these sites. The last cluster was found

in only one site, suggesting high isolation. This site was a remote mountain area located in the vicinity of one of the main Barau's Petrel colonies. The behavioural study was conducted on this isolated feral cat population. Mark recapture analysis suggested that feral cats were present at low density and had large home ranges, which is probably explained by reduced food availability. Finally, we make several recommendations for refining feral cat management programmes on inhabited islands.

Introduction

One third of the terrestrial biodiversity hot-spots includes oceanic islands and most of them are in the tropics (Myers et al. 2000). Oceanic islands are characterised by a high proportion of endemic species (Carlquist 1974; Myers et al. 2000; Kier et al. 2009) contributing to the uniqueness of island communities (see Burlakova et al. 2011). Insular species are particularly naive and vulnerable to the introduction of exotic predators (Moors and Atkinson 1984; Medina et al. 2011; Legge et al. 2017), which are known to be the main drivers of species extinction and biodiversity loss on islands (Moors and Atkinson 1984; Courchamp et al. 2003; Leclerc et al. 2018; Russell and Kueffer 2019). Domestic cats (*Felis catus*) have established feral populations on many islands worldwide (hereafter referred to as feral cats; Nogales et al. 2013). They present a high invasive ability (Van Aarde 1986) and are one of the most damaging species introduced on islands (Fitzgerald 1988; Courchamp et al. 1999b; 2003, Medina et al. 2011; Nogales et al. 2013; Jones et al. 2016). This generalist and opportunist predator has caused numerous extinctions of insular species and particularly of endemic vertebrates (Nogales et al. 2004; Nogales and Medina 2009; Doherty et al. 2016). There is an urgent need to counteract the biodiversity loss due to feral cat predation by optimising methods to eradicate or regulate this invasive predator (Myers et al. 2000; Kier et al. 2009; Burlakova et al. 2011).

Feral cat eradications, which consist of a complete and definitive removal of the feral cats, have been frequently conducted on islands (see Medina et al. 2011). However, their implementation on large, inhabited islands remains challenging. The main difficulties to eradicate feral cats from large inhabited islands are low social acceptability, inappropriate legislation, lack of long-term political commitment, important financial cost and reduced technical feasibility of such large-scale operations (Oppel et al. 2010; Glen et al. 2013; Russell et al. 2018). The situation is even more complicated by the presence of domestic cats which can be accidentally culled and which permanently supplement the feral cat population through breeding (Choeur et al. 2022). One alternative to eradication is long-term control of feral cats in key areas, in order to maintain the population below a threshold that results in a low and acceptable impact on biodiversity (Doherty et al. 2017; Palmas et al. 2020). However, in most cases, controlled

areas are not isolated from nearby uncontrolled areas and are continuously re-invaded by cats (Lazenby et al. 2015; Palmas et al. 2020). The re-invasion rate depends on various factors, such as the density of cats in uncontrolled nearby areas, the connectivity between controlled and uncontrolled areas and the dispersive behaviour of the cats (Palmas et al. 2020; Choeur et al. 2022). When cat control is implemented in key areas, there is a strong need to understand the individual dispersion (Pulliam 1988; Hanski 1999) and space use at global and local scales to estimate the rate of re-invasion and to optimise the cost-effectiveness of control campaigns (Palmas et al. 2020).

Population genetics is an efficient tool for informing the management of invasive mammalian species (Browett et al. 2020). Genetic-based techniques can be used to identify the origin of the invaders, to trace the invasion pathways and to appropriately target a population of manageable size with low re-colonisation risk (Robertson and Gemmell 2004; Abdelkrim et al. 2005; Rollins et al. 2006, 2009). This information can be used to design the best strategy for successful control campaign. For instance, introduced feral cats on the main island of the Kerguelen Archipelago are now well established over the entire island, suggesting that a complete eradication would be extremely difficult (Simberloff 2003; Pontier et al. 2005; Barbraud et al. 2021). However genetic analyses highlighted limited connections between sites, indicating that local control may have long-term benefits (Pontier et al. 2005). On the island of Hawai'i, the genetics of feral cat populations indicated high genetic diversity, population expansion and weak, but significant structure amongst three sites (Hansen et al. 2007). These results indicated that the most isolated site could be targeted for control (Hansen et al. 2007). On Christmas Island (Indian Ocean), no genetic structure was detected amongst feral cat populations, suggesting high connectivity and higher risk of re-invasion after local control. This indicates that, in this case, feral cats of the entire island should be removed or simultaneously controlled (Koch et al. 2020).

Camera trapping and Spatially Explicit Capture-Recapture (SECR) are effective tools to understand species behaviour and spatial ecology (Bridges and Noss 2011; Rovero et al. 2013; Royle 2015). SECR models are hierarchical models that account for both the spatial organisation and movement of individuals in relation to the placement and effectiveness of the detection devices (Kane et al. 2015). This method provides key information for designing effective feral cat control and for optimising management techniques (Robley et al. 2010; Lazenby et al. 2015; McGregor et al. 2015). Palmas et al. (2020) tested the feasibility and efficiency of an intensive control of feral cats in a semi-isolated peninsula in New Caledonia. SECR modelling suggested that feral cats recolonised the controlled area in three months, recovering to the same density as the one determined before the culling (Palmas et al. 2020). Recolonisation by feral cats was faster than expected despite the favourable geographical situation of the peninsula. In such cases, genetic studies may offer a strong benefit to management actions by highlighting the connectivity between controlled and uncontrolled populations.

Réunion Island (21°00'S, 55°39'E) is a large (2512 km²), young (about two million years) inhabited (861,200 people in 2021) volcanic island of the Mascarene Archipelago, western Indian Ocean. The topography is extremely rough with a maximum

elevation of 3,071 m a.s.l., several summits above 2,500 m and three massive eroded calderas surrounded by huge vertical cliffs (of 1 km high). This topography has generated an important ecological heterogeneity (Strasberg et al. 2005). Réunion Island is part of the biodiversity hotspot of Madagascar and surrounding islands (Myers et al. 2000; Roberts et al. 2002; Mittermeier et al. 2005; Kier et al. 2009). Since the colonisation of the Island by humans in the late 1600s, this biodiversity has been strongly impacted by habitat loss, unregulated hunting and invasive species. A total of 57% (17 of the 30 species) of the native vertebrates of the Island are now extinct (Gargominy et al. 2020). One of the most problematic alien predators is the feral cat. This species was introduced in 1702 (Cheke and Hume 2010) and is known to prey upon several endemic species including the endangered Barau's Petrel (*Pterodroma baraui*; Faulquier et al. 2009) and the critically endangered Mascarene Petrel (*Pseudobulweria aterrima*; Riethmuller et al. 2012).

The objectives of our study were to estimate the genetic connectivity and space use of feral cat populations near the breeding colonies of the two endemic petrels. Based on 10 polymorphic microsatellite markers, we evaluated genetic diversity, population structure and gene flow amongst six groups of feral cats located at a maximum of 10 km from known petrel colonies. We used feral cat capture-mark-recapture (CMR) data and SECR models to estimate the density and the home range of feral cats near the well-studied Barau's Petrel breeding colony of Grand Bénare. We determined their density and general activity (movements and detection probabilities) in relation to the types of habitat used (trail vs. vegetation cover). Finally, genetic data and behavioural data were combined to propose an adapted feral cat control strategy.

Materials and methods

The endemic petrels of Réunion Island

The population size of Barau's Petrel is estimated between 10,000 and 30,000 breeding pairs (Virion et al. 2020). The first breeding colony was discovered in 1995 (Probst 1995; Probst et al. 2000). Several breeding sites have been discovered since then and two of them are monitored annually: Bras des Etangs (west side of Piton des Neiges, 2,400 m a.s.l.) and Grand Bénare (2,600 m a.s.l.). The breeding habitat is characterised by steep cliffs between 2,200 and 2,800 m a.s.l. mainly covered by endemic shrubs, such as *Erica reunionensis*, *Stoebe passerinoides* and *Sophora denudata* (Cadet 1977; Probst et al. 2000; Strasberg et al. 2005). Barau's Petrels breed seasonally between September and April. They completely leave their colonies after breeding. Feral cats have been reported at all known colonies. Faulquier et al. (2009) showed that feral cats established at Barau's Petrel colonies prey intensively upon adults, inducing a strong negative impact on populations, as this long-lived species is particularly sensitive to any additive mortality on adults (Russell et al. 2009; Dumont et al. 2010). Rats and mice are also present at Barau's Petrel colonies, at low density, probably because these altitudinal habitats are suboptimal for these species (authors' unpubl. data).

The population size of Mascarene Petrel is estimated at 250 breeding pairs (Attie et al. 1997). Two breeding colonies were discovered in 2016 and 2017 (Virion et al. 2020; Juhasz et al., in press) and have been monitored annually since. Burrows are located on steep cliffs from 650 to 1,200 m a.s.l. where the habitat is dominated by shrubs, such as the indigenous *Olea lancea* and the endemic *Monimia rotundifolia* (Juhasz et al., in press). The Mascarene Petrel breeds seasonally between August and March. They completely leave their colonies after breeding. Preliminary studies conducted at the breeding colonies suggest that predation by exotic mammals (rats and cats) and habitat loss constitute the main threats for this critically-endangered seabird species (Juhasz et al. in press; authors' unpubl. data).

Genetic sampling of feral cats

We sampled feral cats from July 2015 to December 2016 at six sites. Five of these sites are included in the National Park of Réunion Island and located in native mountain forests (Fig. 1A, B). The site of Cilaos is in the southernmost massive caldera of the Piton des Neiges volcano (called "Cirque de Cilaos"). The site of Les Makes is located 9 km to the southwest of Cilaos. Dimitile and Grand Bassin are located respectively at 6 and 8 km to the southeast of Cilaos. These four sites are located between 1,200 and
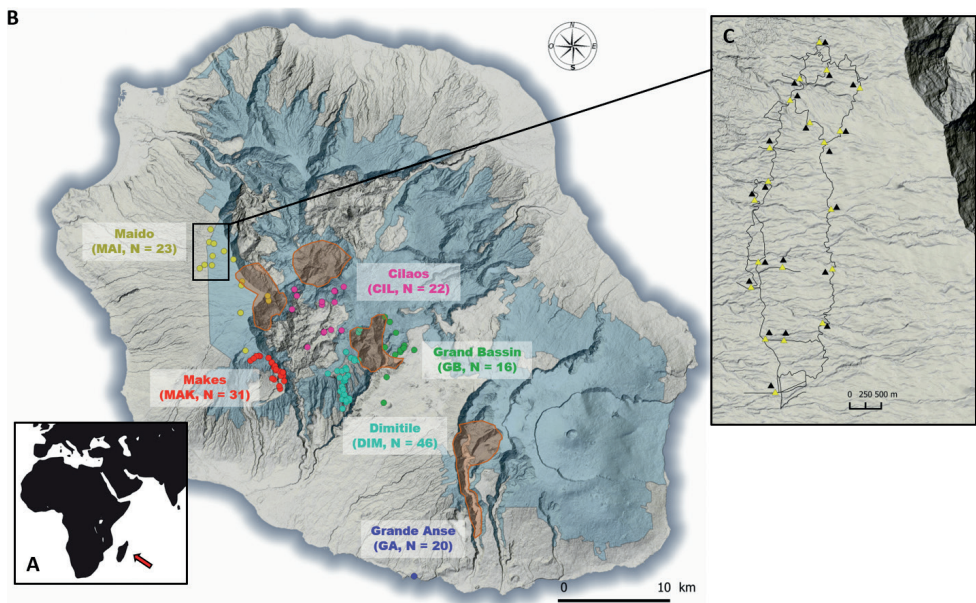
Figure 1. Maps illustrating **A** the locality of Réunion Island **B** genetic sampling sites, in 2015–2016 and **C** camera trapping sites in 2016. Each colour of dots corresponds to a different geographical area. Area codes and sample sizes are indicated in parentheses. The grey area corresponds to the National Park and the orange areas correspond to the presence of Barau's and Mascarene Petrels. Triangles correspond to the localities of camera traps on trails (yellow triangles) and under vegetation cover (black triangles). The black lines show the trails.

Table 1. Estimates ± standard errors of genetic diversity for 10 microsatellite loci of feral cats (total N_{sample} = 158 individuals) in six geographical areas in Réunion Island, 2015–2016.

Area	Code	N_{sample}	N	AL	PA	AR	H_O	H_E	F_{IS}
Maïdo	MAI	23	22.80±0.20	5.20±0.53	1	4.68±0.45 a	0.58±0.05	0.58±0.04	-0.02±0.03
Makes	MAK	31	30.30±0.37	7.20±0.47	4	6.11±0.35 b	0.65±0.04	0.70±0.02	0.06±0.04
Cilaos	CIL	22	21.60±0.31	6.90±0.41	3	6.35±0.38 b	0.68±0.03	0.70±0.03	0.01±0.03
Dimitile	DIM	46	45.30±0.40	6.90±0.53	4	5.49±0.36 ab	0.68±0.04	0.66±0.04	-0.05±0.04
Grand Bassin	GB	16	15.70±0.15	6.00±0.47	3	5.90±0.45 ab	0.58±0.06	0.65±0.04	0.08±0.05
Grande Anse	GA	20	19.80±0.13	6.50±0.27	2	6.20±0.24 b	0.74±0.03	0.71±0.03	-0.07±0.03

For each area, we give the mean number of genotyped individuals (N), the mean number of alleles per locus (AL), the mean allelic richness per locus, based on minimum sample size of 15 diploid individuals (AR; means followed by the same lower case letter are not significantly different [i.e. $P > 0.05$] according to the pairwise Wilcoxon's signed rank tests with Bonferroni correction), the private allelic richness (AP), the observed heterozygosity over all loci (H_O), the unbiased expected heterozygosity (H_E) and the fixation index (F_{IS}; Weir and Cockerham 1984).

1,400 m a.s.l. The fifth site, named Maïdo, is a volcanic plateau sloping to the west and located 9 km to the northwest of Cilaos. Maïdo lies between 1,500 and 2,850 m a.s.l. and is characterised by subalpine shrubland. The sixth study site, Grande Anse, is a coastal peri-urban area located 20 km to the south of all other sites at 0 to 110 m a.s.l. (Fig. 1B). All sampled sites are located at less than 10 km from a breeding colony of Barau's Petrel or Mascarene Petrel (Fig. 1B) and four of them (Cilaos, Dimitile, Grand Bassin and Maïdo) are located less than 3 km from the nearest petrel colony.

Cats were live-trapped with Tomahawk cage traps baited with sardines and brought to the veterinary clinic for sanitary inspection. The veterinarian checked for individual pit-tags and tattoos to identify potential owned cats. The behavioural profile of the cat was then evaluated to estimate the possibility to adopt it. If adoption was impossible because the cat was too wild, the cat was euthanised after the legal guard period of four days. The euthanasia was made by intra-venial injection of pentobarbital. Kidney tissue samples were collected from each euthanised cat and stored in 70% ethanol at -80 °C until laboratory analysis. The protocol was approved by the CYROI institutional ethical committee, certified by the French Ministry of Higher Education and Research (NoAPAFIS#6916-20151 00213267087 v.6). A total of 158 feral cats were trapped including 87 males, 67 females and 4 indeterminate (Table 1). None of them was identified as an owned or adoptable cat.

Microsatellite genotyping

Total DNA was extracted from a small piece of kidney tissue using the QIAmp Blood and Tissue kit (Qiagen, Hilden, Germany). Genotyping was conducted for 10 polymorphic microsatellite loci (described in Menotti-Raymond and O'Brien 1995 for Fca43 and Fca96, Menotti-Raymond et al. 1999 for Fca31, Fca69, Fca76, Fca173, Fca275, Fca441 and Fca531 and Menotti-Raymond et al. 2003 for Fca1027) on DNA extracts from 158 individuals. A 3-primer PCR approach, using a M13 tail for the forward primer, was used for microsatellite loci amplification following Schuelke (2000).

Four different dyes (6-FAM, PET, VIC, NED) were used for the universal M13 forward primer to enable fragment analysis multiplexing. Simple PCR amplifications were performed using a GeneAmp PCR System 9700 (Applied Biosystems, Waltham, Massachusetts, USA) in 10 µl reaction volume containing 5 µl of MasterMix Applied 2× (Applied Biosystems, Waltham, Massachusetts, USA), 0.3 µl of the forward primer with M13 5'-tail (1 µM), 0.3 µl of the reverse primer (10 µM), 0.3 µl of dyes (10 µM), 2.1 µl of sterile deionised water and 2 µl of genomic DNA (20–40 ng/µl). PCR amplifications were carried out under the following conditions: an initial denaturing step at 95 °C for 5 min, followed by 40 cycles of 95 °C for 30 sec, 56 °C for 30 sec and 72 °C for 30 sec and a final elongation at 72 °C for 20 min. Up to four different simplex PCR plates, each with a different dye, were mixed and PCR product sizes were determined, using a 3730XL DNA analyser (Applied Biosystems, Waltham, Massachusetts, USA) at the Gentyane platform (Clermont-Ferrand, France) and were sized with LIZ(500) standard using GeneMapper (Applied Biosystems, Waltham, Massachusetts, USA).

Genetic diversity

Evidence of null alleles, large-allele dropout and stutter peaks in all microsatellites was examined using MicroChecker 2.2.3 (Van Oosterhout et al. 2004). Each locus-pair combination was tested for linkage disequilibrium with GenePop 4.7.5 (Rousset 2008). The *P*-values were corrected using the Benjamini and Yekutieli (2001) method for multiple comparisons (Narum 2006). The mean observed number of alleles per locus (AL) and the number of private alleles per area (AP) were computed using GenAlEx 6.5 (Peakall and Smouse 2012). Allelic richness (AR; El Mousadik and Petit 1996), adjusted for discrepancies in sample size by incorporating a rarefaction method as implemented using FSTAT 2.9.3 (Goudet 2001), was used to make comparisons of the mean number of alleles amongst areas. The means of allelic richness amongst areas were compared using pairwise Wilcoxon's signed rank tests with Bonferroni correction. Observed heterozygosity (H_O), unbiased expected heterozygosity estimated according to Nei (1978) (H_E) and Wright's F-statistics (F_{IS}) according to the method of Weir and Cockerham (1984) were calculated for all and each population using GenAlEx 6.5 (Peakall and Smouse 2012). Deviations from Hardy-Weinberg equilibrium (*HWE*) were tested for each of the six areas using the package pegas 0.13 (Paradis 2010) using R 3.2.0 (R Core Team 2021), with the exact test based on 10^3 Monte Carlo permutations.

Genetic differentiation and structuring

Assignment tests, based on multi-locus microsatellite genotypes, were evaluated using two different clustering approaches. First, we used a Bayesian genotype clustering procedure in STRUCTURE 2.3.3 (Pritchard et al. 2000). The admixture model was used with the LOCPRIOR setting, which considers sample location and allows structure to be detected when genetic structure is weak or when the number of loci is small (< 20; Hubisz et al. 2009). The r-index was also used to determine the relevance

of the sampling location (LOCPRIOR), with low values of r indicating that sampling locations are informative to the overall model (Falush et al. 2003). Correlated allele frequencies were assumed (Pritchard et al. 2000). For each value (1–10) of the number of independent genetic clusters (K), we ran 10^6 iterations 10 times (after a burn-in of 10^5 steps). For choosing the optimal number of clusters, two criteria were used; the log likelihood given K (L(K); Pritchard et al. 2000) and the second-order rate of change of mean log-likelihood (ΔK; Evanno et al. 2005). Both criteria were calculated using STRUCTURE HARVESTER online Web server (Earl and vonHoldt 2012). CLUMPAK software (Kopelman et al. 2015) was used to find the optimal individual alignments of replicated cluster analyses and to visualise the results.

Population structure was also explored by integrating spatial coordinates of samples using a Bayesian model executed in a Markov Chain Monte Carlo, as implemented in the R package Geneland 4.0.5 (Guillot et al. 2005, 2008). The geographical information was used to detect spatial delineation of genetic discontinuities, where the number of area units is treated as an unknown parameter. We ran the MCMC ten times independently to verify the consistency of the results. We used K from 1 to 10, 10^5 iterations with 100 burn-in generations, an uncertainty attached to spatial coordinates fixed to 200 m (i.e. the precision of our sample locations) and the maximum number of nuclei in the Poisson–Voronoi tessellation fixed to 300. The analysis was run with correlated allele frequency models, true spatial and no null allele models. Finally, all runs were examined for consistency.

Genetic differentiation amongst all pairs of areas was assessed by calculating pairwise F_{ST} values following Meirmans (2006) and pairwise Nei's G'_{ST} distances (Nei 1978). Statistical significance was tested by 10^4 permutations of genotypes amongst areas under Bonferroni's correction, using GenoDive 3.04 (Meirmans and Van Tienderen 2004).

Pairwise genetic and geographic distances amongst sampling locations were used to test patterns of isolation by distance (IBD) using a Mantel test (Mantel 1967). We used the scaleGen function in adegenet 2.1.3 package (Jombart 2008) to calculate the Euclidean genetic distances amongst samples. Euclidian geographical distances between each pair of samples were calculated. The significance of the correlation coefficient between sample pairs was estimated using a Mantel test with 10,000 randomisations in R. In addition, we repeated IBD analyses using only the subset of natural areas to investigate the effect of geographic distance of Grande Anse peri-urban area from other areas, which might disproportionately contribute to IBD patterns.

Estimates of recent gene flow

To determine possible source populations that could be targeted for control (Rollins et al. 2006), we estimated recent migration rates amongst areas using two methods. First, we used Bayesian assignment tests with BIMr 1.0 (Bayesian Inference of Migration rates, Faubet and Gaggiotti 2008). BIMr infers the proportion of recent immigrants in a population from their genotypes and calculates corresponding asymmetrical

migration rates amongst pairs of populations. BIMr determines recent migration even amongst weakly-differentiated populations (i.e. $F_{ST} > 0.01$) with unequal sample sizes (Faubet and Gaggiotti 2008). Due to overlapping generations in feral cats, BIMr estimates were interpreted as a relative index of recent gene flow rather than a precise estimate of gene flow in the previous generation. A burn-in period of 20,000 iterations followed by 10^5 iterations for each run was used. The default values were used for all other parameter settings. Migration rate estimates were obtained by choosing the run with lowest Bayesian deviance, measured by the assignment values (Dassign; Faubet and Gaggiotti 2008). Posterior mean and mode migration rates and 95% high density predictive interval (HDPI) were estimated using the package HDInterval (Kruschke 2011) in R.

Estimates of recent migration rates and approximate 95% confidence interval (CI) were also explored by the Bayesian approach as implemented in BayesAss 3.0.4 (Wilson and Rannala 2003). Five runs were first performed by changing the number of seeds (s = 10, 100, 500, 750 and 1000) to obtain a suitable convergence. The number of iterations was 10^6, of which 10^5 were burn-in and the sampling frequency was 100. Mixing parameters were 0.6 for allele frequencies, 0.9 for inbreeding coefficients and 0.5 for migration rates. The final run consisted of the same mixing parameters and 100 numbers of seeds.

Spatially explicit capture-recapture study

CMR data of feral cats were obtained during a single season of camera trap survey at Maïdo (Fig. 1C). This site was selected for: (i) the presence of scats and direct observations of feral cats, (ii) its proximity to a monitored Barau's Petrel colony (about 5 km) where feral cat predation is known to occur (Faulquier et al. 2009), (iii) the proximity of trails which were supposed to maximise the feral cat detection probability (Meek et al. 2014; McGregor et al. 2015) and (iv) the technical feasibility. We deployed and geo-referenced with GPS (Garmin 64 s; 5 m accuracy) 20 camera-traps (9 Scoutguard-MG882K-12mHD, 10 Bushnell Trophy Cam HD and 1 Reconyx HC600 Hyperfire) from 17 February to 25 April 2016 (68 days). Camera-traps were first placed along trails (17 Feb – 23 March), then under vegetation cover (23 March – 25 April). This study period encompassed the second half of the chick rearing and the beginning of the fledging period of Barau's Petrels. The mean distance ($\pm$ sd) between cameras was 2,114.0 $\pm$ 1,273.0 m (min = 49 m, max = 5,626 m). Neither bait nor lure was used, to maintain homogeneous detection probabilities. Devices were set using a high-sensitivity trigger to capture three images per event at rapid-fire interval (0.13 s), with no delay between trigger events, to maximise feral cat identification. During the first week, half of the capture stations were equipped with two cameras placed on the opposing side of trails to capture both flanks of passing animals. Each observed feral cat was identified, based on natural marking such as spots, stripes and ocelli on both sides when possible (Bengsen et al. 2012; McGregor et al. 2015; Lavery et al. 2020; Palmas et al. 2020). A sampling occasion lasted one day (24 h, hereafter named "trap-night";

Otis et al. 1978; Wang and Macdonald 2009). For each sampling occasion, individuals were photographed ("captured"), identified ("marked") and "released". All feral cats previously identified and re-sighted were considered as a recapture. A capture event was defined as all pictures of unique individuals within a 30-min time period (Di Bitetti et al. 2006). Cameras were checked every 10 days to download data from memory cards and replace batteries. No feral cats were captured for the genetic study in the CMR study area during and 6 months before the behavioural study. However, from September to December 2015, four feral cats were captured at 5.9 to 7.8 km from the nearest camera trap.

The trapping effort (in trap-nights) was calculated by adding for each camera the number of days where each camera was active over the study period. The capture efficiency (in number of capture events/100 trap-nights) was calculated by dividing the number of feral cat capture events for all cameras divided by the total trapping effort and multiplied by 100 (Palmas et al. 2020).

Since we designed a short study period (to avoid emigration, immigration or mortality) and we did not consider kitten pictures in the dataset (to avoid recruitment), we applied SECR models that require a demographically closed population. These models assume no emigration or immigration, no mortality and no recruitment during each trap session (Otis et al. 1978; Efford 2004). The matrix of spatially explicit histories of capture-recaptures was constructed for each feral cat by linking each capture of each individual with the coordinates of the camera and with the occasion. Each camera was associated with a spatial covariate (trail vs. under vegetation) to check if trap location affects the detection probability. Data analyses were performed using the SECR package (Borchers and Efford 2008; Efford et al. 2009) in R 4.0.3. First, we estimated the mean maximum distance moved (MMDM) by the individuals between captures. Then, we implemented SECR models. The trap detector type « count » was chosen for the analysis, allowing more than one detection per animal. A habitat mask was used with a buffer width of 3,000 m around each camera-trap (determined with the SECR package; Efford 2021), but excluding the deep cliffs considered as inaccessible for feral cats. This resulted in a sampling area of 60.55 km^2. We assumed that home ranges of feral cats were distributed following a homogeneous spatial Poisson process during the trapping period (Efford 2004; Borchers and Efford 2008; Efford et al. 2009). The half-normal detection function was selected as the most appropriate for our models. This detection function is defined by two parameters: the animal detection probability considering that the camera-trap is located at its home range centre (g0) and the movement parameter, i.e. the distance scale of the detection function (σ). Models were used to investigate the effects of camera locations (on trail vs. under vegetation) on g0 and σ. Model performances were compared using the difference in Akaike Information Criterion modified for small sample size (AICc). Each model presenting a ΔAICc < 2 was considered a competing best model. Finally, based on the estimates of the best model, we determined: (1) the site-specific population density D; in number of cats/km^2 and (2) the home range (HR$_{95}$) and core area (HR$_{50}$) in km^2 of feral cats (see Ringler et al. 2014).

Results

Genetic diversity

No null alleles, large-allele dropout nor stutter peaks were detected for the 10 microsatellite loci. The percentage of missing data was 1.58%. Linkage disequilibrium amongst loci was detected for four of the 45 loci pairs ($P < 0.05$), but no significant linkage disequilibrium was observed amongst any of the loci after the Benjamini and Yekutieli (2001) correction for multiple tests, suggesting that all loci were independent. The mean allelic richness (AR), based on a minimum sample size of 15 individuals, ranged from 4.7 (Maïdo) to 6.4 (Cilaos) alleles per locus and was relatively similar amongst areas, except for the less variable Maïdo area (Table 1). All areas contained one (Maïdo) to four (Makes, Dimitile) private alleles (Table 1). Observed heterozygosity for Maïdo (H_O = 0.58) was similar to Grand Bassin, but it was lower than all other areas (Ho range 0.65–0.74; Table 1). Deviations from HWE were not significant for all areas (all $Ps > 0.05$). The raw microsatellite genotypes of the 158 individual feral cats are available in the supporting information (Appendix 1).

Genetic structuration and gene flow

Clustering of microsatellite genotypes using STRUCTURE analysis indicated that mean values of the r-index used to determine the relevance of the sampling location in the clustering analysis was low (0.31 ± 0.14), suggesting that sampling locations are informative to the model. Analysis clearly showed that the best-supported model contained three genetic clusters (maximum value of Evanno's likelihood at K = 3, maximum value of L(K) and minimum standard deviation of L(K) at K = 3, Appendix 2). The first genetic cluster was almost exclusively detected for samples from Maïdo (91% of the genetic pool from Maïdo samples). The second cluster was detected amongst samples from Dimitile (77% of Dimitile's samples), Grand Bassin (38%) and Cilaos (25%). The third cluster was shared between Makes and Grand Bassin (more than 90% of samples), then Cilaos and Grand Bassin (about 70% of samples) and finally Dimitile (about 18% of samples; Fig. 2, Appendix 2).

Analysis using Geneland yielded a modal number of populations with a higher proportion of three putative genetic groups (K = 3; Appendix 3: Fig. A2F). The run with the highest average posterior density was selected. Sampled feral cats were clustered into five groups. Two inferred groups (part of Cilaos and Grande Anse) had very low posterior probabilities (Appendix 3: Fig. A2D and E, respectively) and the areas of these groups were already represented in groups with strong posterior probabilities (Appendix 3: Fig. A2A–C). The last three putative groups roughly corresponded to the areas defined using the topography of Réunion Island (Appendix 3: Fig. A2A–C); Maïdo, Dimitile, and the other areas, and corresponded to the results obtained using non-spatial analysis with STRUCTURE.
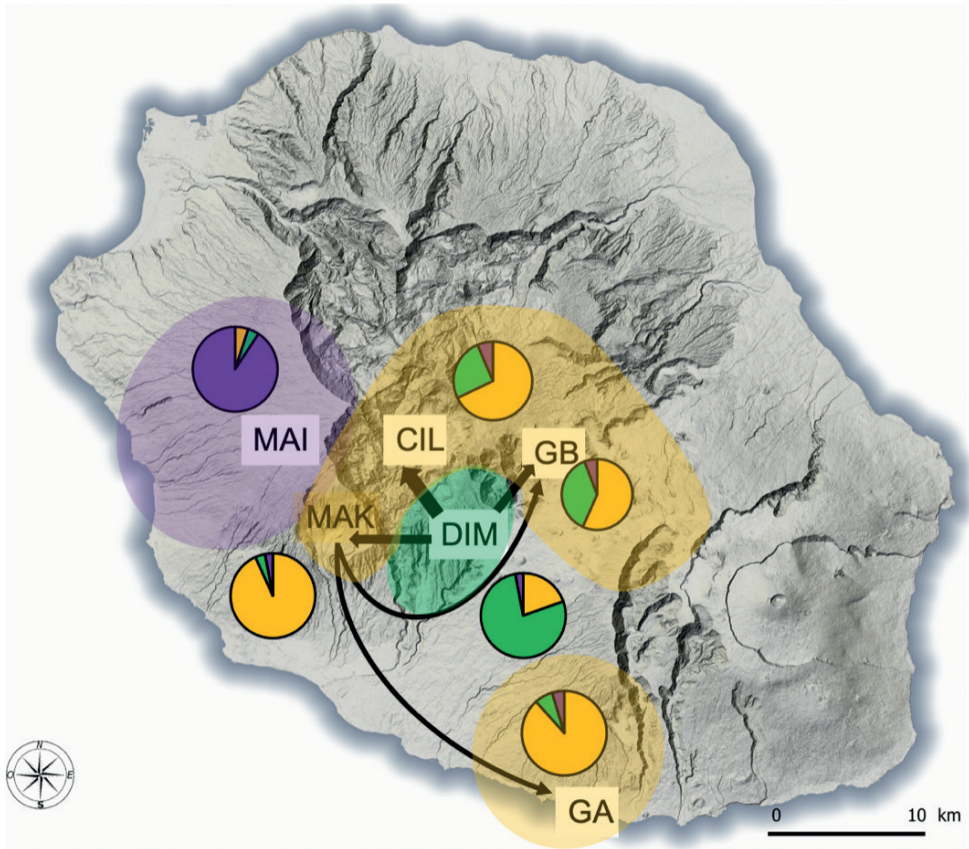
Figure 2. Distribution of microsatellite clusters based on Bayesian clustering analysis using STRUC-TURE (pies) and Geneland (coloured areas) and map of the migratory pathways suggested by BIMr and BayesAss (black arrows, the thickness is proportional to the amount of gene flow) of the feral cats (N = 158 individuals) in Réunion Island, 2015-2016. Area codes: MAI for Maïdo, CIL for Cilaos, MAK for Makes, GB for Grand Bassin, DIM for Dimitile and GA for Grande Anse.

Pairwise F_{ST} values ranged between 0.011 and 0.149 with a global F_{ST} of 0.026 ($P < 0.001$). The highest values were for the comparison of Maïdo to the other areas. *Nei* distances showed the same pattern. For both indexes, 8 of the 10 loci showed p-values less than 0.001. Based on the two differentiation index values, three groups were distinguishable: (1) Maïdo, (2) Dimitile and (3) all other areas, suggesting an isolation of Maïdo particularly and Dimitile to a lesser extent, as previously suggested by the clustering analysis (Appendix 4).

Genetic distance amongst individuals showed no significant relationship with geographic distance either at the global scales (Mantel r-test, $P = 0.189$) or after excluding Grande Anse (Mantel r-test, $P = 0.385$).

Recent mean migration rates determined using BIMr ranged from nearly zero amongst most pairs of areas to nearly 0.05 between Grand Bassin and Dimitile

(Appendix 5). Based on non-overlapping 95% HPDIs, we only recorded significant asymmetric dispersal between Dimitile and Cilaos, with clearly highest migration from Dimitile to Cilaos (Appendix 5). Globally similar results were obtained using Bayes-Ass, suggesting asymmetric dispersal between these two areas. Moreover, all the mean values of recent migration rate were clearly higher compared to those from BIMr and six values had a confidence interval not including zero (Appendix 5), suggesting the migratory pathways presented in Fig. 2.

Camera trapping and SECR results

During the camera-trapping survey, we collected 41,905 pictures including 376 (0.9%) pictures of feral cats. All photographed feral cats were identified and included in the study. Ten individuals were identified. There was no picture capturing more than one feral cat simultaneously (see details in Table 2).

Table 2. Summary of the results obtained from both camera trapping sessions of feral cats, 2016, Réunion Island. For each session, the trapping effort corresponds to the product of the number of occasions per session and the number of active cameras. The capture efficiency is the number of detections divided by 100 trap-days.

Location	Period (days)	Date	Number of cameras	Trapping effort (trap-day)	Number of pictures	Number of cat pictures (%)	Total number of cats	Total number of recaptures	Capture efficiency (detections/100 trap-days)
Trail	35	17 Feb – 23 Mar	20	550	21,524	114 (0.5%)	6	34	7
Vegetation	33	23 Mar – 25 Apr	20	532	20,381	262 (1.3%)	8	12	4
	68	17 Feb – 25 Apr	20	1082	41,905	376 (0.9%)	10	50	5.5

In total, we obtained 60 feral cat detections between 17 February and 25 April 2016, corresponding to 10 captures and 50 recaptures for 10 individuals. For cameras on trails, we obtained six captures and 34 recaptures of five individuals at 14 of the 20 cameras. When camera traps were placed under vegetation, eight feral cats were first detected (including four feral cats previously identified on trails) and five of them were recaptured (12 detections) at eight of the 20 cameras (Table 2; Appendix 6). The global trapping effort was 1,082 trap-nights with a capture efficiency of 5.5 detections/100 trap-nights. The mean maximum distance moved (MMDM $\pm$ se) by feral cat was 1,926 $\pm$ 589 m. We tested the effect of camera types and the linear time trend over occasions on the detection probability g0. No effect was detected.

The model with the greatest support was the null model (Table 3). This model had a maximum detection probability at each camera trap (g0) of 0.06 (95% CI [0.03; 0.09]) and a spatial scale of movement (σ) of 971 m (95% CI [791; 1,193]; Appendix 7). The estimated population density of feral cats was 0.25 feral cats/km² (95%CI [0.12; 0.47]). The mean home range was estimated at 15.0 km² (HR_{95}) with a core area of 2.5 km² (HR_{50}).

Table 3. Model selection testing the spatial effect of camera trap location (on trail vs. under vegetation) on the detection parameters (g0 and σ) on Réunion Island, 2016. D is the density, g0 is for the probability of feral cat detection at the home range centre and σ is the scale parameter of the detection function. Models are ranked by their AICc values. The best model (ΔAICc < 2) is in bold.

	D	g0	σ	Npar	AICc	ΔAICc	W (%)
1.	~ 1	~ 1	~ 1	**3**	**639.25**	**0.00**	**76**
2.	~ 1	~ location	~ 1	5	641.60	2.35	24
3.	~ 1	~ 1	~ location	5	649.70	10.45	0
4.	~ 1	~ location	~ location	7	680.84	41.59	0

Npar: number of estimated parameters, AICc: Akaike Information Criterion modified for small sample size, ΔAICc: difference in AICc values in relation to the most parsimonious model, W: model AICc weight.

Discussion and conclusion

Genetic diversity, structure and gene flow in feral cat populations

The genetic diversity of feral cats on Réunion Island is similar to that observed on cat populations recently introduced on other islands (Kerguelen, Pontier et al. 2005; Hawai'i, Hansen et al. 2007; Christmas & Cocos Island, Spencer et al. 2016). It is also similar to the diversity observed in non-insular contexts, in isolated populations with low dispersal rates (France, Say et al. 2003; Australia, Cowen et al. 2019). It is assumed that most feral cats of Réunion Island are descendants of cats introduced from France (Dreux 1990). Interestingly the genetic diversity of feral cats on Réunion Island is lower than that observed in Europe (Pierpaoli et al. 2003), which may be explained by a founding effect leading to a genetic drift as expected in such isolated contexts (Slatkin and Excoffier 2012; Bélouard et al. 2019).

Microsatellite analysis and Bayesian clustering analysis suggested significant structuring amongst studied populations. Genetic structure was strong compared to populations of Hawai'i (three sampled sites, $F_{ST} < 0.05$; Hansen et al. 2007) and the Kerguelen Archipelago (four sampled sites, $F_{ST} \leq 0.09$; Pontier et al. 2005). We found three genetic clusters amongst which, one was observed only at our highest sample site, Maïdo. This suggests very low gene flow between this site and other lower populations. The isolation of Maïdo was also supported by a lower allelic richness compared to other areas, as expected in isolated populations (Frankham 1996; Peter and Slatkin 2015). This pattern is probably due to the very rough topography of the island. Indeed, Maïdo is separated from other sites by a vertical cliff of more than 1 km, which probably represents a geographical obstacle for feral cat dispersal.

The second and third genetic clusters were detected in the five other areas (Dimitile, Cilaos, Grand Bassin, Makes, Grande Anse, Fig. 2). Although differentiation indexes indicated an isolation of Dimitile, feral cats sampled in this area were mostly assigned to a genetic group that was also detected in the four other areas. The low F_{ST} and Nei distance estimates, coupled with a lack of isolation by distance, suggest that Grande Anse, Makes, Cilaos and Grand Bassin areas were weakly isolated from each other, despite large geographical distances between Grande Anse and the others (minimum of 20 km). This result suggests either or both natural and human-mediated

dispersal of feral cats amongst these areas. The human-mediated dispersal hypothesis is reinforced by the lack of genetic isolation through geographical distances, which would be expected if a progressive colonisation process occurred amongst neighbouring sites (Kimura and Weiss 1964; Slatkin 1993).

Density and home range of feral cats

Comparing home range of feral cats from the literature is challenging because of the large diversity of the methods used, ranging from GPS tracking to SECR modelling (Jones and Coman 1982; Nogales et al. 2004; Bengsen et al. 2012; McGregor et al. 2015). However, our results suggest that feral cats at Maïdo are present at low density (0.25 feral cat/km^2) with large home ranges (15 km^2). To our knowledge, the only cases where feral cats live in such low densities in the tropics are also in mountainous habitats (Hawai'i, Smucker et al. 2000; Goltz et al. 2008). This suggests that some bottom-up limitation due to low densities of prey are occurring in these extreme habitats, resulting in a low carrying capacity for feral cats (see Liberg et al. 2000; see Bengsen et al. 2016). Furthermore, in the case of feral cats living at seasonal seabird breeding colonies (which is the case of both petrel species), the carrying capacity of their habitats fluctuate in relation to the phenology of the petrels.

This space use strongly contrasts to that observed in a low altitude area of Réunion Island transformed by human activities. A recent study has shown that, at sea level, cat density can reach 27 ± 2 cats/km^2 (Choeur 2021), with an average home range of 0.12 km^2 (Choeur et al. 2022). This peri-urban habitat is characterised by extremely abundant food resources for cats including anthropogenic food wastes, supplemental feeding and introduced prey such as mice, rats and lizards.

Management implications and perspectives

The combined results of the genetic and behavioural studies of feral cats indicate that, in mountainous habitats of Réunion Island, such as Maïdo, harbouring Barau's Petrel colonies, cats are likely to be isolated and at low density. This is favourable for long term feral cat control. The genetic isolation implies there might be a low re-colonisation rate from surrounding cat populations (e.g. Lieury et al. 2015; Millon et al. 2019; Palmas et al. 2020).

In terms of feral cat control optimisation, the CMR study produced results that can be used to design the operations. First, in order to increase the number of feral cats exposed to control devices while minimising the number of devices, we propose to use the estimated sigma to optimise the spatial arrangement of the trapping grid (Goltz et al. 2008; Bengsen et al. 2012). In our case, with such an arrangement, each trap should be set every 950 to 1,000 m. This method minimises the number of cages to deploy (which minimises the human effort) while maximising the chance of a cat encountering at least one cage in its home range. Second, we suggest deploying traps near trails as the maximum detection probability has no variation between trail and vegetation cover for this site. This grid design presents the advantage of reducing the workload and

the time spent in the field by facilitating the access and maintenance of the traps. Of course, this recommendation is limited to habitats that have trails nearby. This design of device deployment can also be used after an intensive cat control to deploy camera traps for early detection of any re-invasive cats.

In addition to these recommendations, we propose trapping operations be conducted before the breeding season of Barau's Petrels (i.e. in austral winter, July and August, which correspond to the period when food availability for cats is the lowest, because of the absence of petrels). We also recommend the implementation of an early detection protocol, based on a network of camera traps to detect any re-invasion by cats and to respond with appropriate control actions.

For other sites located at lower altitudes, the absence of genetic isolation indicates strong connectivity between feral cat populations and, thus, a high risk of re-invasion after a feral cat control. Other strategies should be adopted to prevent or limit feral cat impact: 1) permanent feral cat control at colonies and in their vicinity and 2) predator-proof fences around bird colonies (Smith et al. 2020). However, the technical feasibility and financial costs of such operations may limit their implementation on the Island.

Feral cats are known to also prey upon other introduced mammals, such as rats or mice (Faulquier et al. 2009). Thus, in theory, a control of cats may result in the release of these prey, which in turn may impact birds, the so-called "mesopredator release effect" (Courchamp et al. 1999a). However, for such a release to occur, rat or mice populations must be controlled by feral cat predation (top-down control) rather than by their resources (bottom-up control; Courchamp et al. 1999a; Russell et al. 2009; Dumont et al. 2010). In the tropical context, it has been shown that rat and mice populations are controlled mostly by their resources through rain seasonality (Russell et al. 2011), which reduces the risk of a meso-predator release in case of feral cat control (Russell et al. 2011; Ringler et al. 2015). Furthermore, for long-lived animals, like seabirds, the population growth rate is more sensitive to change in adult survival than in breeding success (Le Corre 2008; Russell et al. 2009; Dumont et al. 2010). Feral cats prey upon adults and fledglings, whereas rats prey exclusively on eggs or chicks (Faulquier et al. 2009; authors' comm. pers.). Thus, even if rat population were released as a consequence of cat control, this would have less impact on the population growth of petrels than the impact of cats. Thus, we recommend to implement cat control at petrel colonies wherever possible.

Another more general recommendation would be to improve the public awareness and sensitisation at the scale of the entire island to stop human-mediated displacement of cats, to stop abandonment of domestic cats or kitten in the wild and to sterilise as many domestic cats as possible (Dias et al. 2017; Russell et al. 2018; Choeur et al. 2022).

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Appendix I

Table A1. Raw microsatellite genotypes for 158 individuals of feral cats from six geographical areas, in Réunion Island, 2015–2016. Area codes are described in Fig. 1.

Samples	Area	531	531	173	173	43	43	1027	1027	76	76	441	441	96	96	69	69	275	275	31	31	X	Y
LP0004	CIL	137	143	137	145	148	148	258	258	152	152	174	182	226	230	110	124	156	156	251	253	339151	7664054
LP0005	CIL	143	145	145	147	148	150	258	258	152	152	174	182	236	244	110	110	156	158	235	255	338905	7664691
LP0008	CIL	137	141	137	137	136	148	258	262	150	152	174	182	226	226	110	126	0	0	235	251	338905	7664691
LP0009	CIL	133	133	137	137	148	150	262	262	154	154	170	182	238	244	110	128	156	160	235	235	342891	7664514
LP0012	CIL	133	133	137	145	148	148	256	258	152	152	174	178	242	244	110	126	156	156	235	251	342962	7664490
LP0013	CIL	133	133	141	149	148	148	258	258	150	152	174	182	230	244	110	126	156	162	235	239	342912	7664572
LP0014	CIL	137	139	137	139	148	148	258	258	150	150	174	182	226	244	110	126	156	156	251	251	339151	7664054
LP0016	CIL	145	145	125	131	140	150	250	258	150	152	174	186	226	226	110	126	156	156	255	255	341653	7663152
LP0019	CIL	133	133	137	149	148	150	258	262	152	154	174	182	242	244	110	126	156	156	235	239	342891	7664514
LP0020	CIL	143	147	137	145	148	148	258	268	138	154	174	182	226	226	110	126	154	156	235	235	338669	7662701
LP0040	CIL	133	137	139	149	148	148	258	262	150	154	182	182	0	0	110	110	156	156	239	239	342891	7664514
LP0041	CIL	143	143	141	141	148	148	258	258	152	152	178	182	236	244	110	118	156	158	235	235	343834	7664954
LP0089	CIL	133	143	125	125	138	148	268	268	148	152	174	174	226	238	110	128	156	164	243	255	343614	7660602
LP0092	CIL	133	147	137	145	148	150	262	262	154	154	182	182	226	226	124	124	0	0	235	243	341651,884	7663464,38
LP0094	CIL	133	147	137	143	150	150	258	262	138	154	174	174	226	238	118	124	156	164	249	255	341651,884	7663464,38
LP0120	CIL	133	143	143	145	138	148	258	258	150	152	174	182	232	244	110	128	0	0	253	253	343614	7660602
LP0125	CIL	137	143	137	147	148	150	258	258	144	154	178	182	234	244	118	126	156	156	235	235	343614	7660602
LP0146	CIL	133	133	143	147	148	148	262	268	148	152	182	194	226	232	124	126	156	158	255	255	341826	7660378
LP0150	CIL	143	143	137	145	148	150	256	256	148	152	174	186	232	244	126	126	162	162	253	253	342568	7660656
LP0153	CIL	143	143	145	145	142	150	258	258	124	152	174	178	226	244	110	110	156	158	253	253	341874	7660450
LP0181	CIL	133	143	143	145	140	148	258	262	144	152	182	182	226	230	110	126	152	156	235	235	342917	7663413
LP0182	CIL	143	143	125	141	148	154	258	258	152	152	178	186	226	226	110	126	156	170	243	249	340204,556	658931,34
LP0006	DIM	133	133	141	145	148	148	262	258	152	152	186	186	226	226	110	126	156	158	235	235	343194	7656559
LP0007	DIM	133	143	125	145	148	148	258	262	152	152	174	174	244	244	110	126	162	162	255	255	344251	7656100
LP0010	DIM	137	145	145	145	148	150	262	258	152	152	174	182	226	226	122	126	162	162	251	255	342242	7655286
LP0011	DIM	137	137	145	145	148	150	258	258	152	152	186	186	232	238	124	126	158	158	235	251	345322,17	657642,09
LP0028	DIM	133	143	143	143	148	150	256	258	152	152	174	174	226	236	110	126	156	158	235	253	344056,112	658441,64
LP0029	DIM	137	147	145	145	148	152	258	260	152	152	174	174	226	226	110	126	156	158	255	255	344251	7656100
LP0032	DIM	143	143	141	141	152	152	258	258	152	152	178	182	226	232	110	126	156	156	235	249	343844	765518

Samples	Area	531	531	531	173	173	43	43	1027	1027	76	76	441	441	96	96	69	69	275	275	31	31	X	Y
LP0034	DIM	137	143	137	147	145	138	148	256	258	152	152	174	178	226	236	126	126	156	156	235	255	343974	7655595
LP0036	DIM	137	143	137	145	137	148	148	258	258	152	152	182	186	232	236	124	126	156	158	235	253	345322,17	7657642,09
LP0046	DIM	133	137	125	145	125	148	148	258	258	152	154	174	186	232	236	110	128	156	162	235	253	345311,993	7660541,02
LP0052	DIM	143	143	125	145	125	148	150	258	258	152	154	174	182	226	244	110	122	156	158	235	235	344025	7656863
LP0053	DIM	133	143	125	145	125	148	148	256	258	152	154	174	182	226	230	122	124	162	170	235	237	344251	7656100
LP0056	DIM	139	145	137	137	137	140	150	258	262	152	152	178	178	232	232	110	124	156	160	235	253	343953	7655725
LP0057	DIM	143	145	143	143	143	148	148	258	258	152	154	174	178	226	236	124	128	156	158	235	253	343660	7656552
LP0058	DIM	147	147	145	145	145	148	150	256	258	0	0	174	178	236	238	114	118	156	158	243	251	344001	7655866
LP0060	DIM	133	143	145	145	145	148	150	256	258	152	152	174	174	0	0	124	126	158	170	235	253	344109	7656689
LP0072	DIM	145	145	145	145	145	148	150	258	262	152	154	182	182	236	244	110	110	0	0	235	255	344551,001	7657867
LP0074	DIM	143	145	145	145	145	148	148	256	258	152	152	174	174	238	240	110	124	156	158	251	251	345312,053	7660387,19
LP0075	DIM	137	145	145	145	145	148	150	256	258	152	154	182	186	232	236	124	128	156	158	235	253	344064,189	7658444,27
LP0076	DIM	137	143	145	145	145	148	150	258	260	152	154	178	186	226	236	114	126	156	158	235	251	344553,72	7657861,89
LP0085	DIM	133	143	139	139	139	148	150	258	262	138	152	174	178	242	244	126	130	156	160	235	255	345452,189	7660727,29
LP0086	DIM	143	143	137	137	137	140	148	258	260	152	152	174	178	226	236	110	110	156	162	255	255	344056	7653594
LP0087	DIM	137	145	125	147	125	148	152	260	262	152	152	174	174	226	226	120	122	156	162	255	255	344056	7653594
LP0088	DIM	137	143	141	147	141	148	148	258	258	0	0	174	174	226	232	124	126	158	158	235	235	344086	7653441
LP0096	DIM	133	145	139	139	139	148	148	258	262	152	152	170	186	226	236	118	120	156	158	235	235	344064,189	7658444,27
LP0103	DIM	133	145	125	145	125	148	148	256	258	152	152	178	186	234	236	110	124	158	162	235	235	343762	7654114
LP0109	DIM	137	137	145	145	145	148	152	258	258	152	152	174	182	242	244	110	110	158	170	235	251	343711	7652783
LP0110	DIM	137	137	141	141	141	148	148	258	260	152	152	174	174	226	226	124	126	162	162	235	255	344401	7653628
LP0114	DIM	133	147	145	145	145	138	148	260	262	152	152	174	174	226	236	110	124	156	162	235	255	343662	7653716
LP0115	DIM	137	137	143	147	143	138	148	258	268	138	152	174	182	236	236	128	126	156	162	251	255	344169	7653841
LP0117	DIM	143	143	139	147	139	148	150	258	262	152	152	178	182	226	236	110	110	156	158	249	257	344400	7653782
LP0119	DIM	143	145	145	145	145	148	150	258	258	152	154	186	186	226	238	110	126	156	158	235	253	343946	7654171
LP0122	DIM	143	143	141	145	141	148	150	258	260	152	152	174	182	226	244	124	128	156	158	235	253	343488	7654539
LP0123	DIM	137	145	145	141	145	148	152	258	258	152	152	178	178	232	236	110	126	158	162	249	235	343745	7654812
LP0124	DIM	133	143	143	147	143	148	150	258	258	152	152	174	174	226	236	110	124	156	158	235	235	344169	7653841
LP0133	DIM	137	145	125	145	125	148	152	256	262	150	152	178	182	232	244	110	110	162	170	235	235	343745	7654812
LP0138	DIM	143	143	145	145	145	148	148	256	258	152	152	174	174	226	238	110	122	154	156	235	235	344400	7653782
LP0144	DIM	143	143	145	125	145	148	150	256	258	0	0	174	174	226	244	122	118	156	162	235	235	343776	7654707
LP0147	DIM	143	143	141	145	141	148	148	258	258	152	152	174	182	226	244	118	110	162	170	235	253	343711	7652783
LP0151	DIM	143	143	145	141	145	148	148	246	262	152	154	174	182	226	226	110	110	156	158	251	253	343660	7655007
LP0158	DIM	137	145	145	145	145	148	150	258	258	0	0	174	186	232	238	124	126	156	158	235	251	344901,611	7657760,99

Samples	Area	531	531	173	173	43	43	1027	1027	76	76	441	441	96	96	69	69	275	275	31	31	X	Y
LP0164	DIM	143	145	145	145	150	154	262	268	130	150	182	182	226	234	124	126	156	158	255	255	343899	7654209
LP0165	DIM	143	145	141	147	148	150	246	258	138	152	174	182	202	232	124	126	156	156	235	243	344056	7653594
LP0175	DIM	137	143	145	147	148	148	256	260	150	152	178	182	236	238	110	124	156	158	0	0	343776	7654707
LP0177	DIM	143	145	141	147	148	150	258	258	150	152	174	182	226	236	110	114	156	192	243	249	344905,252	7657584
LP0179	DIM	143	147	141	145	148	148	258	258	150	154	174	174	226	238	114	124	156	158	243	251	343427	7655879
LP0042	GA	143	143	145	147	148	148	256	258	148	152	178	182	226	232	124	124	156	156	235	243	350858,198	7636083,08
LP0043	GA	133	139	145	147	148	148	246	262	150	154	174	174	226	226	122	124	158	158	235	255	350858,198	7636083,08
LP0045	GA	133	133	141	145	148	148	258	262	138	152	174	178	230	244	124	126	162	166	235	255	350858,198	7636083,08
LP0047	GA	143	145	145	145	148	150	258	262	146	150	178	178	226	230	120	128	156	156	235	255	350858,198	7636083,08
LP0048	GA	137	143	141	143	138	150	258	258	152	152	182	186	230	238	110	126	156	162	235	251	350858,198	7636083,08
LP0049	GA	139	143	143	143	140	142	254	258	132	150	174	178	226	240	124	126	158	158	243	243	350858,198	7636083,08
LP0050	GA	143	143	147	147	150	150	258	258	152	152	182	182	0	0	126	126	156	158	235	235	350858,198	7636083,08
LP0064	GA	143	145	143	147	140	154	258	258	146	152	174	178	226	226	120	124	156	156	249	251	350858,198	7636083,08
LP0065	GA	143	143	125	145	142	148	256	258	152	152	178	178	232	236	124	126	156	156	243	249	350858,198	7636083,08
LP0067	GA	143	147	143	145	138	148	254	268	152	152	162	178	228	230	110	110	156	158	235	245	350858,198	7636083,08
LP0070	GA	133	143	125	141	138	150	258	258	152	152	0	0	226	236	118	120	156	162	235	245	350858,198	7636083,08
LP0071	GA	133	143	141	145	148	148	258	262	152	152	174	182	236	244	110	126	156	166	235	245	350858,198	7636083,08
LP0073	GA	133	143	125	145	154	154	258	262	152	152	178	178	226	236	110	124	156	162	239	243	350858,198	7636083,08
LP0078	GA	133	143	125	137	146	148	246	262	152	152	162	178	226	226	124	126	134	156	235	255	350858,198	7636083,08
LP0079	GA	133	143	125	145	142	150	258	268	152	152	178	182	226	226	124	126	156	156	239	243	350858,198	7636083,08
LP0080	GA	133	143	125	147	146	150	258	262	152	152	162	182	226	236	118	126	156	156	235	235	350858,198	7636083,08
LP0081	GA	143	143	143	147	138	150	254	258	148	148	178	178	230	232	120	128	156	156	235	255	350858,198	7636083,08
LP0082	GA	143	147	125	147	140	146	254	258	152	154	174	178	226	232	124	126	156	166	235	243	350858,198	7636083,08
LP0083	GA	143	145	137	145	148	148	258	258	146	152	178	182	236	236	110	126	156	162	235	255	350858,198	7636083,08
LP0084	GA	143	143	137	141	138	150	246	258	152	154	178	182	226	226	120	126	134	156	235	235	350858,198	7636083,08
LP0015	GB	143	147	137	145	148	150	256	258	152	152	178	178	226	244	110	124	164	168	235	235	348970	7658171
LP0022	GB	143	147	137	147	148	148	258	266	152	152	174	182	236	236	110	116	152	156	253	253	349484	7658622
LP0030	GB	143	143	137	145	154	154	258	258	152	152	174	174	226	244	110	110	156	156	251	251	347824	7653382
LP0051	GB	141	143	125	145	142	142	256	262	150	152	174	182	226	236	124	128	156	156	255	255	349880	7659100
LP0059	GB	143	147	147	147	148	148	256	258	152	152	162	178	236	236	110	110	156	158	235	253	349720	7658792
LP0062	GB	145	147	141	145	150	150	258	258	152	152	174	174	242	244	110	120	158	158	251	251	349608	7658645
LP0063	GB	143	145	125	147	148	148	256	258	152	152	174	182	236	244	110	126	158	162	235	245	349483	7658437
LP0111	GB	143	143	137	137	140	148	258	258	152	152	174	186	226	236	114	126	156	156	253	255	347935,24	7658920,11
LP0112	GB	145	145	131	137	148	150	258	258	152	152	174	182	236	244	110	126	156	156	235	255	349481	7658623

Samples	Area	531	531	531	173	173	43	43	1027	1027	76	76	441	441	96	96	69	69	275	275	31	31	X	Y
LP0142	GB	143	143	143	145	147	148	148	258	266	152	152	174	178	236	236	110	114	0	0	253	255	347932	7661950
LP0145	GB	143	145	145	137	147	148	148	258	258	152	152	174	174	226	244	110	110	156	156	235	255	349883	7659101
LP0148	GB	143	143	143	137	145	150	150	258	258	146	152	174	182	226	226	110	110	156	156	235	255	348429	7661450
LP0167	GB	133	143	145	145	145	0	0	0	0	150	150	178	182	232	234	114	126	156	156	235	255	348116	7655939
LP0168	GB	133	143	143	125	145	144	148	258	258	150	152	174	174	226	230	110	110	158	162	235	243	350872	7658655
LP0169	GB	133	145	145	131	141	148	150	256	258	152	152	174	174	226	246	110	110	156	158	235	255	349045	7660365
LP0183	GB	139	143	145	145	145	138	150	256	262	150	152	178	178	202	234	124	124	156	156	235	255	349824,913	7658843,05
LP0027	MAI	133	143	145	145	145	144	148	258	258	152	152	174	182	230	236	110	120	156	156	235	255	333677,367	7665497,52
LP0037	MAI	133	143	137	137	145	148	148	258	258	152	152	178	178	226	244	120	124	134	156	235	255	332819,755	7667694,89
LP0044	MAI	143	143	143	145	145	148	148	258	262	152	152	182	182	236	236	118	124	156	158	235	255	336242,024	7664056
LP0054	MAI	133	133	137	145	145	142	148	250	260	148	152	178	178	226	230	112	118	158	158	235	255	334019,61	7658585,33
LP0068	MAI	133	133	145	145	145	140	148	250	258	152	154	182	182	230	236	118	124	158	158	235	235	336340,044	7663521,99
LP0069	MAI	133	143	145	145	145	148	148	258	258	152	152	174	178	230	236	110	118	156	156	235	235	336330,619	7663582,43
LP0093	MAI	133	143	137	137	145	148	148	250	258	152	154	178	182	226	230	114	128	156	156	235	235	330867,51	7669268,36
LP0104	MAI	143	143	145	145	147	140	150	250	258	138	152	174	182	226	236	110	128	156	158	243	255	330737,89	7668030,97
LP0105	MAI	133	133	137	137	147	148	148	258	258	152	154	174	178	226	244	110	110	156	162	235	235	330404,71	7669412,77
LP0106	MAI	133	133	137	137	137	148	152	250	260	152	152	178	178	228	230	110	124	156	156	235	235	333532	7662357
LP0107	MAI	143	143	137	145	145	148	148	258	258	152	152	178	178	226	244	120	128	134	156	235	235	331878	7668510
LP0113	MAI	133	133	143	137	145	148	148	258	258	152	152	182	182	230	244	110	124	156	156	235	235	333532	7662357
LP0126	MAI	133	133	133	137	137	148	148	258	258	152	152	178	178	226	230	110	124	156	156	235	235	333532	7662357
LP0131	MAI	133	133	143	137	145	144	148	258	262	150	154	182	182	230	244	120	124	162	162	235	235	330867,51	7669268,36
LP0132	MAI	133	143	135	135	145	144	148	256	258	0	0	178	182	226	226	110	120	156	162	235	235	330537,86	7670690,27
LP0134	MAI	143	143	135	135	145	148	148	258	262	0	0	182	182	226	244	110	124	156	158	235	255	333532	7662357
LP0136	MAI	133	143	145	145	147	148	148	258	260	152	152	174	174	226	236	110	110	156	156	235	253	329934,94	7667151,6
LP0137	MAI	133	143	137	145	145	152	152	258	258	152	152	174	178	226	236	110	120	156	158	235	255	330668,26	7667098,23
LP0143	MAI	133	143	137	137	145	150	152	250	258	152	152	178	182	226	236	110	110	156	156	235	235	333609	7665097
LP0152	MAI	133	133	137	137	145	144	148	258	262	130	152	182	182	226	230	110	110	162	162	235	235	333532	7662357
LP0154	MAI	133	143	145	145	145	140	148	246	262	152	152	182	182	234	236	126	126	156	156	235	235	336242	7664056
LP0173	MAI	137	143	135	135	145	148	148	256	258	152	152	178	178	228	230	110	110	156	160	235	235	329454,482	7666797
LP0185	MAI	133	133	135	135	145	148	150	260	260	144	152	178	182	228	234	128	128	156	158	235	235	330668,259	7667098,23
LP0017	MAK	143	143	127	127	139	148	148	258	258	152	152	174	182	226	236	110	110	156	158	235	255	336631	7657360
LP0018	MAK	133	133	127	127	147	146	148	258	258	152	152	174	182	230	232	112	128	156	156	235	243	337083	7656762
LP0021	MAK	143	143	145	145	145	148	148	258	258	150	152	174	182	230	230	124	126	156	156	255	255	337476	7654771
LP0023	MAK	143	147	145	145	145	148	150	256	258	132	132	162	170	236	236	110	110	156	158	235	251	336649	7657420

| Samples	Area	531	531	173	173	43	43	1027	1027	76	76	441	441	96	96	69	69	275	275	31	31	X	Y
LP0031	MAK	143	143	137	147	148	150	258	258	150	150	178	186	226	238	110	126	156	168	239	255	335467	7658028
LP0033	MAK	133	147	145	145	140	148	258	268	152	152	182	182	226	232	110	110	156	156	235	235	336325	7657861
LP0035	MAK	133	145	125	131	138	148	256	262	150	152	182	182	226	226	110	124	154	164	243	249	336325	7657861
LP0038	MAK	133	143	139	145	148	148	258	262	150	154	178	182	226	232	110	124	156	168	235	243	337056	7656624
LP0039	MAK	143	143	137	145	138	142	256	262	138	154	174	182	0	0	110	128	156	156	235	235	335342	7658063
LP0055	MAK	143	143	145	147	148	150	258	268	152	152	174	182	226	236	110	124	0	0	235	243	334516,79	7657580,56
LP0061	MAK	143	143	137	147	148	148	258	258	148	152	172	186	226	226	110	110	156	162	243	255	336881,726	7655700,6
LP0066	MAK	143	143	137	147	138	148	258	258	150	152	172	178	226	226	110	126	156	162	243	251	337776,677	7656129,04
LP0091	MAK	143	143	137	145	138	150	258	258	150	152	178	182	226	238	126	126	156	168	239	251	334840,713	7657807,07
LP0095	MAK	133	143	131	141	148	148	262	262	132	154	174	182	234	236	118	124	134	156	235	255	336879,698	7656881,21
LP0097	MAK	143	143	145	145	142	142	246	262	152	152	182	182	232	232	124	126	156	156	235	255	335364	7658061
LP0098	MAK	133	143	131	145	148	148	258	262	150	154	174	174	226	236	110	124	156	156	235	255	336879,698	7656881,21
LP0099	MAK	133	133	127	137	148	148	246	256	150	154	178	182	226	232	114	128	156	162	235	235	337446	7656509
LP0100	MAK	133	133	137	141	138	148	256	262	130	152	174	182	224	236	110	110	134	134	235	235	337758	7656424
LP0101	MAK	139	147	127	141	148	150	256	262	152	154	174	178	0	0	110	110	0	0	235	251	336694	7655803
LP0102	MAK	133	147	137	141	148	148	262	262	152	154	178	182	230	232	110	124	156	158	235	251	335104	7658028
LP0108	MAK	133	133	137	137	138	148	258	258	152	152	162	178	236	236	110	126	134	168	235	235	336970,406	7657053,94
LP0116	MAK	143	145	141	149	148	150	258	262	152	152	172	174	202	238	124	124	158	164	247	255	337784	7656044
LP0118	MAK	143	143	137	139	150	150	258	262	152	152	174	178	226	226	110	114	156	156	235	255	337890	7655551
LP0121	MAK	133	139	137	147	146	148	256	258	152	152	178	182	232	232	110	110	0	0	235	243	337402	7655051
LP0128	MAK	133	143	127	145	148	150	258	258	152	154	178	182	226	230	110	120	156	156	235	243	334840,713	7657807,07
LP0130	MAK	139	143	143	145	154	154	258	258	150	152	174	186	226	236	110	110	164	164	235	255	337758	7656424
LP0139	MAK	133	143	145	147	142	142	258	258	150	152	162	182	226	226	126	128	156	156	243	255	337568	7656070
LP0140	MAK	143	145	125	125	148	150	258	262	0	0	174	174	226	226	110	110	158	158	243	251	337758	7656424
LP0141	MAK	133	143	131	141	148	148	262	262	0	0	174	182	226	226	110	124	156	156	251	255	336970,406	7657053,94
LP0149	MAK	143	143	137	145	148	150	246	258	132	152	174	182	226	226	110	118	156	156	251	255	336970,406	7657053,94
LP0166	MAK	143	145	125	137	148	148	246	268	150	152	182	186	226	234	110	110	156	156	235	253	337069	7656738

Appendix 2

A

B
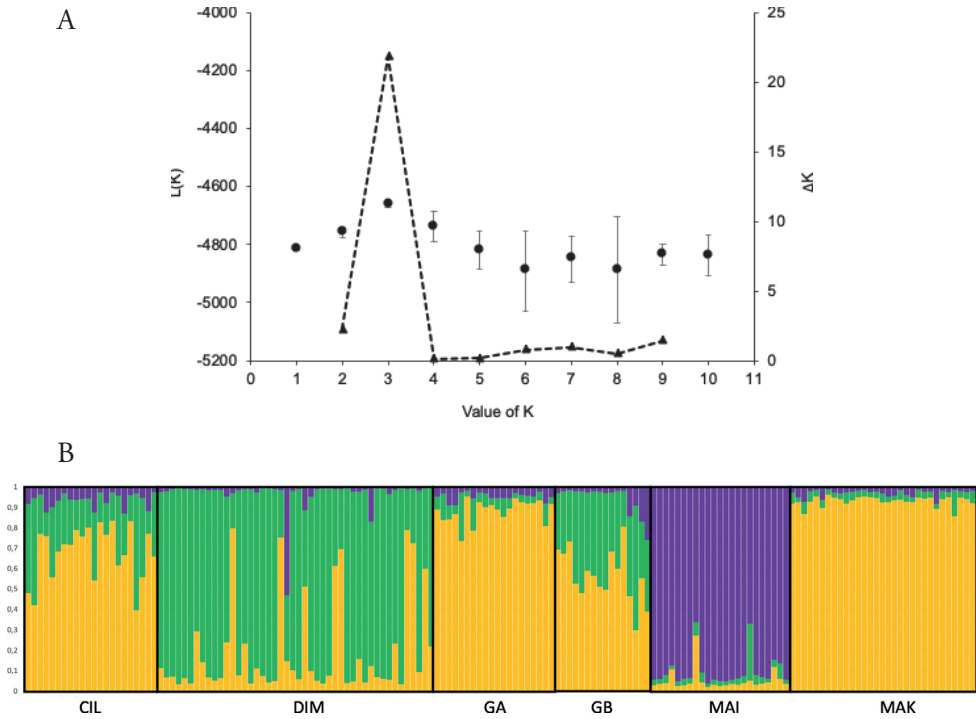
Figure A1. Cluster analysis of 158 feral cats from six geographical areas, on Réunion Island, 2015–2016 **A** detection of the number of genetic clusters K using the log-likelihood mean values L(K) (black circles; ± standard deviation) and ΔK statistic (black triangles; Evanno et al. 2005) as derived from STRUCTURE with K ranging from 1 to 10 with each value obtained by averaging the posterior probabilities over 10 independent runs **B** proportional membership probability to a given genetic cluster. Colours correspond to genetic clusters. Area codes are detailed in Fig. 1.
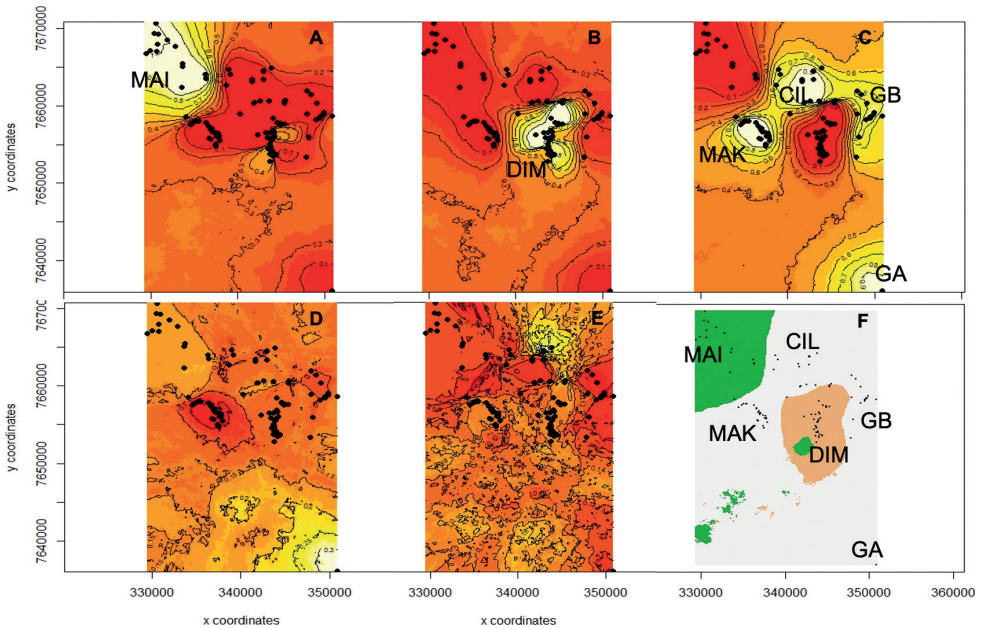
Appendix 3

Figure A2. Spatial distribution of each group defined by Geneland for sampled feral cats (n = 158), on Réunion Island, 2015–2016. Black dots represent sample locations **A, B, C, D** and **E** are maps of posterior probability to belong to each group. Clusters are indicated by areas with different intensities of colour. Probability of population membership increases as shading intensity decreases (values of probability are indicated on each contour line) **F** shows the mode map of the posterior probability to belong to each group (see Table 1 for area codes). Unit of axis is metre.

Appendix 4

Table A2. Pairwise F_{ST} (above diagonal) and Nei distance estimates (below diagonal) for 6 areas where feral cats were sampled (n = 158) on Réunion Island, 2015–2016. Area codes are described in Fig. 1.

Area/Area	MAI	MAK	CIL	DIM	GB	GA
MAI	–	0.120***	0.132***	0.145***	0.149***	0.136***
MAK	0.043***	–	0.011 [NS]	0.096***	0.036 [NS]	0.049 [NS]
CIL	0.047***	0.003[NS]	–	0.100***	0.055 [NS]	0.093 [NS]
DIM	0.055***	0.030***	0.032***	–	0.056 [NS]	0.096***
GB	0.057***	0.012 [NS]	0.018 [NS]	0.019 [NS]	–	0.097 [NS]
GA	0.048***	0.015 [NS]	0.028*	0.030***	0.031 [NS]	–

Appendix 5

Table A3. Posterior mean and mode migration rates over the last generations amongst the six geographical groups of sampled feral cats on Réunion Island, 2015–2016. 95% high density predictive interval (HDPI) estimated by software BIMR and means of the posterior distributions of the migration rate (with 95% confidence intervals) using BayesAss are indicated. Asymmetric immigration is shown in bold text. Means values using BayesAss with a confident interval not including zero are in italic. Area codes are described in Fig. 1.

| From-Into	BIMr		BayesAss	
	mean, mode	HDPI 95CI	mean	95CI
CIL-CIL	1, 1	[1;1]	0.681	[0.653;0.709]
CIL-DIM	**6.90e-09, 1.05e-08**	**[2.41e-13;1.79e-08]**	**0.016**	**[-0.006;0.037]**
CIL-GA	1.27e-08, 1.32e-08	[4.27e-13;3.35e-08]	0.014	[-0.012;0.040]
CIL-GB	2.70e-08, 2.94e-08	[4.56e-13;8.12e-08]	0.015	[-0.013;0.044]
CIL-MAI	4.60e-09, 1.13e-08	[3.37e-13;1.23e-08]	0.012	[-0.011;0.035]
CIL-MAK	3.19e-09, 5.80e-09	[1.09e-13;8.41e-09]	0.012	[-0.011;0.036]
DIM-CIL	**0.020, 0.101**	**[2.08e-12;0.126]**	*0.186*	*[0.098;0.275]*
DIM-DIM	0.903, 1	[0.50;1]	0.913	[0.859;0.967]
DIM-GA	1.29e-08, 1.21e-08	[1.06e-12;3.40e-08]	0.088	[-0.005;0.179]
DIM-GB	2.67e-08, 2.91e-08	[1.56e-13;8.02e-08]	*0.203*	*[0.130;0.276]*
DIM-MAI	4.66e-09, 9.99e-10	[1.98e-13;1.23e-08]	0.048	[-0.017;0.113]
DIM-MAK	3.17e-09, 3.73e-09	[3.47e-13;8.36e-09]	*0.133*	*[0.015;0.250]*
GA-CIL	6.80e-09, 2.28e-08	[3.96e-13;1.79e-08]	0.012	[-0.011;0.035]
GA-DIM	0.009, 1.16e-08	[1.23e-12;0.065]	0.007	[-0.007;0.022]
GA-GA	1, 1	[1;1]	0.680	[0.655;0.705]
GA-GB	2.67e-08, 1.42e-08	[5.34e-13;8.00e-08]	0.015	[-0.013;0.044]
GA-MAI	4.58e-09, 1.11e-08	[9.69e-14;1.21e-08]	0.012	[-0.011;0.035]
GA-MAK	3.20e-09, 1.24e-09	[1.09e-13;8.36e-09]	**0.011**	**[-0.011;0.032]**
GB-CIL	6.73e-09, 1.31e-08	[9.26e-13;1.79e-08]	0.012	[-0.011;0.034]
GB-DIM	0.047, 0.176	[1.18e-12;0.291]	**0.007**	**[-0.006;0.020]**
GB-GA	1.28e-08, 1.03e-08	[2.21e-13;3.38e-08]	0.013	[-0.012;0.038]
GB-GB	1, 1	[1;1]	0.682	[0.653;0.711]
GB-MAI	4.59e-09, 2.31e-09	[3.24e-13;1.22e-08]	0.012	[-0.010;0.033]
GB-MAK	3.20e-09, 1.58e-09	[1.52e-13;8.43e-09]	0.010	[-0.008;0.027]
MAI-CIL	6.78e-09, 2.40e-09	[4.07e-14;1.77e-08]	0.075	[-0.007;0.157]
MAI-DIM	0.008, 1.83e-08	[3.09e-12;0.051]	0.024	[-0.012;0.059]
MAI-GA	1.27e-08, 1.01e-08	[9.34e-13;3.36e-08]	0.054	[-0.023;0.130]
MAI-GB	2.64e-08, 1.23e-08	[2.92e-12;8.00e-08]	0.019	[-0.016;0.055]
MAI-MAI	1, 1	[1;1]	0.894	[0.818;0.970]
MAI-MAK	3.17e-09, 1.87e-09	[1.81e-13;8.33e-09]	*0.089*	*[0.011;0.166]*
MAK-CIL	6.72e-09, 2.31e-09	[6.59e-14;1.77e-08]	0.036	[-0.024;0.091]
MAK-DIM	0.013, 1.23e-08	[3.97e-13;0.085]	0.034	[-0.006;0.073]
MAK-GA	1.29e-08, 1.22e-08	[6.76e-13;3.423e-08]	*0.152*	*[0.047;0.257]*
MAK-GB	2.63e-08, 1.34e-08	[2.83e-12;7.89e-08]	*0.065*	*[0.004;7.0.126]*
MAK-MAI	4.63e-09, 3.98e-09	[9.623e-14;1.23e-08]	0.022	[-0.016;0.060]
MAK-MAK	[9.623e-14;1.23e-08]	[9.623e-14;1.23e-08]	0.747	[0.619;0.875]

Appendix 6
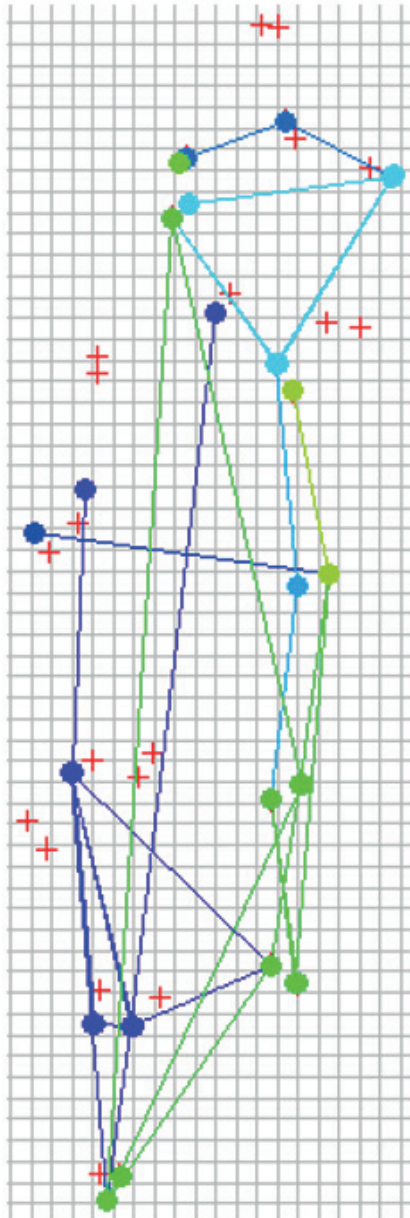
Figure A3. Plot of detection histories of feral cat over the detector maps during the study period, in Réunion Island, 2015-2016. Red crosses are for camera-trap locations and each dot represents a capture event (one colour per individual).
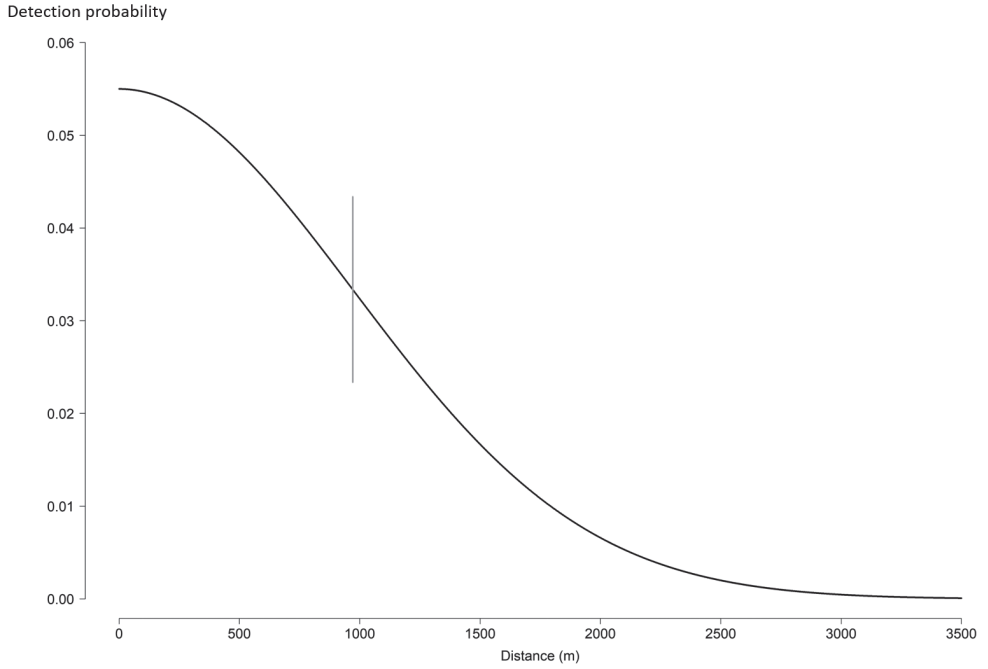
Appendix 7

Detection probability

Figure A4. Variation of the detection probability with the distance of the home range centre. The dark grey mark is for the value of the spatial scale of the movement parameter for a half-normal detection function.