Research Article

Population Structure and Management of Invasive Cats on an Australian Island

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ABSTRACT Invasive predators have a major impact on endemic island species; therefore, information about invasion dynamics is essential for implementing successful control measures. The introduction of feral cats onto Dirk Hartog Island, Western Australia, has had devastating effects, with presumably 10 of 13 native terrestrial mammal species being lost because of predation. Detailed records of historical introduction events were lacking; therefore, we analyzed genetic variation of the current population to gain information about past invasion dynamics and current gene-flow patterns. We analyzed the genetic structure and diversity of feral cats on the island and 2 mainland populations (Peron Peninsula and Steep Point). Analysis of mitochondrial DNA (ND5 and ND6) showed 2 primary haplotypes that we attribute to 2 main introduction events. Pairwise G00 ST values indicated high connectivity on the island but some isolation to the mainland populations. Mitochondrial and nuclear data showed no evidence for genetic differentiation of island and mainland populations; however, kinship analyses rejected evidence for on-going immigration of members of the current cat populations. Overall, our data suggested that gene flow following the main introduction events ceased some years ago. Because current island populations appear to be reproductively isolated from mainland populations, a sufficiently large-scale eradication measure might successfully diminish feral cat populations long-term. © 2014 The Wildlife Society.

KEY WORDS conservation, dirk hartog Island, eradication, Felis catus, genotyping.

Ecosystems on offshore and oceanic islands around the world are particularly vulnerable to introduced species such as domestic cats, Felis catus (Fitzgerald and Veitch 1985, Keitt et al. 2002, Pontier et al. 2002, Blackburn et al. 2005, Medina et al. 2011). Terrestrial vertebrates and bird populations on these islands generally show high rates of endemism and often predator-naïve behavior (Dickman 1992, Vitousek et al. 1995, Fritts and Rodda 1998, Bonnaud et al. 2007).

Dirk Hartog Island, the largest island off the Western Australian coast, lost 10 of 13 native terrestrial mammal species presumably because of predation by cats (Baynes 1990, Abbott and Burbidge 1995, McKenzie et al. 2000, Burbidge and Manly 2002). Since 1860, the island has been managed as a pastoral lease and grazed by sheep (Ovis aries) and goats (Capra hircus; Burbidge and George 1977). When first cats were introduced to the island is unclear, but the main introduction events of cats are assumed to have taken place during its pastoral use in the late 19th century (Burbidge and George 1977, Burbidge 2001). Prior to its establishment as a National Park in November 2009, the main commercial activity had changed from livestock to tourism, leading to more opportunities for cats to be transferred to the island. Dirk Hartog Island is now protected in the framework of a National Park to maintain several threatened species as well as to re-establish the original native mammal fauna. Previous studies showed that successful mammal reintroduction of native taxa depend on eradication of all invasive pest species, such as feral cats (Christensen and Burrows 1995, Gibson et al. 1995, Myers et al. 2000, Medina et al. 2011). The most effective method for controlling feral cats is aerial baiting, if non-target species are not at risk (Algar and Burrows 2004, Algar and Brazell 2008). Algar et al. (2011) conducted a pilot study in May 2009 at the northern end of Dirk Hartog Island (hereafter referred to as DHI) to evaluate the efficacy of baiting, which is the proposed primary control technique in the eradication campaign. Cats were fitted with global positioning system (GPS) data logger radio-collars providing detailed information on their activity patterns and home ranges. These data were subsequently used to plan the spacing of flight transects during an aerial baiting efficacy trial across the north of the island. Although cats have been established possibly for a century, we still have little information about the invasion dynamics, population genetic structures, and gene flow to verify this hypothesis. The knowledge of the population structure, however, will allow us to determine possible eradication units to prevent possible recolonization and...
reestablishment of this invasive predator species within the island (Robertson and Gemmell 2004; Abdelkrim et al. 2005, 2007, Hansen et al. 2007). Genotyping of individuals provides information on parent–offspring relationships and thus data on the connectivity and structure of the population (Pontier et al. 2005). This helps to ensure biosecurity by providing managers with the ability to determine possible survivors or new colonists after an eradication attempt (Abdelkrim et al. 2007).

We genotyped feral cats on Dirk Hartog Island at 3 sites as well as populations from the 2 main potential access points from the mainland using mitochondrial DNA and 10 microsatellite loci. We determined genetic structure and differentiation of populations, as well as relatedness among individuals. The main objectives were to assess if the island was invaded multiple times by cats and to test the hypothesis that island and mainland populations are reproductively isolated. We investigated the possibility of defining eradication units and give implications to aid future management for a successful eradication of feral cats to facilitate a sustainable reintroduction of endangered native species.

STUDY AREA

The largest island off the Western Australian coast, Dirk Hartog Island, is approximately 850 km north of Perth, Western Australia, and covers an area of 620 km² (Fig. 1). We conducted our study over a 400-km² area on the island using tracks between Cape Inscription in the north and Little West Well lying in the southern half of the island. We completed 3 trapping periods in 3 different sites on the island between March and April. The first trapping took place in the northern part of the island in 2009 (Johnston et al. 2010, Algar et al. 2011); the second and third sites were located in the middle and southern part of DHI with trapping being conducted in 2012. The second study site was on Peron Peninsula at the Big Lagoon (25°72’32’’S, 113°43’29’’E) of Francois Peron National Park approximately 35 km north of Denham. The third location was situated at Steep Point (26°14’38’’S, 113°16’06’’E) the westernmost point of the Australian mainland and the narrowest sea channel, the South Passage, between the mainland and DHI.

The climate of the region is semi-desert Mediterranean (Beard 1976, Payne et al. 1987). Mean maximum daily temperatures are 38 °C in summer and 21 °C during winter. January and February are the hottest months, whereas June and July are the coolest. Rainfall averages 220 mm per year, mostly from May to July (Commonwealth of Australia 2013, Bureau of Meteorology). Vegetation on the island is generally sparse, low and open and comprises spinifex (Triodia) and hummock grassland with an overstorey of Acacia or pittosporum shrub-land in the north. The western coast is mixed open shrubland with patches of bare sand and a few birridas (salt pans). On the east coast there are patches of mixed open heath of Diplolaena dampieri, Myoporum sp. and Conostylis sp. shrubs (Beard 1976).

METHODS

We trapped feral cats at locations around the track network on Dirk Hartog Island. We conducted trapping in the northern (DHIN), middle (DHIM), and southern part of the island (DHIS) as well as on 2 mainland locations: Steep Point and at Big Lagoon, Peron Peninsula. Trapping on Peron Peninsula commenced during an eradication program at a fenced in enclosure designed to remove all cats before the start of a fauna translocation program (Onus and Rolfe 2011). Steep Point is a remote and isolated cape and the westernmost point of the Australian with little access to the rest of the mainland. The trapping technique used padded leg-hold traps Victor Soft Catch® traps No. 3 (Woodstream Corp., Lititz, PA) with a mixture of cat feces and urine and an olfactory lure (Cat-atroscopic, Outfoxed, Melbourne, Australia) as the attractant. Trap sets were parallel to the track along the edge at 0.5-km intervals. We recorded trap locations with a Garmin GPS 60Cx (Garmin, Olathe, KS). We euthanized trapped animals using a 0.22 calibre rifle and recorded their sex, weight, and broad estimation of age (as either kitten, juvenile, or adult). We determined the pregnancy statuses of females by examining the uterine tissue for embryos. We collected tissue samples of the ear tip and stored samples in a buffer solution (Longmire et al. 1997) for DNA analysis. The Department of Environment and Conservation, Western Australia, Animal Ethics Committee approved protocols 06/2006 and 35/2009, which describe activities undertaken in this project.

DNA Extraction and Amplification

For genomic and mitochondrial DNA isolation, we used the Nucleospin Tissue Kit (Macherey-Nagel) for tissue samples. We genotyped all samples with a 12-microsatellite loci in a single multiplex reaction (MeowPlex). This included as a standard component a sex-identifying sequence tagged site from the domestic cat Y-chromosome SRY gene, which was as part of the multiplex set not separable for this study (Butler et al. 2002, Menotti-Raymond et al. 2005, Menotti-Raymond et al. 2012). We sequenced a stretch (1,800 bp) of mitochondrial DNA genome corresponding to the ND5 and ND6 region using primers and a polymerase chain reaction (PCR) protocol developed by S. Hendrickson-Lambert (personal communication; Supporting Information 1). We performed amplifications in a Biorad C1000 Thermocycler (Bio-Rad Laboratories, Hercules, CA) using 96-well microtitre plates. The PCR temperature cycles (20 cycles: 94 °C for 15 s, 60 °C decrease −0.5 °C per cycle for 60 s, 72 °C for 2 min; followed by 20 cycles: 94 °C for 15 s, 50°C for 60 s, 72 °C for 2 min) were preceded by a denaturation step of 10 minutes at 94 °C and finished by an extension step of 10 minutes at 72°C (S. Hendrickson-Lambert, personal communication). We determined DNA sequences using an ABI 3730 sequencer (Applied Biosystems, Carlsbad, CA) and analyzed sequences using Geneious 5.6.6 (Biomatters, Auckland, New Zealand) software for mtDNA and Genemarker V1.95 (Soft Genetics, State College, PA) software for nuclear fragment analysis.
Genetic Analysis

We used MICROCHECKER 2.2.3 (Van Oosterhout et al. 2004) to detect the presence of null alleles at each microsatellite locus. We used the GENEPOP 4.0 software (Rousset 2008) for the entire dataset to calculate basic population genetic parameters: mean number of alleles per locus ($N_A$) and expected ($H_E$) and observed ($H_O$) heterozygosity as well as significance values for deviations from Hardy–Weinberg equilibrium (HWE). We assessed patterns of historical genetic diversity for the sample locations for the mitochondrial ND5 and ND6 region using the number of variable sites, the number of haplotypes, haplotype diversity ($h$), and nucleotide diversity ($\pi$) in DNASP V5.1 (Librado and Rozas 2009). We employed NETWORK version 4.6.1.0 (Bandelt et al. 1999) to generate a median joining network with the frequency $>1$ criterion inactive.

We used the ML-RELATE (Kalinowski et al. 2006) software and estimated genetic relationships between all individuals. We used the maximum likelihood estimate of relatedness ($r$) and identity by descent coefficients (IBD; Blouin 2003) to discriminate between the pedigree relationships: unrelated, half siblings, full siblings, and parent–offspring. If estimated putative relationships among individual pairs were full sibling or parent–offspring relationships, we used the same software to estimate $P$ values with 1,000 simulations using an alternative relationship. We corrected $P$ values for relationships found between the island and mainland for multiple comparisons using the false discovery rate (FDR) approach (Benjamini et al. 2006). A small $q$ value indicates that the putative relationship fits the data significantly better than the alternative relationship. To verify the results, we calculated the average pairwise

Figure 1. Study area on Dirk Hartog Island in Western Australia with 3 sampled areas: northern (DHIN) shaded in light gray, middle (DHIM) shaded in dark gray and southern trapping area (DHIS) not shaded. Feral cat trapping locations (2009 or 2012) on Dirk Hartog Island are indicated by small dots for DHIN and DHIS. We did not record global position system (GPS) locations for DHIM. For GPS points see Supporting Information 1. Sampled areas on the mainland: Steep Point and Peron Peninsula.
relatedness using the relatedness estimator (Queller and Goodnight 1989) implemented in GENALEX 6.5 (Peakall and Smouse 2012; Supporting Information 2). We calculated population genetic parameters, such as allele frequencies, allelic richness, and $F_{IS}$ coefficients (Weir and Cockerham 1984) as a measure of the level of inbreeding using FSTAT 2.9.3 (Goudet 1995). Furthermore, we used STRUCTURE 2.3.2 (Pritchard et al. 2000) to infer the number of genetic clusters ($K$) and to assign individuals to these clusters. We estimated $K$ using independent runs for each $K$ ($K = 1–5$) with burn-in period of 50,000 steps and 500,000 Markov chain Monte Carlo repetitions. We did not include prior population delineation information and assumed correlated allele frequencies and population admixture. We then calculated the optimal $K$ based on $\Delta K$ using Structure Harvester (Earl and vonHoldt 2012). We used GENALEX 6.5 (Peakall and Smouse 2012) to determine the number of private alleles in each population and to run a principal coordinate analysis (PCoA) to further identify major patterns of genetic differentiation. We calculated average number of pairwise differences between population pairs ($G_{ST}$ values) and their significance estimates with 1,000 permutations and 1,000 bootstraps (Meirmans and Hedrick 2011) using GENALEX 6.5 (Peakall and Smouse 2012). We used BOTTLENECK version 1.2 software (Piry et al. 1999) to test for a genetic signature of recent declines in the effective population sizes. We estimated the observed and expected heterozygosity under the 2-phase model with settings of 10% infinite allele model (IAM), 90% stepwise mutation model (SMM), and default settings (30% IAM and 70% SMM) with 1,000 iterations. We tested excess of heterozygosity using a Wilcoxon test. We applied NEESTIMATOR V1.2 (Peel et al. 2004) to estimate effective population sizes ($Ne$) for 3 populations (we pooled DHI samples [DHIS, DHIN, and DHIM] into a single population).

**RESULTS**

We genotyped 59 individuals from DHI and the 2 mainland populations at 12 polymorphic microsatellite loci. We excluded 1 locus (F85) because MICROCHECKER revealed the presence of null alleles (Van Oosterhout et al. 2004). All microsatellite loci were polymorphic, with an average of 6 alleles per locus, ranging from 3 to 11 alleles. Genetic variability analysis indicated a mean of 0.76 and 0.70 for ($H_{E}$) and ($H_{S}$), respectively (Table 1). The allelic richness did not show large variation among the samples from DHI and Peron Peninsula, and a revealed a slightly increased value for Steep Point (Table 1). We were able to successfully sequence 53 individuals of the 59 samples of 5 sampling locations for mitochondrial ND5 and ND6 genes. The haplotype network revealed 16 haplotypes among 53 individuals. The branching patterns showed 2 common haplotypes (haplotype 1 = 56.6% and haplotype 2 = 13.2%) with several rare haplotypes differing by 1–5 substitutions (haplotypes 3–16 = 30.2%). Haplotype 1 comprised individuals from all sampling locations and included 40.9% of DHIN, 33.3% of DHIM, 75% of DHIS and Peron Peninsula and 100% of Steep Point individuals. Haplotype 2 included only individuals from DHIN (31.8%), DHIS (12.5%), and Peron Peninsula (12.5%; Fig. 2). Among all samples, $b$ was 0.568 ($\pm$0.066) and $\tau$ was 0.0011. The mean number of nucleotide differences between haplotypes was 1.53 and ranged from 0 to 1.8 (Table 2).

We calculated relatedness estimates with 2 different approaches resulting in similar patterns (Table 3, Supporting Information 2). Estimation of the relatedness factor (r) in ML-Relate for individuals from Dirk Hartog Island and mainland locations detected 1,950 possible pair combinations with values ranging from 0.004 to 0.12 (1,468 unrelated, 409

<table>
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<td>22</td>
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$Ne$ approx. 95% CI 65.8–129.1 16.2–32.8 5.2–11.8

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**Table 1.** Descriptive statistics of genetic diversity in feral cats in Western Australia (2009 and 2012) from 10 microsatellite loci illustrating sample size ($N$), average number of alleles per locus ($NA$), observed heterozygosity ($H_{E}$), expected heterozygosity ($H_{S}$), inbreeding coefficient ($F_{IS}$), $F_{ES}$ P-values (random $F_{IS} \geq$ observed $F_{IS}$), private alleles per population ($PA$), allelic richness averaged per locus and population ($PA/N$), and effective population size ($Ne$) with values for 95% confidence intervals. We sampled on Dirk Hartog Island (DHI) in 3 areas: north (DHIN), middle (DHIM), and southern (DHIS) and 2 mainland locations: Peron Peninsula (PE) and Steep Point (SP).

**Figure 2.** Haplotype network including 59 feral cat samples from mainland Australia (Peron and Steep Point) and Dirk Hartog Island (DHI) collected in 2009 and 2012. Numbers in circles indicate number of individuals assigned to that haplotype. Circles without numbers indicate only a single individual represented the haplotype. Lines connecting haplotypes represent the number of mutations separating the haplotypes. In case of more than 1 mutation, we show the number of mutations.
Table 2. Measures of genetic diversity of feral cats in Western Australia (2009 and 2012); samples size (n), number of haplotypes (H#), haplotype diversity (h), and nucleotide diversity (π) for mtDNA ND5 and ND6 genes variation within 53 sampled cats. We sampled on Dirk Hartog Island (DHI) in 3 areas: north (DHIN), middle (DHIM), and southern (DHIS) and 2 mainland locations: Peron Peninsula (PE) and Steep Point (SP).

<table>
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<tr>
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Half siblings, 49 full siblings, and 24 parent–offspring relationships). Among individuals of Dirk Hartog Island, we found all levels of relationship categories with significant values for r. Full sibling relationships were present between 10 cats from Peron (P < 0.06) and 2 cats from Steep Point (P = 0.03). We detected parent–offspring relationships for 2 cats from Peron (P = 0.01). Relatedness analysis for individuals between the island and mainland (corrected for multiple comparisons) significantly rejected evidence of first-degree relationships (parent–offspring and full sibling) between island and mainland individuals. A comparison of both relatedness estimator approaches indicated second-degree genetic relationships between the island and mainland populations (Supporting Information 2, Table 3).

The results of the Bayesian assignment approach implemented in STRUCTURE were largely inconclusive and lacked structure to identify the most likely K value above 1. The principal coordinates analysis (PCoA) plot, however, indicated clear differences between mainland and island populations (Fig. 3). Overall, the first and second axes explained 32% and 16% of the overall genetic distances, respectively. Pairwise $G^2_{ST}$ values between the 5 populations ranged from 0 to 0.57 with all comparison except DHIM and DHIN were highly significant (Table 4). We found no recent bottleneck in any population, and values for effective population sizes (Ne) ranged from 7.4 to 88.1 for Peron Peninsula, Steep Point, and DHI (Table 1).

**DISCUSSION**

The overall genetic diversity of feral cats in DHI and the 2 mainland populations ($H_O = 0.7$, number of alleles $A = 6$) is similar to that of another examined island population (Hawai‘i; $H_O = 0.7$, $A = 7.57–9$; Hansen et al. 2007). It was also similar to that of European domestic cats ($H_O = 0.7$, $A = 14.2$; Pierpaoli et al. 2003) but higher than the genetic diversity on Kerguelen, Grand-Terre ($H_O = 0.53, A = 3.6–7$) a sub-Antarctic island populated by cats from France (Pontier et al. 2005). This is to be expected because the Kerguelen founder population originated from 4 individuals introduced only 50 years ago (Pascal 1984, Pontier et al. 2005). The allelic richness values of cats on Dirk Hartog Island indicate multiple introductions; we found similar values between the island and the mainland populations. An increased genetic variation of introduced populations, as found in our study, is assumed to be indicative of multiple introductions from different sources (Allendorf and Lundquist 2003, Kolbe et al. 2004, Dlugosch and Parker 2008, Fitzpatrick et al. 2012). Early pastoralist likely first introduced cats onto DHI around 1860 when the island was used for farming sheep and goats (Burbridge and George 1977, Burbridge 2001) and that these cats had an European ancestry (Abbott 2002; K. Koch, Biodiversity and Climate Research Centre [BiK-F], unpublished data). We assume that cats were brought regularly to the island during that time because numerous shepherds and sheep shearers, as well as residents at the pastoral homestead (Burbridge and George 1977, Abbott 2008) and lighthouse (Ibbotson 2000), had frequent contact with the mainland. We found evidence of introductions following this first invasion period. The estimates of allelic richness and the presence of 2 common mitochondrial haplotypes, is an indication of several introductions. Genetic analyses of feral cats across Australia showed that haplotype 1 was also found in several mainland locations (K. Koch, unpublished data). We suggest that this haplotype represents the ancestral haplotype, which originated from cats brought by early European settlers to Australia during the first introduction period. Haplotype 2 therefore represents a recent haplotype comprising of cats from Peron Peninsula and Dirk Hartog Island.

The principal coordinates analysis (PCoA) revealed 2 main clusters and $G^2_{ST}$ values ranged from 0 to 0.57, which indicates genetic differentiation between island and mainland populations and gene flow between Peron Peninsula and Steep Point populations. However, a Bayesian assignment approach was unable to differentiate among mainland and island populations; additionally, we did not detect differentiation at the mitochondrial locus. First-degree relationships between island and mainland populations were significantly rejected. Thus, both analyses, relatedness and population structure analyses of nuclear and mitochondrial DNA, suggest that recent gene flow between the islands and the
mainland did occur; however, migration events during the last years were rare or ceased completely. Immigration was possible through pastoral use, extensive tourism, and visiting fishing vessels from the mainland. Therefore, we suggest that successful establishment of island populations took place after the first invasion period but ceased some years ago. Analyses of microsatellite data showed that genetic differentiation among populations on DHI were low, suggesting high connectivity. Estimates of relatedness on DHI display a significant kin structure suggesting high numbers of successfully breeding individuals also supported by large Ne estimates. We found no evidence for bottlenecks on DHI and Peron Peninsula, although the major part of the Peninsula underwent a management and eradication program in the past years (Short et al. 1994, Algar et al. 2007). However, the genetic impact of a bottleneck is reduced through rapid recovery and expansion or new immigrants, which is especially found in invasive populations (Nei et al. 1975, Cornuet and Luikart 1996) and therefore applicable to our results.

The reproductive biology and life history of feral cats allows great potential for population recovery (Myers et al. 2000). Male cats reach sexual maturity between 8 and 10 months and females between 6 and 8 months and can breed 2–3 times a year (Hansen et al. 2007). Cats on DHI revealed great dispersal abilities with home range analysis indicating a mean area of 12.7 km² for male and 7.8 km² for female cats (Johnston et al. 2010). These data display the extensive movement and recovery abilities of feral cats on DHI. The feral cat population on the north of the island was reduced by 80% in 2009 after sampling for this study (Algar et al. 2011). Further studies will provide an opportunity to investigate the specific reinvasion capability of feral cats on DHI during a period of 4 years. Cats on DHI show low genetic diversity and extensive dispersal abilities, which prevents us from determining eradication units on the island and indicate a complete island eradication program is needed.

In conclusion, we found that several introduction events lead to the ancestral haplotype 1 that is present on the island and mainland locations and a more recently introduced haplotype 2 on the island and Peron Peninsula. Genetic differentiation values indicate that gene flow has occurred between the island and mainland. However, the genetic relatedness between island and mainland individuals suggests

### Table 4. Genetic differentiation among 3 populations of feral cats from Dirk Hartog Island (DHIN = north, DHIM = middle, and DHIS = southern populations) and 2 mainland populations (PE = Peron Peninsula and SP = Steep Point) in Western Australia (2009 and 2012). The lower matrix contains \( G_{ST} \) values (average number of pairwise differences between population pairs) and the upper matrix indicates significance. Asterisks (*) indicate significant \( G_{ST} \) (>0.05) and (−) indicate non-significant differences calculated with 1,000 permutations.

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Figure 3. Principal coordinates analysis (PCoA) plot indicating genetic distances between individuals from 5 populations of feral cats in Western Australia in 2009 and 2012. The PCoA is based on co-variance distance matrix values using microsatellite data. Filled symbols indicate mainland populations. Diamond shapes indicates samples from northern (DHIN), circles are from middle (DHIM), and polygons are from southern (DHIS) trapping locations on the island. Triangles represent Peron Peninsula (PE) and squares represent Steep Point (SP) locations.
a ceased gene flow for some generations. Even though our sample size for some of the populations was relatively small and results need to be considered carefully, we found no evidence for gene flow among individuals of current generations.

MANAGEMENT IMPLICATIONS

In our study, cats’ high dispersal rates and population connectivity on the island prevented us from determining the appropriate eradication units. Thus, the planned eradication program requires a large-scale control that limits feral cats’ dispersal across the island. This might be achievable by a fence at the islands isthmus to prevent recolonization across the island. Furthermore, to achieve a successful eradication program, management plans need to encompass genetic monitoring after control programs start to identify potential survivors or new colonists in order to ensure permanent biosecurity. The techniques used in this study for the management of feral cats on Dirk Hartog Island are an example of the effective usage of genetic methods in combination with classical management tools (Johnston et al. 2010, Algar et al. 2011). These techniques provide information to support and improve invasive species management strategies.

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