Genetic diversity and phylogeography of Australian feral cats

by

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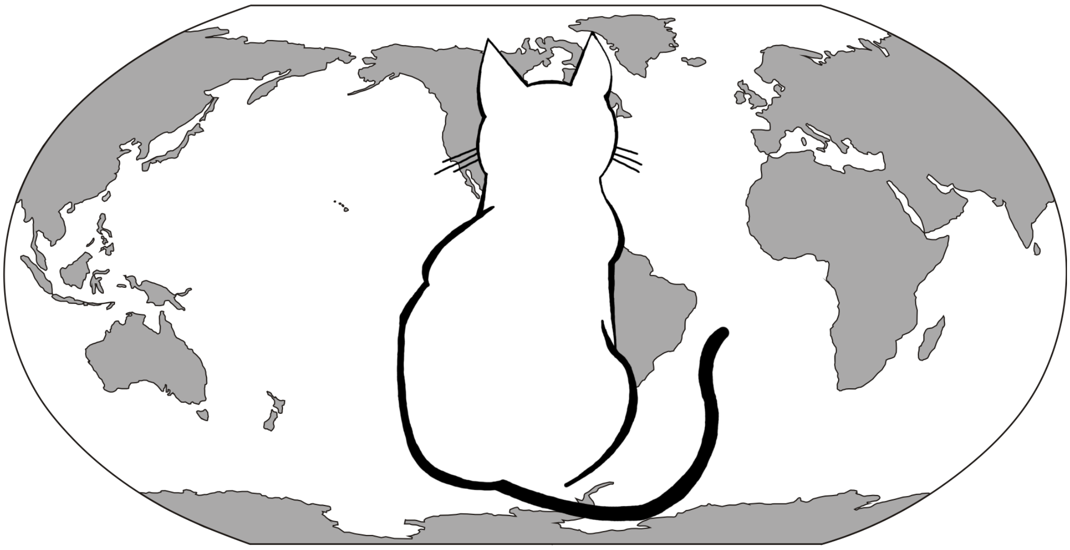

Contents

Abstract

Biodiversity is not only threatened by habitat loss, climate change and pollution, but also by invasive species. The impact of introduced species is immense and causes substantial ecological and economical costs worldwide. With the start of domestications of the African wildcat (*Felis lybica*) in the Near East, the transport of house cats (*Felis catus*) around the world as a commensal and domesticate began. The general aim of my thesis was to investigate the impact of invasive feral cats on native species as well as underlying population genetic structures, diversity and phylogeography. This was studied in the context of the demographic history in Australia and Hawai'i. My studies confirmed that the main introductions of cats to Australia began in the 19th century via ships of European settlers, traders and workers. Similarly, I was able to confirm cat introductions to Hawai'i by European traders and explorers; which has to the present a devastating effect on Hawaiian endemic species. Likewise, cats are widespread across Australia, can be found on most islands and are recognized as one of the major threats to Australian native species. A selective feeding behaviour by invasive predators was found in one of my studies. This study additionally gives an indication for possible population recovery of small Western Australian vertebrate species after predator removal. Advancement and the combination of various management techniques allow, if adequately funded, a more efficient planning and implementation of eradication campaigns. Population genetic approaches are able to give insights into population genetic structure, diversity and kinship, thereby enabling management campaigns to be more cost effective and successful. No pattern of isolation by distance between populations of Hawai'i and Australia indicated that trade routes, such as the 'Golden Round' of the maritime fur trade, facilitated a link between far off global cat populations. Multiple introductions to Australia and intermixing with domestic breed cats resulted in feral cat populations which show no signs of reduced genetic variability. My studies also revealed the advantages of bioproxies in combination with phylogeography, which enable the inference and reconstruction of introduction routes, history and origin of invasive species. Genetic signals of historically introduced genotypes are still discernible on islands with low number of introductions over time and thereby low intermixing with domestic fancy breeds. Feral cats' adaptability as an invader was reconfirmed and possible underlying genetic mechanisms enabling their success as a global invader ('global supercat') are discussed. Research into the feralisation process of cats will provide new information regarding the domestication of cats, the genetic basis of feralisation and allow additional insights into cats' adaptive potential.

General Introduction

Biodiversity

Biological diversity or biodiversity refers to the variety within the living world (Convention on Biological Diversity 1992).

The Convention on Biological Diversity, CBD 1992 (Article 2) defined biodiversity as: 'the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and ecosystems'. Here, the three fundamental and hierarchically-related levels of biological organisation define the separate elements of biodiversity: genes, species and ecosystems.

The global biodiversity typically represents the number of species (approximately 1.8 million) in different taxonomic groups that have been described and named to date. The estimate of the total number of species existing on earth varies between 5 to nearly 100 million (Global Biodiversity Assessment 1995). The term 'biodiversity hotspots' describes geographical regions under threat from biodiversity loss, that were defined as areas with conservation priority, since they harbour a significant numbers of endemic species found in relatively small areas (Myers 1988, 1990; Myers *et al.* 2000b). Regions in Australia and the Hawaiian Islands have been recognized as such biodiversity hotpots. However, the loss of biodiversity is not confined to biodiversity hotspots, but is rather a global issue.

The IUCN Red list recorded 896 extinctions, with 804 species listed as extinct and a further 65 as extinct in the Wild (IUCN 2009). A reassessment of the world's mammals species showed that nearly one-quarter (22%) are considered globally threatened or extinct and 15% of species are Data Deficient (IUCN 1994; Schipper *et al.* 2008).

Consequently to safeguard global biodiversity, an international legally binding treaty was signed and recognized at the Convention on Biological Diversity (CBD 1993) recognizing three main objectives: ‘conservation of biological diversity, sustainable use of its components and fair and equitable sharing of benefits arising from genetic resources’.

One of the main targets of the convention objectives is the reduction of biodiversity loss rate, which despite increased conservation efforts has increased. Several main drivers for biodiversity loss have been identified including habitat loss; climate change/global warming and pollution and the threat from invasive species.

Invasive species

An invasive species is defined as: ‘a species that is non-native to the ecosystem under consideration and whose introduction causes or is likely to cause economic and environmental harm or harm to human health’(National Invasive Species Council 2008).

The invasion of non-indigenous species and their impact on native species communities and ecosystems is widely recognized as a major threat to global biodiversity by scientists, governments and the CBD (Elton 1958; IUCN 2000; Lodge 1993; Simberloff 2011; Vila *et al.* 2011; Vitousek *et al.* 1996).

Biological invasions have often been linked to fortuitous or intentional dispersal events through human migration (Estoup & Guillemaud 2010; Lockwood *et al.* 2005; Mack *et al.* 2000). Although biotic invasions are neither a novel nor strictly human-driven phenomena, the geographical extend, the number of species involved and frequency of introductions has grown enormously especially as a direct consequence of expanding transport and commerce (Mack *et al.* 2000). Vectors for dispersal through human activities include extensive exploration voyages, discovery and settlement of new continents and islands through sea and later air travel (Mack *et al.* 2000). In the past 200 to 500 years the rate of species introductions through human assistance has increased by orders of magnitude (di Castri 1989; Duffy & Capece 2012; Konecny *et al.* 2013; Mack *et al.* 2000), thereby accelerating species dispersal into new remote areas (Estoup & Guillemaud 2010).

Beginning around 10,000 CE years ago ancient human migrations, settlements and trade from the Fertile Crescent during the Neolithic Revolution led to the early spread and domestication of species such as cereals (Poaceae), dates (*Phoenix dactylifera*), cattle (*Bos primigenius*), cats (*Felis catus*) and sheep (*Ovis aries*) (Cucchi *et al.* 2005; di Castri 1989; Driscoll *et al.*

2009). The house mouse (*Mus musculus*) became one of the first human commensals at settlements in the Near East and started colonizing Western Europe and other parts of the world around 1000 CE (Searle *et al.* 2009a). The phylogeography and current geographic distribution of the house mouse as a commensal could be linked to human colonization and settlement patterns from the Iron Age, to the extensive maritime activities of the Vikings in the 9th to 11th centuries and European explorations starting in the 15th century (Jones *et al.* 2013; Jones *et al.* 2012; Searle *et al.* 2009b). Bioproxies, such as house mice, give valuable insight into human demographic history, but also demonstrate the scope of intentional and unintentional introduction of species through history.

The impact of invasive alien species is enormous, insidious and generally irreversible with damaging effects on native species and ecosystems equivalent to global loss and degradation of habitats (IUCN 2000). The major ecological cost is the irreversible loss of ecosystems and native species (IUCN 2000). The main risk considered for approximately 40% of the species listed as threatened or endangered under the Endangered Species Act of 1973 of the US (2012) is the competition with or predation by invasive species (IUCN 2009; Wilcove *et al.* 1998). This percentage most likely underestimates the impact of invasive species since calculations included only threats to extant species without incorporating species considered extinct (IUCN 2009). Additionally, the economic costs caused by invasive species through environmental damage and losses are perceived as a major concern throughout the world (Pimentel *et al.* 2000; Pimentel *et al.* 2005). In the United States with approximately 50,000 non-indigenous species established, the total economic costs are estimated as $120 billion per year (Pimentel *et al.* 2005).

The ability of a species to establish successfully in a new environment and the likelihood of a species being invasive is based on the existence of particular phenotypic traits, such as strong dispersal abilities, ample growth rate, generalist vs. specialist trophic relationships and high levels of competitiveness (Estoup & Guillemaud 2010; Kolar & Lodge 2001; Sakai *et al.* 2001). These ‘invasive characteristics’ have been found to vary considerably between species (Kolar & Lodge 2001) as well as between introduced populations of the same species (Estoup & Guillemaud 2010; Kang *et al.* 2007; Kelly *et al.* 2006). Additionally, differences in new ecological conditions encountered by introduced species and therefore natural selection and adaptation are main features determining the success of an invasion (Estoup & Guillemaud 2010; Facon *et al.* 2006). A species’ capacity to respond to selection and changes in levels of genetic diversity (e.g. through good combination of specific genes/alleles) are important for successful introductions and establishment (Drake & Lodge 2006; Estoup & Guillemaud 2010; Facon *et al.* 2006; Lockwood *et al.* 2005; Memmott *et al.* 2005). The history of an invasion process and the routes of introduction provide valuable information about the genetic composition and origin of an invading population (Dlugosch & Parker 2008; Estoup & Guillemaud 2010). Molecular and quantitative traits of an invading population are greatly affected by the history and origin of invasive species, including demographic factors of their introduction (Estoup & Guillemaud 2010). Here, demographic factors include the genetic diversity of an invading population that is attributable to the genetic composition of source populations, the number of individuals introduces per introduction event and their dispersal following each introduction (Estoup & Guillemaud 2010).

Domestication and spread of the cat

Genetic analyses indicate that the species *Felis silvestris* (wildcat) is comprised of five subspecies: *F.silvestris silvestris* (European wildcat); *F. s. lybica* (African wildcat); *F. s. ornate* (Central Asian wildcat); *F. s. cafra* (Southern African wildcat) and *F. s. bieti* (Chinese desert cat) (Driscoll *et al.* 2007). The mitochondrial DNA analysis estimated the age of ancestral *F. silvestris* to be in the order of 230,000 years, whereas the age of *F. s. lybica* is estimated to be around 131,000 years (Driscoll *et al.* 2007; Figure 1). The African wildcat (*F. s. lybica*) is considered to be the most likely ancestor of the domestic cat with its domestication believed to have taken place around 9,000 to 11,000 years ago through association with humans commensally (Driscoll *et al.* 2007; Randi & Ragni 1991; Serpell 2000; Vigne *et al.* 2004). Behavioural characteristics support this hypothesis as *F. s. lybica* exhibits a gentle temperament living and foraging near human settlements in contrast to *F. s. silvestris* which shows exceptional shyness and intractability even after modern taming attempts (Kitchener 1998; Serpell 2000).

The domestic cat of today subsequently spread from Egypt across Europe following the constantly travelling Roman armies (Sunquist & Sunquist 2002). By the 10th century the domestic cat appears to have been widespread throughout Europe and Asia (Serpell 2000). In the following 2,000 years cats were introduced around the world and can now be found on every continent except the Poles (Lever 1994). Especially in the last 200 to 500 years numerous cats were deliberately or accidental translocated to islands and countries around the globe (Bonnaud *et al.* 2011; Courchamp *et al.* 2003; Vitousek *et al.* 1997). As a biological control for pest species such as rodents, cats were kept on sailing vessels of explorers, traders and colonists or accompanied settlers as pets (Courchamp *et al.* 2003; Dickman 1996; Todd 1977).

Today, domestic cats are one of the world's most numerous pets with 26.7% of the population in Australia (Australian Bureau of Statistics 2006) and up to 37.3% of households in the United States owning cats (The Human Society US 2013). These statistics however do not account for the vast numbers of established stray and feral cat populations. They diverged in the course of history from domestic cats, initially being confined to settled areas, to rural areas or more remote localities (Dickman 1996; Mahoney & Richardson 1988; Moodie 1995).

Domestic cats are defined as pet, house and fancy breed cats with all of their ecological requirements being provided by humans (Moodie 1995). Stray cats rely only partly on human provisions often unintentionally through food and shelter supplied in urban fringe situations such as rubbish tips (Moodie 1995). Feral cats live in self-perpetuating populations with no reliance on humans (Moodie 1995).

Feralisation (the process of becoming feral) of domestic animals is often linked to human-mediated translocations into new territories (Digard 1990; Goodwin 2007; Tesset *et al.* 2009; Vigne 2013). The feralisation of domestic sheep in Corsica for example, probably early within the Neolithic period, led to the emergence of the Corsican mouflon (*Ovis orientalis musimon*; Digard 1990; Tesset *et al.* 2009). However, the underlying genetic factors responsible for this process are unknown. For this thesis I defined feralisation as a process which possibly enables the partial reconstruction of a wild phenotype in domesticated animals that enables self-perpetuating populations with no reliance on humans.

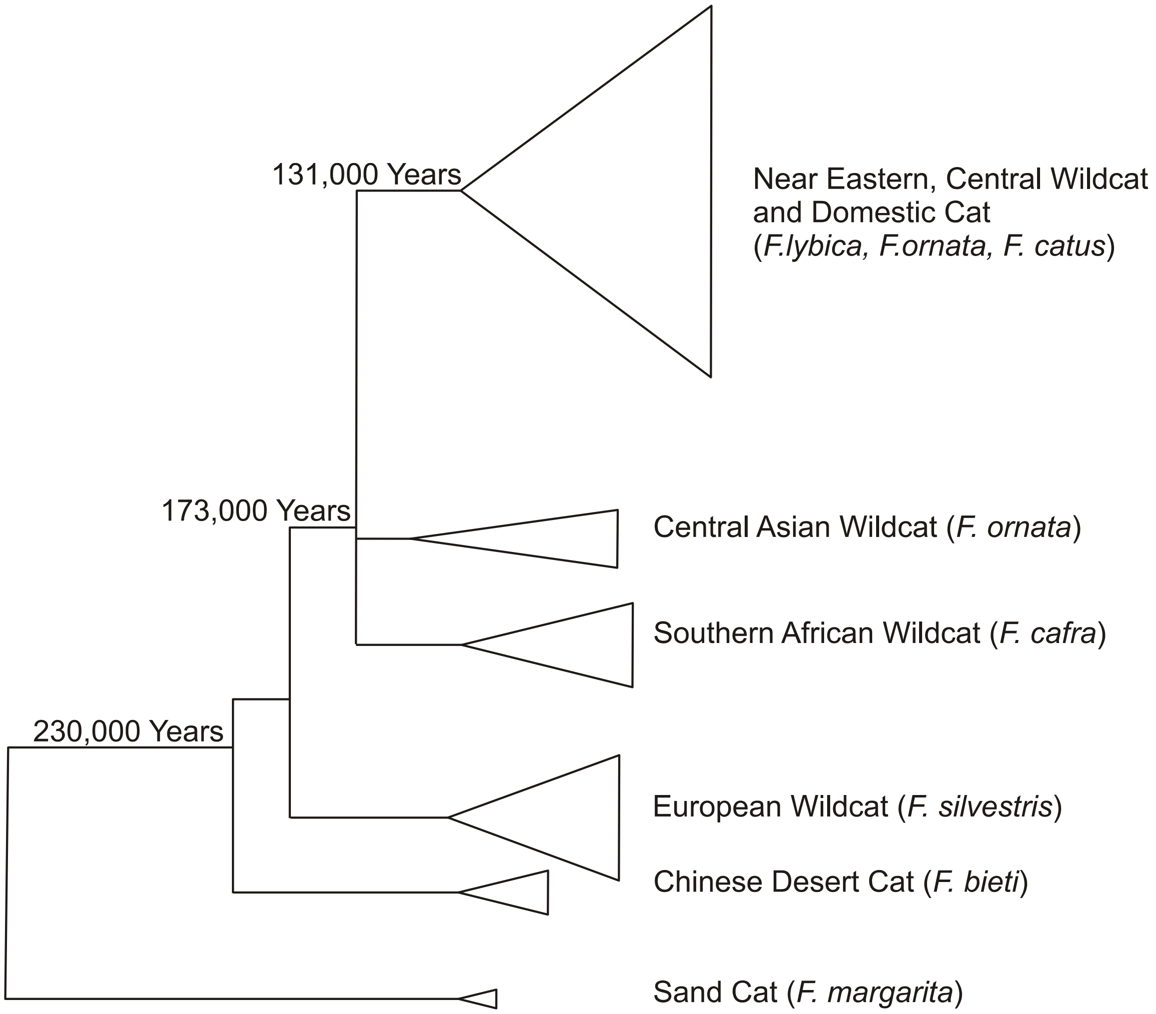

Figure I-1: Adapted phylogenetic tree of mitochondrial DNA sequence of 176 haplotypes discerned from 742 cats sampled across the range of the domestic cat with estimated age of the ancestors (European wildcat, Near Eastern wildcat, central Asian wildcat, Southern African wildcat, Chines desert cat and sand cat; Driscoll *et al.* 2007).

Introduction of cats to Australia

Australia is one of the seventeen megadiversity countries, which hold collectively around two thirds of the worlds of biodiversity (McNeely *et al.* 1990). Up to 89% of Australia's fauna and flora is endemic to the continent (Strahan 1995). Even though Australia is a geographically isolated island continent and historically remained almost free from introduced mammalian species, the arrival of European settlers in the late 18th century changed this with approximately 22 listed introduced mammalian species having established free-living populations since then (Olsen 1998). Australia is currently listed as one of the countries with the most number of threatened mammal species (57 mammal species threatened; IUCN 2009).

Historical changes in land use and habitat transformation, altered fire regimes and introduced species have led to the extinction of approximately 22 terrestrial species and 43 critically endangered species that survive only on offshore islands (Burbidge & Manly 2002; Burbidge & McKenzie 1989; Kinnear *et al.* 1988; Kinnear *et al.* 1998; McKenzie *et al.* 2007; Short & Smith 1994). Of the 22 invasive mammalian species, two predators have been introduced to Australia, which have become a major threat to Australia's wildlife (Wheeler & Priddel 2009). These predators are the European red fox (*Vulpes vulpes*) and the domestic cat (Wheeler & Priddel 2009).

The most likely introduction of the domestic cat to Australia took place with European settlement, although it has been suggested, that the cat may have been introduced earlier through the trade between Malay and Aboriginal people or with explorers and seafarers landing in Western Australia around 1650 (Abbott 2002; Burbidge *et al.* 1988; Macknight 1976; McKay 1996; Oskarsson *et al.* 2012; Robert 1972). Nevertheless, the main and most extensive period of introductions is assumed to have been between 1806 and 1886 (Abbott 2002; Abbott 2008). Apart from their spread to rural settlements as pets, cats were purposely released in the wild and established on rural properties in order to control likewise introduced rabbits (*Oryctolagus cuniculus*) and house mice (Abbott 2008; Rolls 1969). Today cats' distribution in Australia is nationwide including the central desert, Tasmania and various offshore islands (Dickman 1996). Feral cats are now considered a major threat to the Australian native fauna. They are competing with native predators (Glen & Dickman 2005; Moodie 1995), are hosts of disease and parasites (Adams *et al.* 2008; Dickman 1996) and most importantly have a high impact on the decline and extinction of native wildlife through direct predation (Burbidge & McKenzie 1989; Dickman 1996; Environment Australia 1999; Nogales *et al.* 2004; Risbey *et al.* 2000). Attempts to reintroduce threatened species in the arid zone have often failed because of extensive predation by feral cats (Burbidge & Manly 2002; Christensen & Burrows 1995; Gibson *et al.* 1995; Short *et al.* 1992).

Introduction of cats to Hawai'i

The Hawaiian archipelago consists of the younger main Hawaiian Islands and the older north-western Hawaiian Islands. It is the most isolated archipelago in the world, situated in the middle of the Pacific Ocean. The islands harbour a vast array (over 10,000) endemic plants and animal species (Ziegler 2002) and their biodiversity and evolutionary radiation was described to be more spectacular than those of the Galápagos (Cowie & Holland 2008). An elevation range from sea level to 4,025 m results in Hawai'i containing all major known ecological zones and thereby displaying most of the earth's variation in climate conditions (Mitchell *et al.* 2005).

In Hawai'i approximately 300-500 invasive species have been introduced, spreading widely and causing significant environmental and economic damage (Loope & Kraus 2009). These invasions have resulted in the extinction and endangerment of hundreds of native endemic species and large-scale replacement of native vegetation with alien plant communities (Cox 1999; Hobdy 1993; Loope 1998; Stone & Scott 1985; Stone *et al.* 1992).

Feral cats are believed to have been introduced in the late 1700s during the Islands discovery through European explorers e.g. Captain James Cook (Cox 1999; King 1984) spreading subsequently through the forests of the Hawaiian Islands (Perkins 1903; Rothschild 1893). Since then, cats have been reported to contribute highly to the decline and extinction of various endemic Hawaiian bird species (Perkins 1903; Ralph & van Riper III 1985; Smucker *et al.* 2000; Stone & Scott 1985). From 1840 on cats were found to range throughout the Hawaiian Islands from high-density stray cat colonies to remote feral cat populations in montane forests and subalpine areas of Maui and Hawai'i (Brackenridge 1841; Hansen *et al.* 2007; Hu *et al.* 2001; Simons 1983; Tomich 1986; Winter 2003).

Endangered forest birds, terrestrial and colonial nesting seabirds are particularly prone to feral cat predation in Hawai'i (Hess *et al.* 2004; Hess *et al.* 2007; Hu *et al.* 2001; Kowalsky *et al.* 2002; Laut *et al.* 2003; Smith *et al.* 2002). In addition, cats are a host of the parasite *Toxoplasma gondii* contributing to its dispersal and thereby threatening Hawaiian native species (Honnold *et al.* 2005; Work *et al.* 2002; Work *et al.* 2000).

Management of invasive feral cats

Introduced mammalian predators are the most threatening factor for many species, particularly on islands, and are one cause of animal extinctions in the past few centuries (Blackburn *et al.* 2005; Courchamp *et al.* 2003; Croll *et al.* 2005; Salo *et al.* 2007; Vitousek *et al.* 1997; Young *et al.* 2013). Therefore the management, control and eradication of non-indigenous species is a major topic for conservation biologists and a priority for wildlife management (Allendorf & Lundquist 2003; D'Antonio & Kark 2002; Myers *et al.* 2000a; Simberloff 2003; Veale *et al.* 2013). The Convention on Biological Diversity recognised the threat posed by this invasive species and agreed on the prevention, control or eradication and the mitigation of their impacts (Convention on Biological Diversity 1992).

Management strategies of non-indigenous species are generally focused on two main invasion processes: (i) preventing or detecting incursions at an early stage and (ii) rapid eradication actions or/and mitigating effects of well-established invasive species (Hobbs & Humphries 1995; Hulme 2006). Management and eradication campaigns utilize for this purpose advanced ecological management and population genetic techniques (Abdelkrim *et al.* 2007; Allendorf & Lundquist 2003; Clout & Russell 2008; Russell *et al.* 2009; Veale *et al.* 2013; Waples & Gaggiotti 2006).

The invasive feral cat is listed on the International Union for Conservation of Nature (IUCN) compilation of the 100 of the world's worst invasive alien species as well as being recognized as a key threatening factor under the *Commonwealth Environmental Protection and Biodiversity Conservation Act 1999*. The introduction of cats to Hawai'i and Australia with their numerous endemic species has had an dramatic impact on both countries' biodiversity (inter alia: Burbidge & Manly 2002; Dickman 1996; Hess *et al.* 2004; Nogales *et al.* 2004; Perkins 1903; Ralph & van Riper III 1985; Smith *et al.* 2002).

Management techniques for established populations of feral cats and other predators mainly consist of large-scale aerial baiting, monitoring and trapping (Clout & Williams 2009; Moseby & Hill 2011). The development of toxic baits for feral cats (*Eradicat®*) has led to a highly effective technique for the control of feral cats, when there is no risk posed to non-target species (Algar *et al.* 2007; Algar *et al.* 2002; Algar & Burrows 2004; Algar *et al.* 2012; Algar *et al.* 2013; Moseby *et al.* 2011; Short *et al.* 1997). Recent research targets the development of a new toxin and reduce exposure of bait-delivered toxicants to non-target species by producing a bait that implements the toxin compound into an encapsulated pellet (*Curiosity®*) (Hetherington *et al.* 2007; Johnston *et al.* 2011; Johnston *et al.* 2012; Murphy *et al.* 2011).

Feral cat eradication programs on islands have increased in the last years (Keitt *et al.* 2011), preventing the extinction of many species and leading to the recovery of others (Young *et al.*

2013). On strategic mainland locations effective introduced predator control is more difficult because of reinvasions. Through predator-proof fences, large trapping grids and extensive baiting, 'mainland islands' can be created in which cats can be successfully managed (Algar *et al.* 2010; Algar *et al.* 2002; Algar & Burrows 2004; Bloomer & Bester 1992; Burns *et al.* 2011; Saunders & Norton 2001; Young *et al.* 2013). Nevertheless, eradication projects are time consuming and labour intensive and have mostly large economical costs (Abdelkrim *et al.* 2005a; Simberloff 2003). Unfenced areas on the mainland or islands are at risk from eradication campaign failures, especially through the target species ability to recolonize from neighbouring islands or the adjacent mainland (Abdelkrim *et al.* 2005a). Therefore, the control of established invasive populations depends greatly on information about the history, origin and population structure as well as the level of connectivity existing between groups of individuals (Rollins *et al.* 2009). This information is essential to prevent and predict further spread and to develop adjusted population control strategies (Rollins *et al.* 2009; Schwartz *et al.* 2007).

Genetic approaches in invasive species management

Population genetic tools have traditionally been used to characterise wild populations and are now additionally employed for invasive species management (Rollins *et al.* 2006). The use of these techniques in invasion biology studies provides information on the ecology and evolution of invasive and native species (Allendorf & Luikart 2007; Allendorf & Lundquist 2003). Allendorf et al. (2003) suggested that the potential of genetic diversity and population biology studies not only lies in providing knowledge on what caused species to become invasive, but also enables the identification of critical life-history stages during which control will be most successful. The incorporation of population genetic approaches into various eradication and management campaigns has been found to enhance their success and can assist in recognizing possible positive outcomes of containment efforts (Abdelkrim *et al.* 2007; Allendorf & Lundquist 2003; Rollins *et al.* 2006; Schwartz *et al.* 2007; Veale *et al.* 2013; Waples & Gaggiotti 2006). Population genetics is able to identify population structure and diversity, patterns of connectivity within and between populations as well as performing genetic kinship analysis of populations in order to link individuals to a kin group rather than to a population (Broquet & Petit 2009; Palsboll *et al.* 2010; Peery & Pauli 2012; Veale *et al.* 2013). This information consequently allows a management design specifically adjusted to population structure and their connectivity to other populations (Estoup & Guillemaud 2010; Rollins *et al.* 2006; Veale *et al.* 2013).

The use of phylogeography employs genetic variation detected in populations to draw inferences about the origin of a population and its relationship with other populations of the same species (Avise 2009; Bloomquist *et al.* 2010; MacKay *et al.* 2013). Therefore routes of introductions can be reconstructed giving information on the pathways and degree of connectivity between source and invaded populations (Rollins *et al.* 2006; Rollins *et al.* 2009; Schwartz *et al.* 2007). Phylogeography also provides the opportunity to gain insights into the environmental and evolutionary factors possibly responsible for biological invasions (Dlugosch & Parker 2008; Estoup & Guillemaud 2010; Konecny *et al.* 2013). The ability to identify alien species, while describing their invasion history gives the opportunity to detect and prevent further invasions early on (Rollins *et al.* 2009). This allows predicting the relative susceptibility of ecosystems to invasions and invasive population demographics (Allendorf & Lundquist 2003; Estoup & Guillemaud 2010; Rollins *et al.* 2006).

Based on information obtained through population genetic analysis it is possible to assess the scale of which a campaign needs to be implemented as well as the feasibility and effectiveness of a particular control strategy (Abdelkrim *et al.* 2005a; Abdelkrim *et al.* 2005b; Cowled *et al.* 2006; Robertson & Gemmell 2004). Genetic monitoring provides the ability to distinguish between surviving or reinvading individuals during or post-eradication (Abdelkrim *et al.* 2005a; Abdelkrim *et al.* 2007; Berry & Kirkwood 2010; Russell *et al.* 2010), thereby enhancing the efficiency of eradication campaigns, while reducing economical costs (Abdelkrim *et al.* 2005a; Simberloff 2003).

Thesis outline

Aim of this study

The general aim of my thesis is to investigate the impact of invasive feral cats as well as the underlying population genetic structure, diversity and phylogeography in the context of the demographic history in Australia and Hawai'i. In order to achieve this goal I started with an ecological project evaluating the impact of feral cats in Western Australia on native species communities and the efficiency of introduced predator control. Improvements of predator control in the past ten years and successful feral cat eradication projects on islands (Algar *et al.* 2010; Algar *et al.* 2002), have led to a proposal to eradicate feral cats from Dirk Hartog Island, the largest island off the Western Australian coast. Initially, a pilot trial was conducted to examine cat activity patterns and also to assess baiting efficacy, the primary control technique to be used in the eradication campaign (Algar *et al.* 2011; Johnston *et al.* 2010). DNA analysis of feral cat samples collected on the island incorporated population genetic analysis to enhance the control strategies further and give valuable information on possible biosecurity concerns.

Since domestication of cats, approximately 8,000 years ago, cats have been spread, especially in the last 200 years, intentionally and unintentionally through various vectors (e.g. human migration and exploration, trading), around the globe. The routes of introduction and genetic origin of cats found in Hawai'i and Australia is unclear with most theories discussing an introduction through European explorations and settlement at both locations in the late 18th century. This has inspired the second part of my thesis where I examined the genetic origin and pathways of introduction of Australian and Hawaiian feral cats. Island and remote mainland populations were chosen, since their geographical isolation and limited or non-existing human populations restrict influx of house and stray cats. Additionally, it limits the possible number of cat introductions over time allowing a clearer genetic signal of historically introduced individuals.

In particular, my thesis focuses on the following objectives:

1. Evaluating the impact of introduced predator species (cats and foxes) on the native species community for management purposes:
   - Assessment of the impact and food preferences by introduced feral cats and foxes on local biodiversity (**Chapter 1**).

2. Application of molecular markers (microsatellite and mitochondrial DNA) to study the genetic origin and introduction history of feral cats in Australia and Hawai'i:
   - Establishment of molecular markers for population genetic studies (**Chapter 2**);
   - Applicability of population genetic methods to study genetic diversity and structure among populations for invasive species management (**Chapter 2**);
   - Discussion of the history of cat introduction to Australia and an evaluation of possible introductions prior to European settlement (**Chapter 3**);
   - Estimation of genetic structure, diversity and connectivity of feral cats in Australia (**Chapter 3**);
   - Assessment of genetic ancestry of cats in Hawai'i and gene flow between the islands (**Chapter 4**);
   - Discussion of potential introduction routes of cats to islands in the Pacific and Indian ocean (**Chapter 4**);
   - Assessment of genetic isolation by distance between Hawaiian and Australian island populations (**Chapter 4**).

Chapter overview

The first chapter (**Impact of invasive feral cats and foxes on local biodiversity in the southern rangelands of Western Australia**) presents a study demonstrating the high impact and specialisation of invasive feral cats and foxes on native prey species. It also confirms the efficiency of predator control and a decreased predation pressure with evidence of a possible recovery of native species after two years.

The second chapter (**Population structure and management of invasive cats on an Australian island**) focused on the application of population genetic methods for invasive species management. The genetic analysis provided information about the history of the invasion, the origin and the genetic composition of the island population. Strong connectivity and dispersal abilities on the island and potential gene flow from the mainland until a few years ago have led to high genetic diversity in the feral cat population. In practical terms the findings enhance the strategies for the eradication project and addresses biosecurity concerns.

In the third chapter (**A voyage to terra Australis: human-mediated dispersal of cats**) the genetic origin of feral cats in Australia and offshore islands was investigated and the timeframe of the main introduction events was estimated. An overall European origin was endorsed with settlers and migrating workers for the pearling and whaling industry providing the main historical pathways for cats to Australia. Introduction and establishment of feral cat populations from Southeast Asian locations prior to European settlement in Australia were also examined but were found to be highly unlikely. However, the genetic structure of feral cats suggests that introductions from Southeast Asia have occurred within the past 200 years, with first invasions possible through Malaysian workers in the pearling industry of Western Australia. The genetic differentiation among Australian populations is low, but gives an indication for multiple introductions over time. Genetic ancestry can be assigned with high confidence on islands with a small number of introductions and low intermixture with house and stray cats.

In the fourth chapter (**Feral Cat Globetrotters: genetic traces of historic human-mediated dispersal and recent gene flow**) the genetic origin of feral cats on three Hawaiian Islands was examined. The level of genetic diversity and the possible ongoing intermixing of feral cat populations with domestic fancy breed cats were assessed. As found for Australian feral cat populations, results indicated an overall European ancestry, emphasising the significance of human-mediated dispersal of cats throughout the world. The main introduction period was established to have been within the past 200 years during European explorations and the beginning of global trading. The ‘Golden Round’ of the maritime fur trade between 1785 and 1841 is considered to be the most likely route and explains the lack of genetic isolation by distance of Hawaiian and Australian cat populations. Island with low influx from domestic and feral cats were found to carry a signal making it possible to draw inference on their introduction history and genetic origin.

Chapter 1

Impact of invasive feral cats and foxes on local biodiversity in the southern rangelands of Western Australia

K. Koch, D. Algar, M. Onus, N. Hamilton, B. Streit, and K Schwenk.

ABSTRACT

One of the main threats to the survival of native vertebrate species in Australia is predation by introduced carnivores such as feral cats and foxes. Long-term invasive predator control projects aim to decrease their density in strategic areas on the mainland and thereby reduce pressure on local fauna. We examined fauna survey data in comparison to the diet of cats and foxes in order to determine the impact on native vertebrate species. Altered environmental conditions in 2007 (drought, shifted rainfall period) had a major effect on native species abundance, yet total number of species did not change between years and still showed differences between the study sites. Significant differences in abundance of native species groups between study sites as well as differences in the total number of species indicated a major predatory impact by invasive predators on local fauna. Feral cats and foxes had a distinctive diet and showed a prey selection as well as prey switch toward native vertebrate species thereby underutilizing the introduced and most abundant alternate species (house mouse). Feral cats especially specialised on native bird species which comprised up to 31% of their diet. Overall, our data confirm a higher predation risk for native species compared to non-native mammal species by introduced predators and the tendency of threat reduction by predator control over the short period of two years.

INTRODUCTION

Although Australia is a geographically isolated island continent which had historically remained almost free from introduced mammal species, the start of European settlements in the late 18th century changed its isolation with now approximately 22 mammal species introduced since then (Olsen 1998). Two predators unintentionally and intentionally introduced were cats around 1800 (Abbott 2002; Dickman 1996) and foxes around 1870 (Friend 1990; Kinnear *et al.* 2002; Risbey *et al.* 1999). Today both species are widespread across the islands and mainland of Australia (Abbott 2002; Burbidge & McKenzie 1989; Burrows *et al.* 2003). The introduction of these species into Australia and the successive spread has led to a decline and extinction of a number of small to medium-sized native mammal species (Abbott 2002; Burbidge & McKenzie 1989; Burrows *et al.* 2003). Both predators are considered to be major threatening factors to endangered species by direct predation and through the competition with native predators (Burbidge & McKenzie 1989; Dickman 1996; Environment Australia 1999; Nogales *et al.* 2004; Risbey *et al.* 2000). Population recovery or reintroduction attempts of threatened species have often failed because of extensive predation (Burbidge & Manly 2002; Catling 1988; Environment Australia 1999; Short & Turner 2000; Smith & Quin 1996). Long-term predator control projects aim to eradicate cats and foxes on islands and decrease the density of introduced predators in strategic areas on the Australian mainland (Burrows *et al.* 2003; Environment Australia 1999; Kinnear *et al.* 1988; Kinnear *et al.* 2002; Thompson & Thompson 2007; Thomson & Algar 2000).

The predatory impact of feral cats primarily affects birds and small to medium-sized mammals (Bonnaud *et al.* 2007; Dickman 1996; Fitzgerald *et al.* 1991; Hutchings 2003). Reptiles are only preyed upon when available (seasonally in arid to semi-arid areas) (Jones & Coman 1981; Molsher *et al.* 1999). Feral cats and foxes are generally known as opportunistic predators (Bonnaud *et al.* 2007) and prey selection is determined by individual requirements and prey availability (Saunders *et al.* 2004; Winstanley *et al.* 2003). Several studies have found that during seasonal declines in the abundances of primary prey species, feral cats and foxes switch to alternative prey (Catling 1988; Harper 2004, 2005; Molsher *et al.* 1999; Saunders *et al.* 2004). But although it is generally accepted that invasive cats and foxes are one of the major drivers for local declines of native Australian species (Abbott 2002; Burbidge & McKenzie 1989; Burrows *et al.* 2003), we lack detailed information on the prey selection by introduced predators. The impact of feral cats and foxes on total number of species and species abundance (small to medium-sized mammals and reptiles) was examined using two study sites in two seasons over two years (2006 and 2007) in four different habitat types. This was achieved by comparing an area where sustained control of predators was conducted compared with an area where cats and foxes were not controlled over a two-year period. We examined if diet of cat and fox correlated with prey abundances during fauna surveys or if prey species were strongly selected. Furthermore, we analysed if prey selection resulted in a prey-switch or specialisation toward native species.

In conjunction with this study, other aspects of small vertebrate and invertebrate monitoring that were investigated included small mammal and reptile assemblages (Richards *et al.* 2011a), bird assemblages (Richards *et al.* 2011b) invertebrate assemblages (Guthrie *et al.* 2011) and an overall conclusion (Algar & Richards 2010) were reported elsewhere. This paper focuses on the results of the diet analysis of feral cats and foxes in relationship to prey species abundance and species composition incorporating the previously published data.

METHODS

Study Area

Research was undertaken by the Department of Parks and Wildlife (DPaW) and Australian Wildlife Conservancy (AWC), in partnership with the Invasive Animals Co-operative Research Centre (IA CRC). The study was conducted on DPaW acquired pastoral leases of Karara - Lochada and AWC's Mt Gibson AWC Wildlife Sanctuary. Mt Gibson was the treatment (baited) site and Karara-Lochada (henceforth referred to as Karara) the control (non-baited) site (Algar & Richards 2010; Richards *et al.* 2011a; Richards *et al.* 2011b). Both study sites are located approximately 400 km north-east of Perth (29°10'S and 116°40'E) (see Fig. 1) in the mulga-eucalypt zone of Western Australia and cover an area of approximately 130,500 ha. The area is characterised by a semi-arid climate with hot summers and mild, wet winters with temperatures ranging from 19-38 °C in summer to 6-18 °C in winter. There are 9-11 months of dry weather with an annual rainfall of 250-350 mm. Land systems and vegetation associations within Karara and Mt Gibson equal to each other (Algar & Richards 2010; Richards *et al.* 2011a; Richards *et al.* 2011b).

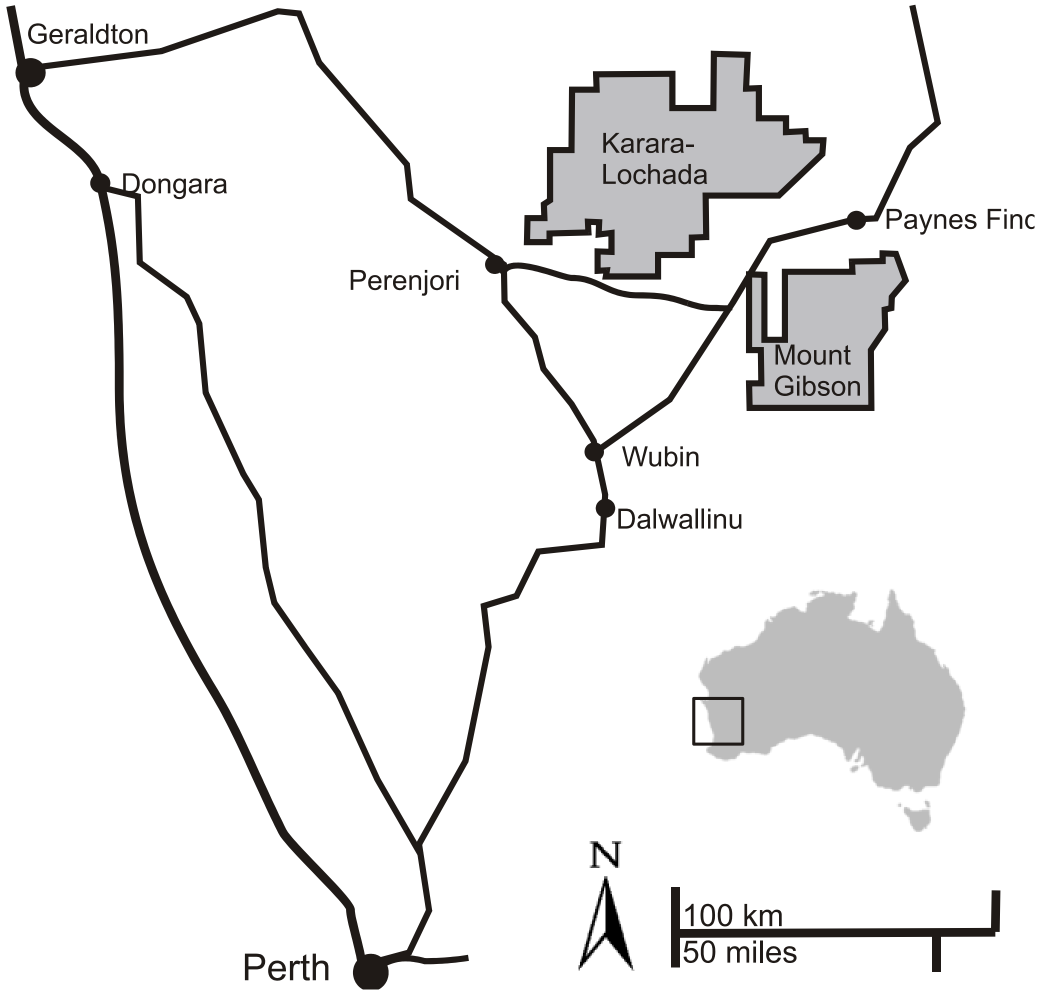

Figure 1-1. Location of trapping sites Karara – Lochada (no predator control) and Mt Gibson (predator control) approximately 400 km northeast of Perth in Western Australia.

Predator control

Fox control was conducted on Mt Gibson between 2004 and 2005 by AWC using dried meat baits with 1080 (sodium monofluoroacetate) laid by hand throughout the sanctuary. In Karara, the 'control' site, both predators were assumed to be abundant since minimal predator control had been conducted on the pastoral lease prior to this study and mostly by neighbouring pastoral lessees in an *ad hoc* manner to bait wild dogs. (*Canis familiaris*) An aerial baiting program was conducted at Mt Gibson Sanctuary between July 2006 and August 2007 with pre- and post-baiting surveys used to establish baiting efficiency. In total 70,000 poisoned *Eradicat*® baits were aerially distributed annually over the entire pastoral lease. Effectiveness of the baiting regime was measured pre- and post-baiting using a track density index. The reinvasion rate was measured on Mt Gibson after baiting stopped at the end of 2007.

Fauna survey

Fauna surveys were conducted twice each year for two years. In winter (20–24 June 2006, 11–15 July 2007 at Mt Gibson and 26–30 June 2006, 6–10 July 2007 at Karara), just prior to aerial predator baiting to assess potential prey abundance at its lowest. The second surveys were conducted in spring (25–29 September 2006, 3–7 October 2007 at Mt Gibson and 19–23 September 2006, 23–27 September 2007 at Karara), when populations had potentially received an influx of new recruits after breeding (Algar & Richards 2010; Richards *et al.* 2011a; Richards *et al.* 2011b). The abundance of small mammals and reptiles was monitored using a grid of pitfall and Elliott traps as described in Algar & Richards (2010) and Richards *et al.* (2011a). Survey sites were located in the four major land systems: Yellow Sand (Joseph), Salt Lakes (Euchre), Open Plain (Pindar) and Granite (Carnegie) (categorised by Department of Agriculture and Food Western Australia 1990) with three replicates in each. Elliott traps were removed from sites between surveys and bucket lids placed over the pitfall traps.

Pitfall and Elliott traps were opened for five days per survey and cleared at sunrise each day. Morphological measurements (species, weight, sex, head-body length, tail length, reproduction condition) were recorded for captured animals, which were temporarily marked with a marker pen and immediately released within 10 m of the point of capture.

Bird surveys were carried out during the five days of small mammal trapping. The surveys were conducted by two researchers in each land system of the small mammal grids. In total, 24 quadrats each of approximately 16 ha, were surveyed. Surveys were conducted an hour after dawn and an hour prior to dusk to determine species presence/absence at each quadrat (Richards *et al.* 2011b).

Cat and fox trapping at Karara

Trapping of cats and foxes was conducted at Karara simultaneously to the fauna survey in winter and spring of 2006 and 2007. The trapping technique used padded leg-hold traps; Victor 'Soft Catch'® traps No. 3 (Woodstream Corporation, Lititz Pa.; U.S.A.). Lures used consisted of a Felid Attracting Phonic (FAP) that produces sounds of a cat call and a blended mixture of faeces and urine. Trap sets were located at approximately 500 m intervals adjacent to the vehicle access tracks with approximately 10-15 traps set per transect depending on available trap sites. The trap locations were established in the four land systems as well used for fauna surveys. Transect locations were always at least 5 km distant to the small mammal trapping grids. Trap sets were recorded with a Garmin GPS 76. Caught animals were euthanized with a 0.22 calibre rifle and their sex, weight and broad estimation of age (as either kitten/cub, juvenile or adult) was recorded. The pregnancy status of females was determined by examining the uterine tissue for embryos. Stomach contents were collected if present and frozen for diet analysis.

Analysis of stomach content and estimation of diet

Stomach material was washed in fine sieves (1,700, 500 and 250 μm) and sorted under a stereo-microscope. Remains from mammalian prey were identified from bones, feet, claws or from microscopic analysis of hairs using cross-section and whole-mount technique (Brunner & Coman 1974) and Hair ID (Software by Ecobyte Pty Ltd CSIRO publishing). Taxonomic classification of the *Sminthopsis* genus was based on methods developed by Brunner and Coman (1974), Archer (1981) and Kitchener *et al*. (1984). Birds were assigned to order by an ornithologist, mainly identified from feather remains and in some cases identified to species level by claw, feet or diagnostic feather patterns (pers. comm. N. Hamilton). Reptiles were identified using various identification keys (Storr *et al.* 1983; Storr *et al.* 1986, 1990, 1999) and invertebrates were grouped by order based on exoskeleton remains (Guthrie *et al.* 2011).
Estimation of the mean individual weight of prey species for each season was based on data obtained from the small mammal and reptile trapping surveys (hereafter referred to as fauna surveys). Unless remains could be identified to species level, generic characteristic weights were assigned to prey types. For example, the representative mean weight of a Passeriforme bird was derived from all passerine species recorded in the study area and equalled 50.45 g. For bird remains, which were identified to species level, we applied their average specific weight for further calculations (Slater 1990). Large prey items (greater than 500 g) were assumed to have provided more than a single meal for a cat/fox and were therefore scored as 185 g (Harper 2005). A prey weight of 2 g and 1 g was used for centipedes and grasshoppers respectively, the two main dietary invertebrates.

Statistical analysis

A test for significant differences in the species richness was conducted using an analysis of variance (ANOVA). Main effects were *study site* (Karara and Gibson), *habitat* (Open Plain, Salt Lake, Yellow Sand, Granite), *season* (July and September) and *year* (2006 and 2007). Species richness represented the dependent variables. Statistica 6.1 (2000) was used to conduct all analysis of variance.

The probability that predators feed selectively was examined using Chi^2 tests. The analysis tested the hypothesis that selective feeding was controlled by prey species abundances. The total numbers of prey species (per category) found in the diet (by predator species and season) were compared with the total numbers of prey species recorded in the fauna survey (pooled across years, separate for both seasons). A second analysis tested if numbers of individuals in defined species groups (i.e. Marsupials, Native Rodents, Invasive Rodent, Reptiles and Birds) differed between both sites using Chi^2 analysis. Chi^2 tests were conducted using PopTools Version 3.0 (Wildlife and Ecology, CSIRO, Canberra, Australia) an add-in for Microsoft Excel®.

Further analysis compared number of individuals per prey species in feral cats and foxes diet with the number of individuals per species recorded during fauna surveys for two seasons (spring, winter) and both years (2006, 2007) using a Chi^2 test.

RESULTS

We incorporated results of a previous study that recorded a total of 1,070 mammal specimens during fauna surveys over a two-year period (Richards *et al.* 2011a). Of these mammal species Mt Gibson apportioned n = 667 individuals and Karara n = 403 (Richards *et al.* 2011a). Additionally a total of 44 reptile species and 94 bird species were documented (Richards *et al.* 2011a; Richards *et al.* 2011b). The most dominant species in both study sites (2006-2007) during the fauna surveys were house mice (*Mus musculus)* (N = 157). A total of 24 feral cats and 39 foxes were trapped in the winter and spring of 2006 and 2007.

Track density index analysis of track counts conducted every three month showed limited reinvasion onto the Mt Gibson site six months post-baiting. Foxes dispersed into the area during the late summer/early autumn annually; but cat numbers were not measurable. Overall very low levels of invasive predators in the baited site were observed.

An analysis of variance (ANOVA) (Table 1-1) showed significant differences in species composition between both study sites for the factors *year, season* and *study site*. Significant interactions were found for *season*study site* and *habitat*study site*.

Additional analysis compared species richness pooled over all habitats in both sites revealing less species in Karara (mean = 7 in 2006, mean = 6.8 in 2007) than in Gibson (mean = 8.2 in 2006, mean = 8 in 2007). Differences were even greater in two habitats (Granite and Open Plain, pooled over both years), revealing that the total number of species recorded (mammals and reptiles) was much lower in Karara (8 and 9.5, respectively) than Gibson (12.5 and 14 respectively).

Table 1-1. Comparison of species composition between Gibson and Karara for two years (2006 and 2007) among four habitats and two seasons. Significance tests are based on an ANOVA analysis. The *P* values of significant results are highlighted in bold.

	f	F	*P* value
Year	1	7.88	**0.006**
Season	1	129.28	**<0.001**
Study site	1	16.57	**<0.001**
Habitat	3	2.22	0.094
Year*Season	1	0.17	0.675
Year* Study site	1	0.17	0.675
Season* Study site	1	9.53	**0.002**
Year*Habitat	3	1.27	0.290
Season*Habitat	3	0.66	0.577
Study site *Habitat	3	4.39	**0.007**
Year*Season* Study site	1	0.31	0.576
Year*Season*Habitat	3	0.71	0.546
Year* Study site *Habitat	3	1.18	0.321
Season* Study site *Habitat	3	1.61	0.194
Year*Season* Study site *Habitat	3	2.00	0.121

Furthermore the comparison of total number of individuals belonging to a predefined species group (Table 1-2, Figure 1-2) showed highly significant differences between the study sites for the groups: marsupials and native rodents (2006) and invasive / native rodents (2007).

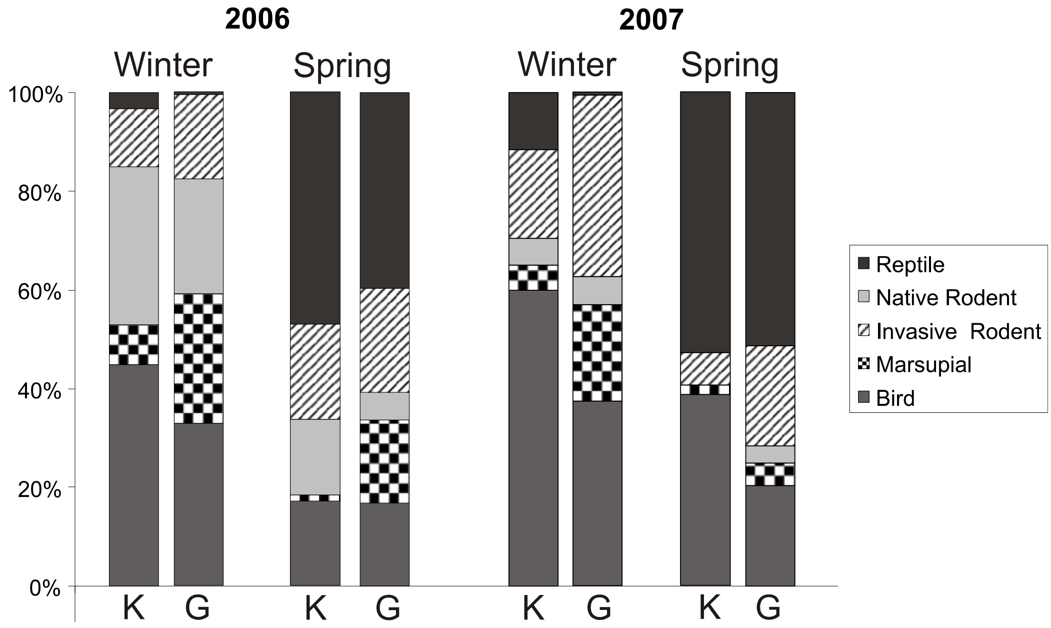

Figure 1-2. Percentage of number of individuals for 2006 and 2007 belonging to a predefined species group: reptile, native rodent, invasive rodent, marsupial and bird at K = Karara-Lochada (no predator control) and G = Mt Gibson (predator control).

Table 1-2 A Chi^2 test was performed to compare the number of individuals belonging to a predefined species group (Birds, Marsupials, Invasive Rodents, Native Rodents and Reptiles) in 2006 and 2007 in Karara (no predator control) and Mt Gibson (predator control). *P*-values in the button row indicate differences between 2006 and 2007 separately for each study site. *P*-values in the row on the right indicate difference between the study sites separately for both years. Total number of individuals shows all animals caught during fauna surveys in Karara and Gibson in 2006 and 2007 excluding the species group birds while including amphibians.

		Karara		Gibson		
		Winter	Spring	Winter	Spring	*P*-value
2006	Bird	56	40	58	54	0.34
	Marsupial	10	3	46	54	**0.03**
	Invasive Rodent	40	36	41	19	0.06
	Native Rodent	15	45	30	67	**<0.01**
	Reptile	4	111	1	128	0.14
	Total number of individuals	264		388		
		Winter	Spring	Winter	Spring	*P*-value
2007	Bird	47	67	53	48	0.09
	Marsupial	4	3	28	10	0.41
	Invasive Rodent	4	0	8	9	**0.03**
	Native Rodent	14	11	52	47	**0.03**
	Reptile	9	90	1	120	0.34
	Total number of individuals	139		279		
	P-value	**<0.01**	**<0.01**	**<0.01**	**<0.01**	

Feral cat and foxes diet

Stomach analyses of feral cats and foxes indicated 176 prey items to be present (cats n = 32, fox n = 144) (Table 1-3). Grasshoppers supplemented the diet of feral cats and foxes in spring (46% cats, 80% foxes) while centipedes were the major invertebrate group represented in their diet in spring (16% cats, 6.3% foxes). The main prey species for cats were birds comprising 31% of their diet in spring and 26% in spring. We found that feral cat predation on birds was primarily on young (nestlings), juveniles and mainly on ground-dwelling or low-dwelling bird species. The most important mammalian prey in spring was *Notomys sp* (21%). This species was not detected in their diet in spring; instead they preyed on *Sminthopsis sp* (15%). Foxes focused their diet mainly on reptiles (up to 13% in spring) and carrion (up to 31% in spring). By contrast cats rarely choose reptiles as prey and no carrion species were detected. Two Short-beaked Echidna (*Tachyglossus aculeatus*) were found in the stomachs of two foxes, with a few spines piercing through the wall of the stomach.

Table 1-3. Percentage of total number of species in the diet of cats and foxes pooled for 2006 and 2007. Aves comprise passerine and parrot species, reptiles comprises skinks, geckos and small dragon species, carrion comprises kangaroo species and sheep.

	Cat		Fox	
Season	Winter	Spring	Winter	Spring
Sample Number Predator	14	10	11	28
Aves	26 %	31 %	11 %	2.3 %
Reptiles	5.3 %	7.7 %	13 %	6.3 %
Carrion			31 %	3.1 %
Sminthopsis sp	5.3 %	15 %	19 %	3.1 %
Notomys sp	21 %			0.8 %
Mus musculus	5.3 %		6.3 %	
Pseudomys hermannsburgensis	5.3 %			1.6 %
Oryctolagus cuniculus	11 %			2.3 %
Grasshopper	5.3 %	46 %		80 %
Tachyglossus aculeatus			6.3 %	0.8 %
Centipedes	16 %		6.3 %	
Total number of prey items	19	13	19	128

The comparison of number of individuals found as prey of cats and foxes versus number of individuals per species recorded during fauna surveys revealed highly significant differences between diet and potential prey for all seasons and years (Table 1-4).

Table 1- 4. A Chi^2 test was performed to compare the number of individuals per prey species in feral cats and foxes diet against the number of individuals per species recorded in fauna surveys in two seasons (spring, winter) and both years (2006, 2007).

Year	Predator	Season	Chi^2 (Pearson's)	f	*P*
2006	Cat	Winter	134.2	18	**<0.01**
	Fox	Winter	113.4	16	**<0.01**
	Cat	Spring	41.8	5	**<0.01**
	Fox	Spring	158.6	11	**<0.01**
2007	Cat	Winter	20.2	10	**0,02**
	Fox	Winter	79.5	18	**<0.01**
	Cat	Spring	18	7	**<0.01**
	Fox	Spring	27	12	**<0.01**

DISCUSSION

Small mammal abundance, especially of rodents, is heavily influenced by rainfall and displays a delayed numerical increase in population size from altered or exceptional rainfall events (Dickman *et al.* 1999; Newsome & Corbett 1975). Additionally, access to shelter, food and water are the principal factors for animal survival and maintenance of breeding (Beatley 1969; Degen 1997; Prakash & Gosh 1975). Richards *et al.* 2011 suggested that the decline in total number of individuals recorded at both study sites (Karara and Gibson) between 2006 and 2007 is most likely caused by severe impact of environmental conditions. This is also shown in significant differences for the factors year and season in the analysis of variance in this study. Significant changes in the community composition are most likely caused by seasonal periodicity of species (e.g. poikilothermic) that are most abundant in warm summer month (Paltridge & Southgate 2001). However, environmental influences such as rainfall or seasonal community abundance shifts are not the only explanation for the significant interaction for the factors study site * habitat. This interaction shows that the impact of predators on biodiversity differs severely between habitats. This may be due to differences in the applicability of individual predator hunting styles (Catling 1988; Read & Bowen 2001) in the varying vegetational coverage of the four habitats. Additionally analysis of total number of species showed that their numbers differed between the study sites independently from the year. Especially native species groups (Marsupials, native rodents) showed significant differences in their abundance between both sites. Results of the fauna survey analysis suggested an overall positive trend of possible species recovery after the two year period of fauna survey and predator control (Algar & Richards 2010). Consequently, our data and the results of the study by Algar and Richards (2010) are in line with recent studies, which found significant predatory impacts on species richness and species abundances (Pavey *et al.* 2008; Pontier *et al.* 2002; Read & Bowen 2001).

Both predators were found to supplement their diet with centipedes and grasshoppers, but otherwise diets diverged considerably. While cats' diet were mainly composed of bird and native vertebrate species, foxes ate mainly reptiles, carrion and various vertebrate species. The small component of reptile and lack of carrion species in cats' diet compared with that of foxes is consistent with the findings of other studies (Jones & Coman 1981; Martin *et al.* 1996; Paltridge & Southgate 2001; Risbey *et al.* 1999). Foxes are highly opportunistic omnivores and scavengers with a lack of special food requirements (Catling 1988; Read & Bowen 2001; Saunders *et al.* 2004), which is also displayed in their prey choice recorded in our study. They were found to fed on Short-beaked echidnas even though their spikes caused severe injuries to the wall of the stomach. Cats however, are assumed to be specialized on available prey with just a few species representing the majority of its diet (Bonnaud *et al.* 2007). Our results showed that cats' specialization included various bird species composing up to 31% of their diet. This level of predation on birds is above any previously documented level of around 10% (Hutchings 2003; Read and Bowen 2001, A.H. Burbidge, DPaW personal communication). The occurrence of introduced predator species has been responsible for the significant decline and extinction of native birds on various islands (Atkinson 1985; Blackburn *et al.* 2005; Bonnaud *et al.* 2007), with ground-nesting birds being particularly susceptible (Sanders & Maloney 2002). Prey selection focused besides birds on native mammal and marsupial species, although the most dominant species was the house mouse.

A review of 72 studies on insular feral cat diets by Bonnaud *et al.* (2011) described several studies in which introduced rodents were regular prey items (Fitzgerald *et al.* 1991; Medina & Garcia 2007). However, cats have been found to switch among alternative prey species when their primary prey is sparse or the alternative prey is high in presence (Bonnaud *et al.* 2007; Harper 2005; Molsher *et al.* 1999; Peck *et al.* 2008). An individual house mouse was found in the diet of a cat over the two year period being divergent to the abundance of the species found in the fauna survey in 2007. Even foxes which seem to have fed opportunistically on all accessible prey still underutilized this highly abundant prey. These findings indicate that both predators have individual prey preferences and show a prey-switch toward native vertebrate species despite their co-invaded natural prey species. A review on invasive cats impact on island vertebrates (Medina *et al.* 2011) examined the influence of introduced alternate prey species. The meta-analysis for bird species, suggests a significantly increased impact of feral cats on birds in the presence of alternative introduced prey (Courchamp *et al.* 2000; Medina *et al.* 2011). We conclude therefore that predator control is an important factor for conservation of species considering that a specialized prey selection increases the threat on endangered species even further.

CONCLUSION

Our analyses confirmed that environmental conditions are accountable for many shifts in species abundance. However the predatory impact on biodiversity through differences in the total number of species between both study sites as well as differences in bird species assemblage (Richards *et al.* 2011b) was proven. Furthermore, we found that feral cats and foxes selectively feed on native vertebrates neglecting their "co-invaded" prey species and thereby increasing the threat on the natives. Overall, we found that predator control through aerial baiting can reduce the threat on native species resulting in their higher abundance during a period of two years.

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Chapter 2

Population Structure and Management of Invasive Cats on an Australian Island

K. Koch, D. Algar and K Schwenk.

ABSTRACT

Invasive predators have a major impact on endemic island species; therefore, information about invasion dynamics are 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. Since detailed records of historical introduction events were lacking, we analysed 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 adjacent 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 G''_{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.

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INTRODUCTION

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

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 (Abbott & Burbidge 1995; Baynes 1990; Burbidge & Manly 2002; McKenzie *et al.* 2000). Since 1860, the island has been managed as a pastoral lease and grazed by sheep (*Ovis aries*) and goats (*Capra hircus*; Burbidge & 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 2001; Burbidge & George 1977). 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 & Burrows 1995; Gibson *et al.* 1995; Medina *et al.* 2011; Myers *et al.* 2000a). The most effective method for controlling feral cats is aerial baiting, if non-target species are not at risk (Algar & Brazell 2008; Algar & Burrows 2004). 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 (Abdelkrim *et al.* 2005a; Abdelkrim *et al.*

2007; Hansen *et al.* 2007; Robertson & Gemmell 2004). 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 km^2 (Figure 2-1). We conducted our study over a 400-km^2 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 (Algar *et al.* 2011; Johnston *et al.* 2010); 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–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).

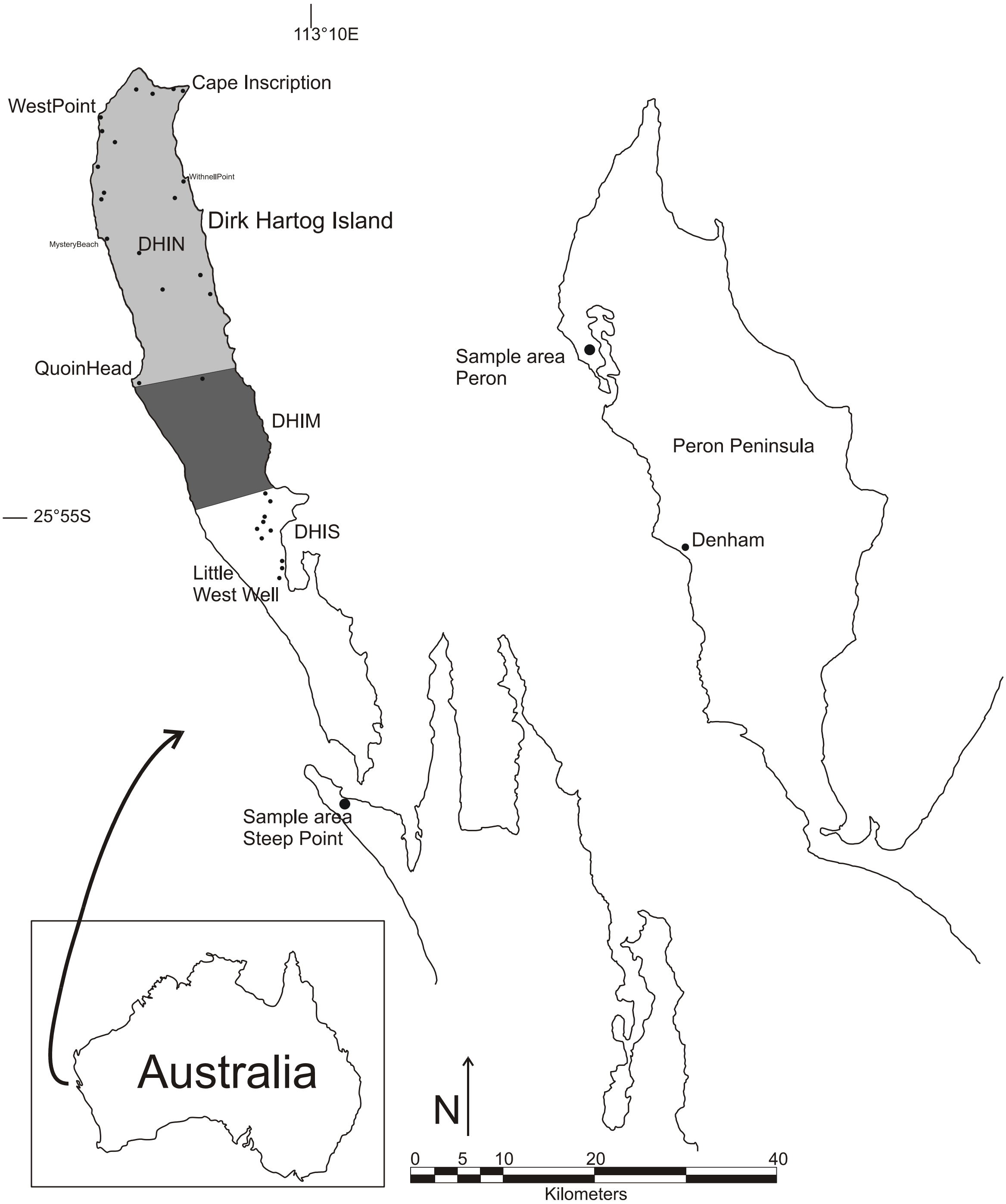

Figure 2-1. Study area on Dirk Hartog Island in Western Australia with 3 sampled areas: northern (DHIN) shaded in light grey, middle (DHIM) shaded in dark grey and southern trapping area (DHIS) not shaded. Feral cat trapping locations (2009 or 2012) on Dirk Hartog Island are indicated by small dots for 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.

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 & 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-astrophic, 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.* 2012; Menotti-Raymond *et al.* 2005). 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 sec, 60° C decrease −0.5° C per cycle for 60 sec, 72° C for 2 min; followed by 20 cycles: 94° C for 15 sec, 50° C for 60 sec, 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 (π) in DNASP V5.1. (Librado & 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 relatedness using the relatedness estimator (Queller & Goodnight 1989) implemented in GENALEX 6.5 (Peakall & Smouse 2012; Supporting Information 2). We calculated population genetic parameters, such as allele frequencies, allelic richness, and F_{IS} coefficients (Weir & 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 10 independent runs for each *K* ($K = 1$ to 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 ΔK using Structure Harvester (Earl & vonHoldt 2012). We used GENALEX 6.5 (Peakall & 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 & Hedrick 2011) using GENALEX 6.5 (Peakall & 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 (*N*e) 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_O), respectively (Table 2-1). 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 2-1). We were able to successfully sequence 53 individuals of the 59 samples of 5 sampling locations for mitochondrial ND5 and ND6 genes.

Table 2-1. 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_o), expected heterozygosity (H_E), inbreeding coefficient ($\mathrm{F_{IS}}$), $\mathrm{F_{IS}}$ P-values (random $\mathrm{F_{IS}} \geq$ observed $\mathrm{F_{IS}}$), private alleles per population (PA), allelic richness averaged per locus and population (R_S), 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).

	DHIN	DHIM	DHIS	PE	SP
N	20	11	9	13	6
NA	7	6	6	6	5
H_o	0.73	0.69	0.74	0.75	0.69
H_E	0.73	0.75	0.73	0.78	0.77
$\mathrm{F_{IS}}$	0.018	0.07	0.007	0.05	0.05
$\mathrm{F_{IS}}$ P	0.36	0.17	0.51	0.13	0.31
PA	6	7	7	11	11
PA/N	0.3	0.63	0.77	0.84	1.83
R_S	4.7	4.5	4.6	4.9	5.3
Ne		88.1		22	7.4
Ne approx. 95% CI		65.8–129.1		16.2–32.8	5.2–11.8

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 to 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%; Figure 2-2). Among all samples, h was 0.568 (±0.066) and π was 0.0011. The mean number of nucleotide differences between haplotypes was 1.53 and ranged from 0 to 1.8 (Table 2-2).

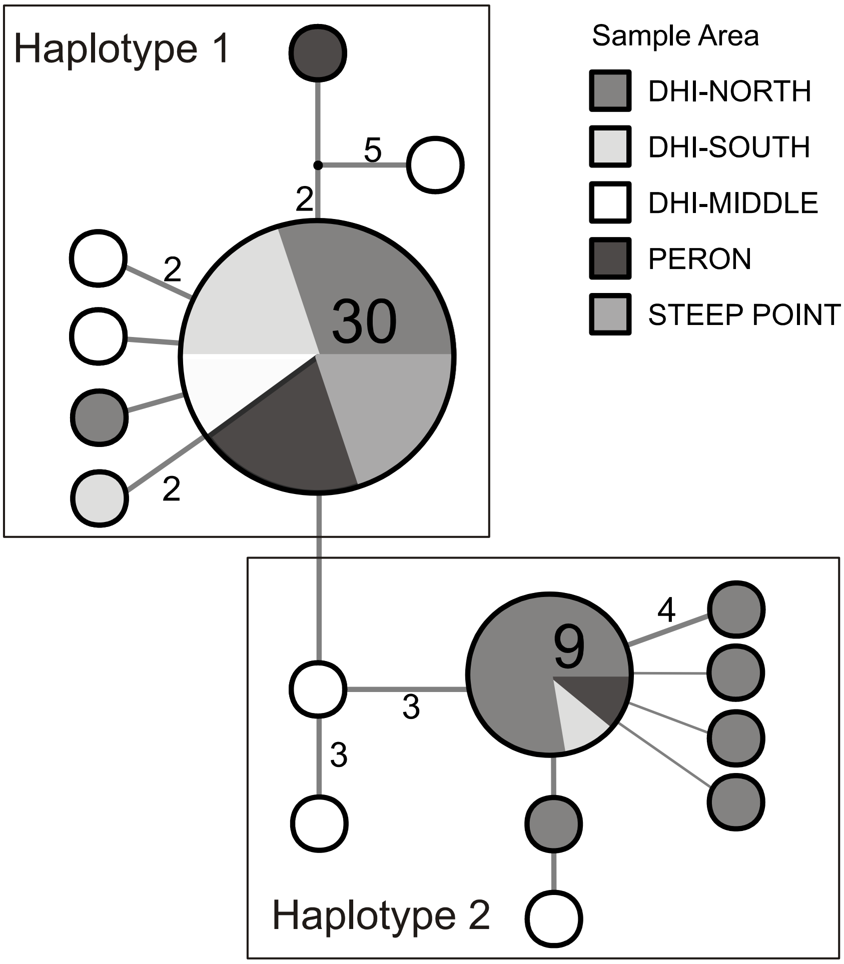

Figure 2-2. Haplotype network including 59 feral cat samples from mainland Australia (Peron and Steep Point) and Dirk Hartog Island (DHI) collected in 2009 and 2012. Numbers in circles indicate number of individuals assigned to that haplotype. Circles without numbers indicate only a single individual 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 2-2. 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).

Population	DHIN	DHIM	DHIS	PE	SP
n	22	9	8	8	6
H#	4	2	5	3	1
h	0.61	0.25	0.80	0.46	0
π	0.00126	0.00054	0.00133	0.00072	0

We calculated relatedness estimates with 2 different approaches resulting in similar patterns (Table 2-3, 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 (1468 unrelated, 409 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 2-3).

Table 2-3. Relationship of individual (ind) 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). Putative relationship (PR; either HS = half sibling or FS = full sibling) between 2 individuals compared to an alternative relationship category (U = unrelated, FS = full sibling, and PO = parent-offspring). We found a single putative FS relationship between individuals from PE and DHIS with alternative relationship categories HS, U, and PO. Significant *q*- values after multiple comparison using false discovery rates (FDRs) indicate rejection of alternative relationship hypothesis.

		PR	*q*-values for alternative relationships		
Ind 1	Ind 2		U	FS	PO
PE 1	DHIS 22	HS	0.05	0.002	< 0.002
PE 1	DHIS 23	HS	0.09	0.002	< 0.002
PE 8	DHIN 3	HS	0.09	0.002	< 0.002
PE 8	DHIS 22	HS	0.09	0.002	< 0.002
PE 9	DHIS 26	HS	0.09	0.002	< 0.002
PE 9	DHIM 35	HS	0.09	0.002	< 0.002
SP 4	DHIN 22	HS	0.09	0.002	< 0.002
SP 5	DHIN 14	HS	0.09	0.002	< 0.002
SP 5	DHIN 22	HS	0.11	0.006	< 0.002
SP 5	DHIM 36	HS	0.12	0.011	< 0.002
PE 1	DHIS 28	FS	0.12	HS = 0.02	< 0.002

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 (Figure 2-3).

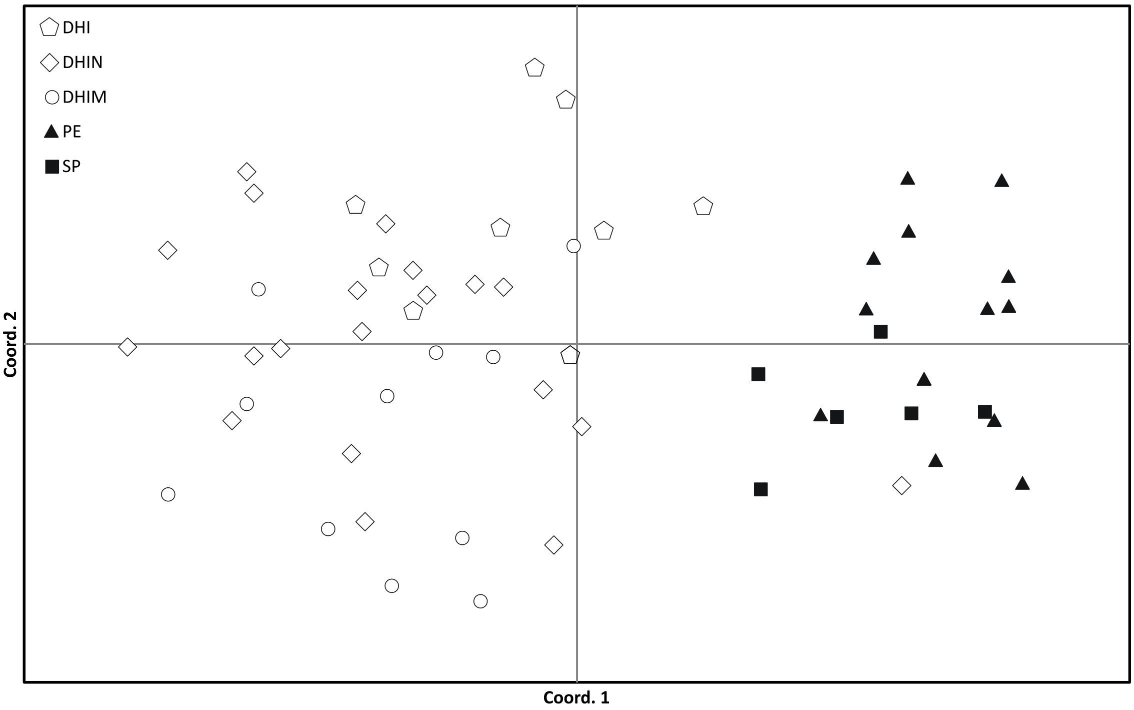

Figure 2-3. Principal coordinates analysis (PCoA) plot indicating genetic distances between individuals from 5 populations of feral cats in Western Australia in 2009 and 2012. The PCoA is based on co-variance distance matrix values using microsatellite data. Filled symbols indicate mainland populations. 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.

Overall, the first and second axes explained 32% and 16% of the overall genetic distances, respectively. Pairwise G''_{ST} values between the 5 populations ranged from 0 to 0.57 with all comparison except DHIM and DHIN were highly significant (Table 2-4). We found no recent bottleneck in any population, and values for effective population sizes (*N*e) ranged from 7.4 to 88.1 for Peron Peninsula, Steep Point, and DHI (Table 2-1).

Table 2-4. 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.

	DHIS	DHIN	DHIM	PE	SP
DHIS		*	*	*	*
DHIN	0.11		–	*	*
DHIM	0.16	0.00		*	*
PE	0.41	0.54	0.57		*
SP	0.54	0.55	0.56	0.37	

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 (HO = 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 since 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 & Lundquist 2003; Dlugosch & Parker 2008; Fitzpatrick *et al.* 2012; Kolbe *et al.* 2004). Early pastoralist likely first introduced cats onto DHI around 1860 when the island was used for farming sheep and goats (Burbidge 2001; Burbidge & George 1977) 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

(Abbott 2008; Burbidge & George 1977) 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''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 (Algar *et al.* 2007; Short *et al.* 1994). However, the genetic impact of a bottleneck is reduced through rapid recovery and expansion or new immigrants, which is especially found in invasive populations (Cornuet & Luikart 1996; Nei *et al.* 1975) and therefore applicable to our results.

The reproductive biology and life history of feral cats allows great potential for population recovery (Myers *et al.* 2000a). 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 km^2 for male and 7.8 km^2 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 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 (Algar *et al.* 2011; Johnston *et al.* 2010). These techniques provide information to support and improve invasive species management strategies.

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Chapter 3

A voyage to Terra Australis: human-mediated dispersal of cats

K. Koch, D. Algar , J. Searle, M. Pfenninger and K Schwenk.

ABSTRACT

Domestic and ship cats have been transported as human commensals around the world, especially in the last 200 years. They have given rise to populations of feral cats in many places. The feral population in Australia is believed to have led to the decline and extinction of native mammal species, but until now the time and origin of the cat introduction into Australia is unclear. Here we investigate the history of arrival of cats to Australia, considering the possibility that this was pre- or post-European settlement, and the potential for admixture. We analyse the genetic structure and diversity of feral cats from six locations on mainland Australia and seven offshore islands as well as samples from Malaysia and Europe using microsatellite and mitochondrial DNA data. Our data suggest that cats in Australia originated from Europe with possible isolated cases of invasions from Asian locations. We find low genetic differentiation between samples from Dirk Hartog Island, Flinders Island, Tasman Island and Cocos (Keeling) Island (Australian Indian Ocean Territory).

Historical records suggest that introduction of cats to these islands occurred at the time of exploration and in connection with the pearling, whaling and sealing trades at the beginning of the 19th century. On-going influx of domestic cats into the feral cat population is causing the Australian mainland populations to be genetically differentiated from those on Dirk Hartog, Tasman and Flinders Islands, which exhibit remnants of the historically introduced cat genotypes.

INTRODUCTION

The deliberate or accidental translocation of species from their native habitat to new environments by humans (Elton 1958; Vitousek *et al.* 1997; Vitousek *et al.* 1995) may trigger substantial environmental consequences (Mack *et al.* 2000; Williamson 1996). The extent of invasions and their consequences for native biodiversity as well as their economic impact has been in the focus of many ecological and conservation-related studies (Elton 1958; Lodge 1993; Vitousek *et al.* 1996). Approximately 40 % of the species listed as threatened or endangered under the Endangered Species Act of the US are considered to be primarily at risk through competition with or predation by invasive species (Wilcove *et al.* 1998). Although the majority of biological invasion events have occurred during recent decades, there are some species that became widely distributed invasives across the globe more than 100 years ago. Feral cats belong to this group of species; cats have had long-lasting and stable invasive populations over large geographical areas. They have had a detrimental impact on native wildlife and are a factor in declines of bird, mammal and reptile species (Bonnaud *et al.* 2011; Fitzgerald 1988; Medina *et al.* 2011). As a consequence, invasive feral cats are considered as a key threatening species under the Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999.*

To be clear what is meant by ‘feral’, cats may be grouped into three categories: *Feral cats* (1) are defined as free-living, independent of humans and reproducing in self-perpetuating populations. *Stray cats* (2) however rely to a small extent on human provision, such as urban fringe situations (rubbish tips). These were originally domestic housecats cats that went astray and now refrain from direct human contact. The third category comprises of *domestic housecats* and fancy breed cats (3) these cats depend almost entirely on humans (Dickman 1996; Moodie 1995).

Clearly, although feral cats do not depend on humans, the feral cats in any particular area derive from cats that have had a closer contact with humans. In considering the introduction of cats into an area, humans must have transported them (usually by boat). The earliest recorded boat transport of cats by humans is extremely ancient: 9500 years ago from the Near East to Cyprus (Vigne et al. 2004). Cats were likely domesticated around 11000 years ago in the Near East in association with early human settlements, and the need to control rodent pests (Driscoll *et al.* 2009; Driscoll *et al.* 2007). Since then, because rodents are constant unwelcome travelling companions of humans wherever they have travelled by boat (Jones *et al.* 2013), this has provided a food source for cats on the same vessels, whether those cats were taken deliberately or as stowaways. This has fostered the dispersal of cats, resulting in a global distribution covering most continents and even remote islands (Bonnaud *et al.* 2011; Courchamp *et al.* 2003; Driscoll *et al.* 2007; Vigne *et al.* 2004). In the last 200 years in particular, domestic cats have been actively transported on sailing vessels of explorers, sealers, whalers and colonists either for controlling rodents or as pets first on board and later in new settlements (Courchamp *et al.* 2003; Dickman 1996; Todd 1977). Clearly, populations of feral cats can derive from this deliberate transport, or from those cats that may have been transported accidentally - as one could imagine happened quite frequently with large sailing vessels.

The Australian fauna, which harbours a large number of endemic species, has been much impacted by feral cats. Predation by feral cats is considered one of the major factors responsible for the decline and extinction of a number of native small to medium-sized vertebrate species (Abbott 2002; Burbidge & McKenzie 1989; Burrows *et al.* 2003; Koch *et al.* in press) as well as reducing their ability to recover (Catling 1988; Environment Australia 1999; Short & Turner 2000; Smith & Quin 1996). The origin and pattern of invasions of cats into Australia is unresolved (Abbott 2002; Abbott 2008; Burbidge *et al.* 1988; Dickman 1996; McKay 1996). Two main hypotheses have been put forward, the first suggests a relatively recent introduction with European explorers and settlers in the late 18th century (Abbott 2002; Dickman 1996). A second hypothesis suggests that cats were brought to Australia prior to European settlement possibly on shipwrecks in Western Australia around 1600, with Malaysian trepangers from about 1650 in northern Australia or even earlier with the introduction of the dingo (*Canis lupus dingo*) around 4500 years ago. (Abbott 2002; Burbidge *et al.* 1988; Macknight 1976; McKay 1996; Oskarsson *et al.* 2012; Robert 1972). The two studies by Abbott (2002; 2008) discuss the origin and spread of cats in Australia based on historical documents mainly covering the period of the early exploration (1788-1883). He precluded an introduction prior to European settlements *inter alia* by reference to the absence of cats in the detailed records of early explorers before 1806 and speculated that the dispersal rate and survival rate of any founding individuals from Asia before 1806 would have been too low for a successful establishment.

We propose a third hypothesis: admixture of cats firstly introduced from Asia with cats from secondary multiple introductions at various occasions by European settlers (Abbott 2002) and continuously since then through stray housecats from mixed geographic origin (Australian Social Trends, 1995, Australian Bureau of Statistics). In order to unravel the evolutionary history and dispersal patterns of Australian feral cats, we applied a phylogeographic approach to the Australian mainland and also offshore islands. Theoretical and empirical studies have shown that hybridization and intermixing through multiple introductions (Allendorf & Lundquist 2003) is less likely to occur on islands than in comparable mainland populations. Thus, island populations may suffer from low genetic variability and may exhibit a gene pool highly similar to the gene pool of the original founder population (due to little or no intermixing with other populations).

We therefore analysed samples from six mainland and seven island locations including Australian Indian Ocean Territories (Christmas Island and Cocos (Keeling) Island; hereafter referred to as Cocos Island) as well as samples from Malaysia and Europe.

Microsatellite and mitochondrial DNA data were used to address the following specific questions regarding origin, genetic structure and diversity of feral cats across Australia: (i) do Australian cats share alleles and haplotypes with European and/or Asian populations and (ii) what is the genetic population structure and how many genetically distinct groups exist across Australia? The findings of this study are discussed in the context of historical reports about the early exploration and settlements in the Australasian region.

METHODS

Cats sampled across Australia and all other locations, except Tip South West and Malaysia, corresponded to the definition of *feral cat*. Individuals of the Tips South West location (TSW) represent house or stray cats including descendants of fancy breeds; they were caught at rubbish tips in Southwest Australia. Samples from Malaysia were collected from a mixture of *feral* and *stray cats*. Trapping and collection of tissue samples from cats was conducted as described in (Koch *et al.* in press). Blood or hair samples were taken as appropriate. Blood samples were collected using NucleoSave Cards (Macherey-Nagel) and hair collections were conducted as described in Berry *et al.* (2012).

DNA extraction

DNA was isolated using the NucleoSpin Tissue Kit (Macherey-Nagel) for tissue and blood samples and the ChargeSwitch Forensic DNA Purification Kit (Invitrogen) was applied for hair samples.

We genotyped all samples at 12 microsatellite loci, which included a gender-identifying sequence tagged site from the domestic cat Y-chromosome *SRY* gene (Butler *et al.* 2002; Koch *et al.* in press; Menotti-Raymond *et al.* 2005). We also obtained DNA sequences of the mitochondrial *ND5* and *ND6* gene regions for comparison with a previously published dataset by Driscoll *et al.* (2007). Sequences selection depended on sequence length and coverage and to represent 3 individuals of each available region of the country of origin published by Driscoll *et al.* (2007). This comprised a segment of 1800 base pairs sequenced using a Biorad C1000 Thermocycler following the protocol of (Koch *et al.* in press). DNA sequences were determined using an ABI 3730 sequencer and analysed using Geneious 5.6.6 (Biomatters) software for mtDNA and Genemarker V1.95 (Softgenetics) software for microsatellites.

Genetic variation and structure

A total of 269 feral cat mtDNA sequences representing the Australian mainland and island populations as well as Asian populations (hereafter referred to as Australasia dataset) were analysed together with a subset of 42 sequences from European locations published by Driscoll *et al.* (2007) (Appendix 1). Genetic diversity of the Australasian dataset and European populations at the mitochondrial *ND5* and *ND6* region was based on estimates of: the number of variable sites; the number of haplotypes; haplotype diversity (h) and nucleotide diversity (π) using DNASP V5.1 (Librado & Rozas 2009). NETWORK version 4.6.1.0 (Bandelt *et al.* 1999) was employed to generate a maximum parsimony median joining (MP) network for the Australasia and the European populations. Pairwise F_{ST} values were calculated according to Nei & Li (1979) using ARLEQUIN 3.5 (Excoffier & Lischer 2010).

The phylogenetic tree was reconstructed via Bayesian inference method using Beast v1.7.5 (Drummond *et al.* 2012). The analysis was run 5 x 10^7 MCMC generations with sampling every 1000th generation. Log files were analysed using Tracer v1.5, to assess convergence and to confirm combined effective sample size (ESS) >200 for each individual parameter. A maximum credibility tree was subsequently produced using TreeAnnotator v1.6.1. FigTree v1.4.0 was used to graphically display the tree and present the 95% highest posterior density (HPD) of node ages.

Analysis of microsatellites included identification of possible genotyping errors due to null alleles using Microchecker (Van Oosterhout *et al.* 2004). The GENEPOP 4.0 software (Rousset 2008) was used for the Australasia dataset to calculate basic population genetic parameters: mean number of alleles per locus (N_A); expected (H_E) and observed (H_O) heterozygosity as well as significance values for deviations from Hardy-Weinberg equilibrium (HWE). Population genetic parameters, such as allele frequencies and F_{IS} coefficients (Weir & Cockerham 1984) as a measure of the level of inbreeding were calculated using FSTAT 2.9.3 (Goudet 1995). To conduct analysis of molecular variance (AMOVA) in ARLEQUIN 3.5 (Excoffier & Lischer 2010) samples were grouped according to four main geographic regions: 1) Australian mainland, Dirk Hartog Island, Tasmania; 2) Cocos Island and Christmas Island; 3) Europe and 4) Asia.

To examine fine-scale population structures we determined the number of private alleles in each population and conducted a principal coordinate analysis (PCoA) on a pairwise distance matrix for individuals (GENALEX 6.5; Peakall & Smouse 2012). In addition, we used STRUCTURE 2.3.4 software (Pritchard *et al.* 2000) to study the relationships among the Australasia dataset populations and to assign samples into clusters using an unbiased Bayesian approach under an admixture model. Burn-in and MCMC iteration settings were 50,000 and 100,000, respectively. Runs for each K were repeated 10 times. The best supported number of clusters based on the ΔK statistic was estimated using STRUCTURE Harvester v 0.6.93 (Earl & vonHoldt 2012). The software CLUMP (Jakobsson & Rosenberg 2007) was used to align multiple replicates for K and the DISTRUCT application (Rosenberg 2004) was used to display the results graphically.

Phylogeographic Model Selection (PMS)

We used MIGRATE-N 3.4 (Beerli & Palczewski 2010) to apply a phylogeographic model selection approach (Depraz *et al.* 2008; Pfenninger & Posada 2002). Two hundred and nine sequences of the 24 sampling sites for the mitochondrial markers were pooled into four geographic groups (Europe, EU; Malaysia/Indonesia, ASIA; Christmas-/Cocos Island, CIQ; Australia, OZ). Considering EU, ASIA and CIQ as possible sources (and, in some cases, sinks) of colonisation of OZ, either direct, or by stepping stone, we developed eleven phylogeographic hypotheses, each of which had a corresponding maximum likelihood migration rate matrix (Appendix 2). The starting parameters were adapted from Jesse *et al.* (2011). We ran a burn-in phase of 10,000 generations and ten short chains with 50,000 generations each, of which every 5,000th tree was recorded. Three long chains of 500,000 generations followed, from which 1,000 trees were sampled after burn-in of 50,000 generations. The transition/transversion ratio was set to 12.8 after estimation using DNASP V5.1. (Librado & Rozas 2009). A final analysis with an unconstrained migration model using a likelihood-ratio-test was performed and Akaike Information Criterion (AIC) scores were obtained for each model.

RESULTS

Genetic population structure and differentiation using microsatellites

A total of 269 individuals representing 14 sampling locations were genotyped at 12 polymorphic microsatellite loci, one of which was excluded because of null alleles (Van Oosterhout *et al.* 2004). For these 11 loci the overall expected heterozygosity values were moderate to high and ranged from 0.43 to 0.88 (mean $H_E = 0.74$) with Australian mainland locations exhibiting the highest genetic diversity (Table 3-1). The mean number of alleles per locus per population varied greatly between sample locations ranging from 2.5 to 12.1, presumably partly in response to sample size (Table 3-1). Christmas Island (CIF) and the Australian mainland location in the south: Cape Arid (CA) had the largest number of alleles with 11.8 and 12.1, respectively.

Table 3-1. Descriptive statistics for microsatellite typing of cat populations in the Australian mainland, Australian islands and Southeast Asia (based on 11 loci), including population sample size (*N*), expected (H_E) and observed (H_O) heterozygosity, mean number of alleles per locus (*NA*), inbreeding coefficient (F_{IS}) and number of private alleles per population over all loci (*PA*).

Group	**Population (abbreviation)**	***N***	***NA***	H_O	H_E	F_{IS}	***PA***	***PA/N***
Territorial islands - Indian Ocean	Christmas Island (CIF)	79	11.8	0.63	0.74	0.11	18	0.22
	Cocos (Keeling) Island (Q)	42	7.0	0.51	0.63	0.18	6	0.14
Western Australia - mainland	Kimberley (KIM)	5	5.7	0.78	0.83	0.06	5	1
	Cape Arid National Park (CA)	23	12.1	0.79	0.88	0.10	14	0.60
	Mount Keith (MK)	8	6.6	0.74	0.80	0.08	7	0.87
	Fitzgerald River National Park (FG)	10	7.4	0.77	0.82	0.06	3	0.30
	Peron (PE)	13	6.9	0.75	0.78	0.03	NA	NA
	Tips South West (TSW)	25	9.8	0.74	0.82	0.10	6	0.24
Western Australia - island	Dirk Hartog Island (DHI)	40	9.6	0.72	0.75	0.03	11	0.27
South Eastern Australia - islands	Flinders Island (FL)	3	1.7	0.36	0.32	0.10	NA	NA
	French Island (FI)	3	3.7	0.70	0.76	-0.15	NA	NA
	Tasmania (TAS)	10	4.8	0.70	0.72	0.04	3	0.30
	Tasman Island (TASM)	5	2.5	0.48	0.43	-0.12	NA	NA
Asia	Malaysia/Sulawesi (ASIA)	3	3.7	0.55	0.78	0.35	NA	NA
	Total	269						

The analysis of pairwise genetic differentiation between populations indicated that Cocos Island and Christmas Island (Q, CIF), the south-eastern islands Tasman Island (TASM) and Flinders Island (FL) as well as the most western island of Australia: Dirk Hartog Island (DHI) were relatively distinct from all other populations, primarily the Australian mainland and large island of Tasmania (PCoA: Figure 3-1; 28.5% and 24.5 % of variation explained by axis 1 and 2, respectively).

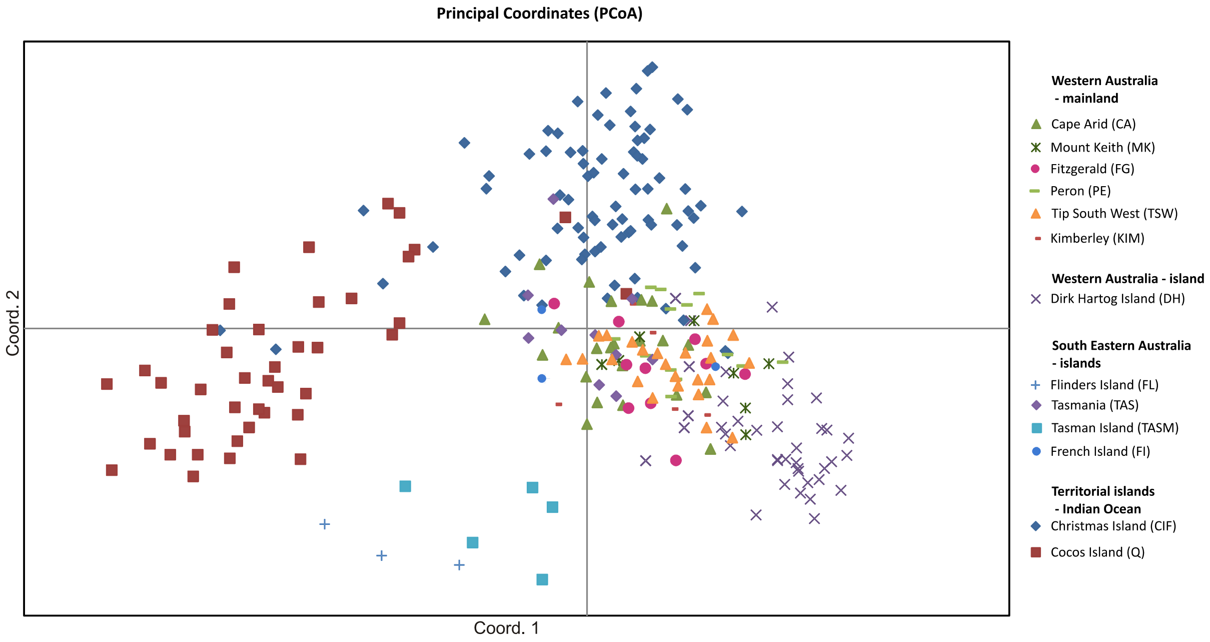

Figure 3-1. Principal Coordinates Analysis (PCoA) plot based on a co-variance distance matrix using microsatellite data (11 loci) scored in cats from 13 populations

For the Bayesian assignment approach implemented in STRUCTURE the Δ*K* statistic revealed a *K* value of five and assignments are shown by population in Figure 3-2. This analysis again grouped the Australian mainland and Tasmanian samples, this time together with the Southeast Asian samples, also included. Cats from the Tasman, Flinders and Cocos Islands (TASM, FL, Q) showed similar assignments to each other, while cats from Christmas Island (CIF) and Dirk Hartog Island (DHI) had assignments that were distinctive from all other populations (Figure 3-2).

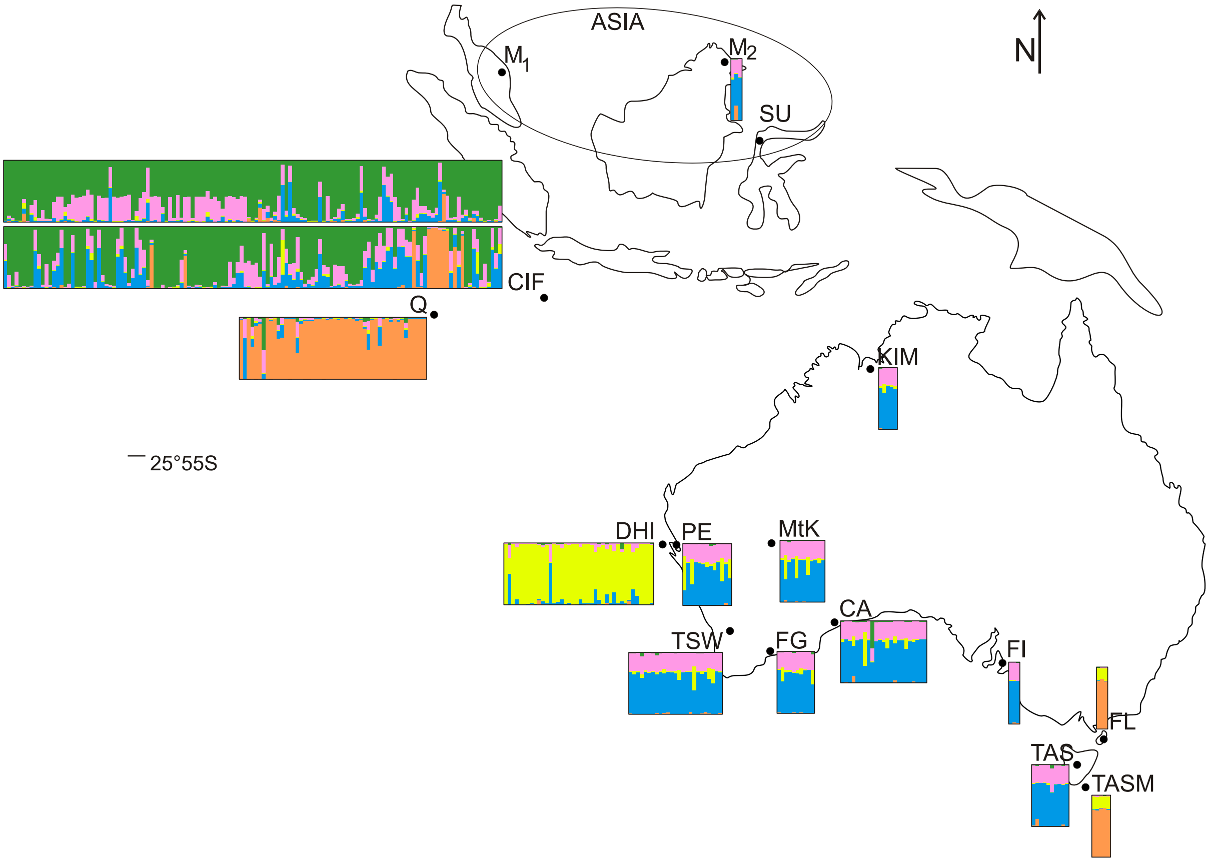

Figure 3-2. STRUCTURE analysis as applied to microsatellite data (11 loci) from cats distributed in mainland Australia, Australian islands and Southeast Asia. Bars indicated graphical output for $K = 5$. Each individual cat is represented by a single vertical line in plots for each location. Abbreviations for locations can be found in Table 3-1.

AMOVA results with the microsatellite data indicated that the major portion of the molecular genetic variation was found within populations (67.8 %; $F_{ST} = 0.32$; $P < 0.001$) with 7.5 % ($F_{CT} = 0.07$; $P < 0.224$) among the four geographic regions (EU, ASIA, OZ, CIQ) and 24.7 % ($F_{SC} = 0.26$; $P < 0.001$) among populations within the geographic regions.

Phylogeography using mtDNA sequences

Populations from Western Australia: Fitzgerald (FG), Cape Arid (CA) and Dirk Hartog Island (DHI) as well as samples from Southeast Asia (ASIA) and Tasmania (TAS) were found to have high haplotype diversity with values ranging between 0.53 and 0.62 (Table 3-2). Highest values were found in European (EU) populations ($h = 0.94$), followed by samples from Tips South West (TSW) ($h = 0.80$). This pattern was also found in the nucleotide diversity with highest values again recorded for EU ($\pi = 0.008$) and TSW ($\pi = 0.002$) populations.

We detected 63 haplotypes in the dataset of which 25 were present in the European populations. All other populations haplotypes ranged from 1 to 6 (Table 3-2).

Table 3-2. Measures of genetic diversity as applied to the mitochondrial *ND5* + *ND6* data for cat populations in the Australian mainland, Australian islands, Southeast Asia and Europe: population sample size (*N*), haplotype diversity (*h*), number of haplotypes (*H#*) and (π) nucleotide diversity

Populations (abbreviation)	***n***	***H#***	***h***	***π***
Christmas Island (CIF)	24	4	0.42	0.0015
Cocos (Keeling) Island (Q)	12	2	0.16	0.0002
Kimberley (KIM)	5	2	0.60	0.0008
Cape Arid National Park (CA)	6	2	0.53	0.0007
Mount Keith (MK)	14	3	0.27	0.0005
Fitzgerald River National Park (FG)	10	3	0.62	0.0017
Peron (PE)	8	2	0.25	0.0006
Tips South West (TSW)	10	5	0.80	0.0020
Dirk Hartog Island (DHI)	39	6	0.59	0.0018
Flinders Island (FL)	3	1	0	0
Tasmania (TAS)	6	2	0.53	0.0014
Tasman Island (TASM)	5	1	0	0
Malaysia/Sulawesi (ASIA)	20	4	0.62	0.0010
Europe (EU)	42	25	0.94	0.0080
Total	214	63		

The phylogenetic tree reconstructed using Bayesian inference revealed four major clades (Figure 3-3A). The largest clade (Clade 2) consists of a mixed group of Australian islands (DHI, TASM, FL and TAS) and mainland (PE, MK, FG, CA, KIM, TSW, VIC, P) populations and samples from Cocos Island (Q), ASIA and EU. Differentiation among clades was low, but a concordant clustering was detected in a haplotype network, which consisted of seven subgroups, labelled A - G (Figure 3-3A). Clade C2 within the phylogenetic tree was subdivided into subgroups that matched the haplotype groupings: Australia mainland and islands, Cocos/Malaysia (A), Midwest Gascoyne (B), Australian Mainland + Britain (C), Australian mainland (D) and ASIA/Tasmania (E). Clade C3 consists of samples from Asia, Christmas Island, Tasmania, Tips South West and some samples from central Europe (haplotype group F, haplotype network; Figure 3-3B). Individuals from southern Europe fell within a separate group forming Clade 4 and group F in the haplotype network.

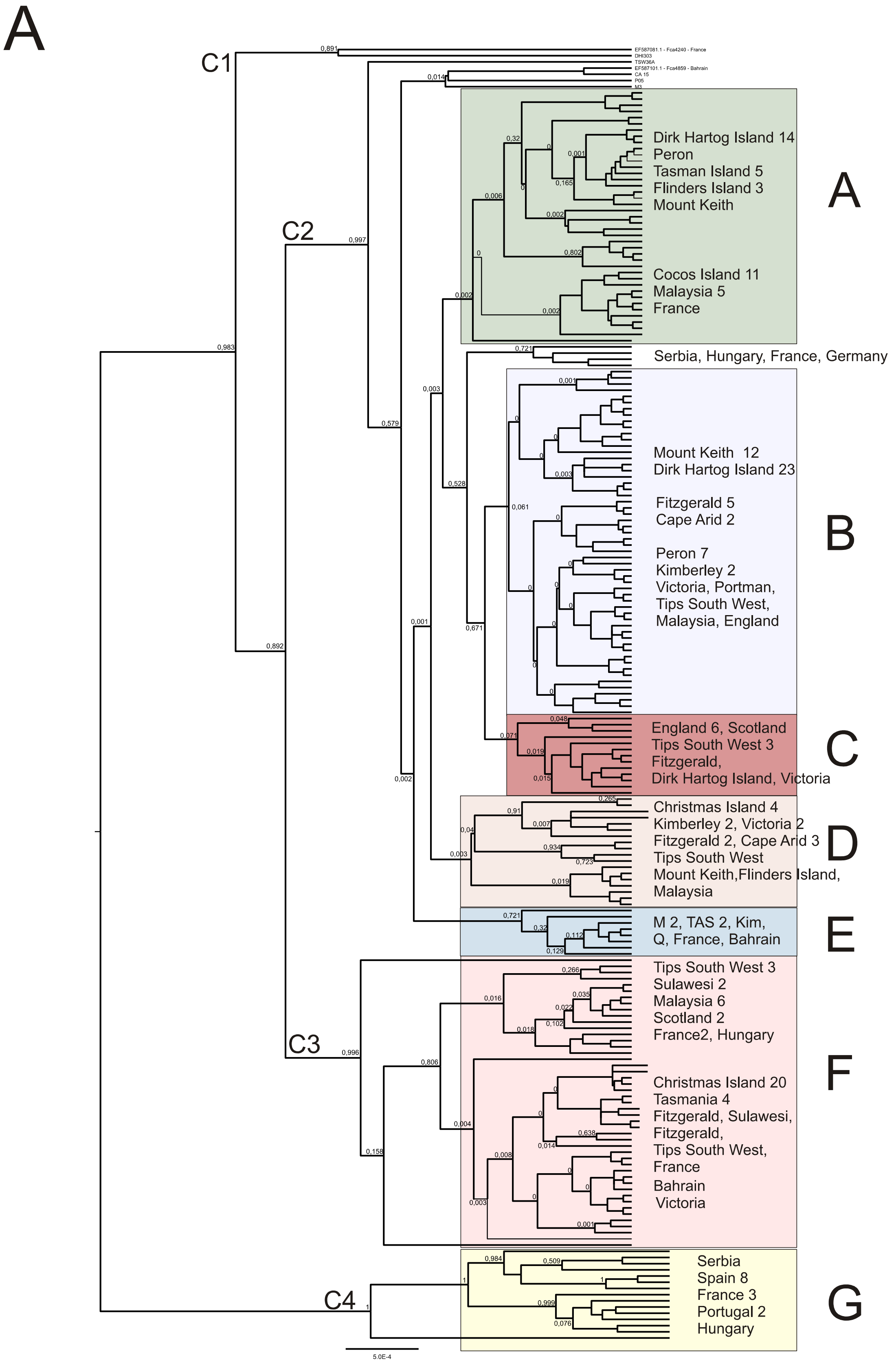

Figure 3-3A. Phylogenetic tree of cat populations based on mtDNA data, reconstructed by Bayesian inference. Four clades (C1-C4) with number of individuals per location found in each clade, defined with 95% highest posterior density (HPD) represented at nodes.

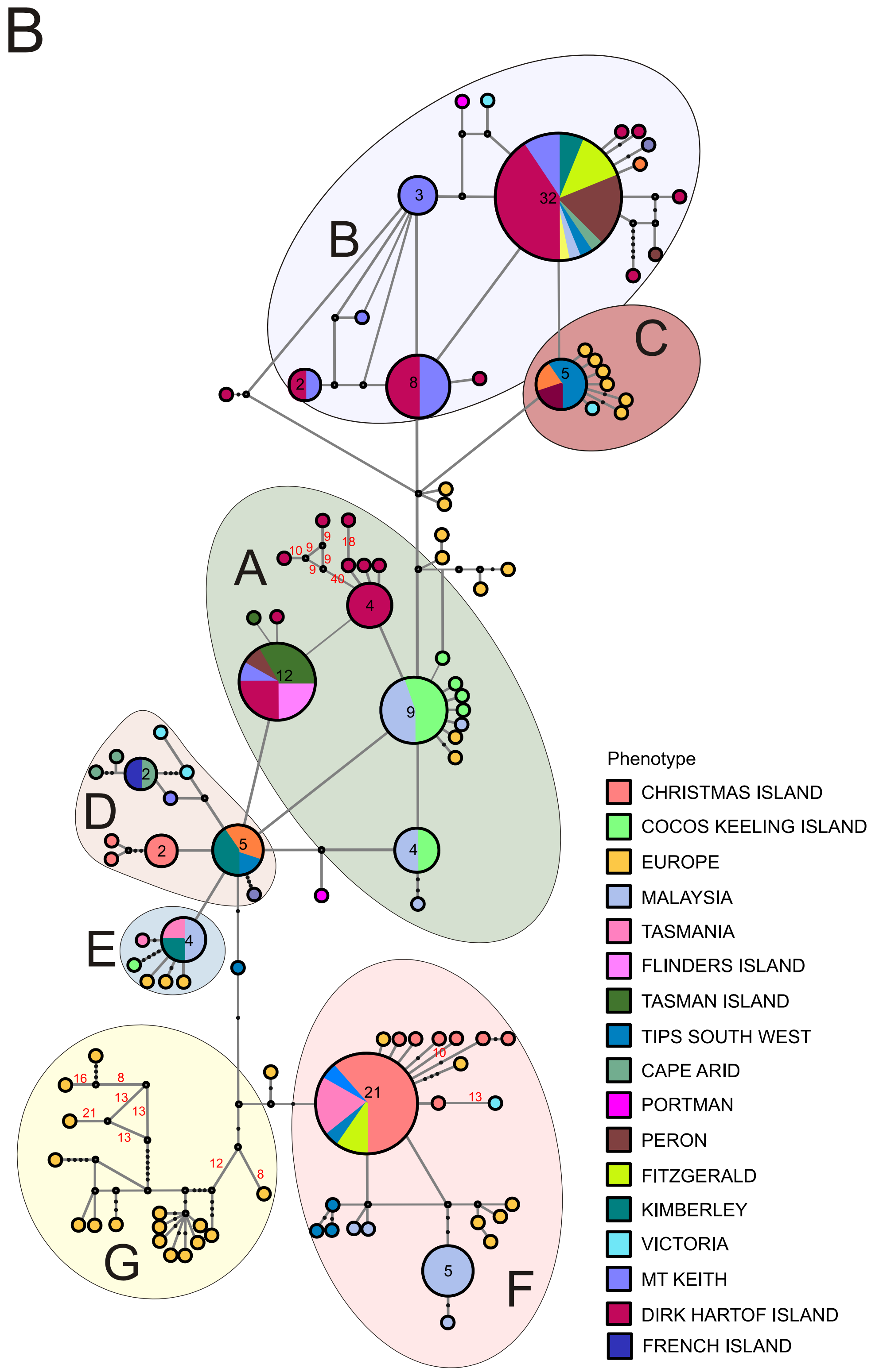

Figure 3-3B. A maximum parsimony median joining (MP) mtDNA haplotype network for Australian, Southeast Asian and European populations of cats consisting of 108 haplotypes divided into seven subgroups. Black dots indicate more than one mutational step. Each additional dot represents one step. Grey filled dors indicate median vectors; a hypothesised sequence which is required to connect existing sequences with network. Numbers in circles indicate number of sequences assigned to the particular haplotype.

Pairwise population comparisons showed low genetic differentiation between samples from Europe and elsewhere (mean F_{ST} of 0.18) and between samples from Asia and elsewhere (mean pairwise F_{ST} of 0.16; Table 3-3). Significant strong genetic differentiation to most other populations was found for Christmas Island (CIF), with the exception for Tasmania (TAS), for Flinders Island (FL) (except TASM, TAS and DH) and Tasman Island TASM (except FL). Very low genetic differentiation is found between TAS, TSW, CIF and EU with pairwise F_{ST} values ranging from 0.03 to 0.09. All samples from the Shark Bay Area, Western Australia (DHI, PE) and the population from Mount Keith (MK) showed low levels of genetic differentiation.

Table 3-3. Genetic differentiation among cat populations based on mtDNA data (lower matrix pairwise F_{ST} values; upper matrix *P*-values). Asterisks (*) and dashes (-) indicate significant and non-significant differences, respectively.

	CA	**DHI**	**FG**	**FL**	**KIM**	**MK**	**PE**	**TAS**	**TASM**	**TSW**	**CIF**	**Q**	**EU**	**Asia**
CA		*	-	*	-	*	*	-	*	*	*	-	*	-
DHI	0.37		*	-	*	-	-	*	*	*	*	*	*	*
FG	0.12	0.09		*	-	-	-	-	*	-	*	*	*	-
FL	0.56	0.34	0.36		*	*	*	-	-	*	*	*	*	*
KIM	0	0.30	0.05	0.53		*	*	-	*	-	*	-	*	-
MK	0.47	0.06	0.07	0.71	0.39		-	*	*	*	*	*	*	*
PE	0.50	0.02	0.07	0.78	0.43	0		*	*	*	*	*	*	*
TAS	0.39	0.56	0.25	0.51	0.36	0.65	0.63		*	-	-	*	-	-
TASM	0.64	0.38	0.43	0	0.62	0.74	0.82	0.60		*	*	*	*	*
TSW	0.24	0.26	0	0.24	0.18	0.30	0.26	0.03	0.39		*	*	*	-
CIF	0.66	0.65	0.49	0.67	0.65	0.72	0.71	0.07	0.69	0.25		*	*	*
Q	0.17	0.63	0.51	0.88	0.27	0.79	0.84	0.63	0.89	0.53	0.76		*	*
EU	0.17	0.28	0.13	0.16	0.15	0.25	0.22	0.09	0.22	0.09	0.23	0.28		*
Asia	0.07	0.18	0	0.27	0.03	0.19	0.18	0.13	0.32	0	0.37	0.31	0.16	

Comparison of potential invasion routes using the model selection approach supported the invasion of cats from Europe and subsequent invasion of Australia and Asian islands (Model 7 and Model 9: LnL of -1381.25 and ΔAIC of 355; Figure 3-4, Table 3-4).

Table 3-4. Results of the migration hypothesis model selection as applied to the mitochondrial *ND5* + *ND6* between Europe (EU), Australia (Oz), Christmas and Cocos (Keeling) Island (CIQ) and Malaysia/Sulawesi (Asia) (Figure 3-4). AIC values measure the fit of the model to the data, taking different parameterisation into account. Smaller values indicate a better fit.

Scenario	no. of parameters	LnL	AIC	delta AIC
Model 1	8	-1867.87	3751.73	1328.23
Model 2	7	-1867.87	3749.73	1326.23
Model 3	7	-1467.33	2948.65	525.15
Model 4	7	-1467.45	2948.90	525.40
Model 5	7	-1467.45	2948.90	525.40
Model 6	8	-1785.60	3587.20	1163.70
Model 7	**8**	**-1381.25**	**2778.50**	**355**
Model 8	7	-1204.75	2423.50	0
Model 9	**8**	**-1381.25**	**2778.50**	**355**
Model 10	11	-1467.45	2956.90	533.40
Model 11	7	-1867.87	3749.73	1326.23

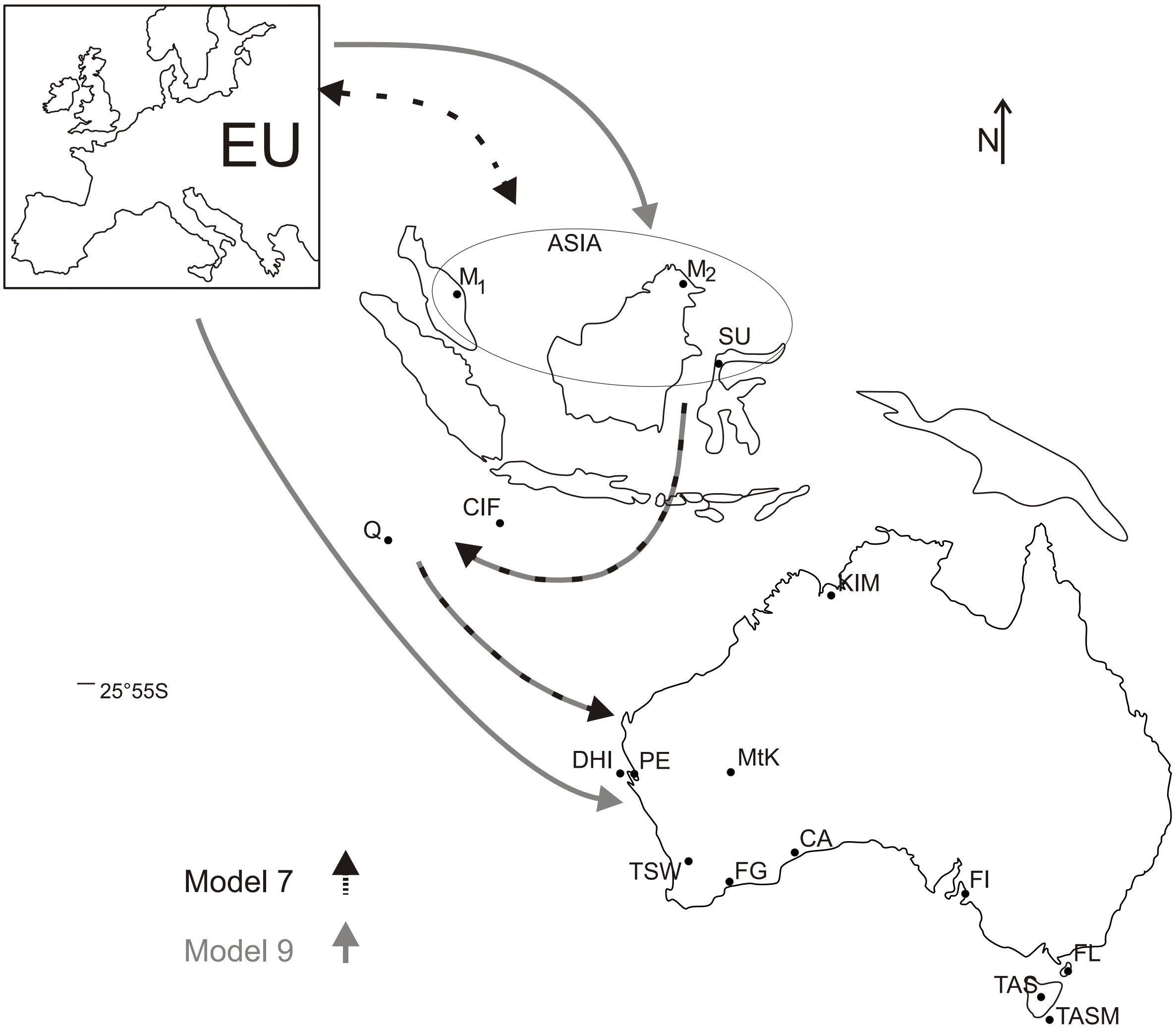

Figure 3-4. A Map of Australia and Southeast Asia with Europe being portrayed in left-hand corner. Arrows of Model 7 (dashed black arrows) and Model 9 (grey arrows) indicate invasion routes with highest support from the model selection approach (Model 7 and Model 9, Table 4).

DISCUSSION

Phylogeography and population genetic approaches are often used to reconstruct dispersal patterns of domesticated and human associated species, in some cases even different species share a common history (Jesse *et al.* 2011; Jones *et al.* 2013; Larson *et al.* 2007; Matisoo-Smith & Robins 2009). Previous studies found that the history of house mice (*Mus musculus*) demography and movements mirrored that of human populations (Jones *et al.* 2013; Jones *et al.* 2011; Jones *et al.* 2012). In Australia, the introduction of house mice was found to be associated with the early European colonization and settlements in the late 18th century (Gabriel *et al.* 2011). Similarly, historical records and comprehensive studies by Abbott

(2002; 2008) document the early introduction events of cats to Australia. Abbott (2002 and 2008) proposes multiple coastal introductions between 1804 -86, rather than a spread from the earliest point of colonization (Sydney, 1788). He also precluded an introduction before European settlements, since he did not detect any records of cat sightings by explorers or early navigators on their landfall (Abbott 2002; 2008). Overall, our analyses support the hypothesis of a European introduction and subsequent establishment of European lineages in Australia. It is most likely that the ancestors of Australian feral cats were introduced mainly from Britain and other Central and Western European locations. The Australian mainland locations show low levels of genetic variation, but genetic differentiation into four to five major groups in the haplotype network. There was no evidence of a separate and stable feral cat population originating from Asian locations. Abbott (2002) postulated that even though there was a possibility of cats being brought before European settlements it would have been unlikely that these few cats would have persisted in the foreign environment with various unknown predators present. It is generally assumed, that the likelihood of survival of a few introduced individuals in a foreign environment is relatively low. If founder populations establish they may suffer from genetic drift and increased levels of inbreeding. These effects have been documented in many empirical studies, e.g. a survey of cats of the Kerguelen archipelago. (Allendorf & Lundquist 2003; Barrett & Kohn 1991; Dlugosch & Parker 2008; Pontier *et al.* 2005). In contrast, moderate or even increased levels of genetic variation of founder populations indicate incidences of multiple invasions. This phenomenon is assumed to be the key pre-condition for a successful introduction and long lasting establishment of invasive species (Allendorf & Lundquist 2003; Dlugosch & Parker 2008; Frankham 2005). It is assumed that multiple introductions lead to inter-mixing among individuals from genetically divergent (previously geographically isolated) populations resulting in higher genetic variation in founder populations than in original populations (Allendorf & Lundquist 2003). Our data do not support the hypothesis of an establishment or spread of cats brought by Malaysian trepangers (Abbott 2002; Macknight 1976) prior the European colonization. However, we found evidence of Asian introduction events possibly following European colonization, since Asian and northern Australian cat population show only a low level of genetic differentiation. The greatest number of cats was brought to Australia in the late 19th century (Abbott 2002), if those cats “hybridized” with a much lower number of potential immigrants from Asia, it is highly unlikely to detect any genetic signature of Asian lineages in current Australian feral cat populations. Therefore, we consider an establishment of cats originating from Asia during the time period between the invasions of the dingo until European colonization as highly unlikely.

Overall we observed that genetic differentiation among mainland Australian populations is low, however island populations were substantially differentiated among each other and differentiated from mainland populations. This population structure is most likely explained by the lower level of gene flow between islands and mainland populations than among mainland populations. Exceptions from these general patterns are explained be human activities and their main pathways of trading and exploitation. Our results showed that the DHI population exhibits a relatively high genetic diversity (Table 3-2) and is genetically distinct from most mainland populations except for nearest coastal populations (PE and MK) and two islands far to the southeast: FL and TASM (Table 3). Additional analyses revealed low genetic differentiation between Cocos Island (Q) north of Western Australia as well as Asian locations (SU, M). In 1863 pastoral occupation of the Gascoyne, administrative regions of Western Australia, commenced (Abbott 2002) and between 1850 and 1920 pearling was at its peak resulting in housing of workers on Dirk Hartog Island and Peron Peninsula (Green 2007). A maximum of 78 vessels operated in the Shark Bay Area with approximately 300 Malaysian, Chinese, Aboriginal and European workers being involved in the pearling industry (Green 2007). Archeological remains indicate a large impact of Malaysian workers in the area and historical records state exchange between their homes in Malaysia and Shark Bay, Western Australia (Edwards 1999; Green 2007). The first report of a cat on a pearling lugger (to prevent seabirds roosting) at Dirk Hartog Island was recorded in 1920 (Abbott 2008; Whitlock 1921). In later times cats were assumed to have been brought over during the island use as a pastoral sheep (*Ovies aries*) and goat (*Capra hircus)* station (Burbidge & George 1977). A recent study showed regular gene flow occurred between the Western Australian mainland and DHI during the last decade, which however has ceased in the last few years (Koch *et al.* in press).

Other islands that were visited by early European explorers are Cocos Island (Q) and Christmas Island (CIF), located in the Indian Ocean approximately midway between Australia and Malaysia (Dampier 1927; Keynes 2001; Slocum 1901). Cocos (Keeling) Island was inhabited around 1820 by European merchants accompanied by Malaysian workers (Molloy 1830; Slocum 1901). One of the merchants built a settlement on Christmas Island supplying the growing industry on Cocos Island (i.e. with timber and provisions) while travelling regularly between Singapore and the two islands (Burstyn 1975; Dampier 1927; Keynes 2001). Extensive travel between Australia, Cocos and Christmas Island as well as Southeast

Asia (Burstyn 1975; Dampier 1927; Keynes 2001) is consistent with the results of the model selection approach. The models selected showed migration from Europe to Australia and Asia and from there to Cocos and Christmas Island.

Therefore, we can assume that shared mitochondrial haplotypes among Cocos Island and DHI populations represent a signature of past human mediated migration events, i.e. traveling of Southeast Asian workers to Cocos Island and establishment of the pearling industry. In addition, we found that the main introduction of cats onto Dirk Hartog Island happened, at latest, between its main use as a pearling site around 1850 and 1920. These cats were of European descent already common in Western Australian settlements through introductions possibly on shipwrecks around 1600 and definitely since 1850 through European explorations (Abbott 2002; Abbott 2008; Burbidge 2001; Burbidge *et al.* 1988). Thus, we have an idea of the mtDNA lineages present in Western Australia after introductions of cats from European and Southeast Asia in the 19th century. The patterns of European invasions were in particular supported by genetic data from Tasmanian populations (TAS) and its neighboring islands, Tasman Island (TASM) and Flinders Island (FL). Although these islands lie closely together (a maximum of 20 km from the coast), feral cats of TAS and FL cluster (microsatellite and mitochondrial DNA analyses) into completely different groups. Furthermore TASM, FL and Cocos Island (Q) form a homogenous group, in particular based on microsatellite data. These three populations show low genetic differentiation among themselves, but large differentiation from all other populations. Differentiation of TASM and FL to all other populations in the phylogenetic tree is not as clear as for TAS, but is supported in all other genetic analyses. Additionally, individuals from Tasmanian populations exhibit a cyclonuclear discordant pattern, since they are clearly separated from all other Australian populations using mtDNA (phylogenetic tree, Figure 3-3), but using microsatellite analyses no separation from Australian populations was detected. Domestic cats were introduced to Tasmania in 1804 during European settlement at Hobart and later became feral (Abbott 2008; Hamilton-Arnold 1994; Nicholls 1977; West 1852). At the beginning of the 19th century various workers (including Asians) were brought to Tasmania to find employment in numerous industries including pearling, whaling, tin mining and sealing (Lawrence 2006; Murray 1927; Nash 2003; Plomley & Henley 1990; Vivian 1985). Tasman Island's Lighthouse was built in 1906 and manned till 1977 (Ibbotson 2000) and feral cats present since the construction of the lighthouse (Bryant & Shaw 2006) were eradicated in 2010 (Campbell *et al.* 2011). Since the early 19th century sealers had established a small settlement on Flinders Island, which was later used to exile the remnants of the Tasmanian Aboriginal population (Alison 2005). All three islands must have therefore been visited regularly by ships and traders on their way to the Australian mainland, European or Asian locations.

The genetic data of Tasman Island (TASM) and Flinders Island (FL) is consistent with their history of human settlements. TASM was not populated before 1977 and FL has a population of approximately 776 (Census, Australian Bureau of Statistics, 2011). However, Tasmania (TAS) has been populated to up to 495,000 people (Census, Australian Bureau of Statistics, 2011) since the first settlement. In 1995 the Australian Bureau of Statistics estimated that 26.7 % of pet owners had cats as household pets and 17.5 % of the households in Tasmania reported problems with stray and feral cats (Australian Social Trends, 1995, Australian Bureau of Statistics). Therefore, we must take into account that large amounts of fancy breed and domestic cats from the Australian mainland were brought onto the island intermixing with the original feral cats explaining cyclonuclear discordant patterns in Tasmanian cats. This is also supported by the genetic differentiation between TAS and Tips South West (TSW), since TSW represents a mixture of stray, feral, domestic and fancy breed cats. In contrast, TASM and FL did not undergo a major increase in human population size and feral cats on the islands have therefore been more or less isolated from interbreeding with domestic fancy cat breeds being introduced as house pets. All three islands were among the first islands on which cats were introduced (Abbott 2008) and are genetically differentiated from all other Australian populations. We hypothesize that these populations consist of the descendants of the original invading lineages during the 19th century. In contrast to many other Australian populations, they remained largely isolated from subsequent mixing, thus these island populations provide valuable information to trace back the global invasion routes of cats.

In conclusion, we found clear evidence for an overall European origin of feral cats in Australia, with remnants of these introduced genotypes on some remote islands. Additionally, we found that a secondary introduction from Southeast Asian locations have occurred during the last two centuries.

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Chapter 4

Feral Cat Globetrotters: genetic traces of historic human-mediated dispersal and recent gene flow

K. Koch, D. Algar and K Schwenk.

ABSTRACT

Endemic species on islands are highly susceptible to local extinction if they are exposed to invasive species. In particular invasive predators, such as feral cats have been introduced to islands around the world, causing major losses in local biodiversity. However, control and management of invasive species depends on information about the source populations and the level of current gene flow. Here we investigate the origin of feral cats of Hawaiian and Australian islands to verify their European ancestry and a potential pattern of isolation by distance. We analysed the genetic structure and diversity of feral cats from eleven islands as well as samples from Malaysia and Europe using mitochondrial DNA (ND5 and ND6 region) and microsatellite data. Our results suggest that Hawaiian cats originate from Europe and overall no pattern of isolation by distance was detected. Instead we found low levels of genetic differentiation between samples from Tasman Island, Lana'i, Kaho'olawe, Cocos (Keeling) Island and Asia. Since these populations are separated by up to 10,000 kilometres, we assume that this pattern is explained by extensive passive dispersal on global maritime trade routes in the beginning of the 19th century, connecting Australian, Asian and Hawaiian Islands. Thus, islands populations which are characterized by low levels of current gene flow represent valuable sources of information on historical, human-mediated global dispersal patterns of feral cats.

INTRODUCTION

Biodiversity loss through population declines, local extinctions and global extinctions of many island endemic species has been determined to be particularly caused by mammal

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invasive species (Atkinson 1985; Bonnaud *et al.* 2011; Courchamp *et al.* 2003; Fritts & Rodda 1998). Feral cats (*Felis catus*) are one of the most widespread introduced invasive predators on islands, having strong negative impacts on the island ecosystems (Fitzgerald 1988; Medina *et al.* 2011; Nogales *et al.* 2004; Veitch *et al.* 2011). The active and passive transport of cats as human commensals led to the extensive spread of the species around the world during the last 200 years (Courchamp *et al.* 2003; Todd 1977). Feral cats live in self-perpetuating populations independent of human care (Moodie 1995) and are dietary generalists which feed on various types of native and introduced prey (e.g. house mice; *Mus musculus*; (Bonnaud *et al.* 2011; Fitzgerald & Veitch 1985; Medina *et al.* 2011; Nogales *et al.* 2004). Cat invasions led to a major loss in biodiversity of insular birds and mammals as well as local extinction of endemic species (Dickman 1996; Donlan *et al.* 2003; Keitt *et al.* 2002; Mack *et al.* 2000).

The Hawaiian and Australian islands are assumed to have been populated by cats most likely through European explorers in the 19th century (Abbott 2002; Brackenridge 1841; Hansen *et al.* 2007; Hess & Jabobi 2011). The European origin of feral cats in Australia has been experimentally tested in a previous study, alternative scenarios, such as possible Asian invasion, were not supported (Koch *et al.* unpublished). In addition, this study showed that in particular small islands with low or no human populations provided valuable information to reconstruct the history and sequence of the invasion process (Koch et al. unpublished). Expanding human migration and trading activities led to the dispersal of invasive species, introducing them to remote locations around the globe (Elton 1958; Gibson 1992; Greene 1993; Hess & Jabobi 2011; Mack *et al.* 2000). Ongoing intermixing between feral and domestic fancy breed cats led to an increased local genetic diversity and population growth (Dickman 1996; Oliveira *et al.* 2008; Say *et al.* 2012).

The time, frequency and pathways of cat introductions to islands around the world are mostly unknown; nevertheless this information is crucial in order to evaluate historical dispersal processes, genetic structure and diversity of feral cat populations on islands. Since a recent study revealed the importance of islands as global archives for feral cats' invasion history, we analysed samples from eleven islands from Hawaii, Australia and Asia using microsatellite and mitochondrial DNA. We addressed the following specific questions regarding the origin, distribution and variability of feral cat genotypes on these islands: i) what is the level of genetic diversity on islands compared to mainland populations and does intermixing with domestic fancy breed cats influence this genetic diversity, (ii) do Hawaiian feral cats originate, as found for Australian mainland and island feral cats, from Europe and

(iii) what is the pattern of isolation by distance between the island cat populations under the assumption of a shared European origin.

METHODS

Sample collection

Feral cat sample collection was carried out on two islands from Southeast Asia (Sulawesi, Malaysia (Borneo)), three Hawaiian Islands (Lana'i, Kaho'olawe, O'ahu) and seven Australian Islands (Dirk Hartog Is., Christmas Is., Cocos Is., Tasmania, Flinders Is., Tasman Is. and French Is.). Trapping, collection of tissue, hair and blood samples as well as genomic and mitochondrial DNA isolation was conducted as described in Koch et al. (in press). A total of 1800 base pairs (bp) of the mitochondrial ND5 and ND6 region were sequenced using a Biorad C1000 Thermocycler following a protocol of Koch *et al.* (in press). All samples were genotyped at 12 microsatellite loci, which included a gender-identifying sequence tagged site from the domestic cat Y-chromosome SRY gene (Butler *et al.* 2002; Koch *et al.* in press; Menotti-Raymond *et al.* 2005). DNA sequences were determined using an ABI 3730 sequencer and analysed using Geneious 5.6.6 (Biomatters) software for mtDNA and Genemarker V1.95 (Softgenetics) software for nuclear fragment analysis.

Analysis of genetic structure and diversity

We analysed a total of 428 feral cat samples from 11 island populations and a subset of 128 cats from European locations (Driscoll *et al.* 2007). Microchecker software (Van Oosterhout *et al.* 2004) was used to identify possible genotyping errors due to null alleles. For microsatellite analysis only Malaysian samples were analysed since samples from Sulawesi did not yield sufficient nuclear DNA for adequate genetic analysis.

Basic population genetic parameters such as mean number of alleles per locus (N_A), expected (H_E) and observed (H_O) heterozygosity as well as significance values for deviations from Hardy-Weinberg equilibrium (HWE) were calculated with GENEPOP 4.0 software (Rousset 2008). DNASP V5.1 (Librado & Rozas 2009) was used to assess the number of variable sites, the number of haplotypes, haplotype diversity (*h*) and nucleotide diversity (π). Allele frequencies were calculated using FSTAT 2.9.3 (Goudet 1995). The average number of pairwise differences between population pairs (pairwise F_{ST} values) (Nei & Li 1979) and analysis of molecular variance (AMOVA) using mitochondrial data were calculated in

ARLEQUIN 3.5 (Excoffier & Lischer 2010). For all analysis performed in ARLEQUIN 3.5 (Excoffier & Lischer 2010) samples were grouped according to four geographic regions: 1) Australian 2) Cocos Island and Christmas Island; 3) Hawaii and 4) Asia. We tested for evidence of isolation by distance comparing pairwise genetic distances *versus* geographical distances of the islands using the Isolation by distance web service (Jensen *et al.* 2005).

A maximum parsimony median joining (MP) network was computed using NETWORK version 4.6.1.0 (Bandelt *et al.* 1999) with frequency >1criterion being active. Samples from Southeast Asia (Malaysia (M) and Sulawesi (S) were analysed separately to accommodate eventual differences in haplotype assignment.

The phylogenetic tree was inferred via Bayesian inference method using Beast v1.7.5 (Drummond *et al.* 2012). Analysis was run 5 x 10^7 MCMC generations with sampling every 1000th generation. Tracer v1.5 was used to analyse log files, to assess convergence and to confirm combined effective sample size (ESS) >200 for each individual parameter. A maximum credibility tree was subsequently produced using TreeAnnotator v1.7.5. We used FigTree v1.4.0 for graphical display of the tree and present the 95% highest posterior density (HPD) of node ages.

In order to detect recent population bottlenecks, each population was tested for heterozygosity excess. We used Bottleneck version 1.2 software (Piry *et al.* 1999) and estimated the observed and expected heterozygosity under the two-phase model with settings of 10% infinite allele model (IAM), 90% stepwise mutation model (SMM) with 1000 iterations.

The number of private alleles in each population executed with GENALEX 6.5 (Peakall & Smouse 2012). STRUCTURE 2.3.4 software (Pritchard *et al.* 2000) was used to study the relationships among the island populations and to assign samples into clusters using an unbiased Bayesian approach under an admixture model. Burn-in and MCMC iteration settings were 50,000 and 100,000, respectively. Each run for K was repeated 10 times. STRUCTURE Harvester v 0.6.93 (Earl & vonHoldt 2012) was used to calculate the best number of clusters depending on ΔK statistics. The software CLUMP (Jakobsson & Rosenberg 2007) was used to align multiple replicates for the chosen K and the DISTRUCT application (Rosenberg 2004) for graphical display of results.

Results

A total of 428 individuals from 11 sampling locations from Hawaii, Australia and Asia were successfully genotyped at 11 polymorphic microsatellite loci, however one locus was excluded because of the presence of null alleles (Van Oosterhout *et al.* 2004). The expected heterozygosity was moderate to high with a mean of H_E = 0.68. Flinders Island (FL) and Tasman Island (TASM) exhibited the lowest genetic diversity with H_E =0.32 and H_E =0.43, respectively (Table 4-1). The mean number of alleles per population ranged from 1.7 to 14.7 (Table 4-1). Largest numbers of alleles per population were found for Christmas Island (CIF) NA = 14.7, Dirk Hartog Island (DHI) NA = 9.6 and Lana'i (L) NA = 9.7.

Table 4-1. Measures of genetic diversity of mtDNA: population sample size (N), haplotype diversity (h), number of haplotypes (H#) and π nucleotide diversity.

Group	Populations (abbreviation)	*N*	*H#*	*h*	π
Territorial Islands - Indian Ocean	Christmas Island (CIF)	118	13	0.39	0.0015
	Cocos Keeling Island (Q)	43	3	0.09	0.0002
Western Australia - Island	Dirk Hartog Island (DHI)	39	5	0.54	0.0013
South Eastern Australia	Flinders Island (FL)	4	1	NA	NA
	Tasman Island (TASM)	5	1	NA	NA
	Tasmania (TAS)	5	2	0.53	0.0022
Hawaii	Kaho'olawe (K)	30	3	0.19	0.0004
	Lana'i (L)	36	3	0.34	0.001
Asia	Malaysia/Sulawesi (MS)	20	5	0.66	0.0026
	Total	300			

The proportion of mitochondrial genetic variation was found to be almost evenly distributed among groups (31.05%), among populations within groups (32.5%) and within populations (36.45%) indicating similar genetic variability between locations respectively within populations (Table 4-2). The PCoA designated three main groups with DHI and Kaho'olawe

(K) forming the first cluster, Cocos Island (Q) the second and CIF the third (Figure 4-1; 27.5% and 22.9% of variation explained by axis 1 and 3, respectively). Tasmania (TAS), Malaysia (M) and Lana'i (L) lay with some overlap between the first and third cluster. Tasman Island (TASM) and Flinders Island (FL) were found separate to other locations.

Table 4-2. Results of hierarchical AMOVA using mtDNA sequences. Levels of significance are based on 1000 random permutations.

Source of variation	***d.f.***	**Sum of Squares**	**Variance components**	**Percentage of variation**	***P* value**	**Fixation indices**
Among groups	6	541.40	1.13626 Va	31.05	*P* = 0.46515	FCT = 0.31054
Among populations within groups	2	14.40	1.18915 Vb	32.50	*P* = 0.01634	FSC = 0.47139
Within populations	292	389.38	1.33352 Vc	36.45	*P* < 0.001	FST = 0.63554

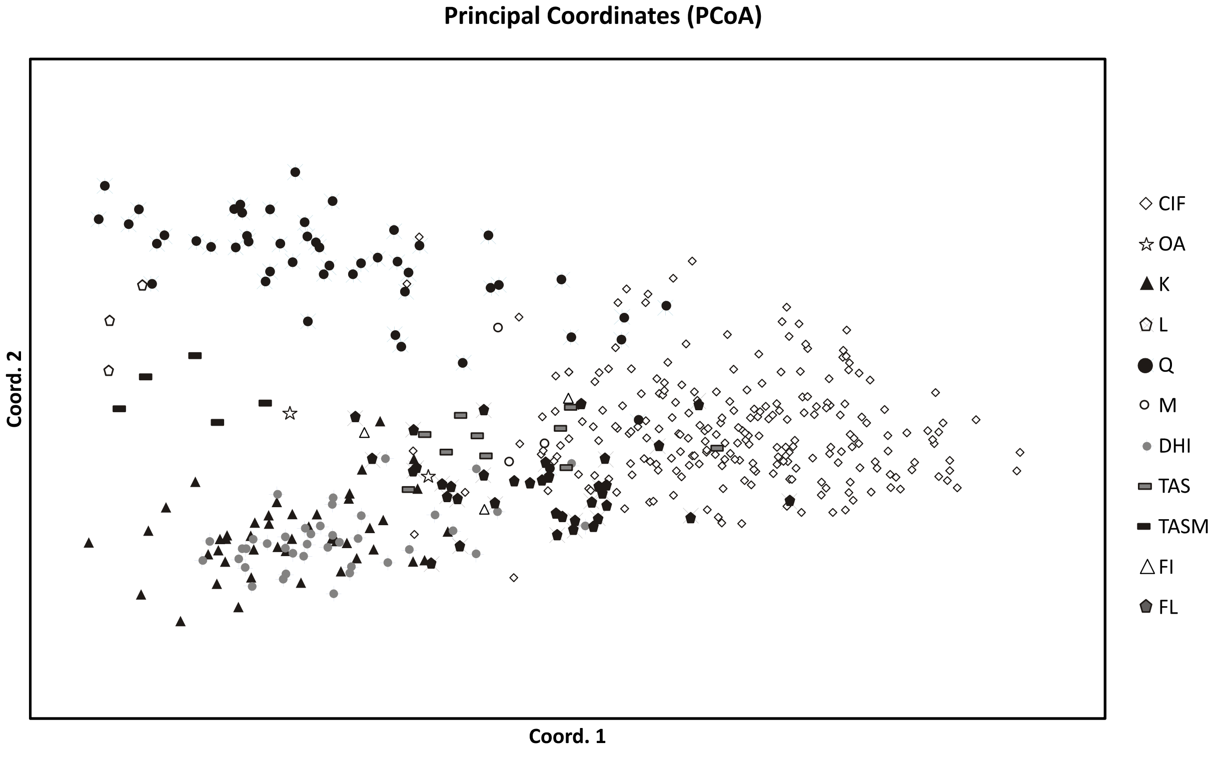

Figure 4-1. Principal Coordinates Analysis (PCoA) plot indicating genetic distances between individuals from eleven populations. PCoA is based on co-variance distance matrix values using microsatellite data.

The results from the Bayesian assignment approach implemented in STRUCTURE assigned five clusters in which Kaho'olawe formed a separate single cluster. Oahu, Lana'i, French Island, Malaysia and Tasmania formed the second and Tasman Island, Flinders Island and Cocos Island the third. Dirk Hartog Island showed strong admixture between clusters (Figure 4-2).

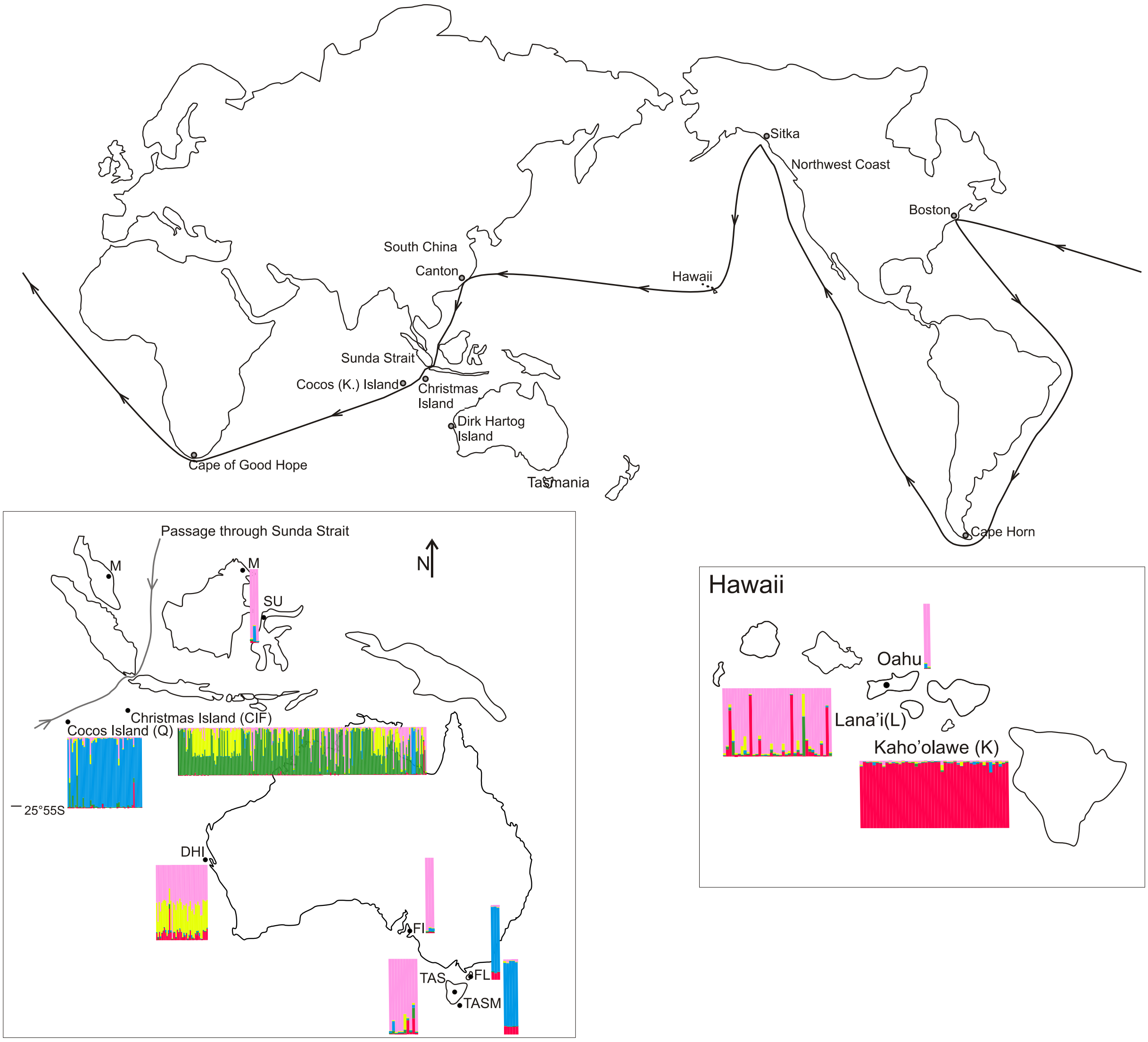

Figure 4-2. Map of the world representing the main route (Golden Round) used by maritime fur trade (black lines). Boxes show sampling locations in Australia, Hawaii and Southeast Asia with bars indicating graphical output from STRUCTURE analysis for $K = 5$. Each individual cat is represented by a single vertical line in population's subset plots which were assigned to their place of origin.

Mitochondrial data analyses were executed for a total of 300 samples of 9 populations and showed a mean haplotype diversity of 0.39 with highest values observed for Malaysia/Sulawesi (MS) h = 0.66, TAS h = 0.53 and DHI h = 0.56. Lowest values for haplotype diversity were observed for Cocos Island (Q) and Kaho'olawe (K) with 0.09 and

0.19, respectively. Nucleotide diversity values displayed a similar pattern with MS and TAS showing the highest values ($\pi = 0.0026$ and 0.0022, respectively; Table 4-3).

Table 4-3. Descriptive statistics and population sample size (*N*), expected (H_E) and observed (H_O) heterozygosity, mean number of alleles (*NA*), inbreeding coefficient (F_{IS}) and number of private alleles per population (*PA*).

Group	Populations (abbreviation)	N	NA	H_o	H_E	F_{IS}	PA	PA/N
Territorial Islands - Indian Ocean	Christmas Island (CIF)	229	14.7	0.68	0.75	0.09	41	0.17
	Cocos (Keeling) Island (Q)	50	7.5	0.51	0.64	0.19	4	0.08
Western Australia - Island	Dirk Hartog Island (DH)	40	9.6	0.73	0.75	0.03	14	0.35
South Eastern Australia	Flinders Island (FL)	3	1.7	0.36	0.32	-0.16		
	French Island (FI)	3	3.7	0.70	0.76	0.10	2	0.6
	Tasmania (TAS)	10	4.8	0.70	0.73		3	0.3
	Tasman Island (TASM)	5	2.5	0.48	0.43	-0.13		
Hawaii	Kaho'olawe (K)	46	6.7	0.73	0.72	-0.009	3	0.07
	Lana'i (L)	37	9.7	0.67	0.78	0.14	9	0.24
	Oahu (OA)	2	3	0.70	0.83	0.22	1	0.5
Asia	Malaysia (M)	3	3,8	0.55	0.78	0.35	4	1.33
	Total	428						

We detected 36 haplotypes with numbers ranging from 13 (CIF) to one in populations with small samples sizes (FL, TASM). The mtDNA median-joining haplotype network consisted of 23 haplotypes attributable to three subgroups (Figure 4-3). Subgroup A consisted mainly of samples from Cocos Island and Lana'i as well as representatives of all populations except Sulawesi (S), whereas subgroup B consisted of most individuals from Christmas Island together with samples from Malaysia, Sulawesi and Tasmania. Subgroup C however, was compost of individuals originating from Dirk Hartog Island, most samples from Kaho'olawe and several individuals from Lana'i and Malaysia. The phylogenetic tree constructed using Bayesian inference (Figure 4-4) showed a similar grouping as detected by the haplotype network analysis.

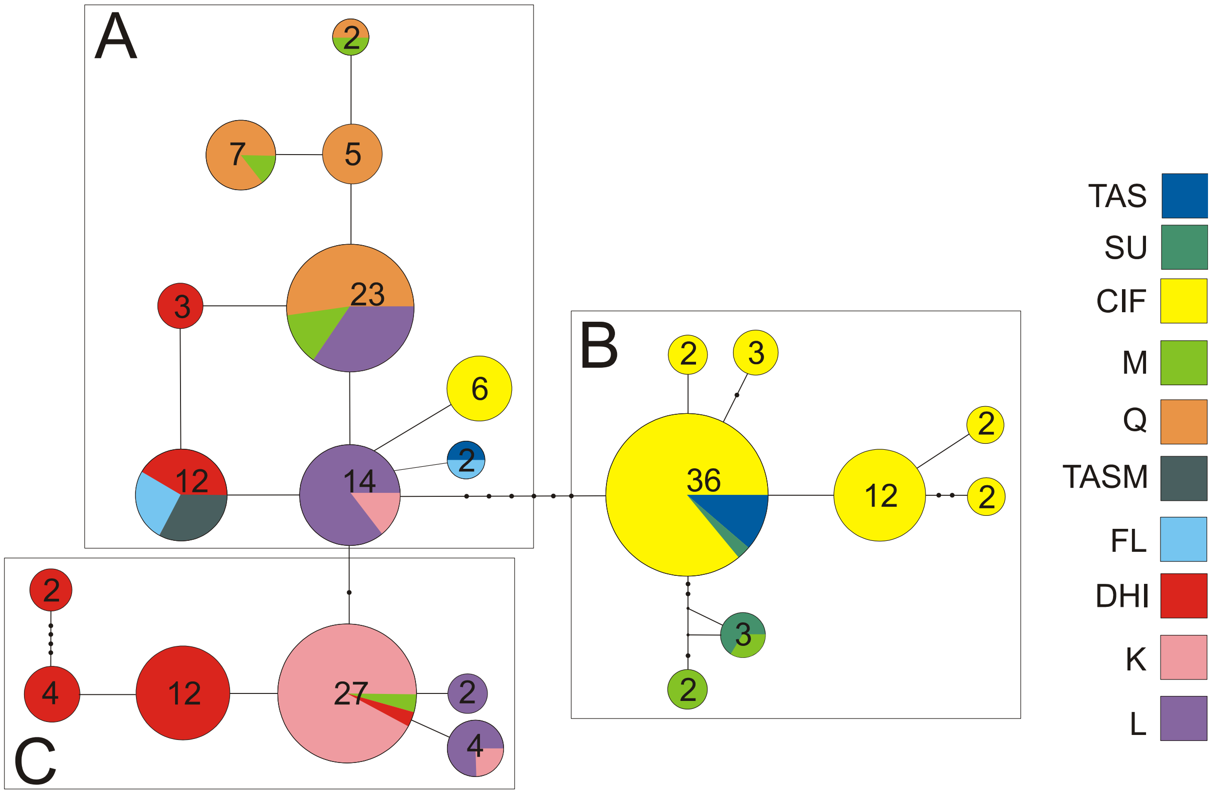

Figure 4-3. A maximum parsimony median joining (MP) haplotype network for Australian, Southeast Asian and Hawaiian populations consisting of 23 haplotypes divided into three subgroups (A-C). Black dots indicate more than one mutational step. Each additional dot represents one step.

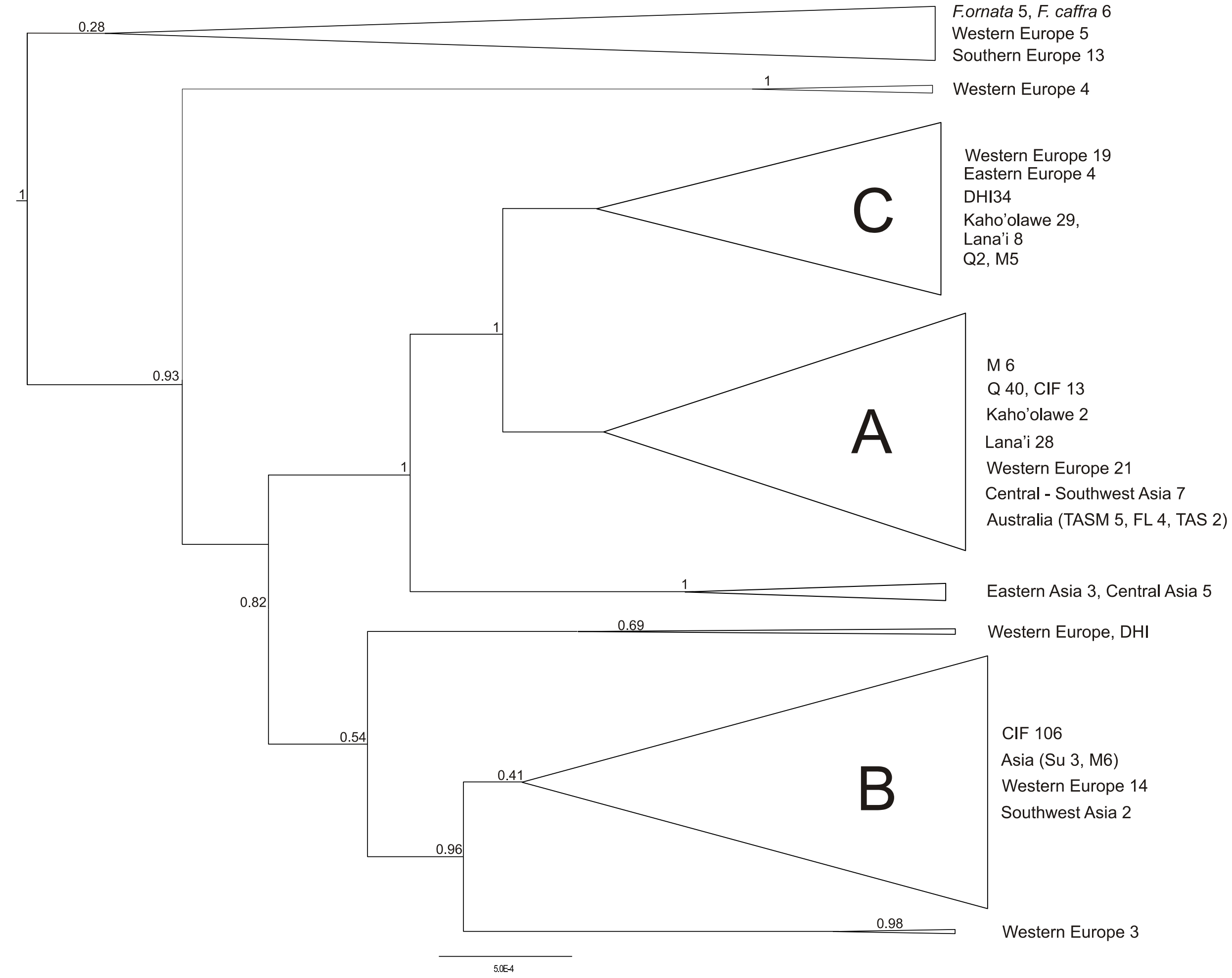

Figure 4-4. Phylogenetic tree inferred by Bayesian inference method. Three clades (A-C) were defined with 95% highest posterior density (HPD) of node ages represented at nodes.

Pairwise population comparison showed low genetic differentiation between samples from Tasman Island (TASM) and samples from Hawaiian Islands (K, L) and Asian locations (MS; mean pairwise $F_{ST} = 0.03$; Table 4-4). Populations from Hawaii (K, L), Asia (MS), Tasman Island (TASM) and Tasmania (TAS) showed no significant pairwise genetic differences. Very low genetic differentiation is found between Cocos Island, Tasmania and Christmas Island with pairwise F_{ST} values ranging from 0 to 0.03. Significant strong genetic differentiations were found between Q, DHI, FL, TASM, L and K.

The genetic distance (F_{ST}) between nine populations was plotted against the geographical distance (Figure 4-5). The resulting R^2 showed that only 0.83 % of the genetic differentiation (F_{ST}) was accounted for by geographical distances. No evidence of recent bottlenecks in any of the feral cat populations (N > 10) was detected.

Table 4-4. Genetic differentiation among populations (lower matrix pairwise F_{ST} values; upper matrix P-values). Asterisks (*) indicate significant and (-) indicate non-significant differences.

	CIF	**DHI**	**FL**	**TASM**	**TAS**	**K**	**L**	**MS**	**Q**
CIF		*	*	*	*	*	*	*	-
DHI	0.66		*	*	*	*	*	*	*
FL	0.76	0.12		*	*	*	*	*	*
TASM	0.68	0.31	0.69		*	*	-	-	*
TAS	0.26	0.36	0.63	0.36		*	-	-	-
K	0.72	0.52	0.88	0.10	0.50		-	-	*
L	0.67	0.36	0.86	0	0.25	0		-	-
MS	0.67	0.38	0.86	0.01	0.27	0	0.00		-
Q	0.03	0.51	0.82	0.60	0	0.80	0.53	0.57	

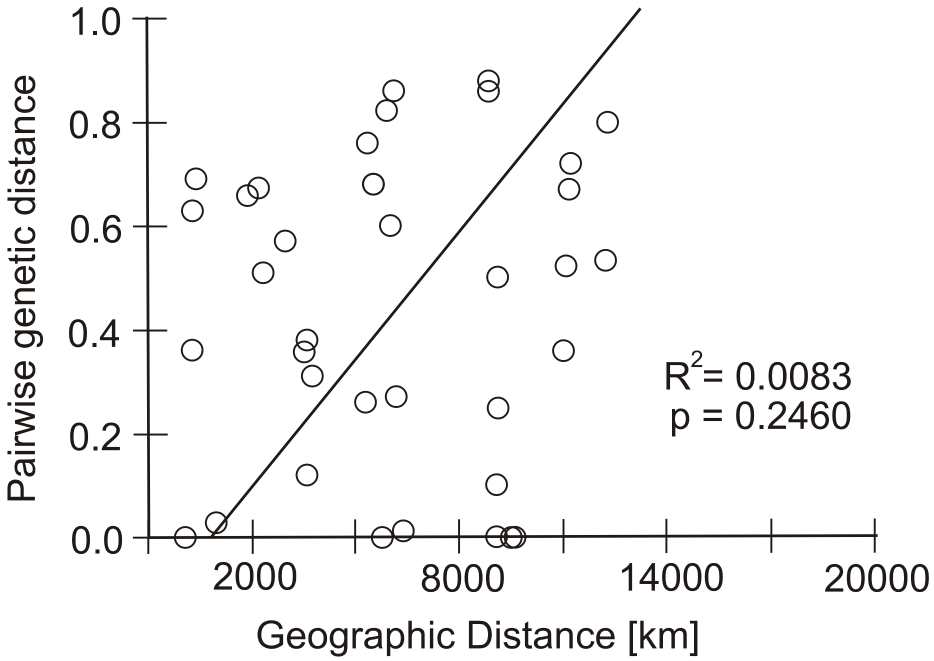

Figure 4-5. The genetic distance (pairwise FST) was plotted against the geographical distance of nine island populations (km). ($R^2 = 0.0083$, $P = 0.238$)

DISCUSSION

All islands in this study are assumed to have been invaded by cats around 200 years ago during a time of extensive European exploration (Abbott 2002; Brackenridge 1841; Hansen *et al.* 2007; Hess & Jabobi 2011). Overall, our analysis supports a strong European ancestry, especially Central and Western European regions, of island cat populations. Previous research documented that fitness deficiencies in small population due to genetic drift might be overcome through multiple introductions from different source populations (Allendorf & Lundquist 2003; Dlugosch & Parker 2008; Frankham 2005). In this study, populations showed no bottleneck effect and exhibited an average level of genetic variability comparable to neighbouring mainland populations (Hansen *et al.* 2007; Pontier *et al.* 2005) (Koch *et al.* unpublished). Our results showed that populations of Christmas Island (CIF), Dirk Hartog Island (DHI) and Lana'i (L) displayed a high genetic diversity, which was found to be similar to the Australian mainland and European domestic cat populations ($A = 8.5$, $H_O = 0.76$ and $A= 14.2$, $H_O = 0.70$, respectively; Hansen *et al.* 2007; Koch *et al.* unpublished; Pierpaoli *et al.* 2003).

Additional mitochondrial DNA analyses indicated that the Hawaiian Island populations originate from European locations, but are genetically differentiated into two groups. Most samples from Kaho'olawe and Dirk Hartog Island composed a single cluster (subgroup C, Figure 4-3) whereas the greatest amount of individuals from Lana'i, Cocos Island, Tasman and Flinders Island formed a second cluster (subgroup A, Figure 4-3). Our data indicated no evidence for isolation by distance between the populations since only 0.83 % of the genetic divergence (F_{ST}) was explained by geographical distances. A previous study revealed high level of gene flow between the populations belonging to the third cluster (Tasmania, Christmas Island and Europe - subgroup B, Figure 4-3) which is most likely facilitated by dispersal of cats through intensive sealing, whaling and pearl trade at the end of the 19th century (Koch *et al.* unpublished).

Low genetic differentiation and no isolation by distance imply a shared haplotype between the Hawaiian Islands and locations in Australia and Asia. Individuals carrying this haplotype would have populated islands with a distance of approximately 10,000 km between them. Hawaii was first visited by European Captain James Cook, who died on his second visit one year later in 1779 (Beaglehole 1974). Cook's accounts of his voyage encouraged merchants and traders from Britain, Russia, America and China to visit Hawaii regularly to replenish their supplies and seek replacement crews on their routes between North America and ports of East Asia (Greene 1993). Cocos and Christmas Island inhabitation by Malaysian workers started around 1850 (Green 2007). Malaysian labourers were also appointed in the pearling and whaling industry on Dirk Hartog Island, Flinders Island and Tasman Island. Since some current Australian populations exhibit individual cats that carry Southeast Asian haplotypes, it seems likely that Asian cats were brought to Australian islands during a second wave of invasions. Consequently these Asian cats intermixed with individuals of the founder populations that were of European origin (Koch *et al.* unpublished).

The maritime fur trade between 1785-1841, which traded in sea otters pelts (*Enhydra lutris)* operated on the "Golden Round" trade route around the world (Gibson 1992; Little 1973; Mackie 1997). On this route most ships would firstly sail from Northwest America to Hawaii and then to southern China. On their way back they would pass Malaysia through the Sunda Strait, Indonesia passing through the Indian Ocean to the Cape of Good Hope, Africa. From there, ships would sail to Boston, Northeast America or Britain and finally travel back to their initial starting point rounding South America at Cape Horn (Gibson 1992; Little 1973; Mackie 1997). Other routes started from India travelling through the Sunda Strait to Hawaii and Northwest America (Gibson 1992; Little 1973; Mackie 1997).

We assume that cats originating from Southeast Asia were brought onto the trading ships during landings in Malaysia or stopovers at Cocos or Christmas Island. The island was habituated by a European merchant trading various goods; i.e. timber and provisions employing Malaysian and Southeast Asian workers (Molloy 1830; Slocum 1901). Thereby it is possible that cats from Southeast Asia were brought on board of trading ships during stopover. Through extensive trade in Southeast Asia and Australia as well as regular traffic on routes such as the "Golden Round" it was possible to transport Southeast Asian and European cats around the world. This dispersal routes explain the low levels of genetic differences between populations which are separated by large geographic distances.

Population genetic data of Hawaiian and Australian cats demonstrate that in particular island populations represent valuable information to trace historical European and Asian dispersal routes of feral cats. Despite the high level of isolation of remote islands, e.g. Hawaii, island populations are surprisingly genetically variable, suggesting rare but multiple invasions from different source populations.

The genetic structure and diversity of invasive island populations is dependent on the level of historical and recent gene flow. Isolation from the recent influx by domestic breed cats into feral cat populations can lead to a pattern of cyclonuclear discordant individuals such as observed with samples from Kaho'olawe. Genetic differentiation among Hawaiian Island populations and isolation of Kaho'olawe in the microsatellite genotype clade is assumed to be attributable to historically low human habitation and no public access since its use as a US Army training ground and bombing range in 1941 (Department of the Navy 1979; Judd 1916; Warren & Aschmann 1993). Low human habitation is assumed to be equatable with few introductions over time and low number of domestic housecats (Dickman 1996; Koch *et al.* unpublished data; Oliveira *et al.* 2008; Say *et al.* 2012). Cat populations on the islands did not originate solely from ship landings by traders or explorers, but also presumably as secondary introductions as human commensals from nearby islands. The recruitment and intermixing of domestic and stray animals into a wild population is well documented (Dickman 1996; Oliveira *et al.* 2008; Say *et al.* 2012), which leads to population growth and an increased genetic variation (Dlugosch & Parker 2008; Kolbe *et al.* 2004). This would be also applicable for Lana'i with relatively high genetic diversity and a high human population size of approximately 3,200 inhabitants and numerous domestic cat owners (US Census 2000, US Department of Commerce). The Tasmanian cat populations were found to group within the Australian mainland cluster possibly representing a recent domestic and stray cat genotype distributed across the Australian mainland. We assume that grouping of O'ahu, Lana'i, Tasmania, French Island, Asia and portions of Dirk Hartog Island individuals into a cluster in the Bayesian assignment approach are based on the intermixing with domestic fancy breed cats. Therefore, is the interpretation of the development of invasive cat populations greatly biased by its introduction history and recent intermixing with domestic cats.

In conclusion we found a mainly European ancestry for cats in Hawaii hardly any genetic differentiation with cats from Australian islands. This population structure is mainly explained by passive dispersal during extensive trading in the 19th century. Drawing inference on the genetic structure and development of invasive species populations, such as the feral cat, is greatly biased by multiple introductions in the course of human habitation with consequential genetic influx from domestic house cats.

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General Discussion

The main aim of my thesis was to undertake a genetic analysis of feral cat populations in Australia and Hawai'i in order to contribute to wildlife conservation projects and invasive species research. The research focussed on determining the genetic origin, phylogeography, structure and management of feral cat populations. I assessed the diet of feral cats and foxes and evaluated the impact and the selective feeding behaviour on native biodiversity (**Chapter 1**). The results of the study back the necessity of island eradications and highlight the efficiency of well design predator control campaigns. The incorporation of population genetic and phylogenetic approaches have been found to enhance eradication and management campaigns further, by giving insights into population structure, degree of connectivity in and among populations, genetic origin and pathways of introduction of invasive species (Abdelkrim *et al.* 2007; Allendorf & Lundquist 2003; Clout & Russell 2008; Rollins *et al.* 2006; Russell *et al.* 2009; Schwartz *et al.* 2007; Veale *et al.* 2013; Waples & Gaggiotti 2006). In order to assess applicability of population genetic methods for feral cat management, I established molecular markers, estimated genetic structure, diversity and connectivity of Australian and Hawaiian feral cats and analysed genetic origin and potential introduction routes (**Chapter 2, Chapter 3 and Chapter 4**). The results of this study indicate that feral cat management can be improved through the application of genetic principles which provide crucial insights into feral cat dispersal history and feralisation. I therefore conclude that the assessment and utilization of genetic approaches must be considered in the design of invasive species studies, their management and research of feralisation processes.

Invasive species management

The first study of this thesis (Chapter 1) was part of a major predator management research project (Algar & Richards 2010; Guthrie *et al.* 2011; Richards *et al.* 2011a; Richards *et al.* 2011b). For a better understanding of invasive predators' impact on indigenous fauna in Australia I conducted a study identifying the extensive threat feral cats and foxes pose on the native species of Western Australia in combination with a prominent selective feeding pattern focusing on native prey species. Additionally, the study demonstrated that during the two year project a tendency of threat reduction and possible recovery capabilities of native Western Australian species could be observed. Through strategic planning an effective predator control can be realised (Algar *et al.* 2010; Algar *et al.* 2002; Algar & Burrows 2004; Bloomer & Bester 1992; Burns *et al.* 2011; Saunders & Norton 2001; Young *et al.* 2013) which then opens the possibility for species recoveries after eradication, respectively continuous management with decreased predator population size (i. e.: Campbell *et al.* 2011; Cooper *et al.* 1995; Keitt *et al.* 2011; Priddel *et al.* 2011; Young *et al.* 2013). This is particularly important considering that the results of this study indicated a specialized prey selection by feral cats on native species, which is presumed to increase the predation threat many times over.

Recent wildlife and invasive species approaches extend the traditional techniques of hunting and trapping through GPS monitoring, custom designed baits and aerial baiting (Silvy 2012). Since several eradication campaigns that included advancements of the scientific and technical basis were successful, it has been implied that islands and larger areas can be addressed, opening opportunities for future effective eradication projects (Campbell *et al.* 2011; Genovesi 2011; Keitt *et al.* 2011; Young *et al.* 2013).

The `Return to 1616` project on Dirk Hartog Island plans therefore to firstly eradicate all invasive species on the island and secondly to restore the vegetation and fauna to its biodiversity state assumed to have been present before 1616 (Department of Parks and Wildlife 2012). A pilot study and a study I was part of conducted for the 'Return 1616' project incorporated advanced management techniques in order to assess the daily activity patterns of feral cats on the island and recommend optimisations of the spacing for aerial baiting and monitoring transects (Algar *et al.* 2011; Johnston *et al.* 2010).

Advanced techniques included aerial baiting with target species custom designed baits (*Eradicat*®, *Curiosity*®) containing highly efficient toxins that were found to give the possibility of rapid and economical knockdown of cat populations (Algar *et al.* 2002; Algar & Burrows 2004; Algar *et al.* 2011). Nevertheless, it has been indicated that toxin-based eradication projects alone failed if they lacked additional application of other management techniques in order to remove remaining animals during and after baiting, to reduce population recovery rate and to capitalise on the population knockdown (Campbell *et al.* 2011). The methods recommended included trapping in cage and leg-hold traps (Algar *et al.* 2010; Algar *et al.* 1999; Algar *et al.* 2002; Burns *et al.* 2011; Saunders & Norton 2001; Young *et al.* 2013), micro-chipping and sterilisation (Hilmer *et al.* 2009) as well as the monitoring effectiveness and feasibility of eradication campaign design (Campbell *et al.* 2011; Phillips *et al.* 2005).

The toxin widely used and incorporated in the *Eradicat*® baits is sodium monofluoroacetate (1080), a toxin derived from plant species (e.g. *Gastrolobium*, *Gompholobium*, *Acacia*), that introduced species are highly susceptible to in Australia, whereas native Australian species are more tolerant (McIlroy 1986). Ongoing research works on the design and assessment of an enhanced toxins that enable a new humane and effective baiting outcome (Murphy *et al.* 2011). Feral cats are highly susceptible to the toxicant para-aminopropiophenone (PAPP) and encapsulated in pellets poses possibly less risk for non-target species (Eason *et al.* 2010; Hetherington *et al.* 2007; Jessop *et al.* 2013; Johnston *et al.* 2011; Johnston *et al.* 2012; Murphy *et al.* 2011). A study conducted on Dirk Hartog Island was able to confirm the toxins applicability, while demonstrating the efficiency and acceptability of encapsulated pellets as transport vehicle for toxins (Johnston *et al.* 2010). In addition to recommended management techniques (e.g. specialised baits, aerial baiting) the incorporation of GPS data-logger radio collars fitted on individuals with mortality features has been found to help to monitor the effectiveness of methods used and enhance eradication campaign design (Algar *et al.* 2011; Johnston *et al.* 2010; Phillips *et al.* 2005; Silvy 2012). Although incorporation of these techniques provide important information for projects working on populations with unclear size, structure and distribution, the outcome of management campaigns is impacted by various factors (Campbell *et al.* 2011).

Eradication and management campaigns have been shown to fail if not accurately planned and adequate financially and institutional supported (Campbell et al. 2011). Although the first study of this thesis (Chapter 1) was not considered to permanently eradicate invasive predators in the study area, it nevertheless proves the efficacy of properly designed eradication campaigns, which incorporate traditional and advanced techniques such as trapping, aerial baiting and follow-up monitoring track counts. Thereby, the results back the necessity of feral cat control in order to preserve Australian species that are under threat on the mainland.

Invasive species management and advances in population genetics

Advancement for eradication and management campaigns has come with the incorporation of population genetic approaches (Abdelkrim *et al.* 2007; Allendorf & Lundquist 2003; Rollins *et al.* 2006; Schwartz *et al.* 2007; Veale *et al.* 2013; Waples & Gaggiotti 2006). The characteristics enabling an invasive species to be successful in the new ecological conditions encountered are crucially dependent on the species ability to respond to natural selection and adaptation at the population level before or during settlement (Estoup & Guillemaud 2010; Facon *et al.* 2006). Substantial genetic variability or alternatively good alleles of specific genes or else good combination of genotypes are expected to favour adaptation to foreign ecological conditions and therefore the settlement and spread of introduced species (Estoup & Guillemaud 2010; Facon *et al.* 2006; Kolbe *et al.* 2004). The history of a population's origin and the historical and demographical features of the introduction greatly influence the genetic variability of invading populations (Estoup & Guillemaud 2010). These features include the genetic composition and number of introductions, the number of individuals introduced and the dispersal following each introduction (Estoup & Guillemaud 2010). Therefore, it is crucial to understand the history of the invasion process, including geographical pathways followed by the founders of the invading populations (Dlugosch & Parker 2008).

In addition to the understanding of the underlying factors enabling successful invasions and settlement, it is vital to evaluate and potentially enhance management through the examination of the populations' genetic structure and diversity and the degree of connectivity among populations (Clout & Russell 2008; Russell *et al.* 2009; Veale *et al.* 2013; Waples & Gaggiotti 2006). Practical applications of population genetic approaches include the feasibility to monitor eradication success and sustainability (Rollins *et al.* 2009; Russell *et al.* 2010; Veale *et al.* 2013).

Strategies for recurrent introductions of invasive species are based on the prevention of theses introductions and are assumed to be most cost-effective (Mack *et al.* 2000). The general approach is the identification of the geographical origin through genetic analysis and the responsible vector, followed by targeting the source and means of dispersal through monitoring and quarantine measures (Estoup & Guillemaud 2010). This however, is not applicable for species which are already established and are widespread over large areas (Hulme 2006). Here, management approaches need to aim for containment or a long-term reduction of the population (Hulme 2006). In the case of the feral cats, which are widespread across Australia, containment on the mainland is labour and cost intensive (Algar & Burrows 2004; Burns *et al.* 2011). The creation of 'mainland islands' with a manageable predator reinvasion rate (Algar & Burrows 2004; Burns *et al.* 2011; Saunders & Norton 2001; Young *et al.* 2013) is possible but still requires consequent planning and financial support (Campbell *et al.* 2011; Saunders & Norton 2001).

Fitzgerald (2012), suggested that population genetic techniques need to be carefully chosen, they must be focused on management-oriented objectives and may only be applicable to answer population genetic questions of invasive species that are tractable over short timescales. Various studies have demonstrated that this has already become common practice in research and planning of management approaches for invasive species (e.g.Le Roux & Wieczorek 2009; Rollins *et al.* 2006; Rollins *et al.* 2009; Schwartz *et al.* 2007; Veale *et al.* 2013). Recent studies and several population analyses conducted within this thesis tested for bottlenecks and were able to distinguish single versus multiple introduction scenarios; thereby enhancing the likelihood of eradication campaign success through insights into invasive populations genetic fitness and its introduction history (Le Roux & Wieczorek 2009; Rollins *et al.* 2006; Schwartz *et al.* 2007; Veale *et al.* 2013).

Generally it is recognized that controlling invasive species, such as feral cats, on islands will be more successful by utilizing islands' natural barriers to prevent or at least reduce dispersal (Algar *et al.* 2010; Algar *et al.* 1999; Algar *et al.* 2002; Campbell *et al.* 2011; Phillips *et al.* 2005; Saunders & Norton 2001; Young *et al.* 2013). The eradication of an invasive species population on a small island with well-defined eradication units (target population intended for eradication) is feasible (Courchamp *et al.* 2003; Robertson & Gemmell 2004). However, populations on larger islands or populations not displaying a distinct structure are more problematic (Hampton *et al.* 2004; Robertson & Gemmell 2004).

Although large-scale eradications on large islands are possible (Robertson & Gemmell 2004; Towns & Broome 2003), they are logistically difficult (Courchamp *et al.* 2003; Robertson & Gemmell 2004). As for mainland populations, attempting to eradicate a fraction of a population on an island, or a sink population within an unidentified source-sink dynamic, will eventually results in rapid recolonisation (Robertson & Gemmell 2004). Population genetic approaches allow determination of spatially isolated populations with significant differentiation (no relatedness) indicating limited dispersal on the island (Abdelkrim *et al.* 2005a; Abdelkrim *et al.* 2007; Hansen *et al.* 2007; Robertson & Gemmell 2004).

Identification of distinct population units with negligible immigration allows defining manageable eradication units with low recolonisation risk, providing a firm basis for a successful eradication (Abdelkrim *et al.* 2005a; Hansen *et al.* 2007; Robertson & Gemmell 2004).

In a recent study Veale *et al.* (2013) discussed the genetic techniques to quantify reinvasion, survival and breeding rates during a control operation on stoats (*Mustela erminea*) on an island in New Zealand using population genetic approaches. They concluded that control efforts were most cost-effective and successful when using information from genetic population assignment and relatedness analysis assessing recolonisation rates from the mainland (Veale *et al.* 2013). In the study, genetic monitoring allowed detecting reinvasions from the mainland during special mast events and detailed kinship analysis identified the number and locations of litters. Control efforts were therefore adjusted to specific areas on the island. Similarly, the assessment of relatedness between individuals on Dirk Hartog Island and the mainland allowed both the exclusion of an ongoing gene flow through recruitment from mainland populations (Chapter 2). It also revealed high connectivity within the island that prevents the definition of eradication units. In contrast to the study by Veale *et al.* (2013) the genetic information obtained from feral cats on Dirk Hartog Island indicated that a reestablishment of the population from the mainland following eradication is unlikely. This allowed adjusting the eradication campaign to the population structure on the island creating a promising basis for successful eradication and reconstruction of native fauna/flora on Dirk Hartog Island. As previously proposed by Rollins *et al.* (2006) and Russel *et al.* (2010), both above-mentioned studies (Veale *et al.* 2013, Chapter 2) demonstrate that population genetic tools allow monitoring campaigns outcome and enable individual adjustment of project design to respective conditions. This consequently allows successful eradication or management of populations which consequently reduces the threat to native species.

Invasive species origin, routes of invasion and the use of bioproxies

Reconstructing introduction routes using genetic data enables the opportunity to test hypotheses concerning the environmental and evolutionary factors responsible for biological invasions (Dlugosch & Parker 2008; Estoup & Guillemaud 2010; Konecny *et al.* 2013). It also provides information on the pathways and degree of connectivity between source and invaded populations (Rollins *et al.* 2006; Rollins *et al.* 2009; Schwartz *et al.* 2007). It has been widely recognized that biological invasions have often been caused by fortuitous or intentional dispersal events linked to human migration (Estoup & Guillemaud 2010; Lockwood *et al.* 2005; Mack *et al.* 2000). Vectors for dispersal through human activities (exploration, discovery and settlement in new continents, sea and air travel, etc.) have increased extensively over the past 500 years (di Castri 1989; Duffy & Capece 2012; Konecny *et al.* 2013; Mack *et al.* 2000). These activities promoted introductions into remote areas and accelerated the spatial expansion after species introduction into new areas (Estoup & Guillemaud 2010).

So far, the origin and pattern of invasions of cats into Australia have been unresolved. Several hypotheses on the basis of historical records have been put forward regarding the introduction of feral cats to Australia, of which two are the most common (Abbott 2002; Abbott 2008; Burbidge *et al.* 1988; Dickman 1996; McKay 1996). The first proposes an introduction prior to European settlement in Australia during the introduction of the dingo (*Canis lupus dingo*) around 4,500 years ago, through Malaysian trepangers from about 1650 in northern Australia and through shipwrecks of European explorers on the Western Australian coast around 1600 (Abbott 2002; Burbidge *et al.* 1988; Macknight 1976; McKay 1996; Oskarsson *et al.* 2012; Robert 1972). The second hypothesis suggests a relatively recent introduction with European explorers and settlers in the late 18th century (Abbott 2002; Abbott 2008; Dickman 1996). Theses hypothesis were considered in the third study (Chapter 3). Genetic analysis results indicated that the main introductions of cats to Australia originated from Europe with the possibility of isolated invasions from Asian locations. Similarly, the results of the fourth study in this thesis indicated that feral cats in Hawai'i also originated from Europe (Chapter 4).

Historical records of translocations alone potentially yield incomplete accounts of introduction events, but with the addition of phylogenetic studies it is possible to infer the colonization history of a species in a geographical context (Fitzpatrick *et al.* 2012; Searle *et al.* 2009b). Similarly, phylogeographic analysis of contemporary and archaeological human remains yield insights into the initial and recent colonisation and demographic histories of humans (Jones *et al.* 2013; Malmstrom *et al.* 2009; Reich *et al.* 2012). Generally knowledge about the human past has been inferred though documentary evidence, analysis of artefacts and other traces of a human lifestyle and the interpretation of human remains (Jones *et al.* 2013). In an extensive review, Jones *et al.* (2013) established the term of 'living artefacts' / bioproxies: organisms dispersed between locations though human migration, which potentially provide significant information for determining human colonisation history. These bioproxies were categorized into three categories of organisms: domesticates (purposefully transported); commensals (unintentionally transported) and pathogens or parasites (Jones *et al.* 2013). They are assumed to enable the unravelling of the complex colonisation history of human descendants, whose genetic signal has been obscured by recurrent immigration and emigration (Jones *et al.* 2013; Jones *et al.* 2012; Searle *et al.* 2009b). However, it has been suggested that great care needs to be taken by interpreting genetic data (Jones *et al.* 2013). Since not only the colonisation history of humans may be obscure, but earlier colonisation events of domesticated species may be replaced by intermixing with more recent introduced animals or new domestic breeds (Jones *et al.* 2013; Larson *et al.* 2007; Larson *et al.* 2012). Therefore commensals, that may have been moved around by people in the last 200-300 years may have a limited value as bioproxies for human history (Jones *et al.* 2013). Exceptions are assumed to be domesticates and commensals that are able to persist independently of humans e.g. in feral populations (Jones *et al.* 2013; Larson *et al.* 2007; Larson *et al.* 2012). My studies indicate that the understanding of historical species migration through human dispersal, is possible by using domesticate and commensal species simultaneously as a ‘living artefact’ and object of investigation (Chapter 3 and Chapter 4). This is especially so for the feral cat, a domesticate and commensal, that exists on islands with a low influx from new domestic breeds and still carries a genetic signal that can be used to reconstruct their own historical migration and invasion pathways (Chapter 3 and Chapter 4).

By incorporating historical records in conjunction with a phylogeographic analysis of various mainland and island feral cat populations my studies were able to determine the most likely origin and possible routes of introduction of feral cats into Australia (Chapter 3) and Hawai’i (Chapter 4). Both studies highlighted the fact that transport and dispersal of cats around the world was so extensive that no indication for isolation by distance was detected between several Hawaiian and Australian feral cat populations (Chapter 4). Global trade routes such as the ‘Golden Round’ of the maritime fur trade generated a link between far off global cat populations. One could argue that no pattern of isolation by distance would be due to ongoing intermixing with globally common domestic breeds that was found to limit the genetic signal to draw inference on the colonisation history of humans (Jones *et al.* 2013; Larson *et al.* 2007; Larson *et al.* 2012) and therefore likewise on the introduction history of cats. Nonetheless, low genetic variation between cats of geographical distant locations was especially recognizable on island populations that were found to have a low possibility for intermixing with domestic fancy breeds due to low or no human habitation (Chapter 3 and Chapter 4). It is therefore possible to confidently infer that the dispersal of cats through human migration and exploration, if sampling is undertaken on locations with low possibility of interactions with domestic fancy breed cats. I recommend further assessment of cat pathways confirming historical global trade routes as major paths for dispersal. This assessment should include additional locations in Asia and North America to enable evaluation of associations between cats around the world based on their introduction history. Additionally, this could confirm the maritime fur trades 'Golden Round' as an important source and link for cat dispersal in the 19th century.

The results of this thesis extend the use of genetic methodologies, that were proposed to enable inference of human history (Jones *et al.* 2013) by highlighting their applicability for the inference of human-mediated dispersal of commensal and domesticated species that considerably affect biodiversity around the world.

Feral cats' success as an invasive species

The general success of an invasive species being able to outcompete and replace native species is based on various phenotypic traits that enhance the likelihood of establishment in new environments (Allendorf & Luikart 2007; Crandall *et al.* 2000; Estoup & Guillemaud 2010; Kolar & Lodge 2001; Sakai *et al.* 2001). The capacity of a species to respond to new ecological conditions, selection and changes in genetic variability is greatly influenced by molecular and quantitative traits (Keller & Taylor 2008; Prunier *et al.* 2011). Then again these traits are significantly effected by the history, origin and demographic features of invading populations (Estoup & Guillemaud 2010). For the understanding of the success of an invasive species, phylogenetic analysis including the number and composition of source individuals/populations are crucial (Estoup & Guillemaud 2010; Sakai *et al.* 2001).

This thesis is based on the general accepted assumption that feral cats are among the most successful invaders on locations around the world (Bonnaud *et al.* 2007; Bonnaud *et al.* 2011; Courchamp *et al.* 2003; Medina *et al.* 2011; Nogales *et al.* 2004; Nogales *et al.* 2013). Possible insufficiency or absence of specific enemies, which allow non-indigenous species higher reproductive rates, is assumed to be one explanation for the success of invasive species (Allendorf & Luikart 2007).

Feral cats face certain natural enemies in Australia (e.g. snakes, Serpentes, Australian dingo, *Canis lupus dingo* and foxes) and the role of top-predators and their suppressive effect on sympatric mesopredators and prey has been discussed (Johnson *et al.* 2006). However, there is no evidence that the success of feral cats in Australia is diminished by top-predators such as the dingo (Allen *et al.* 2013).

Their adaptability to new ecological conditions is underlined by their adaptation capability as a generalist predator. They are found to be extremely adaptable to new biodiversity conditions and readily adjust to different prey items (Coman & Brunner 1972; Fitzgerald & Turner 2000; Konecny 1987). It has been suggested that primary prey selection is solely determined by relative abundance (Van Aarde 1978; Veitch 1985), individual requirements and prey availability (Catling 1988; Harper 2004; Molsher *et al.* 1999). With the first study (Chapter 1) I was able to broaden these assumptions by revealing an additional selective feeding behaviour focusing on native prey species despite the highest relative abundant species present being introduced house mice.

Invasive species introduction and establishments are often associated with population bottlenecks which lead to lower genetic variation than in their native range (Allendorf & Luikart 2007). Additionally, invasions are generally limited to a few individuals resulting in small population sizes, with reduced genetic variation by the founder effects (Allendorf & Lundquist 2003).

Although cats show strong capabilities to succeed in new environments (Bonnaud *et al.* 2007; Bonnaud *et al.* 2011; Fitzgerald 1988; Fitzgerald & Turner 2000; Hilmer 2010; Konecny 1987; Medina *et al.* 2011; Say *et al.* 2002), it is likely that these genetic effects still influence invasive cat populations after their introduction. Reducing the impact of genetic bottlenecks (low genetic diversity) can be alleviated by rapid recovery or expansions of the new immigrants (Cornuet & Luikart 1996; Nei *et al.* 1975). Alternatively, non-reduced genetic variation among invaders can be explained through multiple introductions which counterbalance potential genetic variability loss through genetic admixture of more than one local source populations of the geographical origin (Allendorf & Luikart 2007; Allendorf & Lundquist 2003; Frankham 2005; Kolbe *et al.* 2004; Konecny *et al.* 2013).

Under the assumption that introduced populations generally exhibit low genetic variability, analysis of feral cat populations in Australia indicated little to no reduction of genetic variability associated with founding events. These unexpected patterns of an overall average genetic diversity, when compared to cats' native range, were found to be most likely due to multiple introductions of cats during the last 200 years to Australia and Hawai'i and recent extensive gene flow from domestic breed cats. This evidence is supported when one considers the genetic diversity values found in the populations of this study compared with other cat populations found on islands that exhibit low genetic variation. Kerguelen Island, in the Southern Indian Ocean, is an example of the expected pattern of low genetic variability, with multiple introduction events being highly unlikely, no presence of domestic cats and a population that was founded by a very small number of individuals (Pontier *et al.* 2005).

The results of this thesis are in line with previous studies that found multiple introduction events resulting in a restored genetic variation with high adaptive potential (Allendorf & Lundquist 2003; Sakai *et al.* 2001). However, genetic diversity of cat populations in this study were found to benefit, in addition to multiple introduction events, from extensive gene flow from domestic breed cats and high connectivity of feral cat populations in the mainland of Australia.

In conclusion, feral cats in Australia and Hawai'i are a versatile and successful invading species, which were able to establish populations throughout both countries within the last 200 years. Their capability to adapt to new environmental and ecological conditions e.g. through their ability to shift the primary prey species, allowed them to inhabit all ecological and climate zones found in Australia and Hawai'i. Feral cat populations from Australia and Hawai'i originated from Europe and were transported to these countries during the time of exploration in the 19th century and the following start of global maritime trading. This transportation around the world resulted in a connection between Hawaiian and Australian cat populations indicating that, with respect to their history of dispersal and influx from domestic house cat breeds, there might be an overall link between feral cats around the world - the 'global supercat'.

Outlook

The phylogenetic processes of the beginning of cat domestication and potential nucleotide positions that distinguish wild cats and domestic cats have been discussed (Driscoll *et al.* 2007; McEwing *et al.* 2012) . However, the basic factors responsible for the adaptation potential of feral cats as an invasive species, the process of domestication and features facilitating feralisation in cats are unclear.

In general it is believed that the domestication process progresses along an axis that involves the transformation from the wild phenotype to its domestic phenotype (Zeder 2012). This is driven by a number of selective and random processes including the relaxation of natural selection and the adaptation to the new selective pressure as the species enters a human environment (Zeder 2012). The stages of domestication involve the shift from free-living populations, to managed populations that are able to revert to their wild state, and finally to animals that are unable to survive without provision by humans (Figure D-1.; Zeder 2012)

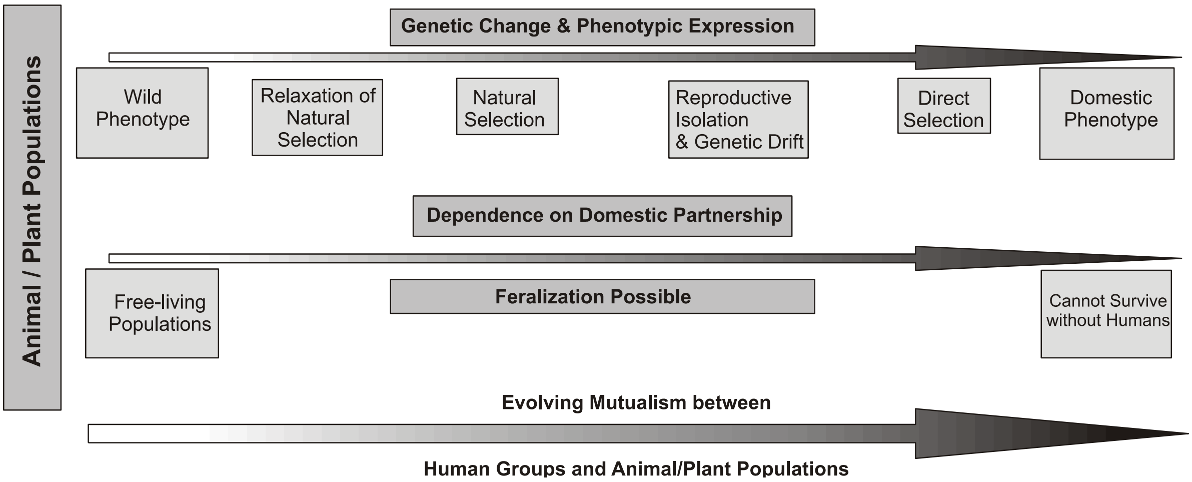

Figure D-1. Adapted from Zeder 2012. Multiple axes along the domestication process (from wild phenotype living in free populations to domestic phenotype that cannot survive without humans).

The domestication history and process of wildcats has been discussed and it has been put forward that phylogenetic and phylogeographic evidence suggested a sympatric divergence from wild to domestic cats (Driscoll *et al.* 2009). It is assumed that a single protracted domestication occurred, which incorporated multiple wildcat matrilines over the broad Near Eastern human cultural area (Driscoll *et al.* 2009). Thereby, each adaptive locus/allele may have been independently selected in different populations through time. This additive effect resulted in the genomic consilience of the now domestic cat (Driscoll *et al.* 2009).

This additive effect of multiple independent domestications is similarly found in various other domesticated and now successfully invasive species (e.g. pigs; Larson *et al.* 2007; Ottoni *et al.* 2013) and sheep (Singh *et al.* 2013).

If an incomplete domestication process allows species to revert to a wild state (Zeder 2012) than it could be hypothesised that the domestication of the feral cat isn't completed yet. Attributes that are thought to be 'pre-adaptive' to domestication in animals are grouped under five general categories of affected behaviours (group structure, sexual behaviour, parent-offspring interactions, responses to humans and flexibility; Zedner 2012). These behaviours make it among other things possible for humans to obtain leadership of group structure of animal communities, determine reproductive timing or assume a parenting role over young animals soon after birth (Zedner 2012). It has been discussed that phenotypic changes of cats, selective breeding in the last 200 years and altered social behaviour indicate a completed domestication process (Driscoll *et al.* 2009; Price 2002; Serpell 2000). This however applies only for domestic or at most stray cats with regular gene flow from domestic fancy breeds. Feral cats display exactly the opposite characteristics outlined for a completed domestication process (Recio & Seddon 2013). This discrepancy of a highly probable completed domestication in domestic cats versus characteristics displayed by feral cats indicates the possibility of an uncompleted domestication in some lineages of house cats. I propose that the domestication of the house cat is completed in regard to fancy breed cats which were created in the last 200 years (e.g. Balinese, Devon Rex; Helgren 2013). However, I hypothesize that isolated feral cat populations, which are most likely descended from domestic shorthaired cats (common house cats, which are of mixed ancestry and not a recognised breed; Helgen 2013), have not completed the domestication process. As a consequence, feralisation and the reversion to their wild state was possible. This hypothesis is backed by the findings of this thesis, which indicate a clear genetic differentiation of feral cat populations on isolated islands compared to mainland population with assumed influx from fancy breed cats. Through data obtained for these cat populations the inference of their genetic origin and introduction history 200 years ago was possible. Isolated feral cat populations showed no pattern of isolation by distance, indicating that this lineage of common house cats hasn't been significantly intermixed with selectively breed cats.

I propose that feralisation of domestic shorthaired cats, which diverged in the course of history from human care and have been isolated from domestic fancy breeds, experienced a shift of allele frequency to inherited 'wild traits' already present through their ancestry. In order to determine a positive selection of ‘wild traits’ that facilitate the feralisation process in feral cats, it is essential to compare these traits between the domesticated and the wild state of the species. Several small wild cat species (e.g. *Felis lybica*, *Felis silvestris*) would allow an extensive comparison with house cats in order to determine a positive selection of ‘wild traits’.

It has been suggested that there are only a few nucleotide positions that distinguish wild cats and domestic cats (Driscoll *et al.* 2007; McEwing *et al.* 2012). The identification of the mutations steps required to differentiate domestic versus wild cats gives the opportunity to genetically define the feralisation process and the state of domestication level in house cats. Drawing inference on feralisation processes in feral cats will give valuable insight into underlying basics of feralisation processes altogether. The understanding of these processes will eventually aid invasive species management to adjust to potential different stages of feralisation and thereby enhance control efforts.

The use of single nucleotide polymorphism markers (SNP) in population genetics provides broad genome coverage with high quality data resulting in an efficient and cost-effective genetic tool (Morin *et al.* 2004; Morin *et al.* 2009). A high density domestic cat DNA Array (Illumina Infinium Feline 63K iSelect DNA array) has been developed that includes SNPs that are able to identify wildcat species as well as phenotypic and phylogenetic important SNPs for felid species (Cat Health Network, Hill’s Pet Food, Inc.). This array will give the opportunity to test hypothesis proposed above and further investigate genetic differentiation of feral cats in Australia.

Genetic differentiation of feral cats in Australia was found to be relatively low compared to island populations (Chapter 3). This was ascribed to high level of intermixing with house and stray cats. However, the extent of gene flow among cats from cities, suburban areas and feral cat populations is unknown. Additional sampling of house cats, stray and feral cats in Australia and the utilization of the ‘Cat DNA array’ will enable to investigate gene flow between the three categories. This ultimately will yield important information for feral cat management in Australia by defining possible source populations of house and stray cats, possible pathways for gene flow and the determination of feral cat population with low influx from suburban areas.

Cats have been introduced around the world including many remote islands and can be found in most climate zones except the Poles (Courchamp *et al.* 2003; Lever 1994; Medina *et al.*

2011; Vitousek *et al.* 1997). Despite unresolved questions regarding the domestication level, populations of feral cats have adapted to diverse climatic conditions. Cats in this study were introduced to semi-arid, tropical and montane areas around 200 years ago. So far it is unclear how these climatic conditions encountered by cats influenced their establishment in Australia and Hawaii. A previous study indicated no influence of climate on the basal metabolic rate of feral cats from Australia's arid and temperate zones (Hilmer 2010). The impacts of seasonal changes influencing the basal requirements were assumed to be due to different prey availability and changing activity patterns (Hilmer 2010). However, ecological differentiation on the gene level could be attributable to a differentiation that is associated to functional genes. Previously discussed positive selection on inherited 'wild traits' would likewise be possible for the adaptation of feral cats to various climate conditions. This again could be investigated using a 'Cat DNA array' covering large areas of the cat genome.

Further studies that acquire information on gene flow from domestic into feral cat populations and the understanding of the feralisation process will be crucial for basic research and invasive species management. Additionally, information on the underlying genetic differentiations that allow adaptation to diverse climate conditions, will give valuable information to understand factors enabling the success of invasive species and adaptation potential of species to different ecological conditions.

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Supplement

Supplement Chapter 2

Table 2-S1. Information on primers used for amplification of 3000 base-pairs amplicon of mitochondrial genes ND5 and ND6. Primer name, primer function and sequences are given.

#	Primer function	Primer Name	Sequence 5' ->3'	Direction
1	PCR & Sequencing	9Hm	AACCCATCATTTACACGAGAAAAC	FWD
2	PCR & Sequencing	10L.int3	TACGGTTGCTCCTCAGAAGG	REV
3	Internal sequencing	9L.int2	GGATGTAGGCCGAATTG	REV
4	Internal sequencing	9Lm	GAGTAATTAGTAGGGCTCAGGCGTT	REV
5	Internal sequencing	10Hm	AACTCCTGTCTCCGCCCTACTCCA	FWD
6	Internal sequencing	10H.int	ACCAACGCCTGAGCCCTA	FWD
7	Internal sequencing	10H.int3	GTAATACACCGCCTCCCATC	FWD
8	Internal sequencing	10L.int4	CTTCAAAGCCTTCTCCAAT	REV

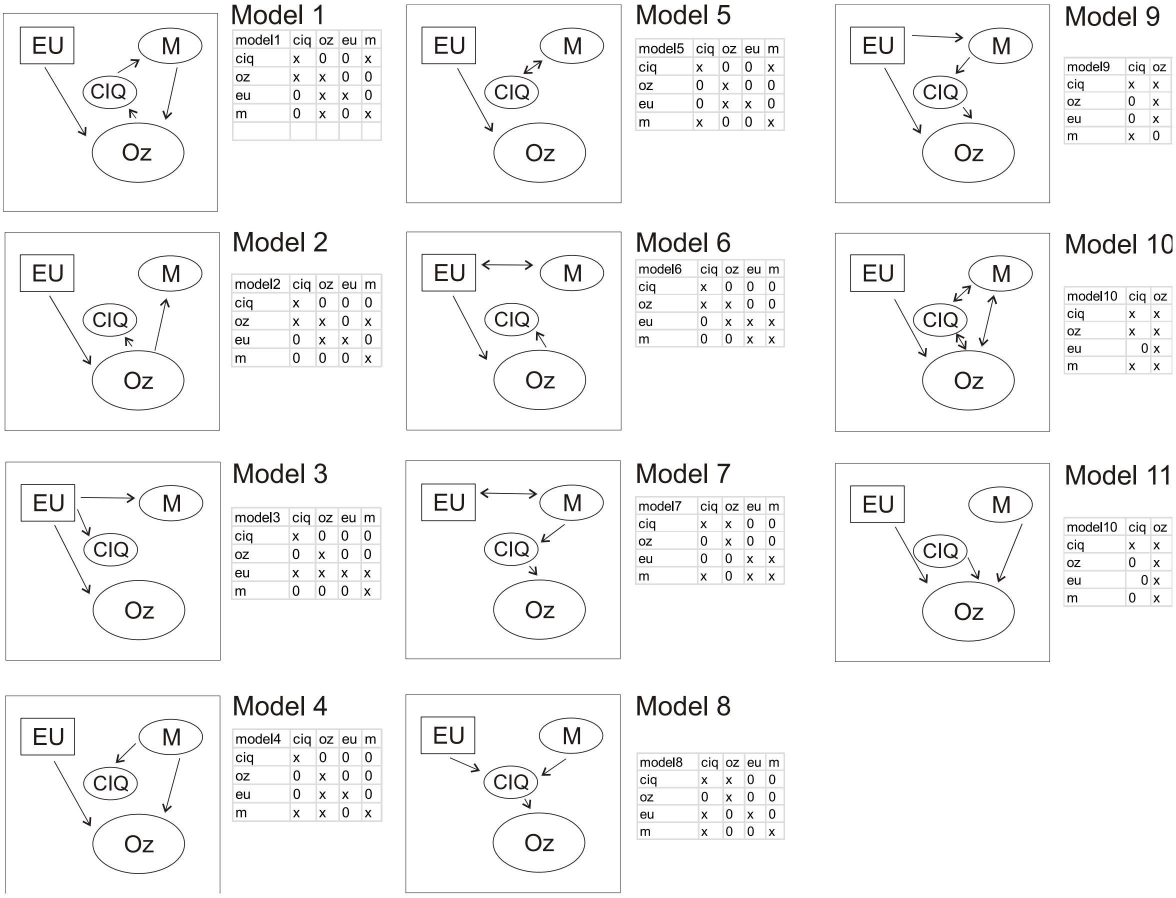
Table 2-S2. STRUCTURE analysis results with probability of each admixture model for clusters 2-5 for feral cats of Dirk Hartog Island, Peron Peninsula and Steep Point.

K	**Reps**	**Mean LnP(K)**	**Stdev LnP(K)**	**Ln' (K)**	**Ln'' (K)**	**Delta K**
2	10	-1785.3900	15.7413	NA	NA	NA
3	10	-1866.3600	94.1506	-80.97000	13.94000	0.148061
4	10	-1933.3900	137.4129	-67.03000	103.8000	0.755387
5	10	-1896.6200	148.8163	36.770000	NA	NA

Table 2-S3. Data of feral cat trapping points from Dirk Hartog Island, Peron Peninsula and Steep Point, Western Australia. Cat Sample ID, trapping area and recorded corresponding geographical coordinates are given.

Cat ID	**Area**	**Latitude**	**Longitude**
DHI-12	South	25º 54’ 850"S	113º 06’ 825"E
DHI-13	South	25º 54’ 607"S	113º 06’ 816"E
DHI-10	South	25º 55’ 345"S	113º 06’ 758"E
DHI-01	South	25º 57’ 442"S	113º 07’ 717"E
DHI-09	South	25º 55’ 635"S	113º 06’ 690"E
DHI-18	South	25º 53’ 269"S	113º 06’ 801"E
DHI-12A	South	25º 54’ 850"S	113º 06’ 825"E
DHI-02	South	25º 57’ 184"S	113º 07’ 618"E
DHI-16	South	25º 53’ 471"S	113º 06’ 690"E
DHI1	**North**		
MB2	North	25° 33’.040"S	112° 57’ 664"E
DHI11	North	25° 36’.714"S	112° 56’ 510"E
MB4	North		
DHI17	North	25° 39’ 069"S	113° 02’ 369"E
DHI16	North	25° 36’ 819"S	113° 02’ 410"E
DHI14	North	25° 30’ 033"S	112° 58’ 260"E
DHI5	North	25° 46’ 277"S	113° 03’ 467"E
DHI6	North	25° 39’ 670"S	112° 59’ 708"E
DHI7	North	25° 34’ 021"S	112° 56’ 295"E
DHI8	North	25° 40’ 865"S	113° 00’ 550"E
DHI9	North	25° 36’ 697"S	112° 56’ 581"E
DHI10	North		
DHI2	North		
DHI15	North	25° 30’ 711"S	112° 57’ 556"E
DHI12	North	25° 41’ 450"S	113° 03’ 208"E
DHI13	North		
DHII3	North		
DHI4	North		
MB7	North	25° 32’ 841"S	112° 56’ 026"E
DHI23	North	25° 30’ 080"S	113° 01’ 030"E
DHI22	North	25° 36’ 244"S	113° 01’ 420"E
DHI21	North	25° 29’ 976"S	113° 00’ 353"E
DHI41	North	25° 43’ 227"S	112° 59’ 695"E
DHI42	North	25° 36’ 974"S	113° 02’ 284"E
DHI	**middle**	25°.84’ 393"S	113°.10’ 401"E
Peron Peninsula		25°.77’ 832"S	113°.45’ 886"E
Steep Point		26°.16’ 474"S	113°.18’ 387"E

Supplement Chapter 3



Model 1

model1	ciq	oz	eu	m
ciq	x	0	0	x
oz	x	x	0	0
eu	0	x	x	0
m	0	x	0	x

Model 2

model2	ciq	oz	eu	m
ciq	x	0	0	0
oz	x	x	0	x
eu	0	x	x	0
m	0	0	0	x

Model 3

model3	ciq	oz	eu	m
ciq	x	0	0	0
oz	0	x	0	0
eu	x	x	x	x
m	0	0	0	x

Model 4

model4	ciq	oz	eu	m
ciq	x	0	0	0
oz	0	x	0	0
eu	0	x	x	0
m	x	x	0	x

Model 5

model5	ciq	oz	eu	m
ciq	x	0	0	x
oz	0	x	0	0
eu	0	x	x	0
m	x	0	0	x

Model 6

model6	ciq	oz	eu	m
ciq	x	0	0	0
oz	x	x	0	0
eu	0	x	x	x
m	0	0	x	x

Model 7

model7	ciq	oz	eu	m
ciq	x	x	0	0
oz	0	x	0	0
eu	0	0	x	x
m	x	0	x	x

Model 8

model8	ciq	oz	eu	m
ciq	x	x	0	0
oz	0	x	0	0
eu	x	0	x	0
m	x	0	0	x

Model 9

model9	ciq	oz
ciq	x	x
oz	0	x
eu	0	x
m	x	0

Model 10

model10	ciq	oz
ciq	x	x
oz	x	x
eu	0	x
m	x	x

Model 11

model10	ciq	oz
ciq	x	x
oz	0	x
eu	0	x
m	0	x

Figure 3-S1. Graphic illustration of migration hypothesis model selection as applied for the mitochondrial *ND5* + *ND6* between Europe (EU), Australia (Oz), Christmas and Cocos (Keeling) Island (CIQ) and Malaysia/Sulawesi (Asia).

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04/2012	**K. Koch**, N. Hamilton, D. Algar (2012) Sampling for DNA analysis of the feral cat population in the southern end of Dirk Hartog Island, DEC Internal Report
11/2010	M. Johnston, D. Algar, N. Hamilton, S. Hilmer, B. Withnell, **K. Koch** (2010) A bait efficiency trial for the management of feral cats on Dirk Hartog Island, Arthur Rylah Institue for Environmental Research, Technical Report Series No.205

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The PhD student's contribution to the article/manuscript	
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Implementation of experimental work	60% K.Koch 40% Co-Authors
Preparation of data and illustrations	100% K.Koch
Interpretation of the results	50% K.Koch 50 % Co-Authors
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Titel: Population Structure and Management of Invasive Cats on an Australian Island

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Titel: A voyage to terra Australis: human mediated dispersal of cats

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Declaration

I herewith declare that this thesis reports my independent work in “Genetic diversity and phylogeography of Australian feral cats”. All used resources are specified and contributions from other authors and third parties are fully acknowledged.

This or another thesis have never been previously submitted in part or in whole to another academic or non-academic institution.

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