SCALE AND IMPACT OF THE ILLEGAL LEOPARD SKIN TRADE FOR TRADITIONAL USE IN SOUTHERN AFRICA

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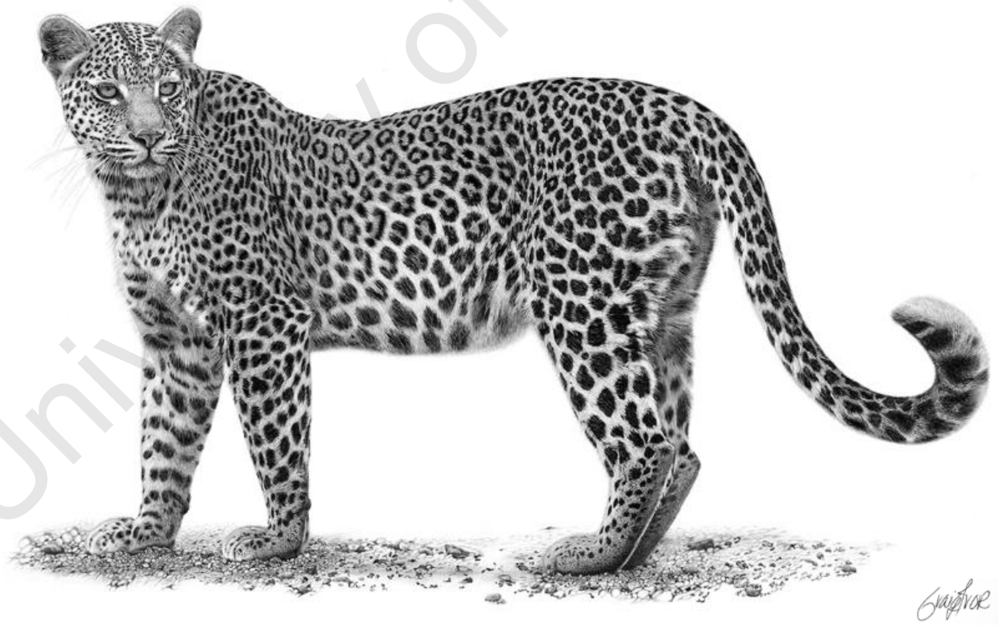

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For Indiana and all those with wild hearts…

DECLARATION

I Vincent Norman Naude, hereby declare that the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. My MSc was upgraded to a PhD by the Doctoral Degrees Board of the University of Cape Town in February 2017 and has been included in this thesis and described as such. I am presenting this thesis for examination toward the Degree of Doctor of Philosophy in Biological Sciences.

I hereby acknowledge that this work was conducted as part of a larger, ongoing collaboration between the Institute for Communities and Wildlife in Africa (iCWild) and Panthera at the University of Cape Town, South Africa. My fieldwork and data collection there thus conducted alongside and with the support of their staff (Tristan Dickerson, Morgan Kudzwayo, Gareth Whittington Jones, Jeffery Dunnink, Guy Balme) and students (Xolani Mabaso and Nolwazi Mongwa).

This thesis has been submitted to the Turnitin module, and I confirm that my supervisors have seen my report and that any concerns raised therefrom have been resolved between myself and my supervisors. I empower the university to reproduce for research either the whole or any portion of the contents in any manner whatsoever.

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ABSTRACT

While leopards (*Panthera pardus*) currently occupy the most extensive geographic range of all large felids, they are also suffering the highest rate of current range loss amongst large terrestrial carnivores. This is primarily because most leopards still range outside of formally protected areas where they are exposed to the full suite of anthropogenic threats affecting carnivores including habitat loss, prey depletion, conflict with humans, and commercial harvest for body parts. The extensive use of leopard derivatives among traditional healers, royalty, and culturo-religious groups poses a known but poorly understood threat to leopards. Socio-political sensitivities surrounding cultural identity and the illegality of much of this use have impeded an objective assessment of both the drivers and impacts of this threat. Through a multi-disciplinary approach, this thesis describes the drivers of illegal leopard skin trade among a significant portion of traditional users in South Africa, quantifies the extent of this trade across the southern African region and assesses its impact on local leopard populations. Together these findings seek to address the lack of conservation- and policy-relevant data regarding the impact and scale of the trade for traditional use in South Africa.

Followers of the recently established ‘Shembe’ Church, with its estimated membership of over four million in South Africa, represent the foremost culturo-religious users of illegal leopard skins in the world. Following the introduction of a *faux* skin alternative, I used longitudinal surveys to explore the drivers of authentic skin desirability and possession amongst *faux* skin recipients. While demand for authentic skins decreased, and *faux* alternatives were generally considered satisfactory, 27% still expressed a desire for an authentic skin, and 15% had acquired one in the three years since receiving their *faux* skin. Both desiring and having obtained an authentic skin were best explained by improved economic status and the perceived weakness of law enforcement. The combined demand of all Shembe followers cannot be sustained by the estimated extant leopard population of South Africa, and it is predicted that traders must be sourcing leopards from surrounding range states to meet local demands.

To investigate this, I created a genetic reference database of leopards across southern Africa (1,452 individuals) and using DNA-based assignment tests, inferred the geographic origins of illegally traded skins sourced within southern Africa. Smoothed continuous assignment techniques revealed leopard source ‘hotspots’ in southwestern Zimbabwe, southern Mozambique and along the eastern borders of South Africa confirming suspicions that the illegal leopard skin trade for traditional use in South Africa is transnational. A similar distribution of leopard source populations was identified from leopard parts obtained in traditional wildlife markets and a large-scale confiscation from a single trader. Together, this suggests the regional trade in leopard parts has been syndicated with predictable harvesting and trade routes into the South African consumer market. Genotyping across all trade samples (237 individuals) revealed a clear bias towards males despite reported sex-ratios being female-biased for natural free-ranging populations. To understand the ecological cost of this sex-biased exploitation of leopards, I compared the spatial, genetic, and demographic data of two South African leopard populations with markedly different histories of anthropogenic mortality. Home-range overlap, parentage assignment, and spatio-genetic autocorrelation showed that extensive historical exploitation, linked to Shembe and other traditional trade, has reduced sub-adult male dispersal, thereby facilitating opportunistic male natal philopatry. The resultant kin-clustering in males is comparable to that of females in the well-protected reserve and has promoted localised inbreeding.

Together these results demonstrate novel evidence linking significant ecological consequences to an underestimated, transnational, and syndicated illegal leopard skin trade driven by demand for traditional and religious use in South Africa. These findings are translatable to all leopard populations threatened by exploitation and emphasise the importance of long-term monitoring of leopard populations within protected areas and improving management interventions to mitigate these effects. Interventions such as anti-poaching can be focussed on the ‘hotspots’ identified in this study while protected area management should prioritise the maintenance of dispersal corridors to promote *in situ* recovery of exploited populations. Lastly, demand reduction strategies such as the continued provisioning of suitable alternatives, together with improved education and increased enforcement, are essential to addressing the growing culturo-religious demand for leopard products contributing to the illegal harvest and trade in this iconic large predator. Success will depend on finding the balance between an improved transnational policy which effectively conserves wild leopard populations and maintaining respect for cultural practices.

CHAPTER 1

INTRODUCTION

Figure 1. Large felids play important symbolic roles in our history and cultural development. However, habitat loss, prey depletion, conflict with humans, and commercial and traditional harvest for body parts in illegal wildlife trade (side panels) are driving global range losses. Leopards have the broadest geographical range of all large felids (middle panels) and as such, suffer range losses that are higher than average among large terrestrial carnivores. This predator acts as a sentinel and model species for understanding the many contemporary threats faced by many large carnivores, especially felids, across these range states. Images are used with permission or under the creative commons license.

1.1. General introduction

The relationship between humans and wild felids (Macdonald *et al.*, 2010) is an ancient, complex, and often paradoxical one (Figure 1). Human history interweaves a deep admiration for big cats as cultural and heraldic symbols of power, fear, and majesty (see 1.3). Still, more recently, they are recognised as ecological keystone species, valuable attractions for tourism-based revenue, 'umbrella' species for ecosystem and biome conservation, and as 'flagships' engendering public support for conservation (Loveridge *et al.*, 2010). However, in regions where wild felids and people coexist, these positive associations are often strongly challenged. Human-wildlife conflict (HWC), through overexploitation of both felid and prey populations (Sandom *et al*., 2018), and habitat loss and fragmentation have led to the extirpation of many wild felid populations and continue to threaten the extinction of many more (Packer *et al.*, 2009; Purvis *et al.*, 2000). How people interact with biodiversity, value natural habitats, and endeavour to understand its complexity is at the very heart of 21st-century conservation.

Carnivores inspire a deep fascination within humankind; they are valued as cultural icons and preserved for their aesthetic, symbolic, spiritual, utilitarian, and ecological value (Loveridge *et al.*, 2010). From Stone Age petroglyphs to cave paintings and abstract modernism, the human artistic record holds a rich archive of our relationship with carnivores. Repeatedly, large felids are presented as heraldic symbols of culture, featuring on coats of arms, adorning many currencies and even appearing on the badges of national sports teams or as political symbols (Figure 2). Historically, they embody gods and characterise ancient cultures, such as lions (*Panthera leo*) in Africa, jaguars (*Panthera onca*) in central America, and tigers (*Panthera tigris*) in South-East Asia (Weber & Rabinowitz, 1996).

Large felids are often highly mobile, and viable populations require vast tracts of suitable habitat and access to adequate prey populations (Andelman & Fagan, 2000; Loveridge *et al.*, 2010; Macdonald *et al.*, 2010). Strategies for the protection of large felids, therefore, offer sanctuary for large 'functioning ecosystems' (Soulé & Simberloff, 1986; Noss *et al.*, 1996; Seidensticker *et al.*, 1999). People and governments are more inclined to protect a charismatic carnivore than a rare and seemingly unremarkable species. A prime example of this protection is the *Paseo Panthera* (the Path of the Panther), a series of biological corridors along the Panamanian islands, designed for jaguars, cougars/pumas (*Puma concolor*), and other wildlife (Rabinowitz & Zeller, 2010). Tigers are another flagship species under whose name significant areas of biodiversity are protected throughout India and along the border regions of India and South-East Asia (Weber & Rabinowitz, 1996; Rabinowitz, 1999; Seidensticker *et al.*, 2010; Sunquist & Sunquist, 2017).

Figure 2. Felid symbology is deeply engrained in our shared cultural identity. Since the first records of imaginative thought (the famous Stadel lion-man; top left), felids have represented strength, power, fear, and prestige, unifying nations, religions, revolutionary movements, civil rights activists, sports teams, car fanatics, and generations of children (as depicted above). Intricately woven into the fabric of our culture, felids continue to symbolise these attributes in increasingly complex ways today. Images are used with permission or under the creative commons license.

1.2. Felids under threat

1.2.1. Conflict with humans

Large carnivores are ecologically predisposed to HWC; their obligate carnivory and tendency to utilise large areas draws them into recurrent competition with similarly widespread and carnivorous human communities (Figure 3; Treves & Karanth, 2003). While the most common cause of HWC globally is livestock predation (Thirgood *et al.*, 2005), actual stock losses to predators are generally low, especially when compared to other factors, such as disease and theft (Rasmussen, 1999; Marker *et al.*, 2003). When losses do occur, these are sporadic and affect the livelihoods of small-scale subsistence farmers far more than that of large-scale commercial agriculture. For example, in Nepal's Annapurna Conservation Area, livestock losses to snow leopards (*Panthera uncia*) equate to approximately a third of local villagers' annual income (Aryal *et al.*, 2014), while an average attack on livestock by African wild dogs (*Lycaon pictus*) in Kenya equates to a fifth of the mean per capita income (Woodroffe *et al.*, 2005). Even when losses are low, the perceived threat that carnivores pose to livestock is often sufficient to encourage widespread and intense retaliatory persecution (Sillero-Zubiri & Laurenson, 2001).

Humans also compete with predators for wild prey, especially when these are of economic or cultural value as a 'game species' (Balme *et al.*, 2009). In Alaska, for instance, hunters blame increasing grey wolf (*Canis lupus*) numbers for declining moose (*Alces alces*) populations and subsequent reductions in hunting quotas (Gassaway *et al.*, 1992). Similarly, Eurasian lynx (*Lynx lynx*) are held responsible for decreases in valuable roe deer (*Caproelus caproelus*) populations in Switzerland (Breitenmoser *et al.*, 1999). In Europe and North America, such conflicts have historically been resolved with lethal control, leading to significant declines in these carnivore populations (Reynolds & Tapper, 1996; Linnell *et al.*, 2001). In addition to livestock and game, carnivores, particularly large felids, kill hundreds of humans every year, and this conflict evokes considerable antipathy (Kruuk, 2002). Tigers in the Sundarbans region of eastern India (along the southern border between Bangladesh and India) kill up to 100 people annually (Sanyal, 1987), while lions in southern Tanzania were reported to have killed 563 people over 15 years (Packer *et al.*, 2005). Lethal attacks in developed countries, however, are far less common; for example, only ten people were reportedly killed by pumas in North America during the last century (Beier, 1991; Behling & Law, 2000). Most attacks are the result of predators being debilitated by injury or old age, although in rural places, such as the Sundarbans in Bangladesh, the vast number of people interacting with carnivores increases the likelihood of conflict (Quigley & Herrero, 2005).

In these regions, predation is usually a minor cause of human mortality; however, it can be critical in determining the tolerance of local communities towards predators, and it is often the fear of carnivores, rather than actual attacks, that drive pre-emptive killing by local communities (Thirgood *et al.*, 2005).

Figure 3. Human-carnivore conflict is pervasive and poses a grave threat to conservation. This conflict is often driven by the real or perceived threat to livestock, competition for resources, and the direct danger posed to human life. Large carnivores are predisposed to conflict, their obligate carnivory, and tendency to utilise large areas, draws them into recurrent competition with humans in peri-urban landscapes. Images are used with permission or under the creative commons license.

1.2.2. Trophy hunting

Hunting of felids for sport dates back thousands of years to the time of Egyptian Pharaohs and medieval English nobles (Figure 4; Guggisberg, 1962). Colonial records show an astounding number of tigers killed by Indian, Nepalese, and visiting British royalty (Sankhala, 1977; Mountford, 1981). In India, during the 1960s, it became clear that hunting tigers would be officially prohibited, so the demand for hunting trophies accelerated, and tiger populations dwindled further (Sunquist & Sunquist, 2017). Throughout colonial Africa, especially across the remote areas of eastern and southern Africa, carnivores were considered vermin and readily killed by farmers, government officials, and the colonial elite who were ‘thrilled by the chase’. Early 20th-century hunting expeditions to the Serengeti removed many carnivores in the misguided belief that this would protect ungulate populations and thereby improve future hunting opportunities (Turner, 1987). In addition to the loss of habitat, prey population declines, and predator eradication initiatives, extensive and unregulated trophy hunting may have also contributed to the historical declines of many large felid populations and, in some regions, was indistinguishable from predator eradication (Pocock *et al.*, 1939).

Contemporary trophy hunting (also known as a sport or recreational hunt) tends to be more controlled, and harvests are often strictly regulated by established and competent management authorities. Many trophy hunters are concerned about and promote conservation values that sustain their livelihoods (Lindsey *et al.*, 2006). Felids are a popular quarry in this industry, where large charismatic species attract sizable trophy fees for government or management authorities and premium running costs to guides and operators (Logan *et al.*, 2004). Trophy hunting revenues can benefit local communities and specialist employment, providing justification and support for conservation. This alternative revenue stream can improve levels of tolerance and acceptance of predators if used to manage populations, protect habitats, and compensate livestock owners for losses to predators (Loveridge *et al.*, 2007a). Hunting ranches may also serve as semi-protected areas outside of national parks (Lindsey *et al.*, 2007), while the hunting of problem or damage-causing animals (DCA) may offer incentives to landowners for managing habitats and encouraging self-sustaining populations (Crawshaw, 2004).

Trophy hunting can, however, have severe demographic consequences for felid populations when poorly managed (see Chapter 4 [Naude *et al.*, 2020]). Sizable adult males are favoured as trophies which can promote accelerated male turnover, leading to high levels of localised infanticide, and potentially reduce reproductive success within the population or contribute to population declines (Greene *et al.*, 1998; Whitman *et al.*, 2004; Gross, 2008; Balme & Hunter, 2013a). While felid populations are relatively resilient to moderate levels of harvest, primarily through immigration (Smuts, 1978), unsustainable rates of exploitation cause more severe social disruptions and have a longer recovery period (Lindzey *et al.*, 1992). Furthermore, in remote areas with little or no official oversight, the strong financial incentive to exploit resources and hunting activities has led to examples of overexploitation. In Selous Game Reserve, Tanzania, for example, inadequate supervision led to 29% of trophy-hunted leopards (*Panthera pardus*) being female, despite official quotas being restricted to males (Spong *et al.*, 2000a). Ensuring that trophy hunting of felids and other wildlife remains sustainable requires effective regulation of hunting activities and enforced compliance with legal hunting quotas (Yamazaki, 1996; Loveridge *et al.*, 2007b; Palazy *et al.*, 2011)

Figure 4. Felids feature as trophies and symbols of power throughout human history. As hunting skills and weaponry evolved, humankind was allowed to ascend the food-chain above their fear-inspiring natural predators. As such, hunting large predators and taking trophies have become socio-psychological symbols of control, power, and authority across many cultures and persist as the foundation of modern sport and trophy hunting today. Images are used with permission or under the creative commons license.

1.2.3. Snaring and by-catch

Opportunistic exploitation remains an underestimated threat for many felid species worldwide (Branch *et al.*, 2013). Large felids rarely feature directly in the bushmeat trade as they are dangerous to catch with simple means and offer relatively little nutritious value compared to their prey species. Despite this, they often suffer severe injuries and mortalities as by-catch in snares (Watson *et al.*, 2013; Loveridge *et al.*, 2017; Everatt *et al.*, 2019a). Wire snares are cheap, durable, and easy to set, making them an extremely efficient means of harvesting bushmeat, especially in areas where firearms are expensive, banned, or regulated (Figure 5). Increasing evidence suggests that snaring is a growing threat. In Niassa National Reserve, Mozambique, for instance, an estimated 40 lion mortalities were attributed to snaring annually (Begg & Begg, 2012), while nearly 85,000 wire snares were removed from the Savé Valley Conservancy, Zimbabwe, between 2001 and 2009 (Lindsey *et al*., 2012; Matseketsa *et al.*, 2019). Perhaps as concerning as the direct threat of snaring to wildlife populations, is the valuable time and energy spent on the removal of snares by many rangers and anti-poaching units throughout protected areas (PAs).

Figure 5. Snaring and bushmeat by-catch is a gravely underestimated and growing threat. Many large carnivores are directly targeted for wire-snaring in retaliation for real or perceived livestock losses or caught as by-catch during indiscriminate bushmeat poaching. Beyond the direct and obvious welfare cost to individuals, valuable time, energy, and resources are wasted on the removal of snares by rangers and anti-poaching units. Images are used with permission or under the creative commons license.

1.2.4. The illegal wildlife trade

Over the last century, the illegal wildlife trade (IWT) has grown into the fourth largest criminal activity worldwide, exceeded only by narcotics, arms, and human trafficking (UNODC, 2010). Each year, billions of animals and their derivatives are traded to meet consumer demand for food, trophies, clothing, decorative items, pets, traditional adornments, and medicine (Karesh *et al.*, 2005). Profits drawn from this global environmental crime syndicate are valued at approximately U$20 billion annually (Alacs *et al.*, 2010; Linacre & Tobe, 2013). In addition to large profits, low conviction rates incentivise and accelerate poaching by illegal trade organisations (Mondol *et al.*, 2014). While the escalating demand and economic value of wildlife trade are alarming, the real challenge for conservation is, of course, the unsustainable exploitation of many species (Ogden & Linacre, 2015). Large carnivores are particularly prone to poaching due to their large home ranges and extensive resource requirements, as well as their potential for conflict with humans (Schipper *et al.*, 2008). Excessive opportunistic exploitation can have cascading effects on targeted populations, altering behaviour and group compositions (Gobush & Wasser, 2009), adult sex ratios (Sukumar *et al.*, 1998), physiology, and population dynamics, ultimately leading to inbreeding (Gobush *et al.*, 2008; Loveridge *et al.*, 2010), range restrictions, and local extirpation (Karanth *et al.*, 2010; Liberg *et al.*, 2011).

While the Convention on Biological Diversity (CBD, established in 1993) explicitly recognises sustainable utilisation as a component of conserving biodiversity and ecosystems, this requires rigorous monitoring and responsible management to minimise overexploitation (see Chapter 4 [Naude *et al.*, 2020]). Enforcement, however, is challenging for societies characterised by resource inequalities, weak environmental control, apathetic enforcement of national and international legislation, and widespread corruption (Sunderlin *et al.*, 2005). The successful conservation of global biodiversity remains fettered by poor governance, corruption, institutional failure, and socio-economic upheaval (Smith *et al.*, 2003). Overexploitation of wildlife resources often tandems with uncontrolled habitat conversion (Rabinowitz, 1999; Nyhus & Tilson, 2004) and poaching of large felids is inexorably linked to existing human–felid conflicts, with illegal trade being a by-product (Kumar & Wright, 1999; Johnson *et al.*, 2006). Household income and food insecurity also predispose people to illegal use of wildlife. In Zambia, for example, improvement in food security reduced poaching and improved commitment to conservation initiatives (Lewis & Jackson, 2005).

Sustainable harvest of large felids is possible, however, as evidenced through the North American cougar fur trade (Obbard *et al.*, 1987); the key to its success has been clear data-driven policy, effectually applied and enforced legislation, and continuous feedback research and population monitoring (Nowell & Jackson, 1996). Unfortunately, these conditions do not exist throughout much of the developing world, where international restrictions do not control fur and medicinal trade. The systematic commercial hunting of spotted cats has, however, seen a steady decline since the implementation of trade restrictions by the United States of America (USA) and the European Union (EU). These restrictions are imposed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and reveal that international action can significantly impact demand-reduction (Nowell & Xu, 2007). Regulation of unsustainable trade in felids appears to depend on robust international legislation and the willingness and capacity of governments and local statutory authorities to implement and police these conservation policies, while disincentivising poaching and IWT. Local and international conservation lobbyists, from influential individuals to non-governmental organisations (NGOs), close this feedback-loop by regulating societal morality and placing legislative pressure on governments and industry (Baker, 1999; Schensul *et al.*, 1999; Scherrer, 2009). Consumer awareness, education, and engagement with stakeholders also appear crucial in reducing or curtailing demand for felid products (see Chapter 2; Challender *et al.*, 2015).

1.3. Cats shape our culture and tradition

1.3.1. The allure of felid fur

The beautiful patterns and insulative properties of felid fur make them attractive to humans. Wild felid derived furs are used in the manufacture of clothing, adornments, and household decoration while wearing them often confers social status, symbolising the wealth and power of its owner (Figure 6). During the 1960s and 1970s, the wearing of coats made of spotted cat pelts became immensely popular among the wealthy of western Europe and the USA. The overexploitation of some wild populations of striped and spotted cats prompted the enactment of the first CITES in 1975. Despite these efforts, demand for tiger and leopard skins has resurged among the newly wealthy in China and Tibet, driving large-scale poaching in source countries, such as India and Nepal (EIA, 2004; EIA-WPSI, 2006).

An example of overexploitation of spotted cats for the fashion industry is the extraction of over 80,000 ocelot (*Leopardus pardalis*) and 15,000 jaguar skins from the Brazilian Amazon in the 1960s (Smith, 1976), prompting the Brazilian government's ban on the export of wildcat skins in 1967. The estimated value of the global fur trade between the 1960s and early 1970s was around U$30 million (Myers, 1973), supporting a lucrative syndicate of poachers (Payan & Trujillo, 2006), intermediaries, and traders from Columbian forests to New York boutiques

(Nowell & Jackson, 1996). Exploitation extended to other spotted cats including margay (*Leopardus weidii*), oncilla (*Leopardus tigrinus*), Geoffroy's cat (*Oncifelis geoffroyi*), and Pampas cat (*Oncifelis colocolo)* all of which were traded in American markets (Mares & Ojeda, 1984; McMahan, 1986).

Figure 6. Commercial fur trade for fashionable culture devastated wild felid populations. With growing wealth and globalisation, the insulating functionality, and majestic symbolism of fur gave way to the commercialisation of social prestige and affluence. Moreover, this trend was exacerbated and continues to be led by famous individuals, the cultural and political icons of modern fashion, and evolving traditional practice. Though now largely sustainable, the fur trade underwent a full cycle of overexploitation, societal consciousness, and self-regulation (see 5.2.3). Images are used with permission or under the creative commons license.

Old World spotted and striped cats were particularly popular with furriers in the 1960s and 1970s, including the leopard, snow leopard, clouded leopard, cheetah (*Acinonyx jubatus*), and tiger (Nowell & Jackson, 1996). Ugandan leopards were legally protected after the export of 9,162 skins from the country in 1960 alone (Treves & Naughton-Treves, 1999). In the early 1970s, the estimated global demand for leopard skins was around 50,000 skins per year, with 17,490 skins exported to the USA between 1968 and 1969 alone. As many of these hunts by tribesmen or subsistence hunters were illegal and often unmanaged, many skins were rejected by middleman traders as a result of damage or being poorly preserved, implying that losses were almost certainly higher than those reported (Myers, 1976). It is estimated that, at the peak of the spotted cat skin trade in 1969, over 61,000 leopards were harvested throughout their range with fewer than 6,000 harvested by 1988 (Martin & de Meulenaer, 1988). In the 1970s, the fur trade shifted to less protected and easily obtainable substitutes, such as the bobcat (*Lynx rufus*) and leopard cat (*Prionailurus bengalensis*), with resultant harvest substantially reducing populations of these species (Fuller *et al.*, 1985; McMahan, 1986).

Contemporary felid fur trade for fashion relies primarily on pelts from Canadian and Eurasian lynx, bobcat, and the leopard cat (Nowell & Jackson, 1996). While strict regulations have allowed for biologically sustainable harvests of bobcat (Elton & Nicholson, 1942), the ecological sustainability of the Canadian lynx harvest is uncertain (Poole, 1994; Slough & Mowat, 1996) and large volumes of leopard cat skins are still imported by China (Nowell & Jackson, 1996; Sunquist & Sunquist, 2017). While Western markets have declined due to strict legislation and strong negative sentiments from the public over furs in fashion, current markets have emerged in the more prosperous regions of eastern Europe and among an increasingly wealthy Chinese populous. The illegal trade in Asiatic leopard (*Panthera pardus fusca*) and tiger skins appear to have increased throughout South-East Asia (Rabinowitz, 1999; EIA, 2004; Nowell & Xu, 2007) with wealthy Han Chinese valuing tiger and other felid skins for the prestige of owning an expensive exotic item and because they are believed to bring good luck (EIA, 2004). In the 1990s, tiger and leopard skins became increasingly fashionable to wealthy urban Tibetans (Figure 7), worn as traditional Tibetan *chubas* (gowns). Skins were also used at traditional ceremonies such as weddings, and a ceremonial tent made of 108 whole tiger skins was seen in 2006 at the Litang Horse Festival in the Chinese Province of Sichuan (EIA-WPSI, 2006). Concern and legal pressure from environmental groups have, however, driven a marked decline in this trade (EIA-WPSI, 2006; Sharma *et al.*, 2013), accelerated by the symbolic burning of tiger and leopard skin robes across Tibet in 2006. This pyrrhic event followed the condemnation of such use of wildlife products by Dalai Lama Tenzin Gyatso

(Graham-Rowe, 2011; Yeh, 2012; Geertz, 2016). While these events have indeed reduced prices and demand (Hu *et al.*, 2006; Huggler, 2006), this highly lucrative trade persists and remains both politically and culturally sensitive. For example, a consignment of 31 tiger, 581 leopard, and 788 otter (subfamily Lutrinae) skins, worth an estimated U$1.2 million, were seized in Tibet in 2003 while being smuggled from India to China (EIA, 2004; EIA-WPSI, 2006).

Figure 7. Tiger and other rare skins have deep culturo-religious significance in Tibetan culture. Depicted here are the elaborate tiger skin *chubas* worn by affluent Tibetan men at the Litang Horse Festival in the Chinese Province of Sichuan and the famous traditional tent made of 108 tiger skins. After facing much political pressure and cultural shame, the 14th Dalai Lama, Tenzin Gyatso, banned the use of endangered wildlife products in traditional Tibetan attire, burning thousands of skins in moral support of the edict. Nevertheless, there remains resistance to this 'modernisation' and loss of tradition among the more conservative followers. Images are used with permission or under the creative commons license.

As is so often the case in IWT, wildlife agencies lack the resources for effective enforcement of policy and laws that have been devised to protect wildlife. Poaching penalties are harsh, but the likelihood of apprehension remains low and that of conviction even lower (Damania *et al.*, 2008). Poaching and illegal trade in tiger products have rebounded and only serve to exacerbate declines due to logging, habitat loss, and expansion of human populations (Rabinowitz, 1999). Between 1994 and 2006, 783 tiger and 2,766 leopard skins were seized in

India, though these are thought to represent only a fraction of skins on the illegal market. This illegal trade in tiger skins between India, Nepal, and China is believed to have driven recent declines in Indian tiger populations (EIA-WPSI, 2006). Depleted source populations in Cambodia, Myanmar, and Thailand have turned commercial poachers to other Asian big cats, such as Asiatic lions (*Panthera leo leo*), leopards, snow leopards, and clouded leopards (*Neofelis nebulosa*) in Malaysia and other range states (Damania *et al.*, 2008). Poaching is frequently undertaken by skilled local hunters using reusable steel traps, wire or cable snares (see 1.2.3), or poisoned bait, with minimal running and opportunity costs, such as time and expected penalties (see 5.2.1). Field operations and trade take place under 'open-access' conditions due to capacity-limited enforcement (Damania *et al.*, 2008).

Wildlife poaching and illegal trade in India reveals a similar tale of a well-organised and lucrative criminal network operating under poor policing and disincentives in the legal system (Kumar & Wright, 1999). While countries like China appear to be enforcing IWT laws more vigorously (Nowell & Xu, 2007), fighting wildlife crime is not a significant priority in many South-East Asian range states. Under-resourced environmental protection agencies, acting under vague policies and fettered political will, offer little deterrent by way of punishment. Nominal fines for possession and trade in wildlife products relative to the market value of a single skin, allow traders to adjust their margins and accommodate any change in judicial pressure, competition, or demand at the retail end of the market, thus frustrating initiatives to diminish poaching (Bulte & Damania, 2005). Moreover, most prosecution is delayed, and rates of conviction are low. For instance, in India, which has a well-developed institutional structure for conservation, only 14 convictions were achieved out of 748 wildcat skin confiscation cases (EIA, 2004). This commercial trade is a transnational syndicate with sources in India, Indonesia, Laos, Thailand, Myanmar, and Vietnam with markets on the Chinese Mainland, in Hong Kong, Taiwan, South Korea, and Japan (Li & Wang, 1999; Rabinowitz, 1999; EIA-WPSI, 2006; Nijman, 2010; Oswell, 2010). Overcoming the IWT requires transnational, multi-disciplinary commitment and cooperation from anti-poaching units and educators to supreme courts and international prosecuting agencies.

1.3.2. Traditional Asian medicine

Despite active trade bans on tiger parts and most big cat derivatives around the world existing for more than a decade, conservationists are increasingly concerned about the IWT for use in traditional Asian medicine (TAM; Rosen & Smith, 2010; MacMillan & Challender, 2014).

Many practitioners of Traditional Chinese Medicine (TCM) now use alternatives, but illegal trade continues (Figure 8). Even with the World Federation of Chinese Medicine Societies (WFCMS) having declared that tiger parts are not necessary for human health care and that alternatives are plentiful, affordable, and effective, poachers continue to kill tigers to satisfy an unreasonable demand for tiger bones to make health tonics. Across South-East Asia, habitat loss is the primary long-term cause of declines in tiger populations; however, poaching of tigers and other felids is a critical short-term threat to the survival of these populations (Mills & Jackson, 1994; Hemley & Mills, 1999; Rabinowitz, 1999; Damania *et al.*, 2008). This trade now threatens clouded leopards, leopards, snow leopards, and lions as their bones are traded as substitutes (Wingard & Zahler, 2006; Williams *et al.*, 2017). The illegal trade in tiger parts, particularly bone, reached epic proportions in the 1980s and 1990s, decimating wild populations. Before South Korea acceded to the CITES, for instance, their customs record showed imports of over 8,951 kg of tiger bone between 1970 and 1993, mostly sourced from Indonesia (Plowden & Bowles, 1997; Nowell, 2000).

Figure 8. Traditional Asian Medicine (TAM**) threatens many felid species across South-East Asia.** The practice of TAM is deeply spiritual, relying on centuries of cultural knowledge systems to prescribe alternative and often charm-like remedies alongside conventional Western medicine. Despite much controversy, this is a recognised and legislated form of alternative treatment which still directly challenges international environmental policy and drives illegal trade. Images are used with permission or under the creative commons license.

Immense efforts have since been focussed on controlling tiger bone trade (Upadhyay *et al.*, 2007; Gratwicke *et al.*, 2008), with an emphasis on international legislation, raising public awareness, and a commitment among TAM specialists to search for alternative medicinal products (Hemley & Mills, 1999). Most countries have banned the domestic and international trade in tiger bone and others like South Korea, have since mostly eliminated it through swift prosecution. In regions where enforcement and prosecution have been apathetic, however, residual trade has proven much harder to control and eradicate (Li & Wang, 1999; Shepherd & Magnus, 2004; Ng & Nemora, 2007; Nowell & Xu, 2007). The existence of several captive-bred populations of tigers in South-East Asia have since emerged, leading to the suggestion that products from ‘farmed’ tigers could serve as a commercial replacement for wild products; however, this remains heavily contested (Kirkpatrick & Emerton, 2010; Abbott & van Kooten, 2011; Tensen, 2016). The consensus among conservationists is that trade in farmed tigers may stimulate demand by providing the means to launder poached tiger derivatives with retrogressive effects on recent successes in reducing the magnitude of this trade (Hemley & Mills, 1999; Gratwicke *et al.*, 2008; Nowell & Xu, 2007).

1.3.3. African religion, spiritualism, and traditional healers

In an African context, it is difficult to understand the social importance of the traditional healer and their trade without taking the concept of traditional African religion and its spirituality into account (Gumede, 1990). The traditional African philosophy of illness, in most cases, encompasses a complex of interactions between God, ancestors, and the universe, and many traditional healers play a dual role as community religious leaders, such as priests or prophets, in independent African churches (Mokgobi, 2014). While the ideology of traditional African religion and spiritualism remains similar across the continent, it can vary in its practice regionally and locally across its 19 major ethnic groups (≥10 million people) and 1,250–2,100 languages (van der Walt, 2003).

Traditional African religion is ancient, encompassing a rich diversity and complex history of peoples and their cultures existing well before the 19th-century challenge for and Westernisation of the African continent (Nigosian, 1994). Contrary to the intentions of colonial authorities, forced conversion to branches of Christianity and Westernisation did not lead to the complete abandonment of the traditional African health care system and religion. Instead, many Africans now practice a blend of Christian or Islamic and traditional African religions concurrently, utilising the services of both traditional African and modern healthcare systems (Nigosian, 1994). Many African religions are founded on a belief in the spirit of the ‘ancestors’, called *badimo* (Bapedi, Batswana and Basotho), *amadlozi* (Zulu), and *iinyanya* (Xhosa) in southern Africa among many others from across the continent (Mokgobi, 2014). These compassionate spirits are blood-relatives of the people who believe in them and are held as superior to living social hierarchies (van Dyk, 2001). Ancestors act as mediators between God and the living, and as such, the practice is considered ancestral reverence rather than ‘ancestral worship’ (Berg, 2003). The chain of communication is often aided by enlisting the services of a traditional healer who advises on how to commune with the ancestors, with the means and type of ritual that needs to be performed depending on the purposes of the communication (Mokgobi, 2014).

‘Traditional healers’ is a collective term encompassing many types of training and expertise across multiple regions (Green & Makhubu, 1984; Freeman & Motsei, 1992; Ensink & Robertson, 1999). These include roles as traditional diviners, healers, herbalists, surgeons, and birthing attendants (Figure 9). Diviners are guided by ancestral spirits and will traditionally ‘cast’ bones to foretell the future and give advice on how to avert an undesirable event or to diagnose and prescribe medication and treatment for different physiological, psychiatric, and spiritual conditions (Mokgobi, 2014; Thobane, 2015). Divination sets will often include the bones of large felids (mostly lion), hyenas (family Hyaenidae), anteaters (suborder Vermilingua), baboons (genus *Papio*), crocodiles (*Crocodylus niloticus*), wild pigs (*Phacochoerus Africanus* and *Potamochoerus larvatus*), domestic goats (genus *Capra*), many antelope species, and other items designated for all psycho-socio-spiritual polarities (Janzen, 1992; Thornton, 2009). While there may be some regional overlap or exceptions based on the individual and their calling, healers and herbalists do not generally divine; rather, they treat ailments using highly specialised, transgenerational knowledge of remedies or charms and through ancestral consultation (Robertson, 2006). Traditional surgeons are often formally qualified and accredited, with their practice and expertise encompassing that of other types of healers such as divination and herbalism. Traditional birth attendants have become skilled midwives through witnessing and assisting in many births; however, this profession is diminishing with many women choosing to give birth in hospitals (Mokgobi, 2014).

An interesting exception among traditional healers is that of prophets or faith healers, such as the Sanusi shamans of North Africa, who may be both diviners and herbalists. Being possessed by the Holy Spirit, they can foretell the future and dispense advice on how to avoid misfortune (Truter, 2007). These prophets or *ba porofeta* emerged from independent Zionist churches in the early 1900s, seeking to ‘Africanise’ Christianity by incorporating African traditions and customs into their religious practice (Green & Makhubu, 1984). These prophets and the ‘Africanisation’ of these independent Zionist churches attract millions of followers, making them the most extensive and appealing in Africa (Marinovich, 2018). While these prophets and other faith healers are not strictly considered traditional healers, as their communion is not with ancestral spirits, they are formally recognised in government policy, such as within the Traditional Health Practitioners Act of South Africa (THPASA; Act No. 35, Government Gazette, 2004).

Figure 9. Traditional healing in Africa, when Western religion meets cultural spirituality. Here traditional healers and diviners are the formal conduits of ancestral guidance and interpreters of divine direction. As such, they often hold dual roles as medicinal healers and spiritual guides. Remedies thus evolve with the holistic needs of their patients alongside conventional Western medicine. As these services are considered sacred, healers and diviners are often pivotal leaders within their communities, care for the psychological wellbeing of their members in crisis, and retain ancient indigenous knowledge systems. Images are used with permission or under the creative commons license.

Wildlife and their derivatives are fundamental to African traditional healing; those selected as ingredients in remedies or components in charms are generally chosen for their appearance, reputation, and behaviour (Simelane & Kerley, 1998). For example, animals that are large or fierce, such as elephants (*Loxodonta* species) and lions, are used when the customer needs strength or protection, whereas species associated with cunning, such as striped weasels (*Poecilogale albinucha)* and polecats (*Ictonyx striatus*), are used as good luck charms, while baboons, perceived as being agile, are valuable for their crushed bones that are used to treat arthritis (Simelane & Kerley, 1998). Remedies are prepared using herbs or a mixture of herbs and animal parts, such as bone, skin, teeth, claws, and fat (Cook, 2009; Thornton, 2009). Animal derivatives are seldom ingested; instead, they are rubbed on to the skin, sniffed or inhaled, burned, applied topically, sprinkled, worn, or wiped on cooking pots (Williams & Whiting, 2016). The traditional use of, and trade in, wildlife (especially endangered species) and its derivatives remain a contentious socio-political issue as wildlife use has deep cultural significance.

Across Africa, traditional healers play a pivotal role in people’s lives as resourceful healers and as educators of traditional culture, cosmology, and spirituality (Yeboah, 2000; Mokgobi, 2014). They also serve as counsellors, social workers, skilled psychotherapists, and custodians of indigenous knowledge systems (Mills *et al.*, 2005). Their services extend well beyond the uses of herbs and animal derivatives for physical illnesses and are recognised by the World Health Organisation (WHO); for example, in post-civil war Mozambique, traditional healers were found to be invaluable in social reconstruction and reestablishment of communities, particularly in rural areas, through rendering culturally appropriate psychological services that included ancestral communion (Honwana, 1997).

1.3.4. Religion to tradition: symbols, affluence, and prestige

Wild felids have served as religious and cultural symbols across the globe for much of documented human history (Table 1). Regional usage is typically linked to the endemic range of wild felids, with Asian cultures making use of tigers, leopards, and snow leopards, African cultures using lions and leopards, and American groups using jaguars and pumas amongst other smaller, endemic species.

The use of felids by different cultures has been largely convergent, assuming that diverse cultural groups have had limited influence on one another (Pickenpaugh, 1997; Pieterse, 2020). This convergence stems from the overarching symbolism of wild felids as being powerful and regal. For example, leopard skins and necklaces made from leopard teeth are traditionally worn by Zulu kings in South Africa (Raum, 1973; Harries *et al.* 1993), leaders in the Oguta Kingdom, Nigeria (Laine, 1991; Arnoldi, 1995), the Kuba king and his regents and the chief of the Enia tribe in the Democratic Republic of Congo (Droogers, 1980; Cornet, 1982; Laine, 1991; Roberts, 1995), and kings in Cameroon (Northern, 1984; Nilsson *et al.*, 2016). Lion tooth necklaces and serval (*Leptailurus serval*) or leopard skins are used by the Luba emperor in the Democratic Republic of Congo (Laine, 1991), and necklaces made from jaguar teeth are worn by chiefs and leaders of the Bororo tribe, Brazil (von den Steinen, 1894), and the Huaorani people of eastern Ecuador (Kane, 1995).

Figure 10. Felids reappear across multiple cultures as symbols of power and prestige. The use of felid derivatives as cultural symbols of power, masculinity, royalty and social prestige in traditional practices is pervasive, persisting and even growing among some cultural groups merging ancient and modern spiritual belief systems. Images are used with permission or under the creative commons license.

In addition to the regalia of royalty, felid skins and body parts are used in cultural ceremonial attire (Figure 10), such as that of the Khampa Tibetan community in China who don *chubas* containing pieces of tiger and leopard skin to celebrate the *Losar* (Tibetan New Year), summer horse festivals, and weddings (EIA-WPSI, 2006; Moyle, 2009). Similarly, in the Kirdi tribe of Cameroon, the female lead dancer performs in a ceremony celebrating the harvest wearing a necklace of leopard teeth (Fisher, 1984) while in the Nigerian Savannah regions, lion skin is used in a thunder ritual (Adeola, 1992). In the Ngorongoro Crater Area, Tanzania, lions are used in ritual killing (referred to as *Ale-mayo*) by Maasai youth to symbolise their coming of age (Ikanda, 2008).

The use of felid derivatives to bring good fortune and protection similarly crosses cultural borders (Pickenpaugh, 1997; Pieterse, 2020). For example, in the Gansu province of China, snow leopard, leopard, clouded leopard, and tiger skins are sought after as prestigious gifts and symbols of fortune to be kept decoratively in the home (EIA-WPSI, 2006). In the Lacandona jungle of Mexico, fat of the ocelot, margay, jaguarundi (*Puma yagouaroundi*), and jaguar is applied to the abdominal area of women who are unable to fall pregnant to bring about the good fortune of fertility (Garcia-Alaniz, 2010). In the Sundarban mangroves of Bangladesh, various tiger derivatives are thought to protect from disease, enemies, and evil spirits while bringing good fortune, respect, and a tiger-like temperament (Saif, 2016).

Leopard bone, eye, and skin are also believed to protect against witches in the Nigerian rainforests (Adeola, 1992) and the feet of spotted cats in the Caribbean regions of Colombia (González-Maya, 2010), the placenta of Asiatic wild cats (*Felis silvestris ornate*) among the Shoka tribes, India (Negi, 2007), and the eyes of the wild cat (*Leopardus* species) and lion teeth amongst some in the cities of São Luís and Caruaru, Brazil (Alves, 2012) are thought to impart good luck. Felid derivatives are extensively used in traditional healing in both Asia (see 1.3.2), South and Central America, and Africa (see 1.3.3). In South and Central America for example, the fat of jaguar, puma, ocelot, margay, and jaguarundi are used in the Mexican Lacandona jungle as a remedy for muscular pain, asthma, and coughs (Garcia-Alaniz, 2010). In the Caribbean regions of Colombia, jaguar fat is used for general healing and the treatment of asthma, derived oil is used for wound healing, and jaguar or puma fat is used to treat rheumatism (González-Maya, 2010). In Asia, various tiger derivatives are used in the Bangladeshi Sundarbans to treat pain and a wide range of ailments (e.g., cancer, chickenpox, heart disease, and dysentery; Saif, 2016), while the Shoka tribe in India use boiled Asiatic wild cats in the treatment of arthritis and the burnt hair and fat of leopards to treat foot and mouth disease and bodily pain, respectively (Negi, 2007), while in the Nigerian rainforest, leopard skin is used as a cure for snake bites (Adeola, 1992).

Despite an extensive awareness of the use of animal body parts and derivatives in many parts of the world, much cultural use of felids remains understudied or undocumented (Pickenpaugh, 1997; Pieterse, 2020). For instance, the Nazareth Baptist ‘Shembe’ Church in

South Africa uses leopard skins as ceremonial regalia at religious gatherings to symbolise that every man is the king of his own household, a practice derived from Zulu culture that is traditionally reserved for kings and royalty (see Chapter 2; Kumalo & Mujinga, 2017; Marinovich, 2018). Elite rowers in the Lozi king's *Kuomboka* festival in western Zambia (Flint, 2006) wear skirts of felid skin, especially serval, as do the Ngoni people at the annual *N'cwala* festivals which take place from Zambia to Swaziland (Breytenbach, 1972; van Binsbergen, 1987).

While some traditional uses of felid parts recorded here are likely historical remnants, lack of research hampers the extent to which this can be assumed. The cultural use of felid derivatives is undoubtedly based on deep historical respect and admiration for these animals; however, growing demand needs to be formally assessed and managed to ensure that it does not continue to impact already vulnerable wild populations.

Table 1. A non-exhaustive table of felid derivatives used in traditional ceremonies around the globe. Some of those listed represent historical exploitation, but as much of traditional use goes undocumented, it is unclear whether these still represent significant cultural use today.

Region or cultural group	Felid species	Body part used	Purpose	Reference
			CENTRAL & SOUTH AMERICA	
Caribbean region of Colombia	Spotted cats	Foot	Luck, protection	González-Maya, 2010
	Jaguar	Fat	Asthma, general healing	
	Jaguar, puma	Fat	Tendon softening, rheumatism	
	Jaguar	Oil	Wound healing	
	Jaguar, puma	Oil	Hand or foot relief	
	Jaguar, puma	Teeth	Gum punctures for healthy teeth in children	
Amazon - Shipibo men	Jaguar	Teeth	Symbol of bravery	Roe & Saunders, 1998
Northern Brazil - Waiwai men	Jaguar, puma	Teeth	Symbol of bravery	Roe & Saunders, 1998
Belize - Mayan people	Jaguar, puma	Teeth	Symbol of bravery	Rabinowitz, 1986
Selva Lacandona, the State of Chiapas, southeast Mexico	Jaguar, puma, ocelot, margay, jaguarundi	Fat	Applied to reduce muscular pain or boiled and drunk to cure asthma and coughs	Garcia-Alaniz *et al.*, 2010
	Jaguar	Fat	Attractant to hunt other jaguars	
	Jaguar, puma	Fat	Herbivore deterrent from crops	
	Ocelot, margay, jaguarundi, jaguar	Fat	Applied to the abdominal area of women who are unable to fall pregnant to enhance fertility	
Amazon, eastern Ecuador - Huaorani culture	Jaguar	Teeth	Necklace worn by the leader and tribal spokesperson	Kane, 1995
Mato Grosso, central Brazil - Bororo culture	Jaguar	Teeth	Necklace worn by the chief	von den Steinen, 1894
North-east Brazil, São Luís	Jaguar	Tail, foot, eyes	For amulets and Afro-Brazilian rituals	Alves *et al.*, 2012
North-east Brazil, city of São Luís	Wild cat	Eye	Black magic to attract good luck	Alves *et al.*, 2012
			CENTRAL & SOUTH-EAST ASIA	
Pithoragarh, Uttaranchal State, India - Shoka tribes	Asiatic wild cat	Whole animal	Skinned and boiled to cure arthritis	Negi & Palyal, 2007
	Asiatic wild cat	Placenta	Good luck	
China and Mongolia	Snow leopard	Skin, bones, meat, claws	Not reported	Swan, & Conrad, 2014; Sutherland, 2020

Linxia, Gansu Province of China	Tiger, snow leopard, clouded leopard, leopard	Skins, some with paw pads and claws (to prove authenticity)	Prestigious gifts, symbols of luck, home décor	EIA-WPSI, 2006
Qing Dao, Shan Dong province, China	Tiger	Penises	Aphrodisiac	Moyle, 2009
Bangladeshi Sundarbans	Tiger	Teeth, bone, claws, meat, fur, whiskers, tongue, genitalia, liver	Pain relief	Saif *et al.*, 2016
		Teeth, bone, claws, meat, fur, whiskers, tongue, genitalia, scat, milk	Treatment of various diseases	
		Teeth, claws, meat, whiskers, liver	Protection from disease	
		Teeth	Protection from enemy	
		Teeth, bone, claws, meat, whiskers	Protection from bad spirits	
		Teeth, bone, claws, meat, scat	As a pesticide	
		Bone, meat, whiskers, genitalia	To improve male sexual virility	
		Bone, tongue, pugmark	Female contraceptive	
		Canines	Brings good fortune	
		Teeth	Earns respect	
		Teeth, claws, scat, pugmark	Tiger like temperament	
		Teeth, claws	Enhances beauty	
Chinese markets	Tiger, leopard	Bones	TCM - treatment of bone disease and hoarded for potential future needs	Moyle, 2009
Tibetan community in China (mostly Khampa)	Tiger, leopard	Skin	Cultural-decoration of traditional attire (*chubas*) worn at the *Losar* (Tibetan New Year), summer horse festivals and weddings	EIA-WPSI, 2006; Moyle, 2009
AFRICA				
Ngorongoro Crater Area, Tanzania	Lion	Whole	Ritual killing (*Ale-mayo*) by Maasai youth to symbolise coming of age	Ikanda & Packer, 2008
South-eastern Democratic Republic of Congo, Luba empire	Lion	Teeth	Emperor wears a necklace of lion canines, a mantle of serval skin and rests his feet on a leopard skin	Laine, 1991
	Serval, leopard	Skin		

Nigerian savannah regions	Lion	Skin	Thunder ritual	Adeola, 1992
	Leopard	Skin	Ritual sacrifice	
	Leopard	Tail	Female fertility	
Nigeria rainforest regions	Leopard	Skin	Ingredient for curing snakebite treatment	Adeola, 1992
		Bone, eye, skin	Protecting against witch invocations	
Pithoragarh, Uttaranchal State, India - Shoka tribes	Leopard	Meat	Promotes strength and virility	Negi & Palyal, 2007
		Bones	Aphrodisiac	
		Hair	Burnt treatment of foot and mouth disease	
		Fat	Massage oil for treatment of bodily pain	
South-central Democratic Republic of Congo, Kuba kingdom	Leopard	Teeth, skin	Regalia of the reigning king and his regent symbolising his alleged ability to transform into a leopard to take revenge on his enemies	Cornet, 1982; Laine, 1991; Roberts, 1995
North-central Democratic Republic of Congo, Enia tribe	Leopard	Skin, teeth	Hat, armbands, shoulder belt and necklace wore by the chief.	Droogers, 1980
Cameroon (interior Grassfield’s region)	Leopard	Teeth, skin	Regalia is worn by the *Fon* (king)	Northern, 1984; Nilsson *et al*., 2016
Cameroon, Oku kingdom	Leopard	Teeth	Regalia is worn by the *Fon* (king)	Northern, 1984; Nilsson *et al*., 2016
The Mandara Mountains of northern Cameroon, Kirdi tribe	Leopard	Teeth	Lead dancer (female) wears a necklace of leopard teeth in a celebration of the harvest	Fisher, 1984
Imo State, southeast Nigeria, Oguta kingdom	Leopard	Teeth	Necklace worn by the king	Laine, 1991
		Teeth, skin	Prime minister (also a priest) wears a necklace of canines and seated on a skin	Arnoldi & Kreamer, 1995
Northeast Liberia and Northwest Ivory Coast, Dan and We tribes	Leopard	Teeth, skin	Successful hunters required to give the skin and canines of the leopard to the village chief	Fischer & Himmelheber, 1984
Zulu culture of South Africa	Leopard	Skin, teeth	Regalia and necklaces worn by kings	Raum, 1973; Harries *et al.* 1993

1.4. Leopard distribution, conservation status, and trade in southern Africa

Leopards currently occupy the most extensive geographic range of all extant large felids (Figure 11); they also suffer the highest rate of current range loss amongst large terrestrial carnivores and remain formally listed as ‘Vulnerable’ across their range by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Stein *et al.*, 2019). The pressures and challenges faced in their conservation mirror those of many endangered carnivore species (Nowell & Jackson, 1996), with five of the nine recognised leopard subspecies listed as ‘Endangered’ or ‘Critically Endangered’ (Stein *et al.*, 2019). Consequently, leopards provide a valuable model for the full range of conservation-related issues that affect the persistence of large carnivores worldwide.

1.4.1. Global distribution and conservation status

Leopards have the most extensive global distribution of all wild cats, with the nine subspecies spanning across Africa, the Caucasus, and Asia (Figure 11). Despite their wide distribution, most populations are thoroughly fragmented and declining, with numerous examples of regional extirpation, such as that of North Africa (Stein *et al.*, 2019). These large, solitary felids inhabit diverse habitats, including grasslands, woodlands, and riverine forest that remain largely undisturbed (Nowell & Jackson, 1996). Leopards remain numerous throughout sub-Saharan Africa, surviving in marginal habitats where other large cat species have disappeared (Pirie *et al.*, 2017). On the Arabian Peninsula, leopard populations are small and heavily fragmented (Spalton & Al Hikmani, 2006; Judas *et al.*, 2006; Al Jumaily *et al.*, 2006) and in Egypt, leopard sightings are exceptionally rare (Soultan *et al.*, 2016).

Throughout western and central Asia, their range is extensive, excluding only deserts, regions with extensive periods of snow cover, and peri-urban areas (Gavashelishvili & Lukarevskiy, 2008) characterised by high levels of HWC (Landy *et al.*, 2018). The highest altitude at which leopard have been detected (by camera trap) was 4,300 m (14,100 ft) in the Kanchenjunga Conservation Area of Nepal (Thapa *et al.*, 2013). Across the Indian sub-continent, leopards are still abundant relative to other pantherids (Stein *et al.*, 2019), even in semi-developed and transformed landscapes near human settlements. Despite their adaptability, leopards rarely linger in these areas as their prolonged survival still requires healthy, abundant prey populations and appropriate vegetative cover for hunting. As solitary, nocturnal (mostly crepuscular) hunters, the elusive nature of leopards means that people are often unaware of their presence (Athreya, 2010). For instance, in Sri Lanka, leopards have been sighted in unprotected forest patches, tea estates, grasslands, home gardens, and both pine and eucalyptus plantations outside of Yala National Park (Kittle *et al.*, 2014).

In Myanmar, leopards are found primarily in the Northern Tenasserim Forest Complex; however, some have recently been sighted in the southern hill forests of Karen State (Moo *et al.*, 2017). Leopards in Thailand are present in the Western Forest Complex, Kaeng Krachan-Kui Buri and Khlong Saeng-Khao Sok PA complexes, and in the Hala Bala Wildlife Sanctuary on the Malaysian border, where they are present in Belum-Temengor, Taman Negara, and Endau-Rompin National Parks along the peninsula (Rostro-García *et al.*, 2016). In Laos and Cambodia, leopards have been recorded in the Nam Et-Phou Louey National Biodiversity Conservation and Nam Kan National PAs (Johnson *et al.*, 2006), the Mondulkiri Protected Forest, and the Dipterocarp forest of Phnom Prich Wildlife Sanctuary (Gray, 2013). During surveys of 11 nature reserves across southern China between 2002 and 2009, leopards were only recorded in the Qinling Mountains (Li *et al.*, 2010). Javan leopards inhabit dry deciduous forests and dense tropical rainforests at altitudes from sea level to 2,540 m (8,330 ft), having been recorded (2008 and 2014) outside of PAs in mixed agricultural land, secondary forest, and production forest (Wibisono *et al.*, 2018). Finally, in the Russian Far East where winter temperatures reach lows of -25 °C (-13 °F), leopards inhabit temperate coniferous forests (Uphyrkina *et al.*, 2001).

While leopards are formally listed as ‘Vulnerable’ across their range by the IUCN Red List of Threatened Species (Stein *et al.*, 2019), the Arabian (*Panthera pardus nimr*) and Far Eastern leopard subspecies (*P.p. orientalis, P.p. japonensis, P.p. delacouri,* and *P.p. melas*) are classified as ‘Critically Endangered’. The Persian (*P.p. saxicolor*) and Sri Lankan (*P.p. kotiya*) leopard subspecies are considered ‘Endangered’, whereas the Indian (*P.p. fusca*) and African (*P.p. pardus*) are classified as ‘Vulnerable’ (Figure 11A). Leopards are threatened by habit loss globally. In total, Jacobson *et al*., (2016) estimate leopard eradication from 63–75% of their historical range (Figure 11B & C).

African leopards once occurred across most of the African continent apart from the hyper-arid interiors of the Sahara and Namib deserts but are now virtually extinct in North Africa, extremely rare throughout West Africa’s coastal belt, and continue to decline outside of PAs across much of East and southern Africa, with only 33% of their preferred habitat remaining (Figure 11B; Bailey, 1993; Jacobson *et al.*, 2016). Leopard populations outside of Africa have fared little better.

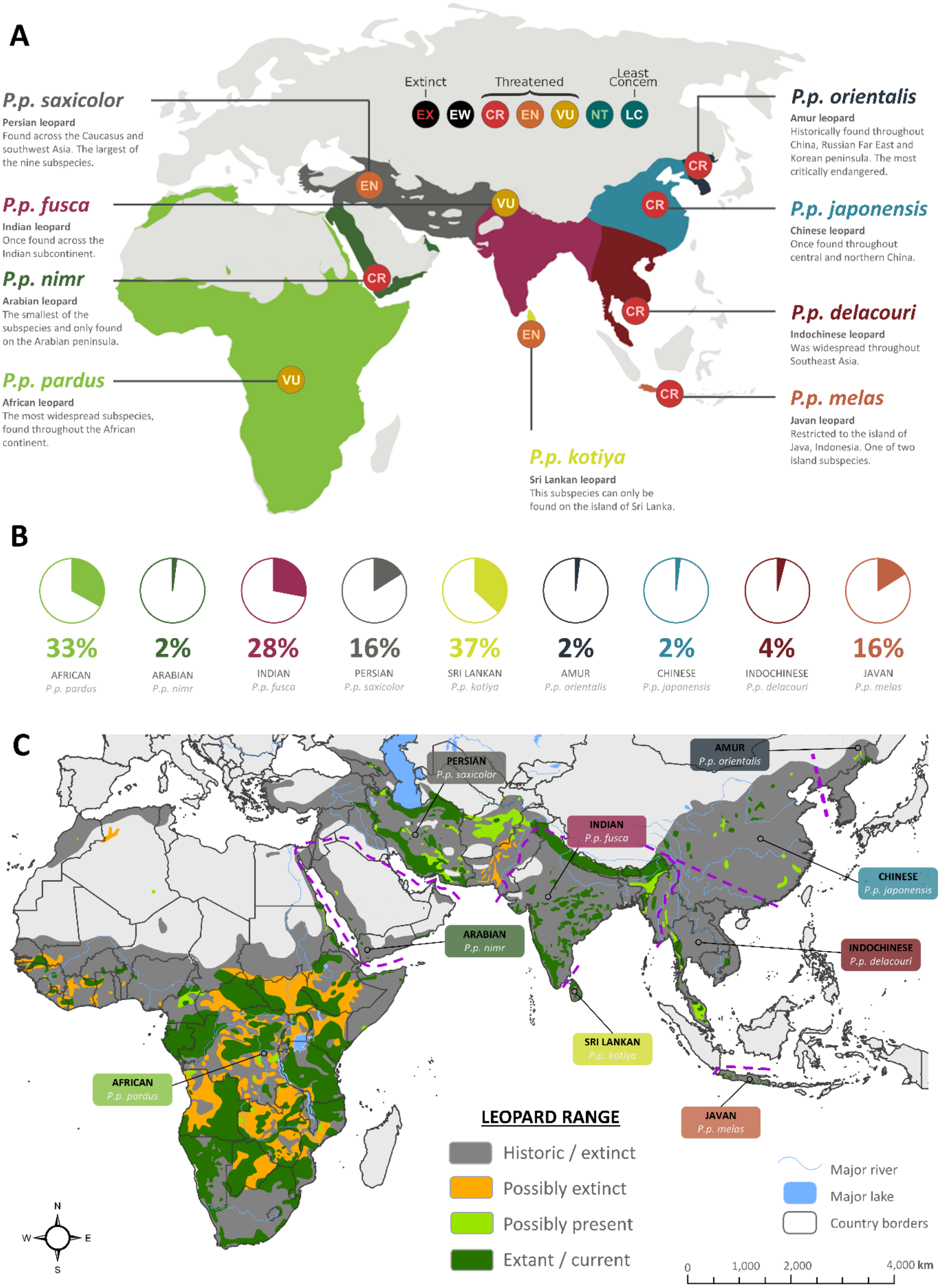
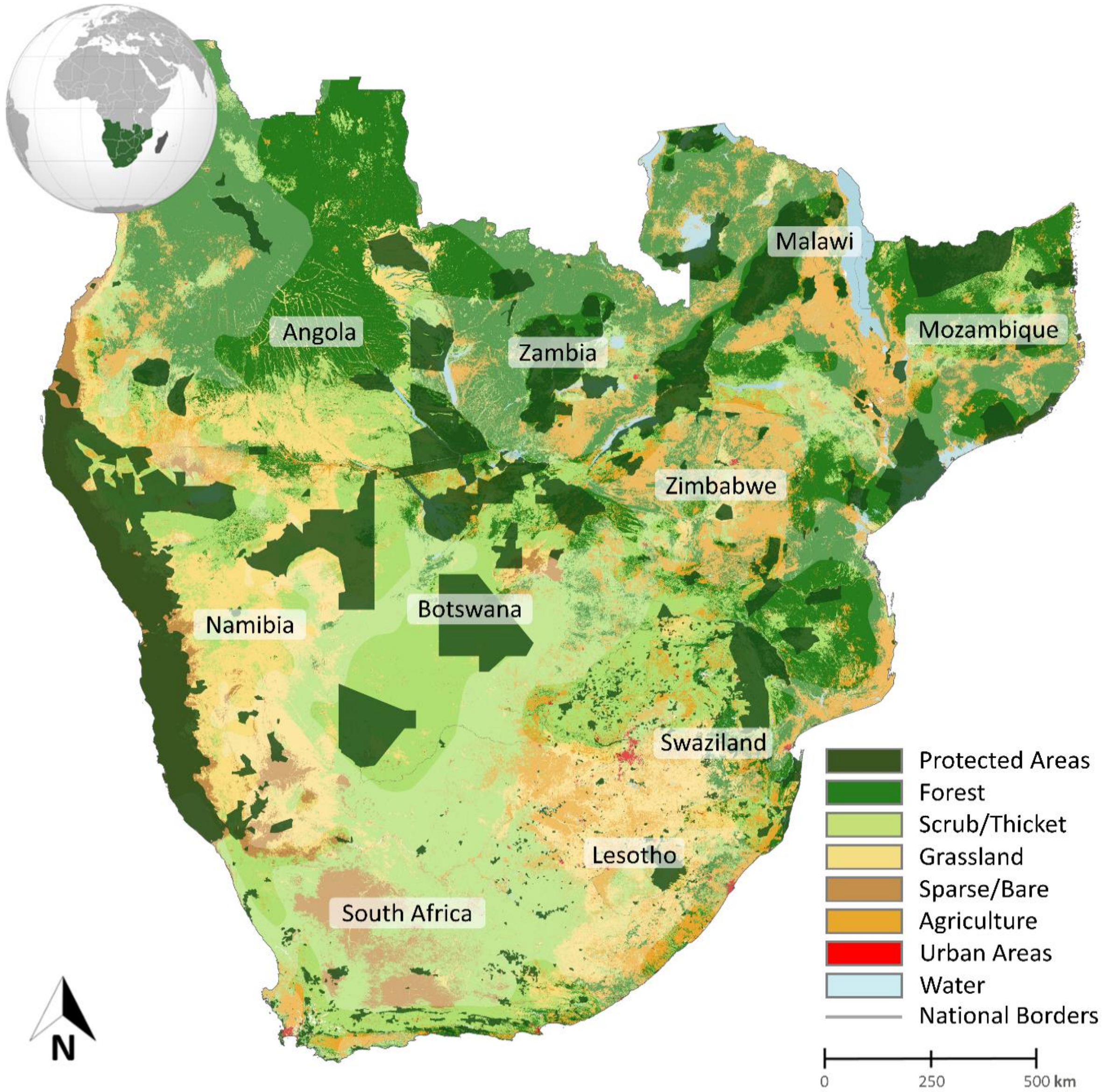


Figure 11. Distribution, status, and remaining habitat of leopard subspecies. (A) The nine recognised subspecies of leopard and their historical distribution, IUCN Red List status, (B) proportion of remaining habitat per subspecies, and (C) fragmentation of extant leopard distribution per subspecies. Adapted from Jacobson *et al.* (2016).

The Arabian subspecies is limited to an estimated 100–250 animals distributed across the remaining 2% of their habitat in the Middle Eastern states of Saudi Arabia, Yemen, Oman, and possibly the United Arab Emirates (Figure 11B; Spalton *et al*., 2006a; Jacobson *et al.*, 2016). Leopard numbers have been significantly reduced across South-East Asia and are decreasing rapidly outside national parks with limited suitable habitat across their range (Persian: 16%, Indian: 28%, Sri Lankan: 37%, Amur: 2%, Chinese: 2%, Indochinese: 4%, and Javan: 16%; Figure 11B; Jacobson *et al.*, 2016; Sunquist & Sunquist, 2017). The northernmost subspecies (*P.p. orientalis*) is now confined to three reserves in North Korea and the Maritime Territory of Russia with numbers fewer than 100 individuals (Miquelle *et al*., 1996). In addition to the direct threat of vastly reduced habitat across their range, remaining leopard populations are becoming increasingly isolated by habitat fragmentation and the loss of connectivity (Figure 11C).

1.4.2. Range states, protected areas, and threats

The current geographic range of leopards encompasses roughly 2.9 million km^2 (48%) of southern Africa (Figure 12) distributed over the range states of Angola (24%), Namibia (20%), Mozambique (15%), South Africa (14%), Botswana (13%), Zambia (8%), and Zimbabwe (6%) with a marginal presence in Malawi (<1%), Swaziland (<1%), and Lesotho (<1%). Southern African leopard range is highly fragmented by habitat restrictions and transformed landscapes, with only 29% of suitable leopard habitat included within formally PAs (Jacobson *et al.*, 2016; Stein *et al.*, 2019). While this is unavoidable given the difficulties in providing adequate enclosure, as well as their elusive nature and remarkable adaptability to a shifting prey base, their presence in unprotected areas (62%) and highly transformed landscapes (9%), such as agricultural land and urban areas (Figure 12), bring them into regular HWC (Athreya *et al.*, 2010; Balme *et al.*, 2010a). As PAs generally provide adequate protection and healthy prey populations, their proportional distribution and relative connectivity across range states are crucial to the long-term persistence and protection of leopards in southern Africa.



Country	Leopard range (km²)	Protected area (km²)	Unprotected area (km²)	Transformed land (km²)	Total (km²)
Angola	683,736 (24%)	60,690 (9%)	545,306 (80%)	77,740 (11%)	1,247,682
Namibia	566,755 (20%)	260,580 (46%)	293,067 (52%)	13,105 (2%)	823,978
Mozambique	441,563 (15%)	74,010 (17%)	304,709 (69%)	62,844 (14%)	786,597
South Africa	397,736 (14%)	74,010 (19%)	286,855 (72%)	36,871 (9%)	1,220,035
Botswana	359,229 (13%)	122,716 (34%)	216,187 (60%)	20,326 (6%)	578,080
Zambia	225,158 (8%)	169,757 (75%)	43,212 (19%)	12,188 (5%)	751,304
Zimbabwe	157,266 (6%)	53,062 (34%)	71,909 (46%)	32,295 (21%)	390,647
Malawi	10,685 (<1%)	7,688 (72%)	1,362 (13%)	1,635 (15%)	118,028
Swaziland	10,039 (<1%)	467 (5%)	6,180 (62%)	3,392 (34%)	17,289
Lesotho	323 (<1%)	286 (89%)	30 (9%)	7 (2%)	30,453
Southern Africa	**2,852,490**	**823,269 (29%)**	**1,768,816 (62%)**	**260,405 (9%)**	**5,964,093**

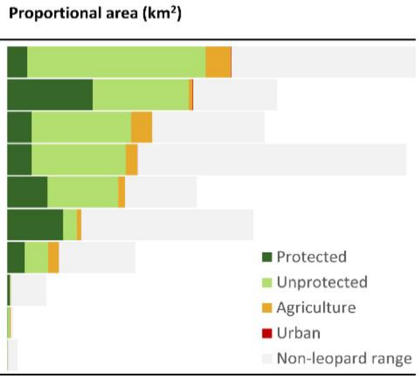


Figure 12. Leopard range relative to land use across southern Africa. Non-extant leopard range is indicated in a lighter hue over the land use map. The total area of leopard range is indicated per country as the proportion of total southern African leopard range and further subdivided into protected versus unprotected area, and transformed land, the proportions of which are scaled relative to the size of each country (km^2). Leopard range data adapted from Jacobson *et al.* (2016). Land use data derived from the South African Biodiversity Institute (SANBI) Archive 2014 - South African National Land-Cover (30 x 30 m raster). Available at: http://bgis.sanbi.org/DEA_Landcover/project.asp.

Zambia has the largest proportion of their known leopard range captured within PAs (75%), followed by Namibia (46%), Botswana and Zimbabwe (34%), South Africa (19%), Mozambique (17%), and Angola (9%). While proportional coverage in Lesotho (89%) and Malawi (72%) are high and in Swaziland, low (5%), the relative representation of these three states in overall southern African leopard range is low (Figure 12). It is concerning that in three of the largest states (Angola: 24%, Mozambique: 15%, and South Africa: 14%), most leopard range falls outside of PAs (80%, 69%, and 72%) and within highly transformed land (11%, 14%, and 9%). Other range state proportions of leopard range to unprotected land and highly transformed habitat within range states are better (Namibia: 20%, 46%, 2%; Botswana: 13%, 60%, 6%; Zambia: 8%, 19%, 5%, and Zimbabwe: 6%, 46%, 21%) but will be variously impacted by climate and population growth variability.

Leopards in southern Africa are vulnerable to threats affecting all large felids in the region, namely loss of habitat, prey depletion, conflict with humans, and harvest for local and international trade in body parts (Durant *et al.*, 2019; Stein *et al.*, 2019; Bauer *et al.*, 2019). They are also harvested by legal trophy hunting (Balme *et al.*, 2010b; Swanepoel *et al.*, 2011; Braczkowski *et al.*, 2015) and illegally for use in traditional practices (Warchol *et al.*, 2003; Whiting *et al.*, 2013; Alves *et al.*, 2013; Williams & Whiting, 2016). Substantial demand exists for leopard skins for their reverence among local traditional royalty (e.g., the Zulu [Harries *et al.*, 1993], Barotse [van Binsbergen, 1987], and Swazi kingdoms [Breytenbach, 1972]) and, more recently, the burgeoning Shembe Church (Kumalo & Mujinga, 2017) that uses leopard skins as ceremonial regalia. Leopard derivatives (e.g., bones, claws, teeth, fat, and skin) are also used in traditional medicine or *muti* (Cook, 2009), spiritual divination, and enchantment (Thobane, 2015; Williams & Whiting, 2016). Traditional use is a significant but generally understated threat to leopard populations, remaining largely undocumented, unregulated, and untraced across southern Africa due to monitoring complexity and culturo-political sensitivities (Dickman *et al.*, 2015).

1.4.3. Undocumented: legal disjunction when lobby becomes law

The South African Traditional Health Practitioners Act (Act No. 35, Government Gazette, 2004) was enacted to formalise, regulate, and protect the teaching and practice of traditional medicine and access of traditional healers to *muti* (Thornton, 2009). However, many of the species prescribed by traditional healers are protected under South Africa’s National Environmental Management and Biodiversity Act (NEMBA; Act No. 10, Government Gazette, 2004), resulting in two national policies in direct contradiction of each other. This unique situation in South Africa proves a challenging legislative landscape that is further complicated by a lack of documentation monitoring traditional use and the sources of wildlife products. This policy remains ill-equipped to deal with the scope of exploitation for traditional use as long as there is a lack of political will to challenge demand due to cultural significance and sensitivities. NEMBA and Threatened or Protected Species (TOPS) regulations protect 'Critically Endangered', 'Endangered', 'Vulnerable', or protected species by legally restricting their use through hunting, collecting, and trade or export (CITES). Despite the poaching and trade of protected species thereby being prohibited and considered punishable offences, the demand for these species for traditional use persists and drives exploitation and IWT, which is largely undocumented and therefore allowed to persist.

1.4.4. Unregulated: cultural sensitivity and political discretion

South Africa has a strained socio-political history; the post-colonial, nationalist apartheid government (1948–1994) formalised racist discrimination against the black majority and the denigration of traditional culture. This context frames the required sensitivity when considering restrictions on culture, customs, and indigenous knowledge systems or practices (Ashforth, 2005). The South African people are understandably insistent that traditional culture and knowledge be accorded respect and not be circumscribed. While the formation of the Traditional Health Practitioners Council of South Africa in 2015, with which all traditional healers are required to register, should have assisted in regulating the practice, effective bureaucratic regulation and enforcement remain limited (Ashforth, 2005; Dickman *et al.*, 2015). These regulations place the South African government in a difficult, if not impossible, position in regulating traditional use of even legally protected species (Ashforth, 2005). Wildlife use and its regulation are further complicated and frustrated by escalating numbers of cultural and religious users, such as followers of the Shembe Church (see Chapter 2; Marinovich, 2018) and traditional royalty who do not necessarily recognise the government's authority in these matters. Furthermore, baseline data on the status of many protected species (see Chapter 4 [Naude *et al.*, 2020]) and the extent of demand for cultural use is mostly absent or incomplete (Balme *et al.*, 2013b), meaning that conservation authorities are poorly equipped to assist the government in making informed decisions.

1.4.5. Untraced: an ‘arms race’ of illegal wildlife trade monitoring

Tracing the origin of poached felid skins for monitoring and prosecution of IWT presents numerous challenges. For reliable ‘forensic’ assessment, seized samples must be identifiable to the individual level, and the geographic origin must be accurately and irrefutably identified (see Chapter 3). The wide distribution of leopards further means that harvest is not always local or in the area of demand. As such, sophisticated, reliable scientific methods are required to trace the geographic origins of seized skins and derivatives to inform poaching hotspots and focus targeted anti-poaching enforcement (Alacs *et al.*, 2010; Mondol *et al.*, 2014). Visual examination cannot distinguish a skin’s origin, especially when it has been processed into a marketable product or is degraded (Alacs *et al.*, 2010). Information on the origin of leopard products disclosed by alleged poachers or traders is likely unreliable and purely qualitative. Molecular techniques may offer the required resolution (Iyengar, 2014), where modifications to common population genetic approaches and techniques (namely, microsatellite genotyping, mitochondrial deoxyribonucleic acid (DNA) sequencing, and phylogenetic analysis) have been employed to identify the origins of illegal wildlife trade and have been largely successful in achieving this to date (Wasser *et al.*, 2004; Baker *et al.*, 2010; Mondol *et al.*, 2014; Gaubert, 2015; Mendoza, 2016; Mwale, 2017).

1.5. Thesis outline

The overall objective of this thesis is to investigate the scale and impact of traditional use as a threat to leopard conservation in southern Africa.

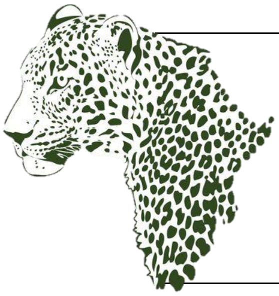
In Chapter 2, I provide an introduction to the Shembe Church in South Africa and use longitudinal questionnaires and telephonic follow-up questionnaires with Shembe followers to explore socio-economic and experiential factors influencing the desirability and possession of illegal leopard skins before and after receiving a *faux* skin alternative.

In Chapter 3, I use molecular techniques to demonstrate the geographical extent of the illegal leopard skin trade in service of various traditional end-users. Specifically, I use DNA-based (mitochondrial haplotype and microsatellite genotype) assignment tests to match confiscates and samples taken from leopard skins entering illegal markets to known leopard populations, thereby identifying ‘hotspots’ of poaching pressure and potential trade.

In Chapter 4, I contrast the genetic and spatial structure of two South African leopard populations with markedly different poaching histories, much of which services the illegal wildlife trade for traditional use. Using these two populations, I explore the potential impacts of unsustainable rates of anthropogenically-linked mortality on the dispersal behaviour and subsequent genetic structure of leopard populations. The data presented herein has recently been published in the Journal of Ecology and Evolution (Naude *et al.*, 2020).

In Chapter 5, I summarise my findings, placing them in a broader context of global leopard conservation and the challenges of illicit wildlife trade, advocating for the reassessment of traditional use as a significant regional threat and emphasising the importance of revised sustainable use policy, continuous monitoring of trade, and effective PA connectivity. I further highlight the unique value of integrating these multidisciplinary methods (socio-cultural engagement, molecular geographic assignment techniques, and population-level ecological monitoring) with the global strategy for the conservation of leopards and other large felids.

CHAPTER 2



UNDER THE SKIN OF A CULTURE: ILLEGAL LEOPARD SKIN TRADE AND LONGITUDINAL ATTITUDE SHIFTS TOWARDS *FAUX* ALTERNATIVES AMONG TRADITIONAL USERS

Figure 13. The Furs For Life (FFL) **initiative aims to reduce demand for leopard skins in the Shembe Church.** Through fostering trust with the foremost culturo-religious users of illegal leopard skins in the world, the FFL provides realistic *faux* leopard skins designed to be accepted by the Church and assimilated into traditional practices, thereby reducing demand for authentic leopard skins and curbing this illegal trade. Images are used with permission or under the creative commons license.

2.1. Abstract

Despite having protected status, poaching for illegal trade and traditional use is one of the primary threats to leopards across southern Africa. Addressing this problem poses particular challenges, not only because it is difficult to uncover and monitor illicit behaviour, but also because law enforcement and alternative intervention strategies need to account for cultural respect and political sensitivities in order to prove effective and sustainable. Followers of the recently established Nazareth Baptist 'Shembe' Church, with its estimated membership of over four million in South Africa, represent the principal culturo-religious users of illegal leopard skins in the world. In this chapter, I use longitudinal, in-person questionnaires (*n* = 8,600) and telephone follow-ups (*n* = 2,300) with Shembe Church followers to explore socio-economic and experiential factors related to the desirability and possession of illegal leopard skins before and after receiving a *faux* alternative as part of the Furs for Life intervention programme. Proportional possession of authentic skins was relatively low among followers who received *faux* skins (21%), with marked declines of 7% and 13% in the subsequent acquisition and stated desirability, respectively. Logistic regression revealed that authentic skin possession, both before and after receiving a *faux* skin, was primarily related to employment status. The desire for authentic skins also increased with recipient age but decreased with improved knowledge of leopard population status since receiving the *faux* skin. Older followers and those who were dissatisfied with *faux* skins were more likely to still express desire for an authentic skin. Most followers (95%) were, however, satisfied with the *faux* alternative, having retained and used it at gatherings, with little noticeable damage or perceived societal judgement. These results indicate that the Furs for Life programme has been largely successful in that although authentic skins are still being acquired, demand has decreased significantly over three years with shifts in perception favouring *faux* skin alternatives.

2.2. Introduction

Recent declines in global wildlife populations are primarily driven by anthropogenic effects (Woodroffe, 2005; Kareiva & Marvier, 2012; Maxwell *et al.*, 2016; Di Marco *et al.*, 2018), but changing human behaviour is seldom the focus of conservation research (Schultz, 2011; Hazzah *et al.*, 2017). Although effective mitigation against over-harvesting of biological resources, destruction of habitat, climate change, and IWT is vital for successful conservation and maintenance of functioning natural ecosystems, the anthropogenic nature of these threats means that actions to modify human behaviour and social systems through innovative solutions and adaptive policy are necessary (Manfredo & Dayer, 2004; Baruch-Mordo *et al.*, 2009; Dobson *et al.*, 2019). Such systemic behavioural change is required across multiple scales, from global markets and governing agencies to the behaviour of individual consumers (Ostrom, 2009).

As key ecological components of natural ecosystems, wild felids have a rich mythology, appearing throughout human history as cultural, political, and religious symbols of power and social prestige (see 1.3; Benavides, 2013). Their skins are particularly revered, as the implicit danger in their acquisition, their fierce visage, and rich patterning are all believed to symbolise affluence, prestige, and power (Loveridge *et al.*, 2010). This relationship is not only evident among ancient, traditional identities (e.g., jaguars and Olmec royalty [Saunders, 2010]; lions and Maasai warriors [Ahmed *et al.*, 2015]; tigers and Tibetan Buddhists [Yeh, 2012]), but is also established in modern culture (e.g., the 20th-century fur trade in Western fashion [Ramchandani & Coste-Maniere, 2017] and recent demand in many Asian cultures [EIA, 2004; EIA-WPSI, 2006; Nowell & Xu, 2007]). Concomitant with species decline and responsive global environmental policy, many traditional groups have denounced or reduced their use of animal skins. For example, following a campaign to raise awareness of tiger declines across South-East Asia in 2006, the 14th Dalai Lama appealed to Tibetans to cease wearing clothing lined with endangered animal skins (Figure 7); this resulted in Tibetans destroying millions of yuan worth of otter, leopard, tiger, and other pelts across the Plateau and an associated significant decline in local demand (Graham-Rowe, 2011; Yeh, 2012; Geertz, 2016). Nevertheless, ongoing respect for the cultural and traditional uses of wildlife material often comes into direct conflict with international and local environmental policy and can impede local enforcement (e.g., the ongoing use of formally protected species in traditional Asian or African medicine [see 1.3.2 & 1.3.3], whose practitioners are often legally recognised and registered [Alves *et al*., 2013; Williams & Whiting, 2016; Nijman *et al.*, 2019]).

Across Africa, wild felid populations including cheetah, lion, and leopard are vulnerable to localised extinction, facing threats of habitat loss, prey depletion, conflict with humans, and harvest for local and international trade in body parts (Durant *et al.*, 2019; Stein *et al.*, 2019; Bauer *et al.*, 2019). Leopards are currently classified as 'Vulnerable' on the IUCN Red List of Threatened Species (see 1.4; Stein *et al.*, 2019). With 62% of their southern African range falling outside of PAs (see 1.4.2; Jacobson *et al.*, 2016), together with a relative tolerance for human-modified landscapes and the ability to adapt to a shifting prey base (Athreya *et al.*, 2010; Balme *et al.*, 2010a), leopards are particularly at risk from retaliatory conflict (Loveridge *et al.*, 2010), legal trophy hunts (Balme *et al.*, 2010b; Swanepoel *et al.*, 2011; Braczkowski *et al.*, 2015), and poaching for illegal use in traditional practices (Warchol *et al.*, 2003; Alves *et al.*, 2013; Whiting *et al.*, 2013; Williams & Whiting, 2016). Across southern Africa, leopard derivatives (e.g., bones, claws, teeth, and fat) are used in traditional medicine or *muti* (Cook, 2009), as well as spiritual divination or enchantment (Thobane, 2015; Williams & Whiting, 2016). Leopard skins are also sought after for their reverence in ceremonial regalia among local traditional royalty (e.g., the Zulu [Harries *et al.*, 1993], Barotse [van Binsbergen, 1987], and Swazi kingdoms [Breytenbach, 1972] and, more recently, the burgeoning Shembe Church [Kumalo & Mujinga, 2017]).

The Nazareth Baptist 'Shembe' Church was founded by the Prophet Isiah Shembe in 1910 and is best defined as an amalgamation of traditional Zulu and Christian beliefs (Figure 13; Tishken, 2006; Tishken, 2015), with strongholds in the Gauteng and KwaZulu-Natal provinces of South Africa. In the last few decades, the broader Shembe community has adopted the traditional Zulu custom of chiefs and royalty wearing leopard skins as symbols of affluence, social power, and prestige (Figure 14D; Dickman *et al.*, 2016; Firenzi, 2012; Papini, 2004). Although there are no reliable figures on the current number of practising Shembe, informal estimates suggest there may be as many as four million followers among its factions, making it a contender for the largest traditional church in Africa (Marinovich, 2018). Shembe religion promotes the ideal that every man is the *inkosi* (king) of his own household and in this way is considered royalty and is thereby eligible to wear a leopard skin (Papini, 2004; Tishken, 2006; Tishken, 2015).

As leopards are nationally protected in South Africa under TOPS regulations, and internationally under CITES (Appendix I), any person wishing to possess or trade in leopard skins requires a permit issued by the provincial conservation authority. To date, however, no permit has been issued to a Shembe follower for the possession of leopard derivatives, while leopard skin adornments are worn and traded openly at gatherings, where enforcement is absent; this is likely because of political sensitivities linked to the policing of cultural traditions (Ashforth, 2005; Moyle, 2009). The ecological consequences of this illegal skin trade on extant leopard populations are largely unknown (see Chapter 4 [Naude *et al.*, 2020]).

Figure 14. Shembe men dancing at the eBuhleni gathering in February 2017. Emphasised: (A) headbands or ‘*umqhele*’ made of spotted cat skins; (B) antelope skins tailored into shoulder capes and artificially ‘spotted’ with ink; (C) other spotted cats skins (e.g., serval and cheetah) tailored into shoulder capes; (D) authentic leopard skins tailored into shoulder capes; (E) drums and vuvuzelas adopted into the ceremony; (F) Furs for Life (FFL) leopard skins tailored into shoulder capes; (G) traditional Zulu Nguni (cow hide) shields called ‘*igqoka*’ or ‘*ihawu*’; (H) ostrich feather headdresses; (I) belts, (J) ankle and (K) arm bands made of spotted cat skin; (L) bare feet on holy ground; (M) holy white surplices or ‘*umnazaretha*’ worn by Nazerites on church grounds; (N) Nguni (cow hide) back skirts or ‘*iBheshu*’; (O) traditional Zulu swatches (fly-whisks) or ‘*izimboko*’ (fighting sticks) and (P) ‘*isinene*’ waist-round skirts of banded animals skins (e.g., genet [genus *Genetta*], mongoose [family Herpestidae], and polecat [*Ictonyx striatus*]). The image is used here with permission.

To reduce demand for leopard skins within the Shembe community, Panthera (a global wild cat non-profit conservation organisation) launched the Furs For Life (FFL) initiative in 2013 (see https://www.panthera.org/furs-for-life). Collaborating with digital designers and clothing companies, FFL created high-quality, durable, and realistic *faux* leopard skins designed to be worn as shoulder capes, known locally as ‘*amambatha*’ (Figure 14F). Panthera has also invested considerable time and effort in establishing a trust-based and mutually respectful relationship with Shembe Church leaders who have endorsed the use of *faux* skins by followers at religious ceremonies. The FFL has since distributed more than 22,000 *amambatha* to Shembe followers at gatherings across South Africa.

The aim of this study was to assess the success of the FFL intervention as determined by reducing the desire for, and possession of, authentic leopard skins. Using longitudinal questionnaires with recipients of *faux* skins (2013–2018), socio-economic and experiential factors that may be related to the possession of and desire for an authentic skin were explored before (2013–2015) and after (2018–2019) receiving a *faux* alternative. Social psychological theories such as the Cognitive Hierarchy, Theory of Reasoned Action, Theory of Planned Behaviour, and the Value-Belief-Norm Theory (Homer & Kahle, 1988; Fishbein & Aizen, 2010; Vaske & Manfredo, 2012; Stern, 2018) propose that an individual's socio-economic characteristics and cognitions (e.g., perceptions, beliefs, and attitudes) can predict their behavioural intentions (e.g., desire for leopard skins) and actual behaviours (e.g., possessing leopard skins). Findings are discussed in the context of scalable conservation intervention strategies, enforcement of environmental policy, and the unaddressed global impacts of traditional uses of wildlife.

2.3. Methods

2.3.1. Ethics statement

This research was retrospectively approved by the University of Cape Town, Faculty of Science Research Ethics Committee (approval number FSREC83–2018). As many respondents were non-literate and to ensure adequate comprehension, all respondents were read a consent clause in their preference of either Zulu or English before providing verbal consent (Appendix 1). Where respondents withheld or withdrew consent, questionnaires were terminated as agreed upon in the consent clause. Respondent identities were numerically coded to ensure anonymity and were maintained as an independent, secure dataset. This record of identities was kept to prevent reissuance of *faux* skins per individual only and not used in any subsequent analyses.

2.3.2. Study area

In-person questionnaires were conducted on-site while distributing *faux* skins at Shembe gatherings held throughout the Gauteng, Mpumalanga, KwaZulu-Natal, and Eastern Cape provinces of South Africa, with marginal representation from Swaziland and southern Mozambique (Figure 15). Gatherings ranged from small weekly congregations (<100 followers) to large annual observances (>50,000 followers). Large gatherings, such as those held at eBuhleni, Nhlangakazi (Holy Mountain), Nongoma, and Eshowe, have deep ceremonial significance and are presided over directly by Shembe leaders, which attracts followers from across southern Africa. Follow-up questionnaires with a randomly chosen subset of *faux* skin recipients (ensuring adequate regional representation) were conducted via telephone.

2.3.3. Survey design and sampling

A total of 8,600 semi-structured questionnaires (see Appendix 1) were conducted throughout the study area (Figure 15) between February 2013 and February 2018 with willing participants before they received a *faux* skin (pre-FFL). Participants were approached opportunistically through convenience sampling during *faux* skin distribution which took place at least twice a year, throughout these five years, with a 100% response rate. All *faux* skin recipients were educated about the impact that demand for authentic skins has on extant leopard populations and legislation pertaining to the purchase and possession of authentic skins as part of the FFL programme. Thereafter (post-FFL), 2,300 semi-structured, follow-up questionnaires were conducted by telephone between June 2018 and October 2019. These questionnaires were conducted with all Shembe followers who had received their *faux* skin within the first three years of distribution (2013–2015), had taken part in the original FFL questionnaire, and indicated that they were willing to partake in the follow-up questionnaire. Of the 3,021 attempted call-backs, 2,300 were contactable (76%), and among these, the response rate was 100%.

Questions relating to authentic leopard skin possession and desirability, as well as perception and experience, among followers relating to *faux* skins were developed via common ethnographic inquiry, including prolonged engagement, participatory observation, multiple source data collection, and recursive interpretations (Bernard, 1998; Schensul *et al.*, 1999).

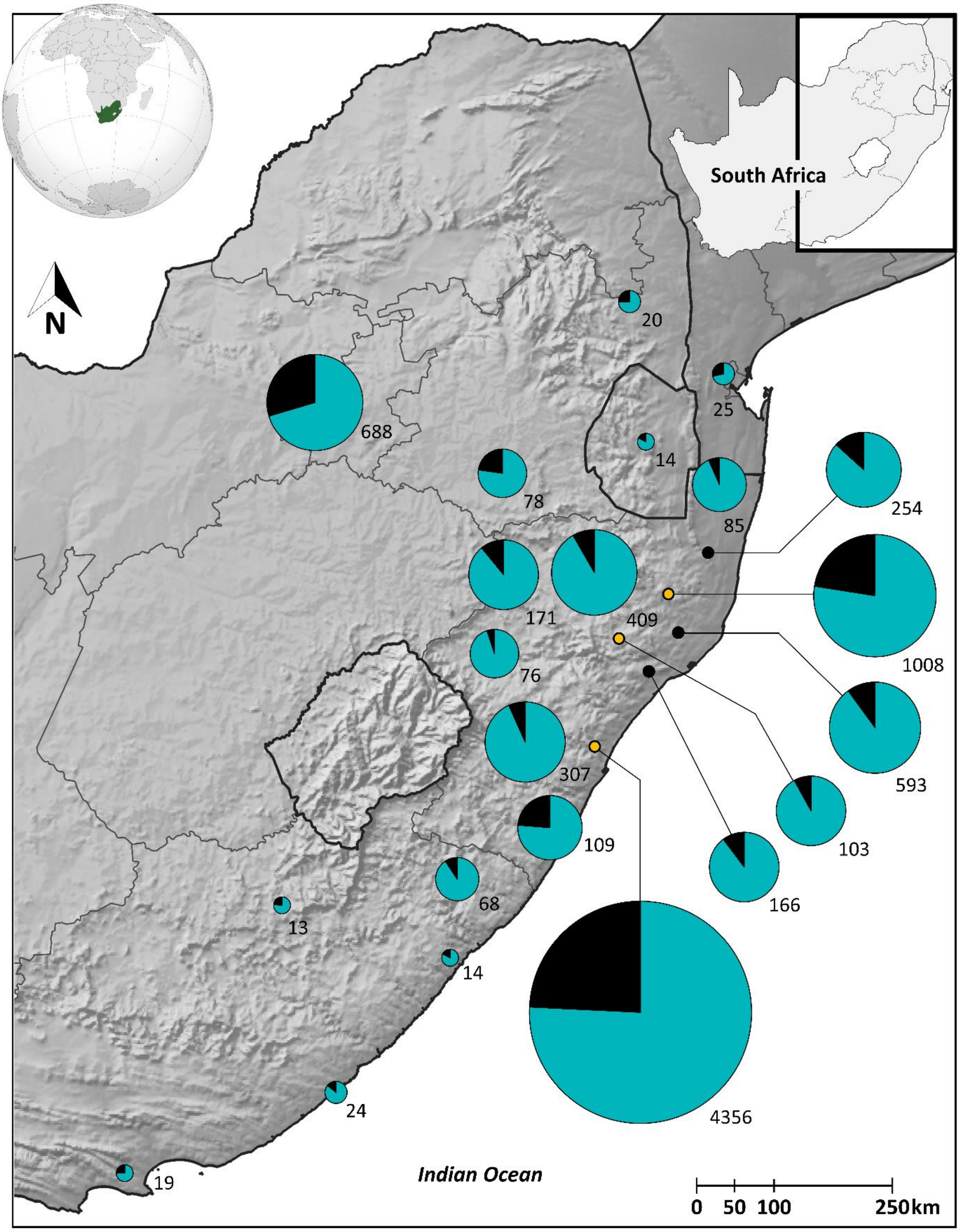


Figure 15. Map of the questionnaire study area in eastern South Africa. Questionnaire surveys were conducted throughout the landscape, where regional summary pie-chart size (sample size; bottom right) indicates the number of pre-FFL intervention surveys conducted (2013–2015; turquoise) and proportion of post-intervention follow-up questionnaires (2015–2018; black). Featured are locations of three of the largest Shembe gatherings (yellow), namely Nongoma (north), Eshowe (central), and eBuhleni (south).

Both pre- and post-FFL questionnaires were pilot-tested with 100 respondents to optimise questions before commencement, and, as such, these data were not included in subsequent analyses. All questionnaires were conducted in Zulu or English, as preferred by the respondent, and communicated by a single interviewer to minimise bias (Browne-Nuñez & Jonker, 2008). Questionnaire transcripts underwent further translation and back-translation by two independent translators to increase their accuracy and reliability (Behling & Law, 2000). Each respondent personally answered the questions with minimal assistance, and there were no missing data.

2.3.4. Data analysis

A subset of the questions used in the pre-FFL questionnaire was included in the post-FFL follow-up questionnaire (Appendix 1). All analyses were conducted in *R* (R Core Team, 2019). Variable frequencies were categorised as indicated (Table 2) for both questionnaires before comparing pre- and post-intervention frequencies through univariate χ^2-tests of independence.

Binary logistic regressions were performed to explore the contribution of relevant socio-economic and experiential factors that may be related to possession and desire for an authentic leopard skin before receiving a *faux* skin (pre-FFL) and subsequent acquisition and desire for an authentic leopard skin after receiving a *faux* skin (post-FFL). Responses to combinations of predictive factors for each question were modelled through logistic regression (generalised linear model with a binomial distribution and logit-link) and the best models selected by minimising the Akaike information criterion (AIC) implemented in the *glmulti* package (Calcagno & de Mazancourt, 2010). Variance inflation factors (VIF; <2) and decomposition proportions were tested in top models to investigate multicollinearity among the predictors (Fox, 1997; Fox & Weisberg, 2011), as well as evidence of outliers, influential observations, and heteroskedasticity. Model fit was then assessed using a combination of log-likelihood ratio ($P \leq 0.05$), global goodness-of-fit tests (Hosmer–Lemeshow; $P \geq 0.05$), and pseudo-R^2 estimates (Nagelkerke *et al.*, 1995; Hu *et al.*, 2006). An odds ratio (OR) with robust standard errors (Wooldridge, 2010) was then calculated for each predictive variable using ‘heteroscedasticity and autocorrelation consistent’ estimators implemented in the *sandwich* package (Zeileis, 2004; 2006). The relative contribution of each factor included in the respective model was determined using both univariate and unique predictive power (pseudo-R^2), whereas factor-level contribution and direction were interpreted through ORs.

Table 2. Socio-economic and experiential factors associated with the leopard skin trade. Factors are described as predictors of possession, acquisition or desire for authentic leopard skins and satisfaction with *faux* leopard skin alternatives in the pre-FFL (n = 8,600; 2013–2018) and post-FFL follow-up questionnaires (n = 2,300; 2013–2015/2018–2019). RSA = Republic of South Africa.

Parameter	**Description**	**Factor type**
Leopard skin possession	Respondents who possess authentic leopard skins at the time of the FFL-questionnaire	Two categories: Yes; No
Leopard skin acquisition	Respondents who acquired authentic leopard skins between the FFL and follow-up questionnaires	Two categories: Yes; No
Leopard skin desirability	Respondents who expressed a desire for authentic leopard skins in each questionnaire after originally receiving *faux* skin alternatives	Two categories: Yes; No
Age class	Age class (per 10-years) of respondents at the time of each questionnaire	Eight categories: 11–20; 21–30; 31–40; 41–50; 51–60; 61–70; 71–80; 81–90
Formal education level	Respondent highest level of formal education (schooling) at the time of each questionnaire	Four categories: None; Primary; Secondary; Tertiary
Employment status	Employment status of respondents at the time of each questionnaire (throughout that year)	Three categories: None; Temporary; Permanent
Leopard population status	Respondent opinion of RSA leopard population status of the at the time of each questionnaire	Four categories: Uncertain; Increasing, Stable; Decreasing
Government intervention	Respondent opinion on RSA government protection of leopards at the time of each questionnaire	Two categories: Yes; No
Legality and permitting	Respondent opinion on the legality of authentic leopard skin possession without a permit at the time of each questionnaire	Three categories: Uncertain; Yes; No
Knowledge of conviction	Respondent knowledge of someone convicted for authentic leopard skin possession without a permit at the time of each questionnaire	Two categories: Yes; No
Will wear *faux* skin	Respondent commitment to wearing *faux* skin alternative at the time of each questionnaire	Two categories: Yes; No
Still possesses *faux* skin	Respondent claims to still possess *faux* skin alternative at the time of the follow-up questionnaire	Two categories: Yes; No
Using *faux* skin	Respondent claims to be using their *faux* skin alternative at the time of the follow-up questionnaire	Two categories: Yes; No
Faux skin damaged	Respondent claims noticeable damage to *faux* alternative at the time of the follow-up questionnaire	Two categories: Yes; No
Faux skin judgement	Respondent feels that they are ‘judged’ or ‘looked down on’ for wearing their *faux* skin alternative at the time of the follow-up questionnaire	Two categories: Yes; No
Faux skin satisfaction	Respondent overall satisfaction with *faux* skin alternative at the time of the follow-up questionnaire	Five categories: Very unhappy; Unhappy; Indifferent; Happy; Very Happy

To test the relative success of the FFL intervention, it was necessary to establish trends between authentic leopard skin possession, subsequent acquisition, and desirability among *faux* skin recipients pre- and post-intervention. Using a subset of the pre-FFL questionnaire responses (n = 6,300; all pre-FFL questionnaire responses [2013–2018] less the subset used in the follow-up questionnaires [2013–2015]), the best-fitting authentic leopard skin possession model was validated by estimating the number of authentic skins possessed (random training subset = 5,000) in a known dataset (random test subset = 1,300). This validated model was then used to predict the number of authentic leopard skins in possession pre-FFL (n = 2,300; 2013–2015) and the number of authentic leopard skins acquired post-FFL (n = 2,300; 2018–2019).

These predicted values were compared to their respective observed (known) frequencies through univariate χ^2-tests of independence. Authentic skin desirability was similarly assessed in the pre- and post-FFL questionnaires, using the best-fitting and validated model for pre-FFL desirability. The relative effect of the FFL intervention could thus be interpreted through significant deviations from these predicted trends.

2.4. Results

2.4.1. Respondent characteristics

Pre-FFL respondents (n = 8,600) were all male between 11 and 83 years of age (Table 3). The majority had secondary education (60%), were unemployed (57%), and were uncertain of both the South African leopard population status (51%) and the legality of unpermitted authentic leopard skin possession (68%) but believed that the government should do something to protect leopards (88%). Few respondents (16%) knew of anyone who had been convicted for possession of authentic leopard skin, and almost all were willing to wear *faux* skin alternatives to Shembe gatherings (93%).

Post-FFL follow-up respondents who had received a *faux* skin (n = 2,300) were a representative subset of the pre-FFL questionnaire respondents (Table 4) with no significant difference in the proportional representation of age classes between questionnaires ($\chi^2_6 = 1.971$; $P = 0.922$). The majority had secondary-level formal education (60%), which was slightly higher (2% increase in tertiary education) than that of the pre-FFL respondents ($\chi^2_3 = 7.804$; $P = 0.05$). Although the majority of respondents were still unemployed (52% versus 59%), the proportion of unemployed respondents was slightly lower than in the pre-FFL questionnaire ($\chi^2_1 = 21.4$; $P < 0.001$).

Table 3. Description of pre-FFL questionnaire respondent characteristics. Shown are the socio-economic and experiential factors included in the pre-FFL questionnaire (*n* = 8,600; 2013–2018). For full parameter descriptions, see Table 2.

Parameter	Level	Count (proportion)
Leopard skin	Possession	1,782 (21%)
	Desirability	3,014 (35%)
Age class	11–20	747 (9%)
	21–30	1,919 (22%)
	31–40	2,183 (25%)
	41–50	1,532 (18%)
	51–60	1,393 (16%)
	61–70	567 (7%)
	71–80	259 (3%)
Formal education level	None	1,525 (18%)
	Primary	1,628 (19%)
	Secondary	5,190 (60%)
	Tertiary	257 (3%)
Employment status	None	4,878 (57%)
	Temporary	1,709 (20%)
	Permanent	2,013 (23%)
Leopard population status	Uncertain	4,414 (51%)
	Increasing	745 (9%)
	Stable	1,362(16%)
	Decreasing	2,079 (24%)
Government intervention	Yes	7,532 (88%)
Legality and permitting	Uncertain	5,807 (68%)
	Yes	1,555 (18%)
	No	1,238 (14%)
Knowledge of conviction	Yes	1,351 (16%)
Will wear *faux* skin	Yes	8,014 (93%)

Knowledge about South African leopard population status also differed between questionnaires (χ^2_3 = 544.3; *P* <0.0001) with a lower proportion (54% versus 27%) of post-FFL respondents uncertain (χ^2_1 = 353; *P* <0.001) and a higher proportion (17% versus 48%) believing that the population was declining (χ^2_1 = 484; *P* <0.001) compared to the pre-FFL questionnaire. Both pre- and post-FFL respondents (87%) believed that the South African government should protect leopards, with no significant difference between questionnaires (χ^2_1 = 0.23; *P* = 0.632). The proportion of respondents who believed it was legal to possess an authentic leopard skin without a permit differed significantly between questionnaires (χ^2_2 = 163.6; P <0.0001), with fewer considering it legal (19% versus 15%) or being uncertain (67% versus 51%) as to its legality (χ^2_1 = 11.48, P <0.001 and χ^2_1 = 122, P <0.001, respectively) in the post-FFL compared to the pre-FFL questionnaire. There was also a significantly greater proportion of respondents (17% versus 23%) in the post-FFL questionnaire who reported knowing someone who had been convicted for possession of an authentic leopard skin without a permit from the statutory authorities (χ^2_1 = 27.46; P <0.001) but no significant change in the proportion of respondents (92% versus 93%) who proclaimed willingness to wear *faux* skins (χ^2_1 = 0.32; P = 0.572).

Furthermore, 98% of respondents still possessed their *faux* skins three years after receiving them, with 94% claiming to have made use of these skins during this time. Only 22 respondents (<1%) reported any noticeable damage, and 108 (<5%) felt ‘looked down on’ for wearing *faux* rather than authentic leopard skins. Most respondents (95%) claimed to be satisfied with their *faux* leopard skin.

Table 4. Descriptive statistics comparing socio-economic and experiential factors associated with leopard skin trade. Factors included in predictive modelling of authentic leopard skin possession and desirability in the pre-FFL questionnaire subset (*n* = 2,300; 2013–2015) and post-FFL follow-up questionnaire (*n* = 2,300; 2018–2019), where individuals were repeat interviewed three years after receiving a *faux* skin. For full parameter descriptions, see Table 2.

Parameter	**Level**	**Pre-FFL**	**Post-FFL**	χ^2_{df}	**P-value**
Leopard skin	Possession	496 (22%)	765 (33%)	78.50_1	<0.001***
	Acquisition	-	343 (15%)	33.68_1	<0.001***
	Desirability	911 (40%)	630 (27%)	76.50_1	<0.001***
Age class	11–20	62 (3%)	75 (3%)	1.08_1	0.298^{ns}
	21–30	444 (19%)	442 (19%)	0.00_1	0.970^{ns}
	31–40	567 (25%)	565 (25%)	0.00_1	0.973^{ns}
	41–50	451 (20%)	446 (19%)	0.02_1	0.882^{ns}
	51–60	406 (18%)	403 (18%)	0.01_1	0.938^{ns}
	61–70	278 (12%)	258 (11%)	0.76_1	0.383^{ns}
	71–80	92 (4%)	89 (4%)	0.02_1	0.879^{ns}
	81–90	-	22 (1%)	-	-
Formal education level	None	482 (21%)	482 (21%)	0.00_1	0.971^{ns}
	Primary	416 (18%)	405 (18%)	0.15_1	0.700^{ns}
	Secondary	1,328 (58%)	1,302 (57%)	0.56_1	0.456^{ns}
	Tertiary	74 (3%)	111 (5%)	7.30_1	0.007**
Employment status	None	1,354 (59%)	1,197 (52%)	21.40_1	<0.001***
	Temporary	380 (17%)	514 (22%)	24.60_1	<0.001***
	Permanent	566 (25%)	589 (26%)	0.560_1	0.454^{ns}
Leopard population status	Uncertain	1,243 (54%)	617 (27%)	3530_1	<0.001***
	Increasing	233 (10%)	187 (8%)	5.31_1	0.021*
	Stable	427 (19%)	399 (17%)	1.08_1	0.300^{ns}
	Decreasing	397 (17%)	1,097 (48%)	484_1	<0.001***
Government intervention	Yes	1,990 (87%)	2,002 (87%)	0.23_1	0.632^{ns}
Legality and permitting	Uncertain	1,150 (67%)	1,181 (51%)	122_1	<0.001***
	Yes	431 (19%)	344 (15%)	11.48_1	<0.001***
	No	319 (14%)	775 (34%)	248.3_1	<0.001***
Knowledge of conviction	Yes	387 (17%)	530 (23%)	27.46_1	<0.001***
Will wear *faux* skin	Yes	2,126 (92%)	2,137 (93%)	0.32_1	0.572^{ns}
Still possesses *faux* skin	Yes	-	2,258 (98%)	-	-
Using *faux* skin	Yes	-	2,176 (94%)	-	-
faux skin damaged	Yes	-	22 (1%)	-	-
faux skin judgement	Yes	-	108 (5%)	-	-
faux skin satisfaction	Yes	-	2,183 (95%)	-	-

Significance (^{ns} = non-significant; $^{\cdot}$P ≤ 0.10; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001)

2.4.2. Pre-intervention authentic leopard skin possession

The pre-FFL questionnaire (*n* = 8,600) indicated that 1,782 respondents (21%) possessed authentic leopard skins (Table 3). After model ranking and selection, authentic skin possession among Shembe respondents was best explained (Nagelkerke pseudo $R^2 = 0.82$) by a model including all factors (Table 5). The model presented a good fit (H-L test: $z_8 = 3.637$; $P = 0.888$) and 96% accuracy in classifying test data (threshold = 0.80; area under the curve [AUC] = 0.97). Respondents with permanent or temporary employment had 91- and 50-times higher respective odds of possessing authentic leopard skins than those who were unemployed (Table 6). Those who believed that it is legal to possess an authentic leopard skin without a permit and that the South African leopard population is increasing had 21- and 9-times higher odds, respectively, of possessing an authentic leopard skin than those who were uncertain in both cases. Increasing age class after 21–30 years was associated with an increased likelihood of possessing an authentic leopard skin, whereas believing that South African leopard populations are decreasing, knowing someone who has been convicted for possessing of an authentic leopard skin without a permit, having tertiary education, and believing that the South African government should do something to protect leopards were associated with a reduction in the likelihood of possessing an authentic leopard skin. Employment status exhibited the strongest univariate predictive power (55%), with its unique explanatory power (16%) close to that of all other factors combined: government intervention (40%, 8%); legality and permitting (30%, 6%); leopard population status (19%, 2%); age class (13%, 2%); level of formal education (2%, 0.4%); and knowledge of conviction (0.4%, 0.1%).

Table 5. Pre-intervention authentic leopard skin possession model selection. Selection of the best logistic regression models explaining Shembe follower authentic leopard skin possession pre-FFL intervention (entire pre-FFL questionnaire: *n* = 8,600; 2013–2018; dependant variable: no = 0, yes = 1). Only additive effects with no possible interactions were tested, and the best model was selected by minimising the Akaike information criterion (AIC) score. K = number of parameters, LL = Log Likelihood, AIC_{Δ} = delta AIC, AIC_{Wt} = AIC weight and $\text{AIC}_{\text{Cum.Wt}}$ = accumulative AIC weight. Emp = Employment status, LPrmt = Legality and permitting, LPStat = Leopard population status, Age = Age class, Edu = Formal education level, KnwCon = Knowledge of conviction and SAGovDo = Government intervention. For full parameter descriptions, see Table 2.

Rank	**Parameters**	**K**	***df***	**LL**	**Deviance**	**AIC**	$\textbf{AIC}_{\Delta}$	$\textbf{AIC}_{\textbf{Wt}}$	$\textbf{AIC}_{\textbf{Cum.Wt}}$
-	*Null*	-	1	-1975.47	3950.94	3952.94	2675.06	0.00	0.00
1	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	7	19	-619.94	1239.88	1277.88	0.00	0.87	0.87
2	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	6	18	-622.87	1245.75	1281.75	3.87	0.13	1
3	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	6	16	-632.11	1264.23	1296.23	18.35	0.00	1
4	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	5	15	-635.25	1270.50	1300.50	22.63	0.00	1
5	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	6	16	-663.81	1327.61	1359.61	81.73	0.00	1
6	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	5	15	-667.37	1334.74	1364.74	86.86	0.00	1
7	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	6	13	-671.12	1342.23	1368.23	90.35	0.00	1
8	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	5	12	-673.91	1347.82	1371.82	93.94	0.00	1
9	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	5	13	-678.17	1356.33	1382.33	104.46	0.00	1
10	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	4	12	-682.09	1364.19	1388.19	110.31	0.00	1
…	…	…	…	…	…	…	…	…	…
100	Emp + LPrmt + LPStat + Age + Edu + KnwCon + SAGovDo	2	6	-1435.03	2870.06	2882.06	1604.19	0.00	1

Table 6. Pre-intervention authentic leopard skin possession model. Binary logistic regression model of socio-economic and experiential factors associated with an increased likelihood of a Shembe follower possessing an authentic leopard skin pre-FFL intervention (entire pre-FFL questionnaire: *n* = 8,600; 2013–2018; dependant variable: no = 0, yes = 1). For full parameter descriptions, see Table 2. The reference parameter is indicated in italics. Model diagnostic plots are in Appendix 2.

Parameter		**Explanatory power (%)**		**β**	**S.E.**	**Wald**	***df***	***P*-value**	**OR**	**95% CI for OR**	
		Univariate	Unique							Lower	Upper
Intercept		-	-	-1.11	0.43	-2.60	1	0.009**	0.33	0.13	0.84
Employment status (*None*)	Temporary	55	16	3.91	0.23	17.19	1	<0.001***	50.09	31.94	80.86
	Permanent			4.51	0.23	19.36	1	<0.001***	91.35	58.42	147.61
Government intervention (*No*)	Yes	40	8	-4.37	0.32	-13.85	1	<0.001***	0.01	0.01	0.02
Legality and permitting (*Uncertain*)	Yes	30	6	3.04	0.22	13.95	1	<0.001***	20.97	14.08	32.03
	No			-0.06	0.21	-0.30	1	0.763^{ns}	0.94	0.61	1.44
Leopard population status (*Uncertain*)	Increasing	19	2	2.20	0.26	8.51	1	<0.001***	8.99	5.12	16.34
	Stable			-0.14	0.18	-0.74	1	0.459^{ns}	0.87	0.59	1.29
	Decreasing			-0.40	0.20	-2.05	1	0.040*	0.67	0.46	0.97
Age class (*11–20*)	21–30	13	2	0.17	0.34	0.52	1	0.605^{ns}	1.19	0.58	2.55
	31–40			0.83	0.32	2.57	1	0.010*	2.29	1.14	4.79
	41–50			1.44	0.33	4.39	1	<0.001***	4.23	2.09	8.94
	51–60			1.88	0.34	5.49	1	<0.001***	6.58	3.18	14.29
	61–70			2.07	0.43	4.86	1	<0.001***	7.92	3.37	19.41
	71–80			2.64	0.43	6.07	1	<0.001***	13.97	5.52	37.28
Formal education level (*None*)	Primary	2	<1	0.06	0.24	0.26	1	0.796^{ns}	1.06	0.66	1.71
	Secondary			-0.25	0.20	-1.23	1	0.220^{ns}	0.78	0.53	1.16
	Tertiary			-2.55	0.36	-7.19	1	<0.001***	0.08	0.02	0.25
Knowledge of conviction (*No*)	Yes	4	<1	-0.52	0.21	-2.42	1	0.015*	0.60	0.39	0.91

Model	**AIC**	1278	**Concordance**	0.97	**Nagelkerke R^2**	0.82
	Sensitivity	83%	**Optimum threshold**	0.80	**Likelihood ratio test**	χ^2 = -1976; *df* = 18; *P* < 0.001***
	Specificity	97%	**Accuracy**	96%	**Global goodness of fit test**	*z* = 3.637; *df* = 8; *P* = 0.888^{ns}

Significance (^{ns} = non-significant; $^{\cdot}$P ≤ 0.10; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001)

2.4.3. Pre-intervention desire for an authentic leopard skin

The pre-FFL questionnaire (n = 8,600) indicated that 3,014 respondents (35%) expressed a desire for an authentic leopard skin after receiving their *faux* alternative (Table 3). After model ranking and selection, authentic leopard skin desirability among Shembe followers at the time of the FFL-intervention was best explained (Nagelkerke pseudo R^2 = 0.56) by a model that excluded (i.e., non-significant predictors) authentic skin possession, willingness to wear *faux* skins at gatherings, and formal education (Table 7). The model presented a good fit (H-L test: z_9 = 0.729; P = 0.682) and 81% accuracy in classifying test data (threshold = 0.50; AUC = 0.88). The desire for authentic leopard skins increased by age class after 21–30, with classes 51–60, 61–70, and 71–80 having 20-, 82-, and 41-times higher respective odds than 11–20 years (Table 8). The belief that the South African leopard population is increasing and that it is legal to possess an authentic leopard skin without a permit resulted in 7- and 3-times higher odds, respectively, of respondents reporting their desire for an authentic leopard skin, whereas believing that the South African leopard population is stable or decreasing, claiming to know of someone who has been convicted for possessing an authentic leopard skin without a permit, and believing that it is illegal to possess one without a permit were associated with a small reduction in the desire for an authentic leopard skin. Age class exhibited the strongest univariate predictive power (29%), followed by leopard population status (19%), knowledge of conviction (9%), and legality and permitting (8%). Legality and permitting had the highest unique explanatory power (31%), followed by leopard population status (21%), age class (18%), and knowledge of conviction (12%).

Table 7. Pre-intervention authentic leopard skin desire model selection. Selection of the best logistic regression models explaining Shembe follower authentic leopard skin desire pre-FFL intervention (entire pre-FFL questionnaire: *n* = 8,600; 2013–2018; dependant variable: no = 0, yes = 1). Only additive effects with no possible interactions were tested, and the best model was selected by minimising the Akaike information criterion (AIC) score. K = number of parameters, LL = Log Likelihood, AIC_{Δ} = delta AIC, AIC_{Wt} = AIC weight and $AIC_{Cum.Wt}$ = accumulative AIC weight. Age = Age class, LPStat = Leopard population status, KnwCon = Knowledge of conviction, LPrmt = Legality and permitting, ASP = Authentic leopard skin possession, SAGovDo = Government intervention, WWear = Willing to wear *faux* skin and Edu = Formal education level. For full parameter descriptions, see Table 2.

Rank	**Parameters**	**K**	***df***	**LL**	**Deviance**	**AIC**	**AIC_{Δ}**	**AIC_{Wt}**	**$AIC_{Cum.Wt}$**
-	*Null*	-	1	-3342.36	6684.71	6686.71	2604.82	0.00	0.00
1	Age + LPStat + KnwCon + LPrmt	4	13	-2027.95	4055.89	4081.89	0.00	0.26	0.26
2	Age + LPStat + KnwCon + LPrmt + SAGovDo	5	14	-2027.50	4054.99	4082.99	1.10	0.15	0.41
3	Age + LPStat + KnwCon + LPrmt + WWear	5	14	-2027.62	4055.24	4083.24	1.35	0.13	0.54
4	Age + LPStat + KnwCon + LPrmt + ASP	5	14	-2027.95	4055.89	4083.89	2.00	0.10	0.64
5	Age + LPStat + KnwCon + LPrmt + Edu	5	16	-2026.18	4052.36	4084.36	2.47	0.08	0.72
6	Age + LPStat + KnwCon + LPrmt + SAGovDo + WWear	6	15	-2027.25	4054.50	4084.50	2.61	0.07	0.79
7	Age + LPStat + KnwCon + LPrmt + ASP + SAGovDo	6	15	-2027.36	4054.71	4084.71	2.82	0.06	0.85
8	Age + LPStat + KnwCon + LPrmt + WWear + Edu	6	17	-2025.37	4050.73	4084.73	2.84	0.06	0.91
9	Age + LPStat + KnwCon + LPrmt + ASP + WWear	6	15	-2027.61	4055.21	4085.21	3.32	0.05	0.96
10	Age + LPrmt + ASP + SAGovDo + WWear	5	17	-2025.76	4051.51	4085.51	3.62	0.04	1
…	…	…	…	…	…	…	…	…	…
100	Age + LPrmt + ASP + SAGovDo + WWear	5	12	-2602.34	5204.68	5228.68	1146.78	0.00	1

Table 8. Pre-intervention authentic leopard skin desire model. Binary logistic regression model of socio-economic and experiential factors associated with an increased likelihood of a Shembe follower expressing a desire for an authentic leopard skin pre-FFL intervention (entire pre-FFL questionnaire: $n = 8{,}600$; 2013–2018; dependant variable: no = 0, yes = 1). For full parameter descriptions, see Table 2. The reference parameter is indicated in italics. Model diagnostic plots are in Appendix 3.

Parameter		**Explanatory power (%)**		**β**	**S.E.**	**Wald**	***df***	***P*-value**	**OR**	**95% CI for OR**	
		Univariate	Unique							Lower	Upper
Intercept		-	-	-0.80	0.17	-4.80	1	<0.001***	0.45	0.33	0.61
Age class (*11–20*)	21–30	29	18	0.01	0.19	0.07	1	0.944^{ns}	1.01	0.71	1.45
	31–40			0.62	0.18	3.49	1	<0.001***	1.86	1.33	2.62
	41–50			1.68	0.18	9.21	1	<0.001***	5.37	3.81	7.65
	51–60			2.99	0.20	14.77	1	<0.001***	19.86	13.84	28.86
	61–70			4.41	0.28	15.69	1	<0.001***	82.07	49.85	138.39
	71–80			3.72	0.28	13.10	1	<0.001***	41.33	23.44	75.23
Leopard population status (*Uncertain*)	Increasing	19	21	1.99	0.18	11.13	1	<0.001***	7.33	5.31	10.27
	Stable			-0.85	0.11	-8.01	1	<0.001***	0.43	0.34	0.53
	Decreasing			-2.24	0.11	-21.01	1	<0.001***	0.11	0.08	0.13
Knowledge of conviction (*No*)	Yes	9	12	-2.89	0.16	-17.98	1	<0.001***	0.06	0.04	0.08
Legality and permitting (*Uncertain*)	Yes	8	31	1.01	0.10	10.31	1	<0.001***	2.75	2.25	3.38
	No			-1.26	0.13	-9.77	1	<0.001***	0.28	0.22	0.36
Leopard skin possession	-	-	-	-	-	-	-	-	-	-	-
Will wear *faux* skin	-	-	-	-	-	-	-	-	-	-	-
Formal education level	-	-	-	-	-	-	-	-	-	-	-

Model	**AIC**	4082	**Concordance**	0.87	**Nagelkerke R^2**	0.56
	Sensitivity	77%	**Optimum threshold**	0.50	**Likelihood ratio test**	$\chi^2 = -3342$; $df = 12$; $P < 0.001$***
	Specificity	82%	**Accuracy**	81%	**Global goodness of fit test**	$z = 0.729$; $df = 9$; $P = 0.682$

Significance (^{ns} = non-significant; $^{\cdot}P \leq 0.10$; $^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$)

2.4.4. Post-intervention authentic leopard skin acquisition

Post-FFL follow-up questionnaires (2018–2019) with a subset of respondents (n = 2,300) who received *faux* skins between 2013 and 2015 indicated that 343 (15%) had since acquired authentic leopard skins (Table 4). This represents a significantly smaller proportion of individuals than in the pre-FFL questionnaire ($\chi^2_1 = 33.68$; $P < 0.001$). After model ranking and selection, acquisition of an authentic leopard skin since the FFL-intervention was best explained (Nagelkerke pseudo $R^2 = 0.61$) by a model that excluded the highest level of formal education and age class (non-significant predictors; Table 9). The model presented a good fit (H-L test: $z_8 = 8.183$; $P = 0.969$) and 89% accuracy in classifying test data (threshold = 0.50; AUC = 0.88). Respondents who had improved their employment status (11% including 'none' to 'temporary' or 'permanent' and 'temporary' to 'permanent') since the FFL-intervention and those who were dissatisfied with their *faux* alternative (5%) had 80- and almost 13-times higher respective odds of having subsequently acquired authentic leopard skins compared to those who had lost or sustained the same level of employment and been satisfied with *faux* skins (Table 10). Already possessing (22%) or having previously expressed a desire for authentic skins (40%) both showed 2-times higher odds of subsequent authentic leopard skin acquisition. Respondents who had gained knowledge regarding the legality and permitting requirements for possession (20%) and better understood the status of the South African leopard population (30%) since receiving their *faux* skin were less likely to be in possession of an authentic leopard skin. Respondents whose employment status had improved had the strongest univariate predictive power (39%) and unique explanatory power (35%) for acquiring an authentic skin, which was more than that of all other factors combined: legality and permitting knowledge gained (13%, 4%); *faux* skin dissatisfaction (10%, 7%); knowledge of conviction gained (3%, <1%); knowledge of leopard population status gained (2%, <1%); authentic leopard skin desire (2%, 1%); and existing possession (<1%, <1%).

Table 9. Post-intervention authentic leopard skin acquisition model selection. Selection of the best logistic regression models explaining Shembe follower authentic leopard skin acquisition post-FFL intervention (post-FFL follow-up questionnaire: *n* = 2,300; 2018–2019; dependant variable: no = 0, yes = 1). Only additive effects with no possible interactions were tested, and the best model was selected by minimising the AIC score. K = number of parameters, LL = Log Likelihood, AIC_{Δ} = delta AIC, AIC_{Wt} = AIC weight and $AIC_{Cum.Wt}$ = accumulative AIC weight. GEmp = Gain in employment status, GLPrmt = Legality and permitting knowledge gained, FSatf = *faux* skin satisfaction, GKnwCon = Gain in knowledge of conviction, GLPStat = Leopard population status knowledge gained, ASD = Authentic leopard skin desirability, ASP = Authentic leopard skin possession, Age = Age class, and GEdu = Gain in formal education level. For full parameter descriptions, see Table 2.

Rank	**Parameters**	**K**	***df***	**L.L.**	**Deviance**	**AIC**	**AIC_{Δ}**	**AIC_{Wt}**	**$AIC_{Cum.Wt}$**
-	*Null*	-	1	-379.84	759.69	761.69	318.66	0.00	0.00
1	GEmp + GLPrmt + FSatf + GKnwCon + GLPStat + ASD + ASP	7	8	-213.52	427.03	443.03	0.00	0.40	0.40
2	GEmp + GLPrmt + FSatf + GKnwCon + GLPStat + ASD + ASP + GEdu	8	9	-213.19	426.37	444.37	1.34	0.20	0.60
3	GEmp + GLPrmt + FSatf + GLPStat + ASD + ASP	6	7	-216.05	432.10	446.10	3.07	0.09	0.69
4	GEmp + GLPrmt + FSatf + GKnwCon + GLPStat + ASD	6	7	-216.30	432.59	446.59	3.56	0.07	0.76
5	GEmp + GLPrmt + FSatf + GLPStat + ASD + ASP + GEdu	7	8	-215.49	430.98	446.98	3.95	0.06	0.82
6	GEmp + GLPrmt + FSatf + GKnwCon + GLPStat + ASD + ASP + Age	8	13	-210.52	421.04	447.04	4.01	0.05	0.87
7	GEmp + GLPrmt + FSatf + GKnwCon + ASD + ASP	6	7	-216.66	433.32	447.32	4.29	0.05	0.92
8	GEmp + GLPrmt + FSatf + GKnwCon + GLPStat + ASD + GEdu	7	8	-215.92	431.83	447.83	4.80	0.04	0.96
9	GEmp + GLPrmt + FSatf + GKnwCon + GLPStat + ASD + ASP + Age + GEdu	9	14	-210.22	420.44	448.44	5.41	0.03	0.99
10	GEmp + GLPrmt + FSatf + GKnwCon + ASD + ASP + GEdu	7	8	-216.31	432.62	448.62	5.59	0.02	1
…	…	…	…	…	…	…	…	…	…
100	GEmp + FSatf + GLPStat + ASP + Age	5	10	-231.73	463.46	483.46	40.43	0.00	1

Table 10. Post-intervention authentic leopard skin acquisition model. Binary logistic regression model of socio-economic and factors associated with an increased likelihood of a Shembe follower acquiring an authentic leopard skin post-FFL intervention (post-FFL follow-up questionnaire: *n* = 2,300; 2013–2018; dependant variable: no = 0, yes = 1). For full parameter descriptions, see Table 2. The reference parameter is indicated in italics. Model diagnostic plots are in Appendix 4.

Parameter		**Explanatory power (%)**		**β**	**S.E.**	**Wald**	***df***	***P*-value**	**OR**	**95% CI for OR**	
		Univariate	Unique							Lower	Upper
Intercept		-	-	-2.83	1.02	-2.77	1	0.006**	0.06	0.01	0.25
Employment status gained (*No*)	Yes	39	35	4.38	0.43	10.08	1	<0.001***	79.48	36.54	198.76
Legality and permitting knowledge gained (No)	Yes	13	4	-2.40	0.51	-4.70	1	<0.001***	0.09	0.03	0.24
Faux skin satisfaction (*Yes*)	No	10	7	2.52	0.41	6.21	1	<0.001***	12.47	5.87	29.42
Knowledge of conviction gained (*No*)	Yes	3	<1	1.59	0.99	1.61	1	0.108^{ns}	4.92	1.20	29.60
Leopard population status knowledge gained (*No*)	Yes	2	<1	-0.70	0.27	-2.57	1	0.010*	0.50	0.28	0.86
Leopard skin desire (*No*)	Yes	2	1	0.81	0.25	3.27	1	0.001**	2.24	1.35	3.77
Leopard skin possession (No)	Yes	<1	<1	0.68	0.26	2.61	1	0.009**	1.98	1.12	3.48
Age class	-	-	-	-	-	-	-	-	-	-	-
Formal education level gained	-	-	-	-	-	-	-	-	-	-	-

Model	**AIC**	443	**Concordance**	0.87	**Nagelkerke R^2**	0.61
	Sensitivity	75%	**Optimum threshold**	0.50	**Likelihood ratio test**	$\chi^2 = -380$; *df* = 7; *P* < 0.001***
	Specificity	89%	**Accuracy**	89%	**Global goodness of fit test**	*z* = 8.183; *df* = 8; *P* = 0.969

Significance (^{ns} = non-significant; $^{\cdot}P \leq 0.10$; $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$)

2.4.5. *Post-intervention desire for an authentic leopard skin*

Post-FFL follow-up questionnaires indicated that 281 respondents (13%) no longer expressed a desire for authentic leopard skins (Table 4). This represents a significant reduction in the proportion of respondents who expressed a desire for an authentic leopard skin, from the pre-FFL to the post-FFL follow-up questionnaire ($\chi^2_1 = 76.5$; $P < 0.001$). After model ranking and selection, desire for authentic leopard skins among Shembe respondents three years since receiving their *faux* skin was best explained (Nagelkerke pseudo $R^2 = 0.46$) by a model including all factors (Table 11). The model presented a good fit (H-L test: $z_9 = 0.729$; $P = 0.682$) and 73% accuracy in classifying test data (threshold = 0.50; AUC = 0.82). Respondents who believed that the leopard population in South Africa was increasing, who expressed dissatisfaction with their *faux* alternative, and were 71–80 years of age, had 2-, 24-, and 19-times higher respective odds of still desiring an authentic leopard skin compared to those who were uncertain of leopard population status, satisfied with *faux* skins, and of the youngest age class (Table 12). Believing that the leopard population status was stable or decreasing, knowing that it is illegal to possess an authentic leopard skin without a permit, knowing someone who has been convicted, and already possessing an authentic leopard skin were all associated with a reduction in desiring an authentic leopard skin relative to those who were uncertain of population status or permitting requirements, had no knowledge of conviction, and did not possess authentic leopard skins. Leopard population status exhibited the strongest univariate predictive (27%) and unique explanatory power (28%), followed by: *faux* dissatisfaction (8%, 7%); age class (7%, 5%); legality and permitting (4%, 2%); knowledge of conviction (<1%, 1%), and authentic skin possession (<1%, 2%).

Table 11. Post-intervention authentic leopard skin desire model selection. Selection of the best logistic regression models explaining Shembe follower authentic leopard skin desire post-FFL intervention (post-FFL follow-up questionnaire: *n* = 2,300; 2018–2019; dependant variable: no = 0, yes = 1). Only additive effects with no possible interactions were tested, and the best model was selected by minimising the AIC score K = number of parameters, LL = Log Likelihood, AIC_{Δ} = delta AIC, AIC_{Wt} = AIC weight and $AIC_{Cum.Wt}$ = accumulative AIC weight. LPStat = Leopard population status, FSatf = *faux* skin satisfaction, Age = Age class, LPrmt = Legality and permitting, Edu = Formal education level, KnwCon = Knowledge of conviction and ASP = Authentic leopard skin possession. For full parameter descriptions, see Table 2.

Rank	**Parameters**	**K**	***df***	**L.L.**	**Deviance**	**AIC**	**AIC_{Δ}**	**AIC_{Wt}**	**$AIC_{Cum.Wt}$**
-	*Null*	-	1	-698.69	1397.39	1399.39	388.99	0.00	0.00
1	LPStat + FSatf + Age + LPrmt + Edu + KnwCon + ASP	7	19	-486.20	972.40	1010.40	0.00	0.69	0.69
2	LPStat + FSatf + Age + LPrmt + KnwCon + ASP	6	16	-490.25	980.50	1012.50	2.10	0.24	0.93
3	LPStat + FSatf + Age + LPrmt + Edu + ASP	6	18	-490.11	980.23	1016.23	5.83	0.04	0.97
4	LPStat + FSatf + Age + LPrmt + ASP	5	15	-493.52	987.04	1017.04	6.64	0.03	1
5	LPStat + FSatf + Age + Edu + KnwCon + ASP	6	17	-495.87	991.73	1025.73	15.33	0.00	1
6	LPStat + FSatf + Age + KnwCon + ASP	5	14	-499.07	998.15	1026.15	15.75	0.00	1
7	LPStat + FSatf + Age + ASP	4	13	-502.73	1005.45	1031.45	21.06	0.00	1
8	LPStat + FSatf + Age + LPrmt + Edu + KnwCon	6	18	-497.95	995.91	1031.91	21.51	0.00	1
9	LPStat + FSatf + Age + Edu + ASP	5	16	-500.07	1000.15	1032.15	21.75	0.00	1
10	LPStat + FSatf + Age + LPrmt + KnwCon	5	15	-501.30	1002.59	1032.59	22.20	0.00	1
…	…	…	…	…	…	…	…	…	…
100	+ FSatf + KnwCon + ASP	3	4	-662.95	1325.89	1333.89	323.50	0.00	1

Table 12. Post-intervention authentic leopard skin desire model. Binary logistic regression model of socio-economic and experiential factors associated with an increased likelihood of a Shembe follower expressing a desire for an authentic leopard skin post-FFL intervention (post-FFL follow-up questionnaire: *n* = 2,300; 2013–2018; dependant variable: no = 0, yes = 1). For full parameter descriptions, see Table 2. The reference parameter is indicated in italics. Model diagnostic plots are in Appendix 5.

Parameter		**Explanatory power (%)**		**β**	**S.E.**	**Wald**	***df***	***P*-value**	**OR**	**95% CI for OR**	
		Univariate	Unique							Lower	Upper
Intercept		-	-	1.38	0.41	3.35	1	<0.001***	3.99	1.57	10.27
Leopard population status	Increasing	27	28	0.89	0.33	2.70	1	0.007**	2.43	1.33	4.58
(*Uncertain*)	Stable			-1.01	0.22	-4.58	1	<0.001***	0.36	0.24	0.56
	Decreasing			-2.67	0.21	-12.81	1	<0.001***	0.07	0.05	0.10
Faux skin satisfaction (*Yes*)	No	8	7	3.18	0.48	6.58	1	<0.001***	24.00	10.72	59.64
Age class	21–30	7	5	0.29	0.39	0.75	1	0.456^{ns}	1.33	0.55	3.27
(*11–20*)	31–40			0.46	0.38	1.19	1	0.233^{ns}	1.58	0.65	3.85
	41–50			-0.32	0.38	-0.85	1	0.394^{ns}	0.72	0.29	1.78
	51–60			-0.10	0.39	-0.26	1	0.794^{ns}	0.90	0.36	2.26
	61–70			0.79	0.43	1.83	1	$0.067^{\cdot}$	2.21	0.84	5.86
	71–80			2.92	0.71	4.10	1	<0.001***	18.56	5.39	68.42
	81–90			-0.42	0.75	-0.56	1	0.575^{ns}	0.66	0.12	3.67
Legality and permitting	Yes	4	2	-0.01	0.23	-0.06	1	0.949^{ns}	0.99	0.59	1.65
(*Uncertain*)	No			-0.77	0.19	-4.15	1	<0.001***	0.46	0.32	0.66
Formal education level	Primary	1	1	0.31	0.25	1.21	1	0.225^{ns}	1.36	0.81	2.28
(*None*)	Secondary			-0.29	0.21	-1.34	1	0.182^{ns}	0.75	0.49	1.14
	Tertiary			-0.53	0.44	-1.21	1	0.225^{ns}	0.59	0.25	1.35
Knowledge of conviction (*No*)	Yes	<1	1	-0.54	0.19	-2.82	1	0.005**	0.58	0.39	0.85
Leopard skin possession (*No*)	Yes	<1	2	-1.04	0.20	-5.19	1	<0.001***	0.35	0.23	0.54

Model	**AIC**	1010	**Concordance**	0.81	**Nagelkerke R^2**	0.46
	Sensitivity	73%	**Optimum threshold**	0.50	**Likelihood ratio test**	$\chi^2 = -699$; *df* = 18; *P* < 0.001***
	Specificity	73%	**Accuracy**	73%	**Global goodness of fit test**	*z* = 0.729; *df* = 9; *P* = 0.682

Significance (^{ns} = non-significant; $^{\cdot}P \leq 0.10$; $^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$)

2.4.6. *Furs for Life intervention success*

Authentic leopard skin possession and desirability models (Table 13) were validated using pre-FFL questionnaire data (2015–2018; n_{training} = 5,000; n_{test} = 1,300), where known counts of authentic skin possession (235 skins) and desire (430 respondents) were accurately estimated as 248 skins (confidence interval [CI]: 234, 265) and 414 respondents (CI: 390, 437), respectively (χ^2_1 = 0.43, P = 0.512; χ^2_1 = 0.37, P = 0.542). The pre-FFL authentic skin possession prediction was 519 skins (CI: 495, 541), which did not differ significantly (χ^2_1 = 0.67; P = 0.414) from the known count of 496 skins (Table 4), whereas the post-FFL authentic skin acquisition known count was 343 skins, which was significantly lower (χ^2_1 =.04; P <0.0001) than the prediction of 467 skins (CI: 445, 491). Pre-FFL authentic leopard skin desirability was predicted for 851 respondents (CI: 819, 885), which was nearly significantly lower (χ^2_1 = 3.31; P = 0.069) than the known count of 911 respondents (Table 4), whereas the post-FFL authentic skin desirability known count was 621 respondents and the predicted count was 644 respondents (CI: 614, 674), which was not significantly different (χ^2_1 = 0.58; P = 0.448).

Table 13. Predictive modelling of FFL intervention success. Socio-economic and experiential factors used to determine (1) the expected number of authentic leopard skin in possession pre-intervention and (2) the expected number of authentic leopard skins acquired post-intervention, and the expected number of followers who claim a desire for authentic leopard skins (3) pre- and (4) post-intervention. For full parameter descriptions, see Table 2.

Model	**Step**	***n***	**Count**			**Comparison**	
			Known	Estimate	CI	χ^2_{df}	*P*-value
	Model (training)	5000	-	-	-	-	-
	Validation (test)	1300	235	248	234–265	0.43_1	0.512^{ns}
Possession[1]	*Pre-intervention*	2300	496	519	495–541	0.67_1	0.414^{ns}
Acquisition[2]	*Post-intervention*	2300	343	467	445–491	23.04_1	<0.001***
	Model (training)	5000	-	-	-	-	-
	Validation (test)	1300	430	414	390–437	0.37_1	0.542^{ns}
Desirability[3]	*Pre-intervention*	2300	911	851	819–885	3.31_1	$0.069^{\cdot}$
Desirability[4]	*Post-intervention*	2300	621	644	614–674	0.58_1	0.448^{ns}

Significance (^{ns} = non-significant; $^{\cdot}P \leq 0.10$; $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$)

2.5. Discussion

Successful intervention strategies require conservationists to have a holistic understanding of human behaviours and how these may influence the ecology of wildlife species. This interaction is crucial to the conservation and sustainable use of threatened populations, while also preserving the rich cultural identity these species have inspired (Manfredo & Dayer, 2004; Hazzah *et al.*, 2017). Longitudinal questionnaires with Shembe Church followers were used to understand the socio-economic and experiential factors related to authentic leopard skin possession and desirability before, and three years after, receiving a *faux* alternative. As part of the FFL programme, *faux* skin recipients were educated about the impact that demand for authentic skins has on extant leopard populations and legislation pertaining to the purchase and ownership of authentic skins. This chapter explored whether these interventions reduced both desirability and possession of authentic leopard skins, while improving perceptions of *faux* skin alternatives.

Through the distribution of over 22,000 *faux* skins, the FFL intervention programme has successfully contributed to a reduction in the acquisition of authentic leopard skins among *faux* skin recipients by 7% post-FFL (Table 4), representing significantly less acquisition than predicted (Table 13). Crucial to the longevity of interventions such as the FFL programme, most recipients (95%) were satisfied with their *faux amambatha* (Table 4), reporting that they still owned (98%) and had made use of it in the last three years (94%), with few reports of noticeable damage (<1%) or societal judgement for its use (<5%). A critical assessment of the relative success of such conservation intervention strategies is challenging, with many studies having neither the appropriate baseline and long-term monitoring data, nor the historical or political context required to substantiate a claim of success (de Vries, 2005; Brooks *et al.*, 2006; Waylen *et al.*, 2010; Cetas & Yasué, 2016). Given the considerable size of the Shembe Church, the logistical scale of widespread demand-reduction, and the cultural sensitivities at play, eliciting acceptance of *faux* alternatives in just three years represents early progress towards a successful long-term intervention. This study provides both a baseline and short-term longitudinal assessment of the FFL intervention, defining success not only quantitatively but also by the degree of cultural acceptance. Authentic leopard skin desirability among *faux* skin recipients decreased by 13% post-intervention (Table 4), as predicted (Table 13), suggesting that authentic skin acquisition is not strictly proportional to the desire for authentic skins.

The persistence of authentic skin desirability prompted further investigation into the factors related to authentic skin possession and acquisition post-intervention. Possession of authentic leopard skins among *faux* skin recipients before the FFL programme was primarily related to employment status and, to a lesser degree, to the limited knowledge or disregard for the illegality of unpermitted leopard skin possession, increasing age, and the belief that the South African leopard population is increasing (Table 6). In contrast, the subsequent acquisition of authentic leopard skins was mainly related to improved employment status (Table 10). Such clear economic predictors (employment status or change therein) emphasise the importance of both social prestige and age in the hierarchical structure of the Shembe Church, a classic indicator for most societal hierarchies where wealth and age are default symbols of respect (see 1.3.4; Tishken, 2006; Dunn & Searle, 2010; Cheng & Tracy, 2013). That age was such a strong predictor for possession before the FFL intervention but became nonsignificant in post-FFL authentic skin acquisition while employment persisted, is important. This suggests not only that age-related cultural inertia to *faux* skin acceptance is transient, given time to experience the alternative but, more ominously, that authentic skin value may not be innately cultural or religiously driven. It follows that any social prestige gained through possession relates to the money spent on an authentic skin rather than the inherent value of the skin itself as a symbol of Church hierarchy. By revealing these substantial economic drivers at play under demand for traditional use, these findings direct Panthera's future intervention strategies towards market-based behavioural change (e.g., creating a competitive market for high-value faux skins) in addition to appealing for Shembe leadership to denounce real leopard skin use and ongoing social engagement and conservation awareness programs. Identifying how economic factors relate to social status are pivotal to understanding the use of and demand for leopard skins among followers, and indeed any illicit use of wildlife products, as it likely limits the success, sustainability, and scalability of intervention strategies (de Young, 1993). While it is true that the traditional Zulu royalty protest this use by the Shembe Church, and there are ongoing tensions, the Church presents an already highly fragmented cultural hierarchy with a fundamental dilemma – the Church has modernised culturo-religious belief in the face of an oppressive colonial past. They cannot risk losing influence among their followers who identify as being culturally Zulu and yet devout followers of Shembe's Zionist Christianity. Moreover, it seems that while traditional authority is recognised, they hold little sway over regalia and its use. For instance, in one questionnaire (n = 8,600), we ask Shembe followers at various gatherings 'If Snoop Dogg – a well known Zionist celebrity, Jacob Zuma – the then President of South Africa and paramount Zulu Chieftan, Inkosi Goodwill Zwelethini – the Zulu King or the Prophet Vela Shembe – a direct descendant of Isiah and current leader of the largest of four Shembe factions) asked you not to wear authentic leopard skins, would you? (these questions are independent and randomised, so they do not make the direct comparison between any of these leaders). 'Yes' ranks as Vela Shembe (57%), Goodwill Zwelethini (22%), Snoop Dogg (11%) and Jacob Zuma (10%), which potentially indicates the underlying hierarchy for the Church and culture above that of national governance (despite Zuma's social ranks), which equates to that of celebrity influence. Following this, it is unlikely that traditional authorities were complicit in the growth of the illegal trade in leopard skins to supply Shembe-driven demand for cultural regalia as they would be indirectly undermining their cultural authority within Shembe communities as it grew. We cannot, of course, exclude inherent corruption along the culturo-political interface as many leaders in southern Africa straddle both cultural and political roles.

Respondents who expressed dissatisfaction with the *faux* product or had a desire for an authentic leopard skin were more likely to have acquired an authentic skin after receiving a *faux* alternative (Table 10), but these were few (<5%) and declined between the two questionnaires (Table 4). Interestingly, respondents who already possessed an authentic skin in addition to their *faux* alternative were more likely to acquire an additional authentic skin post-FFL intervention (Table 10). Although this may represent authentic skin replacement despite the *faux* alternative, it is more likely indicative of resale trade, individual preferential accessibility to leopard products, or an increased desire for authentic skins once experienced. Attempting to change values linked to financial release, trade incentives, and cultural inertia is challenging to any conservation intervention (Dickman & Hazzah, 2016; Nilsson *et al.*, 2016; Hazzah *et al.*, 2017). Improving conservation knowledge and awareness, however, are more susceptible to change (Nilsson *et al.*, 2016; Thomas *et al.*, 2019) and thus form an overarching goal for the FFL educational programme.

Authentic leopard skin desirability decreased among *faux* skin recipients post-intervention (Table 12). This decline was predicted (Table 13) and related primarily to improved knowledge of possession legality, permitting requirements, and leopard population status across age classes of those interviewed (Table 8 & Table 12). In accordance with social-psychological theory, respondents with higher tertiary education levels, greater knowledge about convictions for illegal possession, and a belief that leopard populations are in decline were less likely to have acquired an authentic leopard skin post-FFL intervention (Table 10; Vaske & Manfredo, 2012; Stern, 2018). The finding that most Shembe respondents (88%) were in support of government intervention to protect leopards (Table 3) may facilitate the further implementation of educational programmes. Although conservation awareness is unlikely to eliminate the desire for authentic leopard skins or any traditional use outright, given the entrenched value placed on authentic cultural and religious symbols of devotion or prestige (Beverland & Farrelly, 2010; Geertz, 2016; Pieterse, 2020), they are nonetheless fundamental to effecting individual behavioural change. Such change is pro- rather than retro-active, inspiring a societal sense of intrinsic value and transgenerational equity of wildlife that is vital to intervention sustainability.

It seems that employment gained and therefore income translate directly into the desire for and ultimately, the acquisition of real leopard skins, despite many of the potentially deterring factors considered (e.g., knowledge of legality and permitting, as well as leopard status, knowledge of convictions and years of formal education). This finding has substantial implications for the direction of future intervention strategies. Engagement on the levels of formal education, conservation awareness, and an appeal to the transgenerational morality of Shembe followers has reduced demand and acquisition of skins over these five years. Interventions at these levels are standard practice for many strategies aiming to address sustainable use (conservation or otherwise), are within the capacity of the NGO to implement for the foreseeable future and will likely be the least offensive and most effective way of changing behaviour over time. However, the strong barrier that restricted income affords to the purchase of leopards skins is very worrying. While the global COVID-19 pandemic has undoubtedly impacted the region, the Shembe following continues to grow and gain wealth, increasing their demand for real leopard skins and their capacity to purchase. Moreover, if unmitigated, the decline in local leopard populations, alongside an increase in regional enforcement of transnational trade and the growing number of Shembe followers, are likely to drive a rarity-feedback loop that will likely increase the social prestige of owing a real skin. This will increase demand, but will also widen the purchasing gap, potentially leading to direct sourcing by followers. Either way, it is clear that the most effective short-term strategy, following 1) direct engagement with Vela Shembe and his endorsement of the project, is likely to be an intervention of 2) economic rather than 3) social disruption. Following these principles, we are 1) continuing to foster our relationship with the upper echelons of the church to gain access to, endorsement of and enforcement by Shembe leadership, 2) developing a ‘heritage furs’ brand to strengthen the cultural identity and ownership of faux products, as well as the production of a limited series luxury furs to be sold at a higher value and thereby stimulate competitive demand, and 3) continue our social engagement and conservation awareness outreach work.

Intervention studies carry inherent biases and limitations that must be considered when interpreting results. Importantly, only Shembe followers who approached faux skin distributors were sampled. Nevertheless, their responses provide valuable insights into the likely proportion of possession and probable factors related to the desire for authentic leopard skins among all Shembe followers. In addition, most respondents reported a willingness to wear faux skin alternatives to gatherings (93%) and were satisfied with their amambatha (95%), with only 15% reporting acquisition of an authentic leopard skin in the three years since receiving their faux alternative. Results were also likely affected by possible self-report and social desirability biases in the interview process (i.e., the NGO Panthera provided the faux skins and also conducted these questionnaires in person), as well as the relatively limited time since the intervention (Sutherland *et al.*, 2019). Future research should address these issues in addition to identifying how these intervention strategies may benefit the many other 'at risk' species forming part of the complete Shembe ceremonial regalia. Such studies would also benefit from interviewing non-typical stakeholders (e.g., Shembe women, priests, skin traders, children in the Shembe Church and non-Shembe followers), to understand the innate motivations and ever-changing culture behind felid skin use and trade.

This study is among the first to describe leopard skin use as ceremonial regalia among followers of the Shembe Church **(**Figure 14), which is one of the largest open displays of illegal wildlife exploitation for traditional use in southern Africa. It is the first to try and understand why followers continue to use leopard skin derivatives even after knowing the illegality and conservation implications of their actions. This novel examination of openly unregulated illegal use of wildlife on cultural grounds contributes not only to the sparse literature on longitudinal conservation intervention assessments but is among the most extensive in this field. The offtake of leopard to support the Shembe demand for skins is hypothesized to exceed the capacity of the South African leopard population (Swanepoel *et al.*, 2011). The transnational trade to supply this demand is likely placing considerable pressure on leopard populations throughout the southern African region (see Chapter 3). Despite established TOPS and CITES regulations affording extensive legislative protection to leopards, effective local and regional enforcement is complex, hindered by the scale of use and the culturo-political landscape at play. The results presented in this chapter show that *faux* alternatives are acceptable to followers, significantly contributing to reductions in authentic leopard skin acquisition and desirability through the FFL intervention. Results also highlight the lack of knowledge regarding the required permitting for leopard skin possession and trade among Shembe followers, as well as cognisance of the link between their personal demand and the threat to leopard populations (see 5.2.3). By working to address these disparities, the FFL education and awareness programme has shown tenable reductions in acquisition behaviour. A lack of comparable conservation interventions and studies thereof globally makes contextualising the FFL success challenging but highlights the importance of such retrospective assessment and continued monitoring as part of intervention strategies.

In the face of a rapidly expanding Church, a holistic intervention approach to curbing these effects on leopard populations will require increased enforcement in addition to the provisioning of alternatives and increased conservation awareness. Traditional use as a global threat to wildlife remains largely undocumented (see 1.4.3), unregulated (see 1.4.4), and untraced (see 1.4.5); the socio-political sensitivities surrounding cultural identity and the illegality of much of this use are likely important impediments to this objective assessment. This chapter highlights the consideration, extensive resources, and time required to understand and begin mitigating such threats that exist globally.

CHAPTER 3

SPOTS OF BOTHER: TRACING THE GEOGRAPHIC ORIGINS OF ILLEGALLY TRADED LEOPARD SKINS FOR TRADITIONAL USE

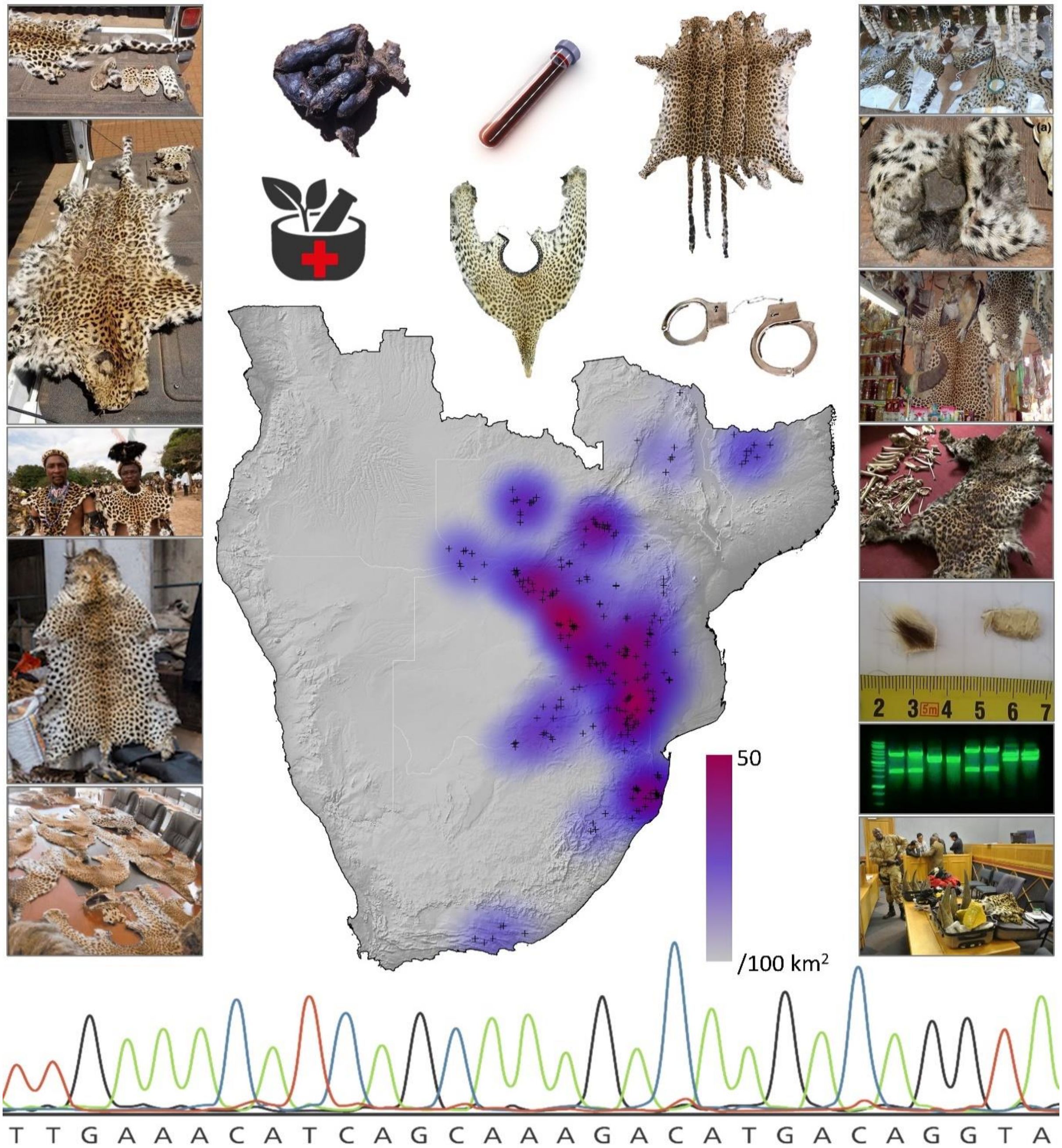


Figure 16. Geographic assignment of illegally traded leopard skins for traditional use. In South Africa, leopard derivatives are traded illegally among traditional healers and burgeoning culturo-religious groups. This undocumented, unregulated, and untraced illegal wildlife trade is certainly putting pressure on wild leopard populations across southern Africa. Images are used with permission or under the creative commons license.

3.1. Abstract

The illegal wildlife trade is a direct threat to the survival of many species. Monitoring such trade would be vastly improved if the geographic origins of illegally traded wildlife products were reliably determined and the areas needing targeted protection identified. Using DNA-based assignment tests (i.e., samples assigned to geographic locations), I investigated aspects of the illegal trade in leopard products for traditional use in South Africa. I created spatially-explicit allele frequencies from a genetic reference database of 1,896 leopards distributed across southern Africa to infer the geographic origins of DNA samples from 303 leopard skins across three sources of illegal trade (i.e., from a police raid, Shembe Church followers, and traders in *muti* markets). Validation and sensitivity analyses for samples of known geographic origin together with the assignment of seized skin samples demonstrated confident spatial sourcing of leopards across southern Africa. Results suggest that the illegal leopard skin trade for traditional use in South Africa is transnational and syndicated, with major poaching 'hotspots' identified in southwestern Zimbabwe, along the eastern borders of South Africa, and in southern Mozambique, many of which are from a single trade source. Leopard samples from *muti* markets have a more localised genetic footprint compared to those obtained at Shembe gatherings and from the police raid samples, both of which are transnational. Results also revealed a significant bias toward male leopards from all three sample sources with some duplication of individuals in *muti* market samples and non-leopard species being sold as leopard product. The techniques developed in this chapter can be used to identify the origins of seized illegal wildlife products and monitor trade routes across the region, redirecting resource-limited antipoaching efforts towards targeted intervention and leveraging transnational policy to increase enforcement.

3.2. Introduction

Illegal trade in wildlife and its derivatives is a transnational and organised environmental crime (see 1.2.4) which operates at multiple socio-economic scales and directly threatens the survival of many species (Baker *et al.*, 1996; Robinson & Bennet, 1999). As the fourth largest international criminal activity after narcotics, arms, and human trafficking (UNODC, 2010), annual profits from IWT worldwide are valued between U$7–23 billion (Nellemann *et al.*, 2014; TRAFFIC, 2016; Scheffers *et al.*, 2019). Trafficking in wildlife and its products can be highly lucrative under relatively low levels of associated risk for poachers, merchants, and clientele (see 5.2). This is particularly true in less developed countries, where corruptibility of local governance and inadequate enforcement of environmental policies leads to poor conviction rates and low judicial priority, further exacerbating poaching pressure and criminal syndication (Smith *et al.*, 2003; Sunderlin *et al.*, 2005; Warchol *et al.*, 2007; ‘t Sas-Rolfes *et al.*, 2019).

Wildlife trade generally follows a rarity-value feedback model or anthropogenic Allee effect (see 5.2.1), whereby increasing rarity drives both higher demand and higher prices for a species (Courchamp *et al.*, 2006; Harris *et al.*, 2017). Recent increases in the frequency of seizures of large consignments of wildlife contraband, including coral, snake skins, rosewood, conch shells, ivory, abalone, and other wildlife products (Clark, 2008; TRAFFIC, 2016; Scheffers *et al.*, 2019), suggest escalating natural resource depletion on a global scale. Such large-scale offtake severely damages ecosystems, disrupting trophic interactions and compounding the adverse effects of climate change (Lewis *et al.*, 2009; Ripple *et al.*, 2014). For example, the unsustainable poaching of large mammals has been shown to have severe downstream effects on targeted populations, altering behaviour, group composition, sex ratios, physiology, and population dynamics (Sukumar *et al.*, 1998; Gobush & Wasser, 2009). Together these impacts may ultimately lead to local inbreeding (see Chapter 4 [Naude *et al.*, 2020]; Loveridge *et al.*, 2007a; Gobush *et al.*, 2008), range restrictions or fragmentation, and even local extirpation (Karanth *et al.*, 2010; Liberg *et al.*, 2011).

Large wild felid populations are particularly susceptible to poaching as their large home-ranges and high resource requirements bring them into frequent contact with humans and their livestock (Schipper *et al.*, 2008), while their body parts are in demand across a wide range of illegal markets for both their cultural and commercial purposes (see 1.2). This is true for several felid species in southern

Africa but particularly so for leopards (Athreya *et al.*, 2010; Balme *et al.*, 2010a) as their body parts are widely used in traditional practices (Warchol *et al.*, 2003; Alves *et al.*, 2013; Whiting *et al.*, 2013; Williams & Whiting, 2016). Traditional use is a significant but generally understated element of the IWT, remaining largely undocumented, unregulated, and untraced on a global scale due to monitoring complexity and its culturo-political sensitivities (Dickman *et al.*, 2015). Across southern Africa, there exists a substantial demand for leopard skins, used as ceremonial regalia by local traditional royalty (e.g., the Zulu [Harries *et al.*, 1993], Barotse [van Binsbergen, 1987], and Swazi kingdoms [Breytenbach, 1972]) and, more recently, the burgeoning Nazareth Baptist 'Shembe' Church (Kumalo & Mujinga, 2017). These and other leopard derivatives (e.g., bones, claws, teeth, and fat) are also used in traditional medicine or *muti* (Cook, 2009) as well as spiritual divination or enchantment (see 1.3.3; Thobane, 2015; Williams & Whiting, 2016).

Under the South African NEMBA (Government Gazette, Act No. 10 of 2004), it is illegal to possess or trade leopard derivatives without authorisation from either national (TOPS) or international (CITES, Appendix I) authorities. However, enforcement may be fettered by cultural, religious, and even political sensitivities (Dickman *et al.*, 2015). While large trade seizures have occurred (as in the case of Ngubane, M.M. versus S, where a repeat offender was caught in possession of at least 150 leopard products), the majority are small, and these cases are often dismissed due to a poor warrant procedure (as in the case above), lack of evidence, or poor chain of custody (Warchol & Johnson, 2009; Wellsmith, 2011; Anderson & Jooste, 2014). As customs authorities generally assume wildlife seizures represent only about 10% of smuggled contraband (Wasser *et al.*, 2004), actual leopard poaching instances may be much higher.

Systematic longitudinal leopard population surveys in key PAs throughout South African leopard range has revealed declines of 7–10% across reserves (M. Rogan, unpublished data). Furthermore, informal interviews with traders in traditional wildlife markets and at Shembe gatherings in South Africa suggest that leopard material is becoming increasingly scarce (N. Mbongwa & T. Dickerson, unpublished data), compelling traders to source material from surrounding range states (e.g., Zimbabwe, Zambia, Mozambique, and Malawi). Using mitochondrial sequencing and microsatellite genotyping, I aimed to reveal the extent of the area impacted by the illegal leopard skin trade in South Africa. I compared the distribution of genetic variation in leopard populations from across southern Africa with leopard skin samples from three sources: (1) samples seized by law enforcement agencies during a raid in KwaZulu Natal in 2016 (from Ngubane, M.M. versus S, hereafter ‘Raid’); (2) samples opportunistically collected at Shembe gatherings from 2015–2019 (hereafter ‘Shembe’); and (3) samples collected at traditional *muti* markets during the same period (hereafter ‘*Muti*’). As traders selling skins destined for ceremonial regalia (e.g., Raid and Shembe) are more likely to sell full or half-pelts (a half-pelt is generally required to produce a shoulder cape) compared to *muti* traders, who might purvey a range of derivatives from full pelts to small patches of skin, fat, claws, and bones from an individual leopard, I predicted that a higher proportion of Raid and Shembe samples would comprise unique individuals compared to *Muti* samples.

Male leopards are natal dispersers and have larger home ranges than females bringing them into increased contact and conflict with people and livestock (see 1.2). I predicted that retaliatory killing for livestock losses combined with indiscriminate snaring both adjacent to and outside of PAs (Balme *et al.*, 2010a; Everatt *et al.*, 2019b) would result in a male-biased sex ratio evident in all three trade datasets. Finally, with the leopard population estimated at only 1,688–6,979 individuals (Swanepoel *et al.*, 2011), illegal demand in South Africa likely exceeds local supply, a concern corroborated by informal interviews with traders at gatherings and markets (N. Mbongwa & T. Dickerson, unpublished data). As ceremonial regalia generally requires more material than *muti,* whole skin traders may need to source leopard products from further afield. Thus, I predicted that *Muti* samples would have a smaller genetic footprint than Raid or Shembe samples and that the origins of Raid and Shembe samples would be transnational compared to *Muti* which would be localised within South Africa. I discuss my findings in the context of regional trade dynamics and anti-poaching efforts, as well as the broader implications of transnational wildlife crime on enforcement and political will in the conservation of leopards across southern Africa.

3.3. Methods

3.3.1. Sample collection

Reference samples (*n* = 1,896) were collected across the subregion by an extensive network of experienced collaborators, including research institutions, statutory authorities, National Parks staff, eco-tourism operators, taxidermists, and citizen scientists. Most of the reference samples (*n* = 1,434) were derived from faeces (Table 14) followed by tissue (*n* = 344) and blood (*n* = 118). Blood samples were stored in BD Vacutainer® EDTA tubes at 4 °C, while tissue and faecal samples were dry-stored on silica beads at -20 °C. Geographic locations were recorded using a global positioning satellite (GPS) unit for all samples collected from 2015–2019 (Figure 17).

Illegal trade samples were derived from three sources: 1) clippings from tailored leopard skins (Raid samples, *n* = 144) seized from a single trading agent in Durban, 2016, allegedly destined for Shembe markets; 2) clippings of leopard capes (Shembe samples, *n* = 85) opportunistically collected from consenting followers at large Shembe gatherings from 2015–2019; and 3) leopard tissue sold at various traditional wildlife markets (*Muti* samples, *n* = 74) across five provinces in South Africa during the same period (Figure 17). Samples were collected under sterile technique and dry-stored on silica beads at -20 °C. Where available, supporting meta-data were recorded for each sample, including seizure date, time and location, cost, and potential geographic origin proffered by the accused, follower, or trader. Collection of these samples was authorised by the South African Department of Environmental Affairs (TOPS permit #S 07503).

Table 14. Summary of all genetic samples collected and analysed from 2015 to 2019. Described are the total number of samples collected, the number of samples for which DNA was successfully extracted, the number of samples confirmed as leopard, the number of individuals (unique genotypes confirmed), and the sex ratio.

Sampling aspect	**Reference**	**Illegal trade**			**Overall**
		Raid	Shembe	*Muti*	
Total samples collected	1896	144	85	74	2199
DNA successfully extracted	1629	137	85	70	1921
Species confirmed as leopard	1524	135	85	66	1810
Unique genotypes confirmed	1452	96	81	60	1689
Female:Male (sex ratio)	639:813 (1.27)	20:76 (3.80)	23:58 (2.52)	22:38 (1.73)	704:985 (1.40)

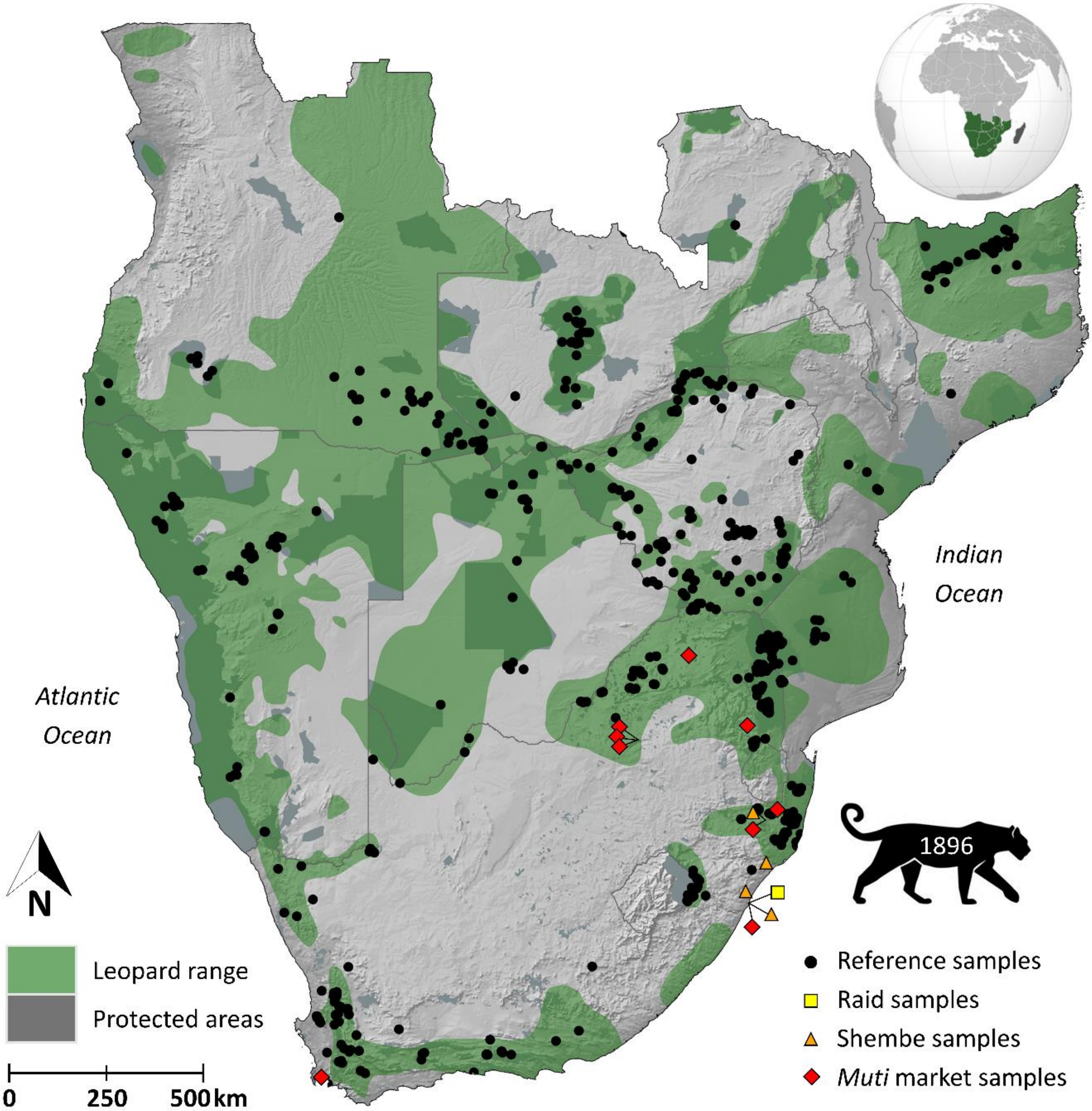


Figure 17. Reference sampling area and leopard range across southern Africa. Indicated are leopard range (extant and possibly present; Jacobson *et al.*, 2016), protected areas (World Database of Protected Areas), and location of leopard reference samples (solid black dots, *n* = 1,896). Locations of a large leopard skin raid (yellow square, *n* = 144), opportunistic sampling at major Shembe gatherings (orange triangles, *n* = 85), and various traditional *muti* markets (red diamonds, *n* = 74) are indicated.

3.3.2. DNA extraction, sequencing, and genotyping

DNA was successfully extracted for 1,629 reference and 292 trade samples (n_{Raid} = 137; n_{Shembe} = 85; n_{Muti} = 70; Table 14). DNA was extracted from faecal samples using the QIAamp DNA Stool Mini Kit and from tissue using the DNEasy Blood and Tissue Kit (Qiagen, Inc., Valencia, CA, USA). Extractions were performed according to the guidelines provided by the manufacturer and were stored at -20 °C.

A 611 bp fragment of the NADH-5 mitochondrial gene was amplified for each sample in two parts overlapping approximately 140 bp using primer pairs F/RL2 and FL2/RL4 (F: 5’-GTGCAACTCCAAATAAAAG-3’, RL2: 5’-TAAACAGTTGGAACAGG-TT-3’, FL2: 5’-CGTTACATGATCGATCATAG-3’, and RL4: 5’-TTAGGTTT-TCGTGTTGGGT-3’) corresponding to positions 12,632–13,242 in the complete *Felis catus* mtDNA sequence (Lopez *et al.*, 1996). These primers, except forward primer F, from Johnson *et al.*, (1997), were developed from leopard sequences in Uphyrkina *et al.* (2001). All samples were amplified following the polymerase chain reaction (PCR)-based methods developed by Uphyrkina *et al.* (2001). PCR reactions contained 50–100 ng DNA, 2 µM each of forward-labelled and reverse primers, 5 µl DreamTaq™ Green PCR Master Mix (Thermo Scientific), and deionised water to a total reaction volume of 10 µl. PCRs were performed on Applied Biosystems 2720 and Veriti® 96-Well Thermal Cyclers. The thermal profile comprised of an initial denaturing step of 95 °C for 5 minutes (min), followed by 40 cycles of a 95 °C denaturation step for 30 seconds (sec), a 58 °C annealing step for 30 sec, and a 72 °C extension step for 60 sec. The final extension step was performed at 72 °C for 10 min before holding at 4 °C. PCR products were visualised by gel electrophoresis on a 2% agarose gel (SeaKem® LE Agarose, Whitehead Scientific (Pty) Ltd). Samples were then sequenced on an ABI300 Genetic Analyser (University of Stellenbosch, Central Analytical Facilities, South Africa).

Samples were genotyped at 22 microsatellite loci (Table S2) developed from the *Felis catus* genome (Menotti-Raymond *et al.*, 1999) and previously shown to be polymorphic in leopards (Uphyrkina *et al.*, 2001; McManus *et al.*, 2014; Ropiquet *et al.*, 2015) together with a Zn-finger linked sexing marker (Pilgrim *et al.*, 2004). PCR reactions contained 50–100 ng DNA, 200 ng bovine albumin serum (BSA), a locus-specific $MgCl_2$ concentration (1.5–2.5 mM), 2 µM each of forward-labelled and reverse primers, 5 µl DreamTaq™ Green PCR Master Mix (Thermo Scientific), and deionised water to a total reaction volume of 25 µl. PCRs were performed on an Applied Biosystems Veriti® Thermal Cycler. Sexing PCR reactions were performed in triplicate for each sample. Samples with identical results for at least two independent reactions were considered reliable for sex identification. Given the generally low quality of DNA extracted from faecal samples, all samples were amplified in singleplex and replicated as necessary (from extraction to amplification) to ensure reproducibility and reliability (at least 15/22 loci genotyped). Locus-specific thermal profiles were developed following Menotti-Raymond *et al.* (1999) and PCR products were pooled according to size and fluorescent labelling for visualization (Table 15). A positive control was used for size scoring between runs and a negative control was included throughout to monitor for possible contamination. Genotypes were analysed (POP7 and 50cm capillary) on a 3100-Avant Genetic Analyzer (Applied Biosystems) at the Central Analytical Facility, Stellenbosch University, South Africa. Genotypes were sized using the LIZ® 600 internal size standard and alleles were scored in GENEIOUS R10 (Biomatters Limited). Automated allele calls were manually checked for accuracy (with every tenth run blind called by an independent researcher). Stutter errors, large allele dropouts, short allele dominance, and significant departures from Hardy–Weinberg equilibrium (HWE) were examined using MICRO-CHECKER 2.2.4 (van Oosterhout *et al.*, 2004) across loci for each population using a χ^2 test for goodness of fit and sequential Bonferroni corrections on the resulting *P*-values (Rice, 1989). FSTAT 2.9. was used to test for linkage disequilibrium (LD) between pairs of loci (Goudet, 2002).

3.3.3. Species, individual, and sex identification

Species confirmation was first conducted to control for misidentified faecal samples in the reference dataset and non-leopard material potentially sold as leopard products in *muti* markets. To do this, NADH-5 sequences were compared to known leopard sequences available on Genbank® (http.//www.ncbi.nlm.gov/genbank). Species sequences were queried in NCBI BLASTN® using the megablast programme, which is optimised for highly similar sequences (Altschul *et al.*, 1990). Query cover (%), unique identity (%), and top species accession matches were considered, and all non-leopard samples excluded from further analyses (Table 14). Blood positive controls (e.g., leopard, lion, serval, and cheetah) were also assessed to ensure consistent species identification.

Table 15. Microsatellite markers used to genotype reference and trade samples of leopards across southern Africa. Individual leopards (*n* = 1,810) were genotyped at 22 loci and a sex-linked marker between 2015 and 2019. Described here by the multiplex pool in which samples were visualised, the forward and reverse primer sequences, product size (bp), the fluorescent tag used, and single reaction-specific annealing temperature. These panels were developed in order to maximise comparability with existing southern African leopard genetic literature (i.e., Menotti-Raymond *et al.*, 1999; Uphyrkina *et al.*, 2001; Pilgrim *et al.*, 2005; McManus *et al.*, 2014; Ropiquet *et al.*, 2015).

Multiplex pool	μSat locus	Forward primer sequence (5'–3')	Reverse primer sequence (5'–3')	Product size (bp)	Florescent tag	Annealing temp. (°C)
1	Zn-Fng	AAGTTTACACAACCACCTGG	CACAGAATTTACACTTGTGCA	163, 166	FAM	48
1	FCA008	ACTGTAAATTTCTGAGCTGGCC	TGACAGACTGTTCTGGGTATGG	122–148	VIC	56
2	FCA026	GGAGCCCTTAGAGTCATGCA	TGTACACGCACCAAAAACAA	136–154	NED	56
2	FCA043	GAGCCACCCTAGCACATATACC	AGACGGGATTGCATGAAAAG	116–128	FAM	56
3	FCA075	ATGCTAATCAGTGGCATTTGG	GAACAAAAATTCCAGACGTGC	103–143	FAM	54
2	FCA077	GGCACCTATAACTACCAGTGTGA	ATCTCTGGGGAAATAAATTTTGG	143–155	FAM	56
2	FCA090	ATCAAAAGTCTTGAAGAGCATGG	TGTTAGCTCATGTTCATGTGTCC	93–120	VIC	56
3	FCA094	TCAAGCCCCATTTTACCTTC	CACCTGAGCCAAAGGCTATC	215–237	FAM	56
2	FCA096	CACGCCAAACTCTATGCTGA	CAATGTGCCGTCCAAGAAC	184–224	VIC	54
1	FCA097	TAATGTTCAACTTGAATTGCTTCC	GAACAGTAGTTTGCCCATACAGG	138–148	NED	56
3	FCA105	TTGACCCTCATACCTTCTTTGG	TGGGAGAATAAATTTGCAAAGC	189–197	PET	52
1	FCA126	GCCCCTGATACCCTGAATG	CTATCCTTGCTGGCTGAAGG	139–145	FAM	56
3	FCA139	AGCATGTTTTTGAGGCAGCT	TTATGGGTAGTGTGAAGTAGGG	141–147	NED	56
1	FCA161	TTACCGATACACACCTGCCA	CACAGACGTGCTCTAGCCAA	179–187	FAM	56
1	FCA211	TGTAGAACATAATGCCTCAGCC	TCTTGAACCTATTTCCCCACA	111–119	PET	52
1	FCA220	CGATGGAAATTGTATCCATGG	GAATGAAGGCAGTCACAAACTG	214–222	VIC	56
1	FCA224	CTGGGTGCTGACAGCATAGA	TGCCAGAGTTGTATGAAAGGG	154–162	PET	52
2	FCA229	CAAACTGACAAGCTTAGAGGGC	GCAGAAGTCCAATCTCAAAAGTC	160–170	PET	52
3	FCA24	GGAAATTAGGAGCTCTGCCA	AAGATTTACCCAGTTGCCCC	145–151	PET	52
2	FCA310	TTAATTGTATCCCAAGTGGTCA	TAATGCTGCAATGTAGGGCA	121–137	PET	52
3	FCA441[†]	ATCGGTAGGTAGGTAGATATAG	GCTTGCTTCAAAATTTTCAC	153–183	VIC	56
3	FCA453	AATTCTGAGAACAAGCTGAGGG	ATCCTCTATGGCAGGACTTTG	186–198	NED	56
3	FCA678	AGCAATCTCCAGAATGTGTGG	TCAAAAGATTAAAGCCTTCCAA	226–234	VIC	56

[†] Tetranucleotide where all others are dinucleotide repeats

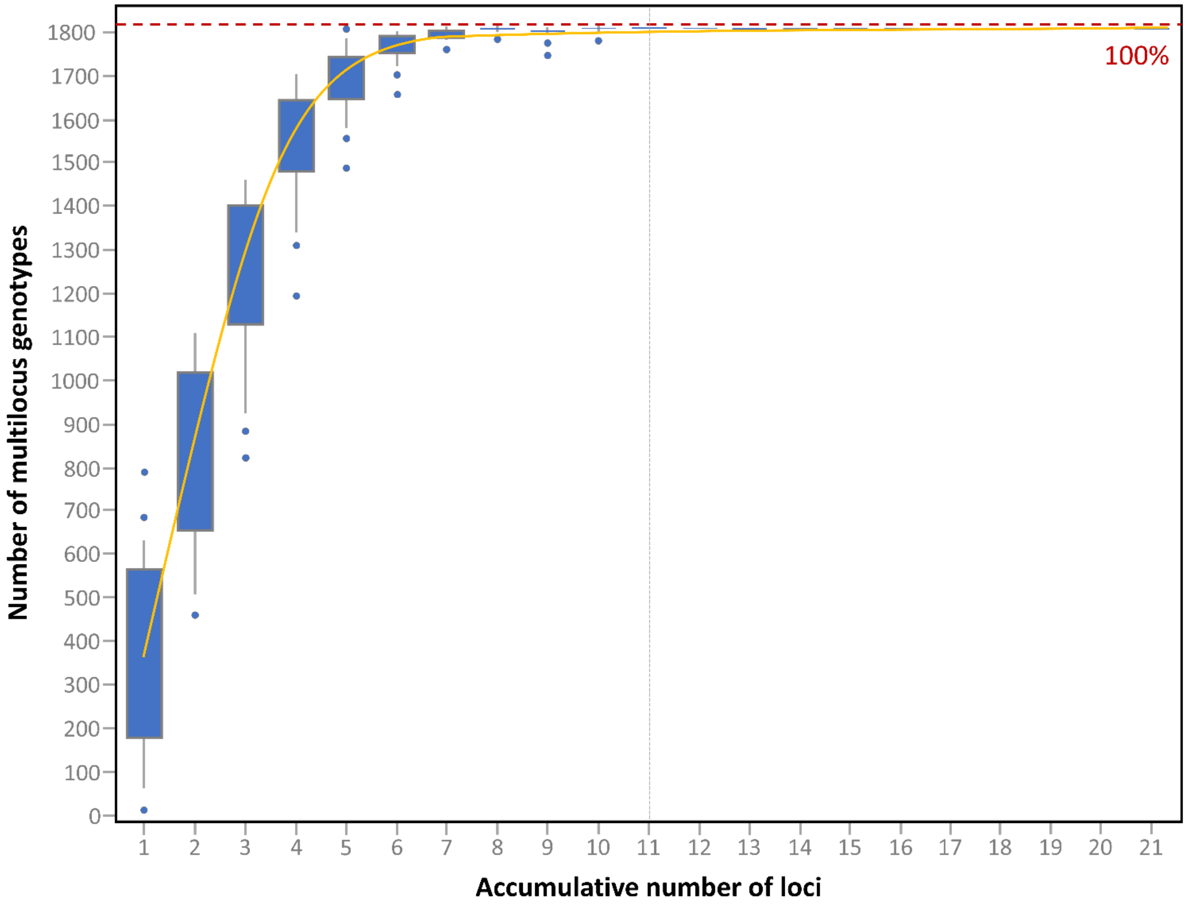


Figure 18. Genotype accumulation curve (GAC) for reference and traded leopards samples. An estimated 1,810 individual leopards (reference and trade) were genotyped at 22 loci throughout southern Africa between 2015 and 2019.

For all individuals confirmed as leopard, identity analysis (through genotype matching) was then implemented in CERVUS 2.0 (Kalinowski *et al.*, 2007) to determine the number and possible duplication of individuals (unique genotypes) both within and across datasets. Pairwise genotype comparison parameters were conservative, permitting a minimum of 10 matching loci (45% of the total number of loci, though results remained consistent through iterations of 10–21 loci) for queries to be considered a match based on a genotype accumulation curve across datasets (Figure 18). The 'fuzzy-matching' function was enabled to identify genotypes that matched at all but one locus (5% genotyping error tolerated). All identity analyses were conducted with and without sex (identified by Zn-finger-linked marker) to ensure the exclusion of similar genotypes between individuals of the same sex.

The significance of sex ratio estimates for each dataset was assessed with a binomial distribution test. I calculated the probability of the observed number of males and females given an expected sex ratio of 0.5. All further analyses were conducted in *R* (R Core Team, 2019) and *QGIS* (QGIS Development Team, 2019).

3.3.4. Geographic assignment analysis

To determine the most likely geographic origins of illegally traded leopard derivatives (Raid, Shembe, and *Muti*), I implemented a Bayesian assignment approach in the programme SCAT 2.1 (Wasser *et al.*, 2004, 2007; Mondol *et al.*, 2014), comparing genotypes of the traded samples with the reference DNA samples collected from leopards of known location. Reference allele frequencies were generated using a Smoothed Continuous Assignment Technique (SCAT) and Markov chain Monte Carlo (MCMC) sampling, as described in Wasser *et al.* (2004; 2007). Several initial runs with multiple combinations of input parameters (burn-in, thinning, and iterations) were conducted. After comparison of results across runs, 10 independent runs with lengths of 100 burn-ins, 10 thinnings, and 100 iterations were performed, using this Continuous Assignment Method (CAM) to assign a location to each sample 100 times. The power of the CAM is that it can estimate smoothed allele frequencies at any location, including those where no georeferenced samples are available, overcoming many of the limitations of standard assignment tests (Wasser *et al.*, 2004). The extension of this Bayesian framework and MCMC algorithm allows for sampling of the posterior distribution, assigning a median of the latitude and longitude for any given sample, where the spread of *n* assignments indicates the overall confidence for all possible locations within the provided boundary (Figure 17).

To validate the geographic assignment of leopard samples based on the reference dataset across the southern African subregion, I conducted i) country-level confidence of assignment and ii) sample-based sensitivity analyses with the reference data. These analyses were done by systematically removing i) entire sampling regions (following Wasser *et al.*, 2004) and ii) one, five, and ten samples (adapted from Mondol *et al.*, 2014) of known origin from the reference dataset, respectively, recalculating allele frequencies without these samples and then cross-validating locations of the removed samples with the same input parameters. The spatial spread of re-assignments, measured as the average difference (in kilometres) between the assignment and the true (or known) location for each sample indicates i) overall assignment confidence per country for 20%, 50%, 80%, and 100% of samples and ii) overall assignment sensitivity as a continuous distance per removal of one, five, and ten samples, respectively.

Assignment analyses were then conducted for the illegally traded samples, with 95% and 99% kernel density estimations (KDE) performed for each trade assignment to identify the landscape with the highest density of points, shown as the median point and two KDE contours on a map of southern Africa. I also categorised the quality of trade assignments (following Mondol *et al.*, 2014) by dataset (Raid, Shembe, *Muti,* and overall) based on the uncertainty of results into three groups: high (one centre in both 95% and 99% contours); moderate (two centres in either contour type); and low (many centres in either contour type). Likely origins were then summarised per illegal trade dataset (Raid, Shembe, *Muti,* and overall) as superimposed assignment points within each 95% KDE on a map of southern Africa and a source country chord diagram was implemented in the *circlize* package (Gu *et al.*, 2014).

3.4. Results

3.4.1. Amplification, sequencing, and genotyping

From an initial sample set of 1,896 reference and 303 illegal trade samples, I obtained DNA extracts from 1,629 and 292 samples, respectively (Table 14). On average, more than 16 loci amplified reliably; however, locus FCA096 was removed from all further analyses due to poor amplification success (47%; Table 16). The mean locus-specific amplification success rate was 87%. All loci were polymorphic and had a mean allele number of 21.9 ± 0.57 (standard error [SE]; range: 16–26 alleles), expected heterozygosity of 0.74 ± 0.03, and observed heterozygosity of 0.77 ± 0.03 (Table 16). Most loci were in HWE (significant deviations included: FCA043, FCA075, FCA077, FCA090, FCA094, FCA441, and FCA453); there were no null alleles nor evidence of LD. The allelic dropout and false allele rates across all loci were below 0.001% (Table 16).

Table 16. Microsatellite diversity of reference leopards (n = 1,810) sampled across southern Africa. Parameter estimates are presented as the number of individuals successfully typed (n), locus-specific amplification success (AS, %), number of alleles (A_n), proportion of allelic dropout (A_d, %), proportion of false alleles (A_f, %), observed heterozygosity (H_O), and expected heterozygosity (H_E). In summary, the mean ($\bar{x}$) and standard error (± SE) for each parameter are shown, and associated P-values are based on the χ^2 statistic of deviation from Hardy-Weinberg Equilibrium. FCA096 was removed from all further analyses due to poor amplification success (AS = 47.1%). No null alleles were found.

Locus	***n***	**AS (%)**	**A_n**	**A_d (%)**	**A_f (%)**	**H_O**	**H_E**
FCA008	1,523	90.2	22	0	0	0.79$^{\text{ns}}$	0.77
FCA026	1,542	91.3	27	0	0	0.81$^{\text{ns}}$	0.81
FCA043	1,458	86.3	22	0.4	0	0.88*	0.77
FCA075	1,552	91.9	26	0	0	0.72*	0.65
FCA077	1,652	97.8	23	0	0	0.95*	0.84
FCA090	1,546	91.5	23	0	0	0.72*	0.80
FCA094	1,304	77.2	21	0.6	0.2	0.87*	0.77
~~FCA096~~	~~795~~	~~47.1~~	26	~~0.7~~	~~1.2~~	~~0.54*~~	~~0.81~~
FCA097	1,559	92.3	23	0	0	0.79$^{\text{ns}}$	0.82
FCA105	1,251	74.1	21	0.5	0	0.67$^{\text{ns}}$	0.61
FCA126	1,631	96.6	25	0	0	0.96$^{\text{ns}}$	0.87
FCA139	1,460	86.4	19	0.2	0	0.45$^{\text{ns}}$	0.42
FCA161	1,559	92.3	18	0	0	0.82$^{\text{ns}}$	0.80
FCA220	1,577	93.4	21	0	0	0.88$^{\text{ns}}$	0.86
FCA221	1,322	78.3	20	0.4	0	0.79$^{\text{ns}}$	0.81
FCA224	1,415	83.7	23	0	0	0.88$^{\text{ns}}$	0.85
FCA229	1,079	63.9	20	0.8	0.6	0.85$^{\text{ns}}$	0.83
FCA247	1,626	96.3	20	0	0	0.75$^{\text{ns}}$	0.74
FCA310	1,337	79.2	21	0.5	0	0.90*	0.85
FCA441	1,588	94.0	16	0	0	0.49$^{\text{ns}}$	0.44
FCA453	1,562	92.5	20	0	0	0.43*	0.36
FCA678	1,568	92.8	23	0	0	0.80$^{\text{ns}}$	0.76
$\bar{x}$	**1,481**	**87.7**	**21.8**	**0.0016**	**0.0004**	**0.77**	**0.74**
SE	**32.06**	**1.9**	**0.6**	**-**	**-**	**0.03**	**0.03**

Significance ($^{\text{ns}}$ = non-significant; ˙P ≤ 0.10; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001)

3.4.2. *Species, individual, and sex identification*

Of the 1,629 reference and 292 trade samples, 105 and 6 (n_{Raid} = 2; n_{Shembe} = 0; n_{Muti} = 4), respectively, were confirmed as non-leopard species (Table 14). Most trade samples were identified as leopard (98%) with three non-leopard species identified (i.e., lion, cheetah, and serval): all Shembe samples were leopard; two Raid samples were confirmed as non-leopard (cheetah and lion); while one cheetah and two servals were identified among *Muti* samples. Identity analysis confirmed a further 72 and 49 duplicated genotypes in the reference and trade samples (n_{Raid} = 39; n_{Shembe} = 4; n_{Muti} = 6; Table 14), revealing a total of 1,452 and 237 individual leopards (unique genotypes) in the reference and trade (n_{Raid} = 96; n_{Shembe} = 81; n_{Muti} = 60; Table 14) datasets, respectively, giving a total estimate of 1,689 individuals corroborated by the global GAC (Figure 18).

Sex was successfully determined for all 1,689 individual leopards (704 females and 985 males) across the reference and trade datasets (Table 17). The overall sex ratio (number of males/number of females) across all samples was 1.40, which was significantly different from parity ($K_{1,689}$ = 985; $z_{0.5}$ = 6.81; *P* <0.001). Both the reference and trade datasets were significantly male biased with sex ratios of 1.27 ($K_{1,452}$ = 813; $z_{0.5}$ = 4.54; *P* <0.001) and 2.65 (K_{237} = 172; $z_{0.5}$ = 6.89; *P* <0.001), respectively. Within the trade dataset (Table 17), Raid samples were most significantly male biased with a sex ratio of 3.8 (K_{96} = 76; $z_{0.5}$ = 5.61; *P* <0.001), followed by the Shembe samples at 2.52 (K_{81} = 58; $z_{0.5}$ = 3.78; *P* <0.001), and the *Muti* samples at 1.73 (K_{60} = 38; $z_{0.5}$ = 1.94; *P* = 0.026).

Table 17. Sex determination and ratios for leopards in reference and trade samples. These were determined using a binomial test, assuming a sex ratio of parity for 237 individual illegal trade samples at 21 microsatellite loci throughout southern Africa between 2015 and 2019.

Source	**Males**	**Females**	**Sex ratio**
Reference (*n* = 1,452)	813	639	1.27***
Trade (*n* = 237)	172	65	2.65***
Raid (*n* = 96)	76	20	3.80***
Shembe (*n* = 81)	58	23	2.52***
Muti (*n* = 60)	38	22	1.73***
Total (*n* = 1,689)	**985**	**704**	**1.40*** **

Significance ($^{\text{ns}}$ = non-significant; ˙P ≤ 0.10; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001)

3.4.3. *Southern African genetic diversity*

Overall, southern African leopards exhibited moderate to high levels of genetic diversity across all loci ($\bar{x}_n$ = 207 ± 123 [SE]; 20–940 samples), with A_n of 9.09 ± 0.48, rarefied A_{r} of 6.22 ± 0.27, A_{p} of 2.86 ± 0.40, H_{O} of 0.57 ± 0.03, and H_{E} of 0.61 ± 0.02 (Table 18). Genetic diversity estimates differed significantly across sampled countries (Kruskal–Wallis rank-sum tests: A_n, H_6 = 143.01, *P* <0.001; A_{r},

$H_6 = 141.73$, $P < 0.001$, A_p, $H_6 = 130.28$, $P < 0.001$; H_O, $H_6 = 141.81$, $P < 0.001$; H_E, $H_6 = 139.18$, $P < 0.001$) and were highest for leopards in Zambia, followed by Namibia, Angola, South Africa, Botswana, Mozambique, and Zimbabwe (Table 18). The global inbreeding coefficient was -0.01 ± 0.03 ranging from -0.09 to 0.12, and there was no significant departure from HWE across sampled countries.

Table 18. Summary statistics of genetic diversity in reference samples of leopard across southern African. Genetic variability was assessed based on 1,452 individual leopards genotyped at 21 microsatellite loci sampled across seven southern African countries. Included are the number of individuals (n), mean number of alleles (A_n), rarefied allelic richness (A_r), private alleles (A_p), observed heterozygosity (H_O), expected heterozygosity (H_E), and inbreeding coefficient (F_{IS}) with 95% confidence intervals (CI; 1,000 bootstraps) with lower (LL) and upper (UL) limits. In summary are shown: the mean ($\bar{x}$) and standard error (± SE) for each, and associated P-values are based on the χ2 statistic of deviation from Hardy-Weinberg Equilibrium.

Country	n	A_n	A_r	A_p	H_O	H_E	***P-value***	F_{IS} **(95% CI [LL, UL])**
Angola	42	8.34	6.42	3	0.62	0.64	0.32	-0.05 (-0.11, 0.01)
Botswana	20	6.73	5.58	2	0.54	0.60	0.44	-0.03 (-0.07, 0.01)
Mozambique	156	10.22	6.15	4	0.49	0.59	0.11	0.08 (-0.00, 0.15)
Namibia	119	9.17	6.87	3	0.68	0.67	0.38	-0.09 (-0.13, 0.01)
South Africa	940	10.54	6.69	4	0.51	0.58	0.23	0.05 (-0.13, 0.19)
Zambia	32	8.98	6.88	3	0.63	0.65	0.34	-0.07 (-0.09, 0.02)
Zimbabwe	143	9.65	4.96	1	0.44	0.52	0.07	0.13 (-0.03, 0.21)
$\bar{x}$	**-**	**9.09**	**6.22**	**2.86**	**0.57**	**0.61**	**-**	**-0.01 (-0.13, 0.08)**
SE	**-**	**0.48**	**0.27**	**0.40**	**0.03**	**0.02**	**-**	**0.03 (-0.19, 0.18)**

3.4.4. Geographic assignment analysis

The CAM was successful in cross-validating reference samples to their country of origin with a mean accuracy of 82.75% ± 2.17 (Table 19). Moreover, considerable confidence in assignment remained even with the sequential exclusion of local sampling areas (Figure 19). When all reference samples were included, 50% of re-assigned reference samples were located within 132 ± 3.92 km of their actual origin, and 80% within 239 ± 6.40 km, whereas under country-level sampling exclusion, 50% of samples were located within 248 ± 3.63 km and 80% within 400 ± 5.55 km (Table 20).

Table 19. Classification matrix for the reassignment of leopard reference samples. Indicated are individual leopard reference sample (*n* = 1,452) assignments across southern Africa (2015–2019) by country and sampling area, using the smoothing-based assignment method. Green to red colour spectrum indicates the frequency of deviations from the correct (green) country and sampling area re-assignment.

Estimated location*		**RSA**							**NAM**				**BOT**			**ANG**		**ZAM**			**ZIM**					**MOZ**				**Accuracy (%)**
		WC	NC	EC	KZ	MP	LM	NW	SW	CN	NW	NE	KG	KH	DL	SW	SE	NG	KF	LZ	NC	NW	SW	SC	SE	LP	SC	CT	NA	
RSA	WC	59	4	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	79%
	NC	2	39	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93%
	EC	2	0	27	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	79%
	KZ	0	0	12	314	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	90%
	MP	0	0	0	4	292	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	94%
	LM	0	0	0	0	6	62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	85%
	NW	0	0	0	0	1	2	51	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	89%
NAM	SW	0	1	0	0	0	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	71%
	CN	0	0	0	0	0	0	0	2	50	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	85%
	NW	0	0	0	0	0	0	0	0	0	24	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	80%
	NE	0	0	0	0	0	0	0	0	0	0	20	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	87%
BOT	KG	0	0	0	0	0	0	0	1	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60%
	KH	0	0	0	0	0	0	0	0	0	0	0	1	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	57%
	DL	0	0	0	0	0	0	1	0	0	0	0	0	0	6	0	0	1	0	0	0	0	0	0	0	0	0	0	0	75%
ANG	SW	0	0	0	0	0	0	0	0	0	2	0	0	0	0	10	1	0	0	0	0	0	0	0	0	0	0	0	0	77%
	SE	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	25	2	0	0	0	0	0	0	0	0	0	0	0	86%
ZAM	NG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	0	0	0	0	0	0	0	0	0	0	0	89%
	KF	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	11	1	0	0	1	0	0	0	0	0	0	73%
	LZ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	0	0	0	0	0	0	0	0	88%
ZIM	NC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	18	2	0	0	0	0	0	0	0	82%
	NW	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	21	2	0	0	0	0	0	0	84%
	SW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	39	2	0	0	0	0	0	87%
	SC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	25	1	0	0	0	0	89%
	SE	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	20	0	0	0	0	87%
MOZ	LP	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48	2	0	0	87%
	SC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	33	0	0	89%
	CT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4	1	57%
	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	56	98%

*Republic of South Africa (RSA), Western Cape (WC), Northern Cape (NC), Eastern Cape (EC), KwaZulu-Natal (KZ), Mpumalanga (MP), Limpopo (LM), North West (NW), Namibia (NAM), South-West (SW), Central (CN), North-West (NW), North-East (NE), Botswana (BOT), Kalagadi (KG)., Kalahari (KH), Delta (DL), Angola (ANG), South-West (SW), South-East (SE), Zambia (ZAM), Ngwezi (NG), Kafue (KF), Lower Zambezi (LZ), Zimbabwe (ZIM), North-Central (NC), North-West (NW), South-West (SW), South-Central (SC), South-East (SE), Mozambique (MOZ), Limpopo (LP), South Central (SC), Central (CT) and Niassa (NA).

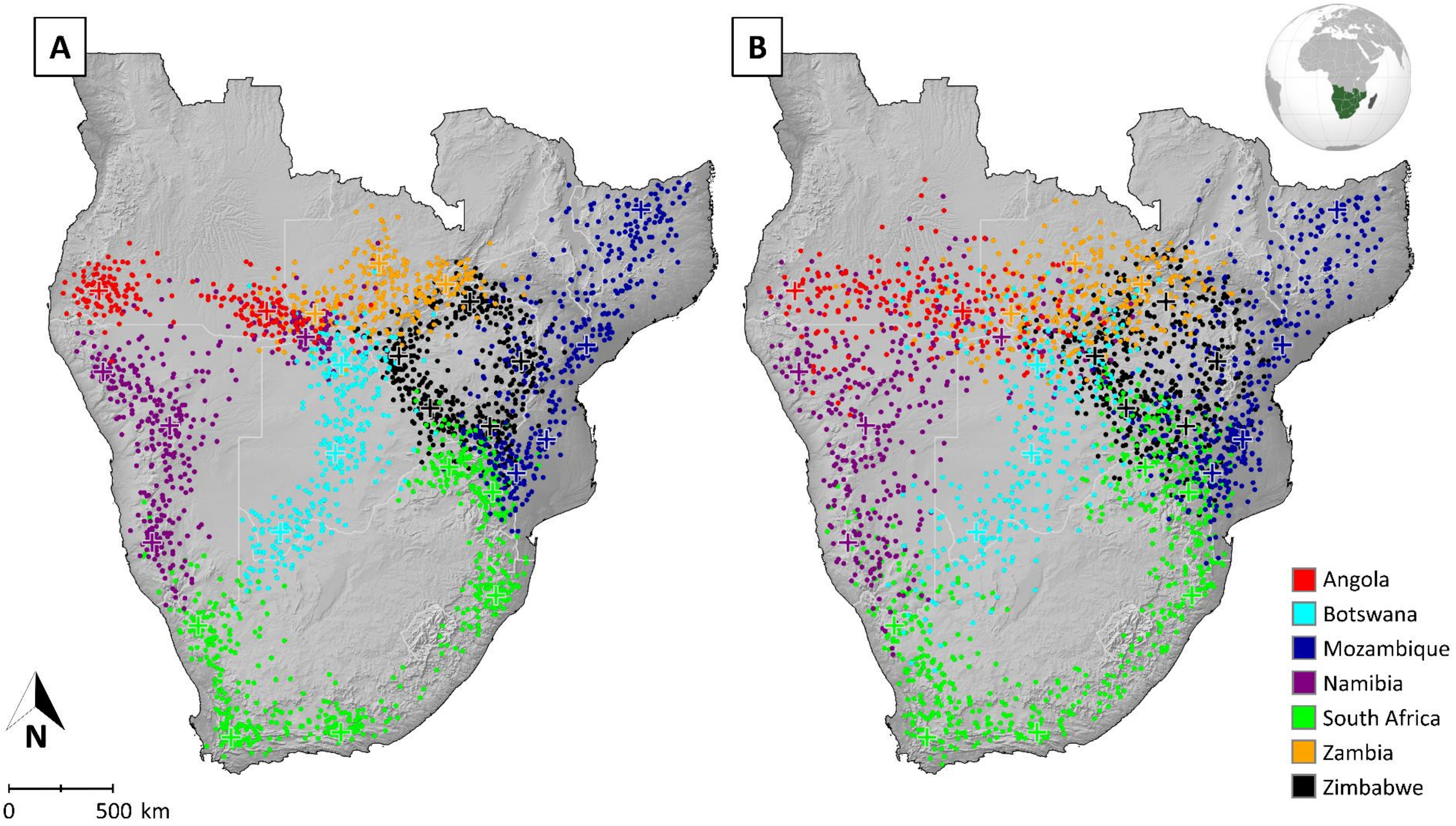


Figure 19. Confidence of leopard sample assignment with regional sampling areas sequentially excluded. These are represented by a single cross per colour. Included are (A) versus excluded (B) assignments per country from the calculation of geographic-specific allele frequencies. The 100 colour-coded circles per area are random draws from the set of all possible locations weighted according to their probability. The concentration of these 100 circles in any given area gives a guide as to the probability that the sample arose from that area under each condition.

Table 20. Continuous re-assignment distances of leopard samples per country. The number of kilometres within which 20%, 50%, 80%, and 100% of leopard reference samples could be correctly relocated through the continuous assignment method to their country of origin.

Country	*Method**	20% (SE)	50% (SE)	80% (SE)	100% (SE)
Angola	*Included*	55 (2.23)	105 (2.57)	185 (6.73)	330 (14.66)
	Excluded	139 (4.60)	311 (13.14)	506 (27.11)	795 (49.65)
Botswana	*Included*	62 (2.18)	135 (1.20)	227 (4.75)	376 (15.69)
	Excluded	112 (3.03)	251 (4.92)	422 (9.34)	661 (17.72)
Mozambique	*Included*	100 (8.74)	228 (19.61)	389 (31.80)	599 (45.53)
	Excluded	99 (7.01)	235 (12.41)	455 (16.08)	714 (26.97)
Namibia	*Included*	53 (1.59)	130 (2.34)	251 (4.54)	450 (13.09)
	Excluded	144 (6.50)	306 (8.56)	472 (8.14)	724 (12.91)
South Africa	*Included*	44 (0.89)	101 (2.27)	203 (5.49)	395 (14.41)
	Excluded	107 (2.95)	214 (3.06)	359 (6.17)	545 (13.45)
Zambia	*Included*	55 (1.92)	125 (2.07)	230 (5.66)	372 (12.02)
	Excluded	145 (5.55)	274 (8.75)	370 (10.29)	554 (19.65)
Zimbabwe	*Included*	51 (0.92)	106 (1.93)	188 (2.97)	309 (8.50)
	Excluded	115 (2.91)	210 (3.65)	310 (4.66)	457 (10.98)
Overall	***Included***	**59 (1.75)**	**132 (3.92)**	**239 (6.40)**	**408 (9.86)**
	Excluded	**120 (2.01)**	**248 (3.63)**	**400 (5.55)**	**613 (9.90)**

*The two methods (included and excluded) refer to all neighbouring samples from that sampling area that were included versus excluded from the calculation of geographic-specific allele frequencies used to assign individuals from that country (see 3.3.4).

Sensitivity analyses (continuous re-assignment of reference sampling) showed that while overall re-assignment quality was high (all reference samples were re-assigned within 223 km of their origin), variability increased in poorly sampled areas, as mean distances between true and assigned median points for one-sample removal ranged from 5–223 km ($\bar{x}_1 = 71.46 \pm 1.39$), from 6–251 km ($\bar{x}_5 = 77.23 \pm 1.54$) for five-sample removal, and 10–500 km ($\bar{x}_{10} = 106.10 \pm 2.79$) for 10-sample removal (Figure 20).

For the geographic assignment of illegally traded samples, I plot both the possible point of origin (median point) and its certainty from the posterior distribution (95% and 99% contours) for each unknown sample (Raid: Appendix 6; Shembe: Appendix 7; *Muti*: Appendix 8). I further categorise assignment quality based on the certainty of assignment results into three groups: high, moderate, and low (Figure 21). Of the 237 amplified trade samples, 84% (*n* = 198) had high, 14% (*n* = 33) moderate, and 3% (*n* = 6) low quality assignments (Table 21). Shembe samples had 87% (*n* = 70) high-quality assignments, whereas Raid and *Muti* samples had 84% (*n* = 81) and 78% (*n* = 47) high-quality assignments, respectively (Table 21).

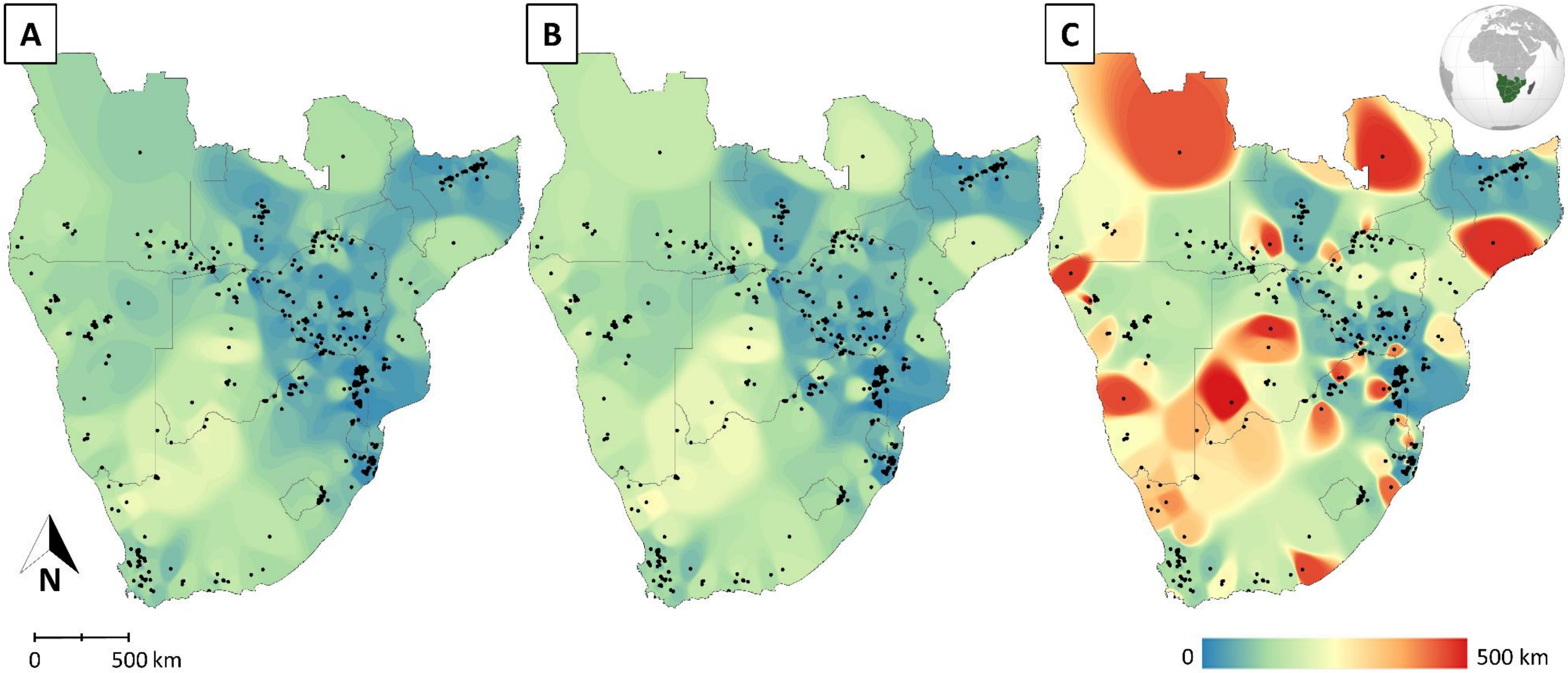


Figure 20. Sensitivity analyses of leopard reference sampling re-assignment across southern Africa. Sensitivity analyses were conducted for 1,452 individual leopard reference samples, through systematic removal and the randomised re-assignment of one (A), five (B), and ten (C) individuals. The colour shading indicates the mean distance (km) between the true reference sample location and the re-assignment of that sample under each condition. Sensitivity scores (0–500 km) are smoothed across the assignment landscape.

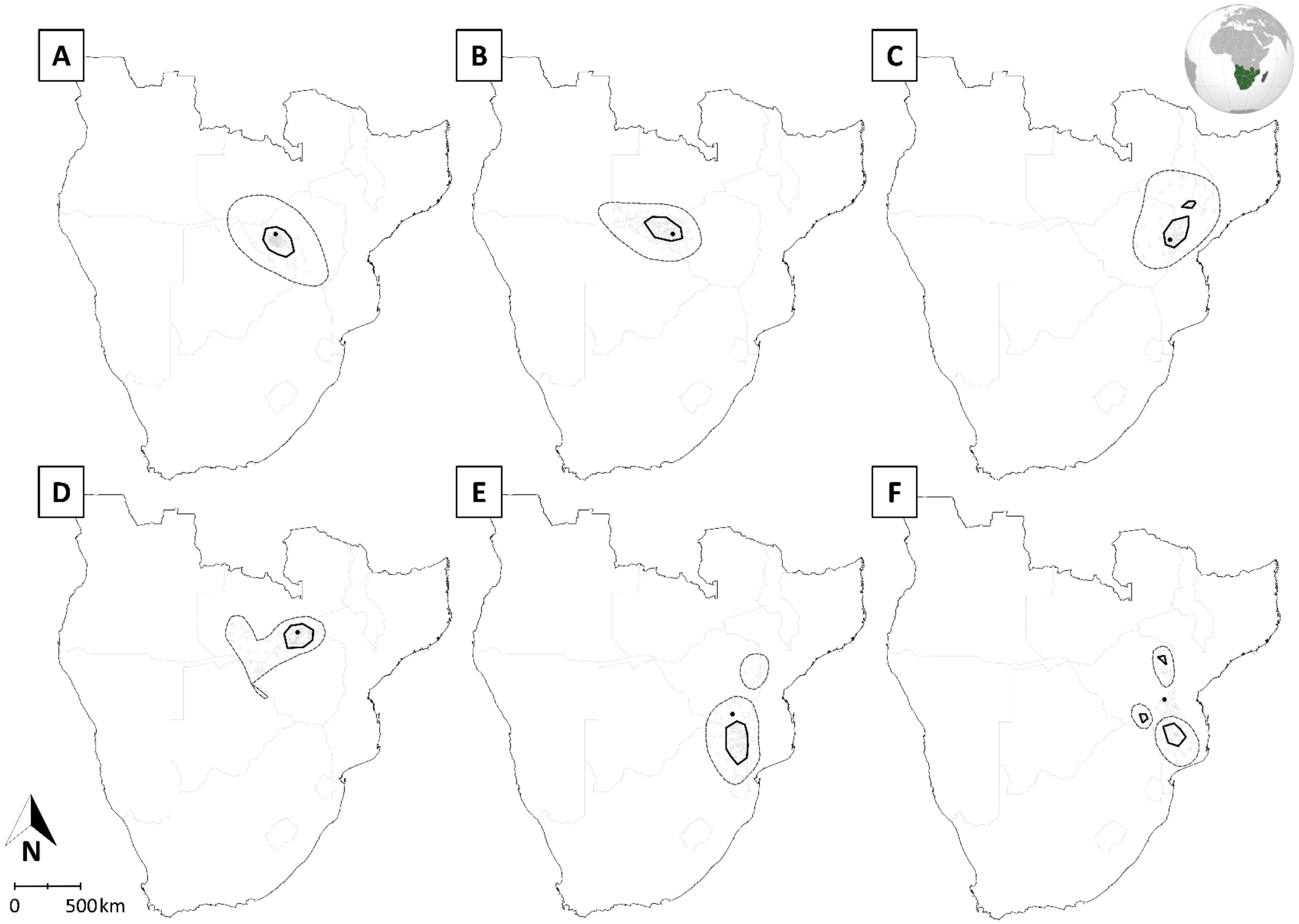


Figure 21. Examples of DNA-based geographic assignment quality for leopards across southern Africa. In testing the 237 illegally traded samples, assignment quality (solid line, 95% kernel density; dashed line, 99% kernel density) is represented by: (A, B) showing high-quality assignments (one centre of point densities in both contours); (C, D, and E) moderate-quality assignments (two centres in either 95% or 99% contours); and (F) a poor-quality assignment (multiple centres in either 95% or 99% contours).

Table 21. Summary of DNA-based assignment quality for leopards across southern Africa. Shown are assignment quality class (high, moderate, and low) counts per illegal trade source. KDE = kernel density estimate.

99% KDE	95% KDE	Certainty	Raid (*n*)	Shembe (*n*)	*Muti (n)*	Overall (%)
One centre	One centre	High	81	70	47	198 (84%)
One centre	Many centres	Moderate	8	6	6	20 (8%)
Many centres	One centre	Moderate	5	4	4	13 (6%)
Many centres	Many centres	Low	2	1	3	6 (3%)
Total			**96**	**81**	**60**	**237**

Several trade samples (22%) were assigned ≥500 km from where they were originally sampled. Western Zimbabwe, north-eastern South Africa, and south-western Mozambique showed the highest assignment densities (up to 20 per 100 km^2) of samples (Figure 22). The superimposed KDEs of assignment or 'genetic footprints' (as defined by Mondol *et al.*, 2014) of trade samples (Figure 22) were significantly associated at the country-level (Fisher exact test: $P = 0.019$). While there was no significant difference in origin country composition (Figure 23) for Raid versus Shembe ($P = 0.260$) and Shembe versus *Muti* ($P = 0.548$), there was a significant difference in Raid versus *Muti* ($P = 0.013$) and Raid and Shembe combined versus *Muti* ($P = 0.013$).

Most illegal trade samples were assigned to Zimbabwe (40%; $n_{\text{Raid}} = 46$; $n_{\text{Shembe}} = 31$; $n_{Muti} = 18$) and South Africa (39%; $n_{\text{Raid}} = 32$; $n_{\text{Shembe}} = 28$; $n_{Muti} = 23$), followed by Mozambique (11%) and Zambia (8%), as well as a few samples (≤1%) each from Namibia, Botswana, and Angola (Figure 23). Mean distance between sampling and assigned locations was significantly different ($F_3 = 0.011$; $P < 0.0001$) across all trade sources ($\bar{x}_{\text{Overall}} = 926 \pm 31$; 136–2,084 km). No significant difference ($t_{173} = 0.014$; $P = 0.989$; CI = -139–137) was observed between Raid ($\bar{x}_{\text{Raid}} = 1{,}002 \pm 46$; 186–2,084 km) and Shembe samples ($\bar{x}_{\text{Shembe}} = 1{,}003 \pm 54$; 136–1,988 km), while both Raid ($t_{153} = 4.092$; $P < 0.0001$; CI = 157–445) and Shembe ($t_{138} = 3.770$; $P < 0.001$; CI = 145–459) were significantly greater than *Muti* samples ($\bar{x}_{Muti} = 701 \pm 57$; 174–1,840 km).

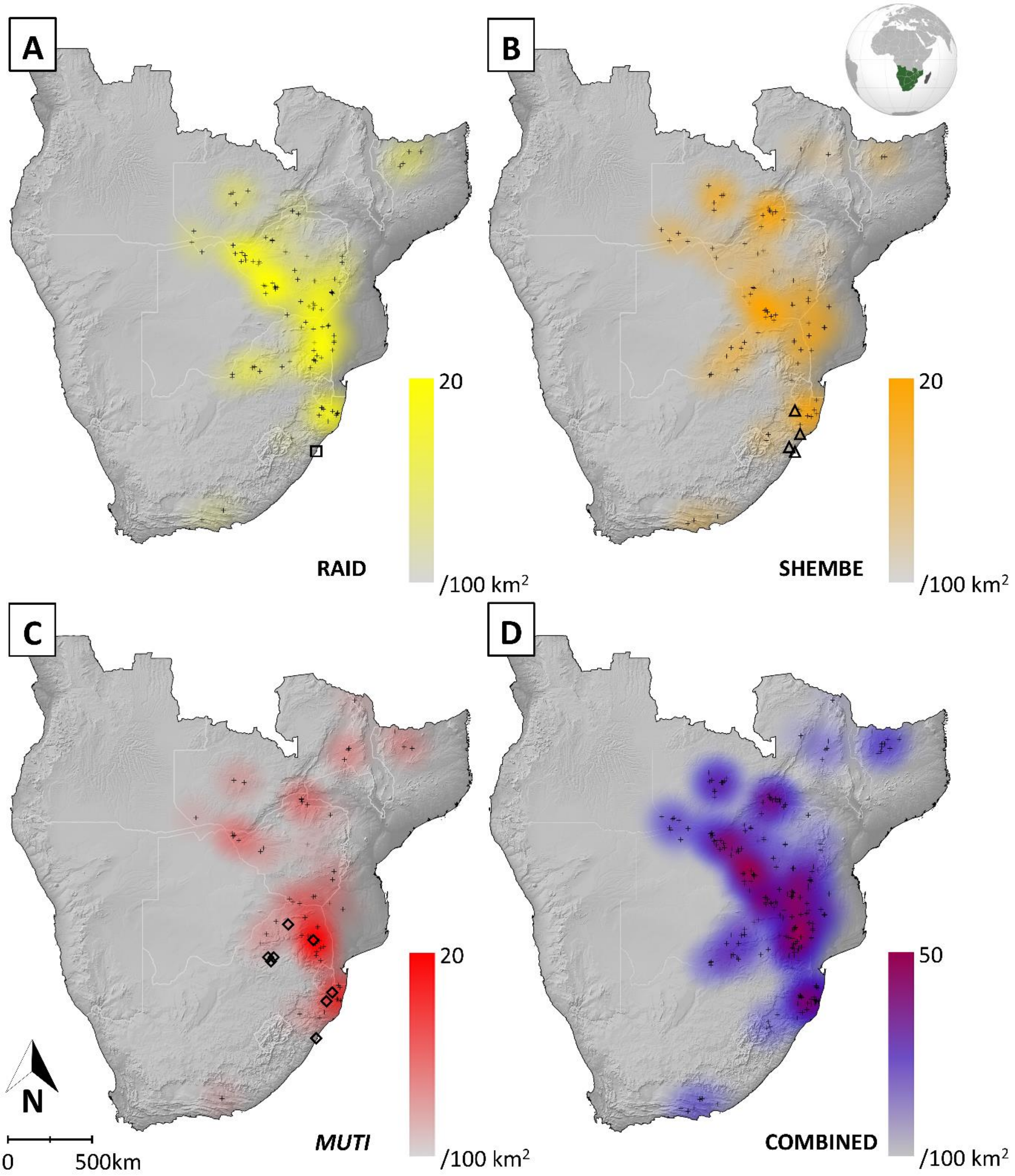


Figure 22. Genetic assignment footprints of leopard samples by trade source in southern Africa. Shown are traded leopard sample geographic assignments ($n = 237$) by (A) raid confiscation, (B) Shembe trade, (C) *muti* markets, and (D) combined. Locations of the large leopard skin raid (A; square; $n = 96$), opportunistic sampling at major Shembe gatherings (B; triangles; $n = 81$), and various traditional *muti* markets (C; diamonds; $n = 60$) are indicated. Colour shading and intensity indicate the mean density of assignments calculated as the median point of 100 random draws from the set of all possible locations weighted according to their individual assignment probabilities (under each condition). Assignments are smoothed across the landscape as (A–C) 0–20 and (D) 0–50 assignments per 100 km^2.

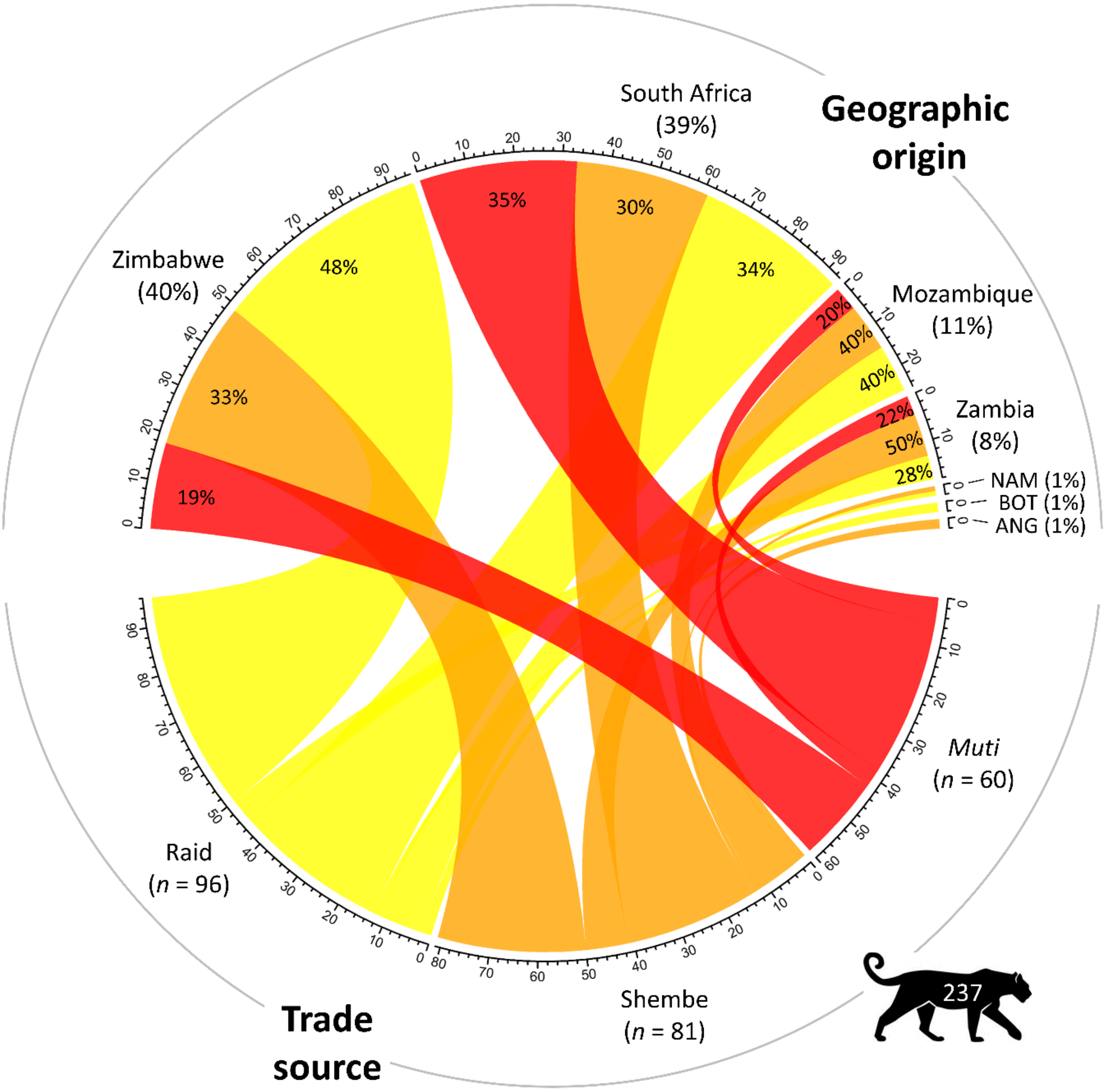


Figure 23. Summary of leopard geographic assignment by trade source and country of origin. Chord diagram summarising 237 individual leopard skin assignments by Raid (yellow), Shembe trade (orange), and *Muti* market samples (red) by their assigned country of origin.

3.5. Discussion

In this chapter, I develop a reference landscape for the DNA-based assignment of leopard derivatives throughout southern Africa and use it to determine the likely geographic origins of samples representative of the illegal trade in South Africa. As predicted, a greater proportion of Shembe samples (95%) comprised unique individual leopards compared to *Muti* samples (91%); however, contrary to prediction, Raid samples (73%) included the highest proportion of duplicated individuals. The high duplication in Raid samples was likely due to syndicated sourcing and tailoring of fewer individual leopards into multiple traditional garments and accessories (e.g., capes, headbands, and wristbands). There is likely to be some degree of sampling effort bias as the Raid was a single seizure, whereas the Shembe and *Muti* samples were collected over time from multiple followers and traders, reducing the likelihood of repeated samples of individual leopards. As predicted, when excluding the Raid samples, there are fewer individual leopards in the Shembe trade than in the *Muti* markets, as predicted.

Most trade samples were identified as leopard (98%). Shembe trade samples were tailored into capes and smaller accessories, and while some *Muti* market samples were tailored as garments, most were sold as small patches of material with versatile uses (i.e., divination, medicinal, and spiritual warding). This left a margin for product imitation by traders, as users may not be able to visually confirm the species being sold. Such counterfeiting of wildlife products is well documented for other species (e.g., tiger [Wetton *et al.*, 2002], bear [Ngoc & Wyatt, 2013], and lion bone [Williams, 2015]) and may be driven by higher market value or cultural significance for rare and protected species such as leopards (see 5.2). However, there are any number of reasons why traders would counterfeit products, such as a limited supply of the genuine material or avoidance of law enforcement (Chestin, 1995; Vigne, 2013; Ludwig *et al.*, 2015).

All illegal trade sources showed significant male-biased sex ratios (Table 17), most markedly in the Raid (3.80) and Shembe trade (2.52) and, to a lesser extent, in the *Muti* samples (1.73). While male leopards generally appear to suffer higher natural mortality rates than females for several reasons (Bailey, 1993; Athreya *et al.*, 2010; Swanepoel *et al.*, 2011), this biased sex ratio is likely explained by variation in intersexual ranging behaviour (see Chapter 4 [Naude *et al.*, 2020]), human-related conflict, size-selective poaching, or a combination thereof. Leopards are largely unrestricted by enclosed PAs (Jacobson *et al.*, 2016) and males are natal dispersers, though this dispersal is generally limited by overexploitation (see Chapter 4 [Naude *et al.*, 2020]; Fattebert *et al.*, 2015a). Nevertheless, males maintain larger territories than females (Fattebert *et al.*, 2015b) and are more likely to come into conflict with humans and fall victim to retaliatory killing (Bailey, 1993; Balme *et al.*, 2010a; Loveridge *et al.*, 2010). Leopards also exhibit substantial size dimorphism with males being near twice the average weight of females (Stuart & Stuart, 2000), potentially resulting in targeted poaching for more material (e.g., skin and fat) per unit effort. Sex-biased targeted poaching occurs in other traded species, such as elephants (Gobush *et al.* 2008) and tropical birds (Regueira & Bernard, 2012), but is perhaps less likely in leopards given that they are typically poached through indiscriminate means such as wire-snaring or poisoning (see 1.2.3).

With no available compilation of prices for leopard body parts, it is difficult to establish evidence for a profit difference between sexes (TRAFFIC, 2019). Anecdotal evidence suggests that male leopards are favoured by the Shembe for their pelt size and quality (T. Dickerson, unpublished data). Both Raid and Shembe samples are assigned to broad geographic ranges (Figure 22) but maintain highly skewed sex ratios, potentially indicative of such targeted poaching. Even if this does not directly point to male-biased poaching, it may still indicate an intentionally male-biased demand in trade because it is logical to assume that the larger the product, the higher the profit (Mondol *et al.*, 2014). Sex-bias in leopard poaching could affect leopard population dynamics, resulting in a loss of genetic variation through a decrease in effective population size (Spong *et al.*, 2000a). Moreover, extensive poaching of males can also lead to localised inbreeding, which further reduces genetic variation within a population (Spong *et al.*, 2000b), as has been observed in Asian elephants (Sukumar *et al.*, 1998) and leopards (see Chapter 4 [Naude *et al.*, 2020]).

Genetic assignment tests showed that with a large set of reference samples across southern Africa (Figure 17) it is possible to determine the geographic origin of leopard samples with a high degree of confidence. Unlike the SCAT method implemented here, most other assignment methods estimate the likely source of each sample assuming they were sampled independently and separately from some set of possible sources (Paetkau *et al.*, 1995). This assumption is problematic in many cases because sampling all possible sources is logistically challenging (Ogden, 2010). The CAM implemented in SCAT overcomes this limitation of standard assignment tests. However, it is critical with such approaches that there is a comprehensive DNA reference database and strict quality control for both reference and unknown sample data. Our data set met both requirements for leopards across the subregion. To my knowledge, this assignment approach has, to date, only been used for ‘wildlife forensics’ in African elephants (Wasser *et al.*, 2004; 2007), chimpanzees (Ghobrial *et al.*, 2010), and Indian leopards (Mondol *et al.*, 2014).

I found qualitatively little variation in assignment across samples using methods described in Wasser *et al*. (2004; 2007) for mean point reassignment of ivory in combination with KDE for illegally traded leopard skin samples implemented in Mondol *et al.* (2014). Mean reassignment accuracy with systematic sampling area removal was high (82.8% ± 2.2; Table 19 & Figure 19); assignment confidence was similar to that of forest elephant ivory assignment in Wasser *et al*. (2004), with low assignment variability for 80% of samples for both country-level inclusive (239 ± 6.40 km) and exclusive (400 ± 5.55 km) re-assignment (Table 20). Overall mean re-assignment distance of reference samples across southern Africa was 127.50 ± 2.50 km, which is within previously reported leopard home range and dispersal distance estimates (see Chapter 4 [Naude *et al.*, 2020]; Fattebert *et al.*, 2015a). Some trade assignment samples had moderate or low certainty and multiple contours (as in Mondol *et al.*, 2014), which would suggest low assignment confidence (Table 21), but these were relatively few (17%) and still gave low spatial variability in geographic assignment.

The valuable reference data used in this chapter is the largest subcontinent-level genetic database of southern African leopards, and the resultant model appears effective for long-term utilisation in regional geographic assignment studies. While more reference data would certainly reduce assignment variability (smaller contour areas), it is important to note that relatively small differences in the spatial assignment can be attributed to variation in leopard ecology and behaviour. With a continuous distribution across the subcontinent, 62% of leopard range falls outside of PAs and close to human settlements (see 1.4.2), with high rates of movement across different landscapes (Fattebert *et al.*, 2013). This may result in low genetic differentiation across the subcontinent and thus in larger differences in the spatial assignment. It is also important to note that these reference samples were collected across generations which may result in conflated similarity and homozygosity scores, which in turn may influence the relative confidence of spatial assignment.

I predicted that Raid and *Muti* samples would have smaller and more localised genetic footprints than that of Shembe samples. However, both Raid and Shembe samples were assigned to multiple origins across southern Africa, with only samples from *Muti* markets having a smaller genetic footprint with most assignments within South Africa (Figure 22). The distance between sampled and assigned locations also differed significantly between these groups (Raid and Shembe versus *Muti*), reaffirming that *muti* trade is more localised to South Africa, while Shembe samples are sourced throughout southern Africa. Raid samples were not expected to follow this pattern as they came from a single seizure. Nevertheless, these were sourced throughout southern Africa and still represent 96 individual leopards tailored for a particular market (allegedly Shembe). This suggests that individuals such as the accused repeat offender in the raid case are acting as conduits to a larger, more syndicated trade of leopard derivatives throughout southern Africa, supplying various illegal markets in South Africa.

Taken together, these geographic assignments support my overarching prediction that Shembe trade is transnational, with >65% of Shembe samples sourced from outside of South Africa (Figure 23). The genetic footprint of Raid samples contrasted my original prediction with 67% originating from outside of South Africa. The spatial similarity between this and the Shembe genetic footprint corroborates their alleged destination, Shembe markets. While *Muti* assignments were transnational, most were concentrated in South Africa (55%), perhaps representative of local harvest supplying local demand.

Collectively, 90% of illegal trade samples analysed in this chapter originated from just three countries: Zimbabwe (40%), South Africa (39%), and Mozambique (11%). While there are many factors which influence genetic diversity, these countries also have markedly lower heterozygosity scores and higher inbreeding coefficients than other sampled southern African countries (Table 18) and those analysed from East Africa (Spong *et al.*, 2000b). Within South Africa, results indicated that the provinces of KwaZulu–Natal and Gauteng are being used as centralised hubs for trade in these body parts (Figure 22). It is not possible to compare these results with other information on leopard trade routes due to lack of such data on a global scale.

The conservation of leopards is challenging because of their extensive geographic distribution, use of human-modified landscapes, and the lack of reliable estimates of population size for this species (see 1.4; Stein *et al.*, 2016). Genetic studies that identify the geographic locations of seizures could significantly enhance future conservation efforts at local and regional scales. In this chapter, I identified poaching hotspots, as well as potential trade routes, across southern Africa. In the future, this reference database could be expanded and merged with parallel studies across other leopard distributions (e.g., Mondol *et al.*, 2014) for assignment of leopard body parts at a range-wide scale. Additionally, the development of approaches to assay genome-wide markers, such as SNP and copy number variations (Ellegren, 2014), could provide opportunities for further high-resolution geographic assignment analyses.

In this study, I assigned the geographic origin of illegally traded animals with high confidence through DNA-based assignment tests, revealing that *muti* markets have a more localised demand compared to regalia-based usage such as that of followers of the Shembe Church. We also found that the trade in leopard derivatives is male-biased, likely syndicated and transnational. Longer-term monitoring of such patterns could provide useful data for law enforcement, such as the location of hotspots and trade routes for the redistribution of resource-limited antipoaching efforts. As leopard skin trade is likely linked to other forms of illicit trade (wildlife or otherwise), there are cascading benefits for law-enforcement to follow up on at these locations within the region (see 5.2 & 5.5). Finally, this chapter could be used to create a reference genetic database for other endangered species based on DNA collected from illegal trade sources and, with that, an improved understanding of where wildlife harvested for traditional use is currently being sourced.

CHAPTER 4

UNSUSTAINABLE ANTHROPOGENIC MORTALITY DISRUPTS NATAL DISPERSAL AND PROMOTES INBREEDING IN LEOPARDS

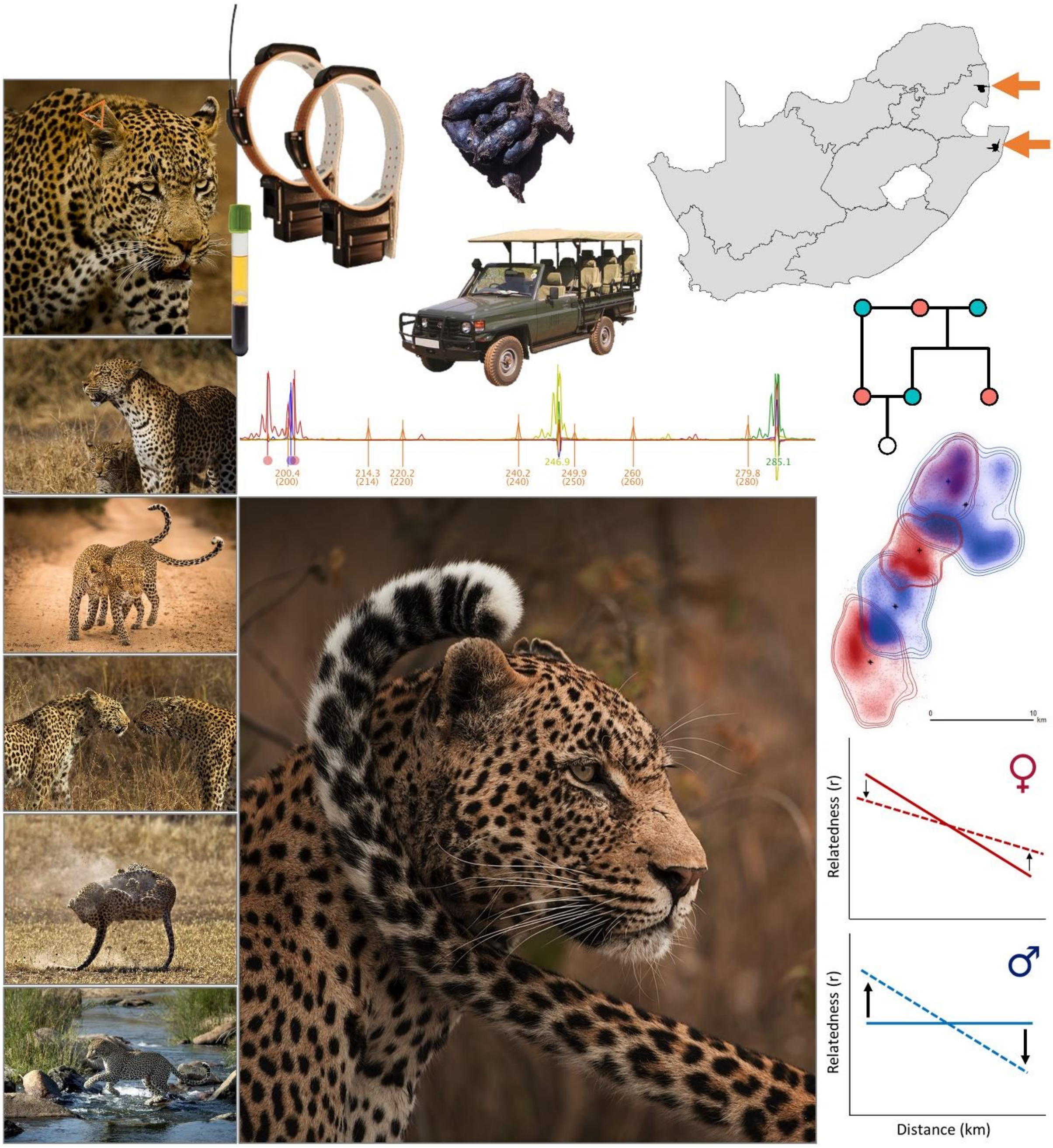


Figure 24. Natal dispersal and migration maintain genetic stability in leopard populations. Exploitation disrupts patterns of sex-biased natal philopatry, limiting dispersal and outbreeding, while *in situ* population-level recovery and connectivity restore genetic stability and structure. Images are used with permission or under the creative commons license.

4.1. Abstract

Anthropogenic mortality of wildlife is typically inferred from measures of the absolute decline in population numbers. However, increasing evidence suggests that indirect demographic effects, including changes to the age, sex, and social structure of populations, and the behaviour of survivors can profoundly impact population health and viability. Specifically, anthropogenic mortality of wildlife (especially when unsustainable) and fragmentation of the spatial distribution of individuals (e.g., home ranges) could disrupt natal dispersal mechanisms, with long-term consequences to genetic structure, by compromising outbreeding behaviour and gene flow. I investigate this threat in African leopards, a polygynous felid with male-biased natal dispersal. Using a combination of spatial (home range) and genetic (21 polymorphic microsatellites) data from 142 adult leopards, I contrast the structure of two South African populations with markedly different histories of anthropogenically-linked mortality. Home range overlap, parentage assignment, and spatio-genetic autocorrelation together show that historical exploitation of leopards in a recovering protected area has disrupted and reduced sub-adult male dispersal, thereby facilitating opportunistic male natal philopatry, with sons establishing territories closer to their mothers and sisters. The resultant kin-clustering in males of this historically exploited population is comparable to that of females in a well-protected reserve and has ultimately led to localised inbreeding. My findings demonstrate novel evidence directly linking unsustainable anthropogenic mortality to inbreeding through disrupted natal dispersal in a large, solitary felid and expose the genetic consequences underlying this behavioural change. Therefore, I emphasise the importance of managing and mitigating the effects of unsustainable exploitation and increased habitat fragmentation on local populations by promoting *in situ* recovery and providing corridors of suitable habitat between contiguous protected areas to maintain genetic connectivity.

4.2. Introduction

When assessing the effects of anthropogenic mortality on wildlife populations, managers and policymakers typically consider only direct numerical responses of populations to human-mediated mortality (e.g., poaching, retaliatory conflict, and unregulated trophy hunting [Woodroffe & Ginsberg, 1998]). Indirect demographic effects (e.g., age, sex, and social structure) and the behaviour of survivors have profound impacts on the health and viability of remaining populations (Rutledge *et al.*, 2010; Ausband *et al.*, 2015; 2017). For example, harvest can facilitate the spatial reorganisation of individuals within populations by creating home range vacancies that may be filled by neighbouring or immigrant conspecifics through a ‘vacuum effect’ (Frank *et al.*, 2017a). This may increase the probability of encounters between unfamiliar individuals leading to elevated rates of conflict, sexually selected infanticide, and increased local extinction risk (Whitman *et al.*, 2004; Gosselin *et al.*, 2015; Creel *et al.*, 2015; 2016). Moreover, directed harvest towards specific sex, age, or size cohorts disrupts dispersal patterns (Milner *et al.*, 2007; Frank *et al.*, 2017b).

By maintaining gene flow within and among populations, dispersal is critical to the persistence of spatially structured metapopulations (Hanski & Simberloff, 1997; Gundersen *et al.*, 2001; Dolrenry *et al.*, 2014). However, by increasing territorial turnover and providing opportunities for subadults to settle locally, harvest limits natal dispersal (in the absence of immigration), affecting both local and metapopulation dynamics (Newby *et al.*, 2013; Blyton *et al.*, 2015). While many studies highlight the demographic effects of unsustainable harvest, the behavioural mechanisms employed to counteract these effects and subsequent consequences to population genetic structure remain poorly understood, particularly in large carnivores (Milner *et al.*, 2007). While inbreeding susceptibility is documented in felids (e.g., lions [Munson *et al.*, 1996] and cougars [Ernest *et al.*, 2014]), few monitoring studies have the requisite longitudinal mortality (i.e., well-documented mortality for entire populations), spatial (i.e., fine-scale movement of known individuals), and genetic (i.e., multi-generational pedigrees of known individuals) data to enable comparison between populations and thereby demonstrate a tenable link between high levels of mortality (often human-mediated), disrupted dispersal, and inbreeding (Onorato *et al.*, 2011).

Across southern Africa, large felids have a long history of both legal and illegal exploitation (see 1.4.2). African leopards have been heavily harvested throughout this region for their economic value as trophies in legal hunts (Balme *et al.*, 2010b; Swanepoel *et al.*, 2011; Braczkowski *et al.*, 2015) and for mostly illegal use in traditional practices (Harries *et al.*, 1993, Kumalo & Mujinga, 2017, Williams *et al.*, 2017). Many leopards are also removed in retaliatory conflict due to their real or perceived threat to livestock (Loveridge *et al.*, 2010). In this study, I investigate how such anthropogenic mortality and persecution disrupts individual dispersal in leopards, altering spatial patterns of kinship, which ultimately promotes inbreeding in this solitary species. Previous telemetry studies suggest that leopards, like many polygynous mammals, generally exhibit female philopatry and male-biased natal dispersal (Fattebert *et al.*, 2015a; 2016; Balme *et al.*, 2017a). Subadult females are thus predicted to compete for philopatry and attempt to breed within or adjacent to their natal ranges, forming spatially defined kin-clusters (Lambin *et al.*, 2001). In contrast, subadult male leopards typically disperse in order to avoid competition with larger, conspecific adult males, thereby reducing the probability of mating with related females (Dobson, 1982; Wolff, 1994). In heavily harvested populations, young male leopards are released from local male-male competition and may exhibit 'opportunistic natal philopatry' to avoid the substantial costs of dispersal, undertaking shorter dispersal distances and establishing home ranges nearer their mothers and sisters (Fattebert *et al.*, 2015b). In such a scenario, the socio-spatial structure of males is expected to approximate the kin-clustered spatial structure of females, which, in the absence of active inbreeding avoidance, ultimately promotes increased levels of localised inbreeding (Støen *et al.*, 2005).

Here, I use home range estimates together with parentage and relatedness analyses to explore dispersal dynamics and the consequent fine-scale genetic structure of two leopard populations with markedly different histories of anthropogenically-linked mortality: a well-protected population at ecological carrying capacity (Balme *et al.*, 2017b; 2019) and a population recovering from a recent history of extensive anthropogenic mortality (Balme *et al.*, 2009; 2010). Under the premise of density-dependent male-biased dispersal and female philopatry, I predict that: (1) female leopards with overlapping home ranges will support higher levels of relatedness than males in both populations, this being particularly evident in the recovering population where mothers can adjust their home ranges to accommodate daughters and unlikely in a population at capacity where this would not always be possible (Fattebert *et al.*, 2016); (2) levels of relatedness between overlapping males and females will be higher in the recovering population due to reduced dispersal distances of sons (Fattebert *et al.*, 2015b); and (3) reduced dispersal distances exhibited by both sexes in the recovering population will result in higher levels of inbreeding. I discuss my findings in the context of local population fitness and the broader implications of disrupted dispersal on persistence and functional connectivity across leopard metapopulations throughout PAs.

4.3. Methods

4.3.1. Study areas

This study was undertaken in two PA complexes of South Africa that differ markedly in their historical rates of anthropogenic mortality. The Sabi Sand Game Reserve (SSGR) is a privately-owned conservancy (est. 1948) in the Lowveld region of the Mpumalanga province (Figure 25A). It covers 625 km^2 but is contiguous along its southern and eastern boundaries with the Kruger National Park and Manyeleti Game Reserve in the north. The SSGR thus forms part of a much larger (22,000 km^2) protected system. Although the western boundary of the reserve is adjacent to a densely populated community, the border fence is impermeable to leopards, and the population seems unaffected by detrimental edge effects (Balme *et al.*, 2019). There is also no legal offtake of leopards inside the SSGR and levels of poaching are very low; anthropogenic mortality accounted for <2% of leopard deaths in the SSGR between 1975 and 2015 and the population appears at capacity (Balme *et al.* 2017b).

The Phinda-uMkhuze Complex (PMC) is situated in the Maputaland region of the KwaZulu-Natal province (Figure 25B) and comprises two neighbouring reserves: Phinda Private Game Reserve (est. 1991) and the public uMkhuze Game Reserve (est. 1912), forming a contiguous protected landscape of 660 km^2. The PMC is surrounded by a mosaic of commercial game ranches, livestock farms, and Zulu communities; these land types are often hostile to leopards (Thorn *et al.*, 2012). Unlike the SSGR, the boundary fence of the PMC is permeable to leopards and individuals move freely between protected and unprotected land (Balme *et al.*, 2010a). The PMC, particularly uMkhuze, also suffers high levels of wire-snare poaching, which can have a marked effect on large carnivores such as leopards (see 1.2.3; Becker *et al.*, 2013). Accordingly, leopards in the PMC face a far greater mortality risk than those in the SSGR; between 2002 and 2012, human-related mortality accounted for >50% of all leopard deaths in the PMC (Balme *et al.*, 2009; unpublished data). Nonetheless, recent policy changes have allowed the PMC leopard population to recover: from a disturbance period (pre-2004) when the population was in decline ($\lambda = 0.978$); through a recovery period (2005–2008), following the implementation of sustainable harvest protocols and other conservation interventions ($\lambda = 1.136$); to a stabilization period (2009–2012), when the population density reached putative carrying capacity ($\lambda = 1.010$; Fattebert *et al.*, 2015b).

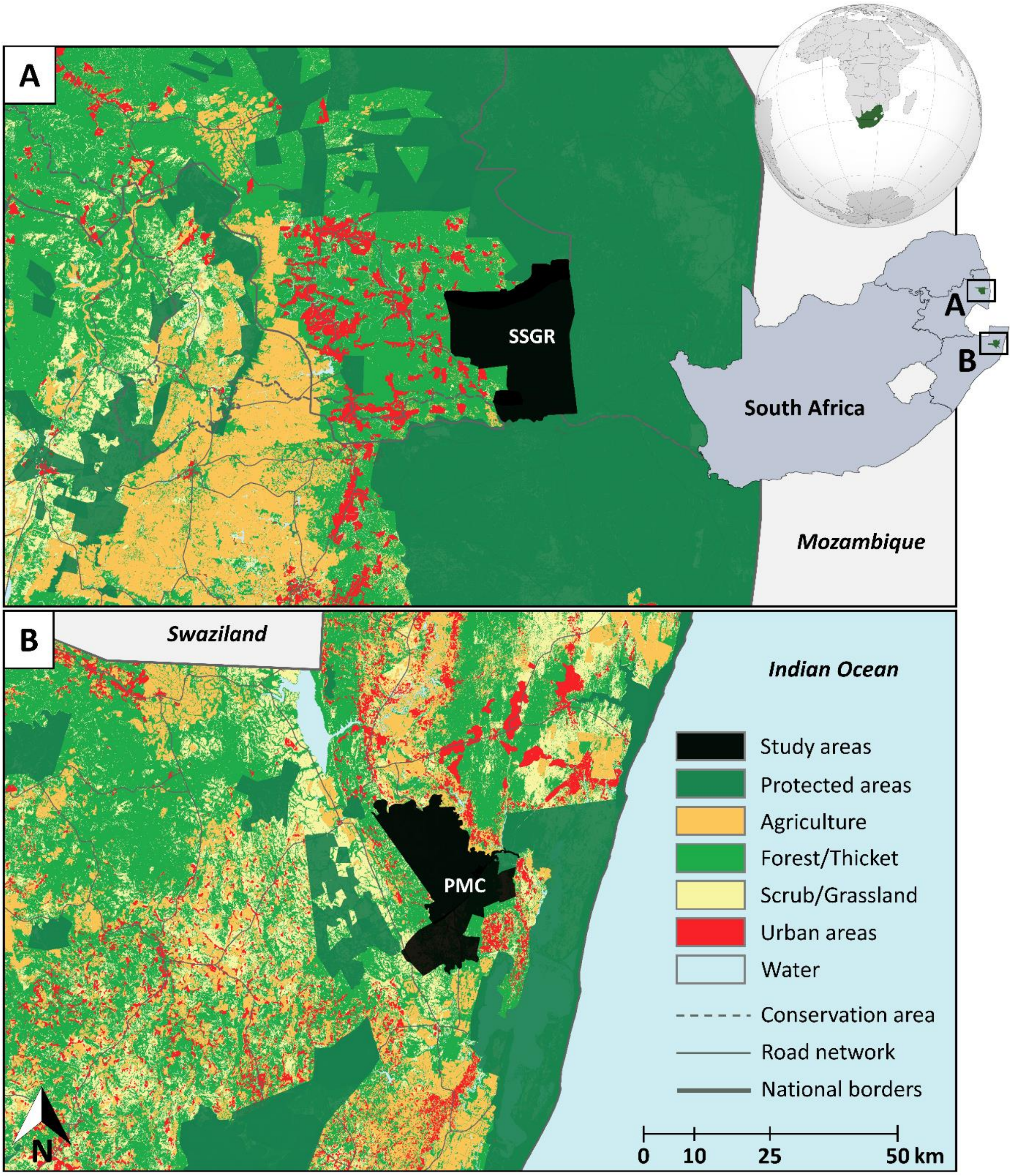


Figure 25. Map showing the two comparative study areas of leopard populations under variable histories of anthropogenically-linked mortality. The surrounding matrix of land use and habitat type are indicated. SSGR: Sabi Sand Game Reserve (A) and PMC: Phinda-uMkhuze Complex (B) are indicated in black. Land use data derived from the South African Biodiversity Institute (SANBI) Archive 2014 - South African National Land-Cover (30 x 30 m raster). Available at: http://bgis.sanbi.org/DEA_Landcover/project.asp.

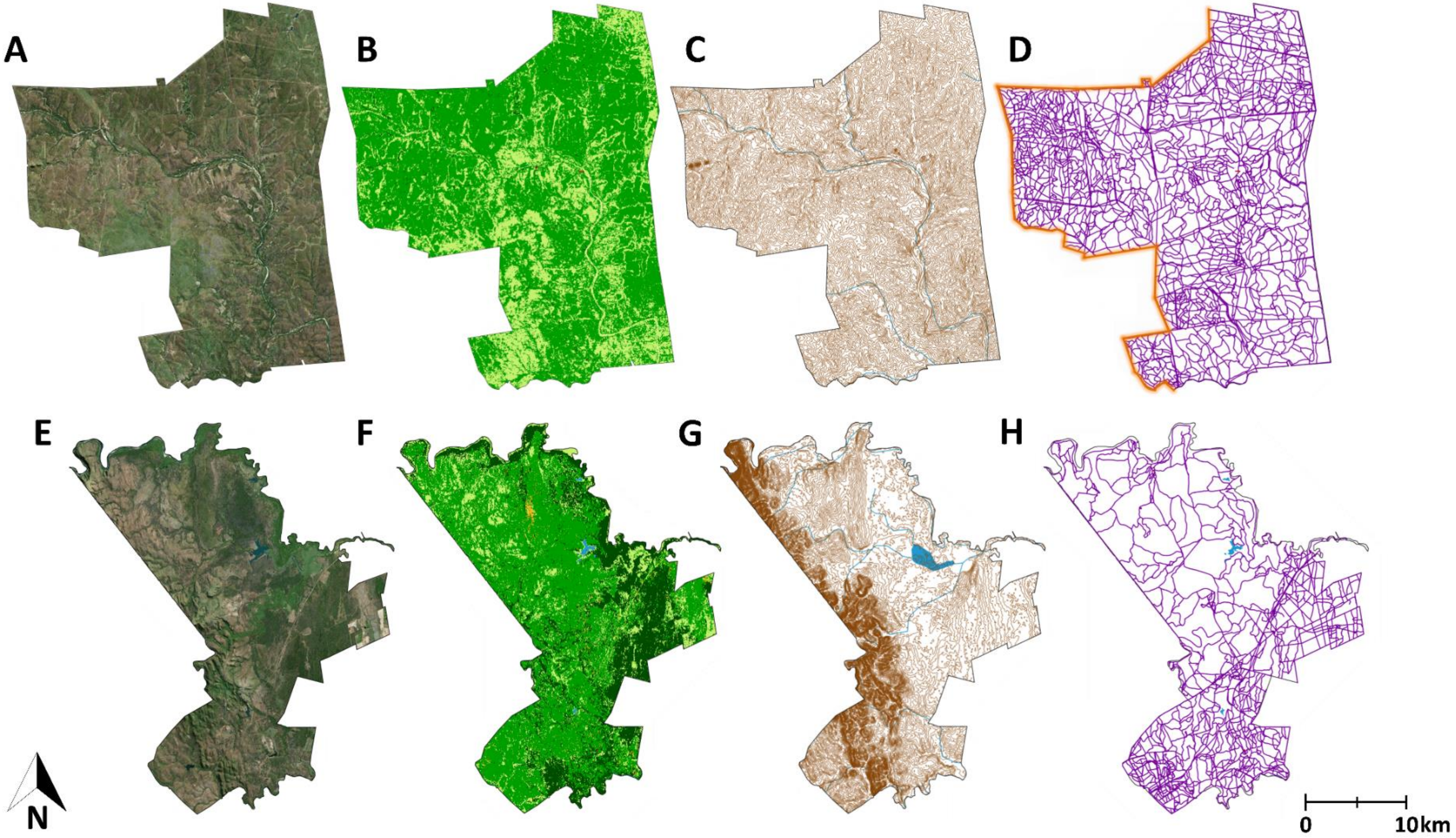


Figure 26. Iterative maps of the Sabi Sands Game Reserve (SSGR; A–D) and Phinda-uMkhuze Complex (PMC; E–H). Indicated are (left to right): high-resolution aerial imagery; landcover (this layer key is identical to that of Figure 25); relative elevation (5 m contours); the two-track or graded road networks (purple); and leopard impermeable fences (orange) in both reserves. These serve to show that leopard habitat is maintained and contiguous throughout both reserves and indeed beyond these borders with no evidence of limited connectivity through physical barriers to dispersal and subsequent genetic connectivity.

Historically, the SSGR and PMC populations were possibly linked via dispersal (Fattebert *et al.*, 2013). The two study sites also have similar habitats (i.e., open to semi-wooded savannah), climates (i.e., mean monthly temperatures ranging from 19 °C–33 °C and an average annual rainfall of ~600 mm), levels of prey abundance, and leopard densities (SSGR: 11.81 ± 2.56 leopards per 100 km^2 [Balme *et al.*, 2019], PMC: 9.51 ± 1.22 leopards per 100 km^2 following recovery [Rogan *et al.*, 2019]), forming contiguous leopard habitat with no physical barriers to dispersal (Figure 26). Accordingly, the observed differences in spatial behaviour and genetic structure are assumed to be the result of human interference rather than due to other environmental or ecological factors, such as competitor presence or density which does not differ between these reserves (Fattebert *et al.*, 2016; Balme *et al.*, 2017b; 2019; Rogan *et al.*, 2019).

4.3.2. Data collection and sampling

In the SSGR, individual location data were collected through direct observation of leopards, using methods detailed in Balme *et al.* (2017b). Briefly, the SSGR hosts several ecotourism lodges that operate high-end photographic safaris. Clients are taken on ‘game-drives’ twice daily led by an experienced guide and tracker. The high density of vehicles (98 ± 2 vehicles per game drive) and extensive road network (mean road density of 3.2 km per km^2) ensures that most of the reserve is traversed daily at a high expected vehicle encounter rate (0.17 ± 0.05 vehicles per km). Drives are not limited to roads, as skilled trackers pursue charismatic species by vehicle or on foot until the animal is located, or the tracks are lost. This intensive search effort results in frequent sightings; on average, 6,428 ± 914 unique leopard sightings are recorded per annum with individual leopards being seen on average every 2.74 ± 0.04 days. Leopards in the SSGR are highly habituated to vehicles and guides are familiar with the individuals residing in their traversing area (individual leopards can be distinguished by their unique vibrissae patterning [Miththapala *et al.*, 1989]). Data captured include the identity of the individual leopard (if known), GPS location of the sighting, the presence and number of offspring, as well as other notable behaviour (e.g., intra- and inter-specific interactions). Although multiple guides sometimes submitted data from the same sighting, we retrospectively filtered the data to ensure that each unique sighting was captured only once, that is, an individual leopard was included in only a single sighting per game drive. To assess the accuracy of the guides’ ability to distinguish individuals, they were asked to submit photographs with the putative identity of the animal from a random subset of sightings; they correctly identified the individual leopard (n = 121) in all photos. We also cross-referenced data submitted by guides from different lodges to assess the consistency of the information captured and found no significant discrepancies (as in Balme *et al.*, 2012). Samples for DNA analysis were obtained from leopard faecal deposits collected by guides in the SSGR. Only samples where the guide observed the leopard defecating (and they were therefore confident of its identity) were used in analyses. In total, 145 samples from 81 individuals were collected between 2015 and 2018. Faecal samples were dry-stored on silica beads at -20 °C.

Spatial data in the PMC were collected using telemetry, following methods detailed in Fattebert *et al.* (2016). Leopards were captured using a combination of free-darting, cage-trapping, and soft-hold foot-snaring and fitted with either a very high frequency (VHF; 250 g, Sirtrack Ltd., Havelock North, New Zealand, 0.5% of adult female body mass) or GPS (420 g, Vectronic-Aerospace, Berlin, Germany, 1.2% of adult female body mass) collar. VHF-collared individuals (n = 41) were located every three days on average to within ~100 m using ground homing or triangulation across the PMC (mean road density of 2.6 km per km^2), whereas GPS collars (n = 28) were programmed to record 2–6 fixes daily. Ear-punch biopsy samples from 69 individuals were collected for genetic analyses during captures from 2002–2012. Tissue samples were stored in >90% ethanol at -20 °C. Capture and collaring of leopards was approved (research permit HO/4004/07) by the provincial conservation authority, Ezemvelo KwaZulu-Natal Wildlife, and by the Animal Ethics Subcommittee of the University of KwaZulu-Natal Ethics Committee (approval 051/12/Animal).

4.3.3. Home range estimation

To determine the spatial distribution and dispersal patterns of individuals in the two study populations, I calculated home range estimates (i.e., size, centroid, utilization density, and overlap) for all sexually mature (≥3 years) leopards post-dispersal (Balme *et al.*, 2013a), using autocorrelated kernel density estimates (AKDEs; Fleming *et al*. 2015), where an analysis of variance (ANOVA) was used to identify significant differences in relocation counts between individuals of different spatial sampling types (i.e., observation, GPS, and VHF). These 95% AKDEs are considered robust for comparisons between different spatial data types (Fleming *et al*. 2015). All pairwise comparisons of spatial overlap between individuals were restricted to periods of temporal co-occurrence (over a continuous four-year sampling period of three generations). Subsequent analyses were focussed on home range overlap (HRO; Bhattacharyya Coefficient [BC]) as the most relevant metric with regard to inbreeding opportunity, as this relates directly to encounter potential and is not affected by between-site variance in home range size (km^2). Variogram calculations, movement model fits, and home range estimations were implemented in the *ctmm* package (Fleming *et al*. 2015; Calabrese *et al.*, 2016). Home range centroids were estimated as the geometric mean of coordinates used to fit the AKDE contours.

Estimated semi-variance (i.e., the frequency with which an individual leopard traversed the same area) was plotted as a function of time-lag (Appendix 9 and 10) to visually inspect the autocorrelative structure of the location data (Fleming *et al.*, 2014). Brownian Motion (BM) or Ornstein-Uhlenbeck (OU) movement models were used at zero to short time lags, where a linear increase in the semi-variance corresponded with uncorrelated velocity, whereas integrated OU (IOU) or OU with foraging (OUF) was used where upward curvature at these time lags indicated autocorrelation in the velocity. Meaning that for individuals where there was relatively little data (frequency of repetition in traversed space), standard BM or OU movement models were used to calculate home ranges. As these did not have sufficient home range crossing data, no individual velocity data could be generated. Where there was sufficient home range crossing time data, IOU or OUF movement models could be used to infer velocity and further inform home range use (i.e., utilisation density) for these individuals. If plotted semi-variance did not approach an asymptote, individuals were not considered to be range residents; these leopards were either not monitored for long enough or did not exhibit behaviours that met the definition of range residents and were removed from further analyses. Thereafter, space use was investigated by assessing behaviour across longer time lags, where range residents were expected to reach an asymptote on a timescale that corresponds to the home range crossing time (Fleming *et al.*, 2014; Calabrese *et al.*, 2016). Maximum-likelihood model fits (Fleming *et al.*, 2014) were ranked by AICc (AIC corrected for small sample size; Calabrese *et al.*, 2016). Home ranges were estimated conditionally on the fitted and selected model per individual. OU models are described using two parameters (i.e., home range crossing time in days and variance in km^2) while OUF models are described using three (i.e., home range crossing time in days, velocity autocorrelation timescale in hours, and variance in km^2). OU models provided home range and crossing time estimates, where OUF models provided these metrics as well as the velocity autocorrelation timescale and average distance travelled per individual. Finally, volumetric space-time utilisation density (UD) and HRO (BC) were estimated based on these selected models (Fieberg & Kochanny, 2005; Winner *et al.*, 2018). All analyses were conducted in *R* (R Core Team, 2019) and *QGIS* (QGIS Development Team, 2019).

4.3.4. *DNA extraction, PCR, and genotyping*

DNA was successfully extracted for 81 individuals from SSGR and 69 individuals from PMC. DNA was extracted from faecal samples using the QIAamp DNA Stool Mini Kit and from tissue using the DNEasy Blood and Tissue Kit (Qiagen, Inc., Valencia, CA, USA) following the instructions of the manufacturers. Individuals were genotyped at 22 microsatellite loci (Table 15) previously shown to be polymorphic in leopards (Uphyrkina *et al.*, 2001; McManus *et al.*, 2014; Ropiquet *et al.*, 2015) together with a Zn-finger linked sexing marker (Pilgrim *et al.*, 2004). PCR reactions contained 50–100 ng/µl DNA, 200 ng/µl BSA, a locus-specific $MgCl_2$ concentration (1.5–2.5 mM), 2.0 µM each of forward-labelled and reverse primers, 5 µl DreamTaq™ Green PCR Master Mix (Thermo Scientific), and deionised water to a total reaction volume of 25 µl. PCRs were performed on an Applied Biosystems Veriti® Thermal Cycler. Given the generally lower quality DNA extracted from faecal samples, all samples were amplified in singleplex and in triplicate (from extraction to amplification) to ensure reproducibility. Locus-specific thermal profiles were developed following Menotti-Raymond *et al.* (1999) and PCR products were pooled according to size and fluorescent labelling for visualization (Table 15). A positive control was used for size scoring between runs and a negative control was included in each run. Genotypes were analysed on a 3100-Avant Genetic Analyzer (Applied Biosystems) at the Central Analytical Facility, Stellenbosch University, South Africa. Genotypes were sized using the LIZ® 600 internal size standard and alleles were scored in GENEIOUS R10 (Biomatters Limited). Automated allele calls were manually checked for accuracy. Genotyping error was assessed per triplicate sample run on each individual and ≥2/3 consensus alleles used in subsequent analyses; where no such consensus was achieved or genotypes failed (≤15/22 loci amplified), whole genotypes were removed. Where available, known parent-offspring relationships were used to find mismatches. Stutter errors, large allele dropouts, short allele dominance, and significant departures from HWE were examined across loci for each population using a χ^2 test for goodness of fit and sequential Bonferroni corrections performed on the resulting *P*-values (Rice, 1989). FSTAT 2.9 was used to test for LD between pairs of loci (Goudet, 2002). The significance of sex ratio estimates for each population was assessed with a binomial distribution test, calculated as the probability of the observed number of males and females given an expected sex ratio of 0.5.

4.3.5. *Kinship, relatedness, and inbreeding*

Parentage assignment and relatedness indices were used to confirm kinship and augment the observed pedigrees for both populations. Individual parentage assignments were estimated within a maximum-likelihood framework implemented in CERVUS 3.0 (Kalinowski *et al.*, 2007). Simulations were generated at a given level of confidence for all offspring analysed. Parameters included: 100,000 offspring, 2% mistyped loci, 89% typed loci for SSGR, and 93% typed loci for PMC, as determined by CERVUS for the dataset. Parentage assignment was only tested if a minimum of 15 loci were successfully genotyped, while candidate parents were limited to adults (≥3 years old) and breeding pairs that were alive at the same time. Parents were assigned based on Likelihood-of-Difference (LOD) scores calculated at both 95% (strict) and 80% (relaxed) confidence levels. The strict assignment was used to build whole pedigrees, whereas the more relaxed assignment was used to provide further insight into likely relationships between individuals when not strictly assigned. Where no 95% assignment was supported, and a clear 80% assignment was available, this was used to assign parentage. Pairwise relatedness between all individuals in both populations was estimated using the Wang relatedness metric (r_w) in SPAGeDI 1.0 (Hardy & Vekemans, 2002; Wang, 2002). This estimator was chosen for its apparent desirable properties among reviewed relatedness indices, namely, low sensitivity to the sampling error that results from estimating population allele frequencies and a low sampling variance that decreases asymptotically to the theoretical minimum with increasing numbers of loci and alleles per locus (Blouin, 2003). For each population, the frequency distribution of relatedness coefficients was summarised for defined kin-categories (i.e., unknown, parent-offspring, full-sibling, half-sibling, and breeding pairs) based on field observations (e.g., mothers with offspring or siblings), parentage analysis, and relatedness scores. Observed pedigrees were supported and expanded for both populations and inbreeding events recorded. In addition, the *adegenet* (Jombart, 2008) and *ape* (Paradis & Schliep, 2018) *R*-packages were used to estimate per locus and population-level inbreeding coefficients (F_{IS}).

4.3.6. Spatio-genetic structure

To test for evidence of restricted or disrupted dispersal, I examined the fine-scale genetic structure of offspring (mother-daughter [M-D] and mother-son [M-S]) and sex-based dyads (female-female [F-F], female-male [F-M], and male-male [M-M]) per unit distance from the natal range in the two study populations. I first superimposed assigned maternal home range centroids with a concentric ring (i.e., the average maternal home range area) surrounded by three concentric rings representing: the nearest-neighbouring maternal home range (1st order); the next peripheral neighbouring maternal home range (2nd order); and all other maternal home range areas beyond this periphery. Here, the width of each band represented the average maternal home range radius by population. Offspring (those assigned through parentage analyses) home range centroids were then plotted in relative x-y proximity to their natal centroid and their frequencies plotted by concentric ring, so as to schematically represent the differences in philopatric home range establishment relative to the natal home range by sex for each population.

I then quantified the association between matrices of pairwise genetic and spatial distances (Smouse & Peakall, 2001; Peakall *et al.*, 2007) through direct correlation, spatial auto-correlation analysis, and Mantel tests implemented in the *ecodist* package (Goslee & Urban, 2007). Under a restricted or disrupted dispersal model, auto-correlograms yield positive correlations at short spatial distances (classes represent the average home range diameter per sex and population), followed by a gradual decrease to zero with increasing geographical distance, and a subsequent random fluctuation of positive and negative values of the correlation coefficient (Smouse & Peakall, 2001). The first x-intercept estimates the extent of non-random genetic structure or defines the point at which random stochastic drift replaces gene flow as the key determinant of genetic structure (Vangestel *et al.*, 2011). As this intercept is dependent upon the true scale of genetic structure, the chosen distance class size, and the sample size per distance class (Peakall *et al.*, 2007), I also performed a second auto-correlation analysis in which I plotted pairwise genetic distances against increasing inclusive distance classes. Here, the distance class at which the auto-correlation coefficient no longer remains significant (999 bootstraps) approximates the true extent of identifiable genetic structure between groups of individuals (Peakall *et al.*, 2007).

4.4. Results

4.4.1. Home range estimates

Home ranges (km^2) were successfully estimated for all 142 adult leopards for which we had genetic data (SSGR: females = 49, males = 24, total = 73, Appendix 9; PMC: females = 31, males = 38, total = 69, Appendix 10). Due to high sampling intensity, rare forays or peripheral movements were witnessed (mostly among young males) and accounted for in all three datasets, where home range relocation counts did not differ significantly between individuals of different spatial sampling types ($\bar{x}_{\text{observed}}$ = 336 ± 7.20 [SE], $\bar{x}_{\text{GPS}}$ = 367 ± 14.20, $\bar{x}_{\text{VHF}}$ = 361 ± 11.7; F_2 = 2.99; *P* = 0.05). Male home ranges were markedly larger than that of females in both the SSGR ($\bar{x}_{\text{female}}$ = 26.93 ± 2.37 km^2, $\bar{x}_{\text{male}}$ = 50.02 ± 5.43 km^2, t_{32} = 3.90; *P* <0.001) and PMC ($\bar{x}_{\text{female}}$ = 31.54 ± 1.34 km^2, $\bar{x}_{\text{male}}$ = 50.32 ± 5.01 km^2; t_{44} = 3.57; *P* <0.001). Female and male home-range size did not differ between study populations (Table 22).

Table 22. Autocorrelated kernel density estimates (95%) of leopard home range size within and between sexes. These were estimated for known leopards (*n* = 142) within the Sabi Sand Game Reserve (SSGR) and Phinda-uMkhuze Complex (PMC), South Africa, from 2002–2018. These are presented as the total number per category (*n*), mean home range size in square kilometres ($\bar{x}$), standard errors (SE), and associated *P*-values based on the t-statistic for independent variables (two-tailed), with Welch-correction for unequal variance, where 95% confidence intervals are presented (CI).

Category		**SSGR**		**PMC**		**Comparison**		
		n	$\bar{x}$ (±SE)	*n*	$\bar{x}$ (±SE)	t_{df}	*P*-value	CI
Female		49	26.93 (2.37)	31	31.54 (1.34)	1.60_{78}	0.113^{ns}	-10.36; 1.13
Male		24	50.02 (5.43)	38	50.32 (5.01)	0.04_{54}	0.968^{ns}	-15.12; 14.51
All Individuals		73	34.50 (2.69)	69	41.90 (3.05)	1.81_{136}	$0.073^{\cdot}$	-15.30; 0.61
SSGR	Female / male					3.90_{32}	<0.001***	-35.16; -11.03
PMC	Female / male					3.57_{44}	<0.001***	-29.41; -8.16

Significance (^{ns} = non-significant; $^{\cdot}$P ≤ 0.10; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001)

4.4.2. Genotyping and genetic diversity

The final dataset (Table 23) consisted of 15–21 loci successfully typed for 142 known individuals in the two study populations. 'Extraction to genotyping success' (number of repeats required per sample) was significantly lower in the PMC than in the SSGR ($\bar{x}_{\text{PMC}}$ = 1.04 ± 0.03 [SE], $\bar{x}_{\text{SSGR}}$ = 2.56 ± 0.09; t_{81} = 15.69; *P* <0.001; CI = -1.71, -1.33) and genotyping failed (<15/22 loci amplified successfully) for only eight leopards (SSGR = 8 and PMC = 0). Locus FCA096 was removed from all further analyses due to poor amplification success (14–30% of individuals). There was no evidence of LD or scoring errors due to large allele dropout and stutter in either population. Mean genotype coverage was higher in the SSGR than in the PMC ($\bar{x}_{\text{SSGR}}$ =68.05 ± 0.39, $\bar{x}_{\text{PMC}}$ = 63.52 ± 1.57; t_{40} = 2.80; *P* = 0.008; CI = 1.26, 7.79). SSGR supports greater heterozygosity ($\bar{x}_{\text{SSGR}}$ = 0.78 ± 0.03, $\bar{x}_{\text{PMC}}$ = 0.65 ± 0.03; t_{40} = 3.01; *P* <0.005; CI = 0.04, 0.22), allelic richness ($\bar{x}_{\text{SSGR}}$ =6.01 ± 0.31, $\bar{x}_{\text{PMC}}$ = 4.89 ± 0.26; t_{38} = 2.78; *P* = 0.008; CI = 0.30, 1.94), and mean number of private alleles per locus than PMC ($\bar{x}_{\text{SSGR}}$ =2.86 ± 0.37, $\bar{x}_{\text{PMC}}$ = 0.52 ± 0.13; t_{24} = 5.90; *P* <0.001; CI = 1.52, 3.15). With the exception of some locus-level deviations, the SSGR population was in HWE (Table 23), whereas PMC was not, with 12 out of the 21 markers out of HWE. The SSGR showed significant female bias (z = 2.81, *P*

= 0.003), with no significant sex bias in PMC (z = -0.72, *P* = 0.235). As there are likely very few unknown individuals in both populations, these sex ratios are assumed to reflect absolute sex ratios and are thus not expected to create a bias in overlap measures.

Table 23. Microsatellite diversity of 142 known leopards within the SSGR and PMC, South Africa, from 2002–2018. Parameter estimates are presented as the number of individuals successfully typed (n), number of alleles (A_n), allelic richness (A_r), number of private alleles (A_p), observed heterozygosity (H_O), and expected heterozygosity (H_E). In summary are shown: the mean ($\bar{x}$), standard error (±SE), and total for each parameter and associated P-values based on the χ^2 statistic of deviation from Hardy-Weinberg Equilibrium. FCA096 was removed from all further analyses due to poor amplification success (14–30% of individuals).

Locus	**Sabi Sand Game Reserve (SSGR)**							**Phinda-uMkhuze Complex (PMC)**						
	n	A_n	A_r	A_p	H_O	H_E	F_{IS}	n	A_n	A_r	A_p	H_O	H_E	F_{IS}
FCA008	69	10	6.36	2	0.78*	0.77	-0.02	63	8	5.12	0	0.72^{ns}	0.76	0.06
FCA026	68	13	7.32	4	0.81^{ns}	0.81	-0.01	68	9	6.97	0	0.85^{ns}	0.83	-0.04
FCA043	70	9	5.39	2	0.88^{ns}	0.77	-0.14	69	8	4.70	1	0.44*	0.61	0.23
FCA075	70	12	5.67	3	0.78*	0.65	-0.19	68	10	5.02	1	0.58*	0.65	0.14
FCA077	70	9	6.92	1	0.95^{ns}	0.84	-0.14	68	9	6.10	1	0.80^{ns}	0.77	-0.05
FCA090	65	9	6.42	3	0.72*	0.80	0.01	63	6	5.05	0	0.68*	0.79	0.15
FCA094	70	9	5.73	4	0.87*	0.77	-0.13	64	5	3.92	0	0.62^{ns}	0.63	0.01
~~FCA096~~	~~11~~	~~13~~	~~9.00~~	~~11~~	~~0.54*~~	~~0.81~~	~~0.32~~	~~21~~	~~2~~	~~2.00~~	~~0~~	~~0.18~~^{ns}	~~0.17~~	~~-0.10~~
FCA097	66	10	6.57	2	0.79^{ns}	0.82	0.03	54	10	7.41	2	0.59*	0.85	0.26
FCA105	68	9	4.94	5	0.67*	0.61	-0.10	68	4	3.16	0	0.70^{ns}	0.64	-0.10
FCA126	68	13	8.53	7	0.96^{ns}	0.87	-0.11	68	6	3.97	0	0.44*	0.61	0.20
FCA139	66	8	4.37	3	0.48^{ns}	0.42	-0.13	68	6	4.51	1	0.75^{ns}	0.70	-0.08
FCA161	66	7	5.76	1	0.86^{ns}	0.80	-0.08	66	6	4.43	0	0.69^{ns}	0.69	-0.01
FCA220	68	10	7.43	5	0.88^{ns}	0.86	-0.03	65	6	4.76	1	0.65*	0.75	0.13
FCA221	70	8	6.11	4	0.79^{ns}	0.81	0.02	61	4	3.95	0	0.61*	0.71	0.11
FCA224	66	12	8.07	5	0.88^{ns}	0.85	-0.05	51	8	6.48	1	0.84*	0.92	0.11
FCA229	68	9	7.13	1	0.85^{ns}	0.83	-0.03	61	8	5.17	0	0.59*	0.58	-0.04
FCA247	66	8	5.53	1	0.75*	0.74	-0.02	40	8	5.68	1	0.77*	0.76	-0.02
FCA310	66	8	6.11	2	0.90^{ns}	0.82	-0.10	65	7	5.39	1	0.75*	0.89	0.14
FCA441	70	5	3.37	1	0.49^{ns}	0.44	-0.13	68	4	2.88	0	0.31^{ns}	0.30	-0.05
FCA453	69	6	2.66	3	0.43^{ns}	0.36	-0.20	68	4	3.29	1	0.60^{ns}	0.59	-0.03
FCA678	70	9	5.80	1	0.80*	0.74	-0.08	68	8	4.67	0	0.56*	0.72	0.21
$\bar{x}$	**65.45**	**8.40**	**6.15**	**3.23**	**0.78**	**0.73**	**-0.08**	**61.59**	**6.64**	**4.76**	**0.50**	**0.65**	**0.70**	**0.06**
SE	**2.62**	**0.46**	**0.32**	**0.51**	**0.03**	**0.04**	**0.02**	**2.45**	**0.46**	**0.28**	**0.13**	**0.03**	**0.03**	**0.03**
Total	**-**	**206**	**-**	**71**	**-**	**-**	**-**	**-**	**146**	**-**	**-**	**-**	**-**	**-**

Significance (^{ns} = non-significant; $^{\cdot}$P ≤ 0.10; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001)

4.4.3. Parentage analysis, relatedness, and inbreeding

Formal computational assignment of parentage, via a likelihood framework, was successful for both populations (Table 24). Maternity (without known paternity) was assigned for 63% of offspring in SSGR and for 48% of offspring in PMC, corroborating all 30 putative field-based maternal assignments in SSGR and 25/31 maternal assignments in PMC. Paternity (given known maternity) was assigned for a 64% of offspring in PMC and 54% in SSGR, confirming all 20 putative sires in SSGR and 16/28 in PMC. Bi-parental assignment was not possible for 30% of offspring in SSGR and 19% in PMC, while the predicted resolving power (95% confidence) of loci sampled was higher in SSGR (99%) than in PMC (96%), with 1% and 4% assigned with 80% confidence in SSGR and PMC, respectively.

Table 24. Parentage assignment success for known leopards within the Sabi Sand Game Reserve (SSGR) and Phinda- uMkhuze Complex (PMC). Parameter estimates are presented as the percentage of individuals for which maternity was successfully assigned, the number of mothers this confirms from field-based observations, the percentage of individuals for with paternity was successfully assigned, the number of fathers this confirms from field-based observation, the percentage of individuals for which bi-parental assignment was not possible, and the resolving power given the variation across these 22 loci within the two populations.

Category	**SSGR**	**PMC**
Maternity assigned	62.90%	47.80%
Field observed maternity confirmed	(30/30)	(25/31)
Paternity assigned	54.30%	64.20%
Field observed paternity confirmed	(20/20)	(16/28)
Assignment not possible (both parents)	30.00%	19.40%
Predicted resolving power of loci across sampled populations[†]	99.00%	96.00%

[†] Percentage of offspring for which CERVUS v 3.0.7 (Marshall *et al.*, 1998) simulation predicts, based on loci sampled, assignment of parentage with 95% confidence.

In both populations, kinship pairs showed mean relatedness coefficients within the limits of their expected distributions (Figure 27), including confirmed breeding pairs in SSGR which were significantly less related than random ($\bar{x} = -0.05$; $t_{12} = 4.27$; $P = 0.001$; CI = -0.08, -0.03). Mean relatedness of confirmed breeding pairs in PMC, however, did not fall within the limits of their expected distribution ($\bar{x} = 0.31$; $t_{11} = 6.07$; $P < 0.001$; CI = 0.19, 0.42). Instead, these were more similar to that expected of the half-sibling distribution ($\bar{x} = 0.31$; $t_{11} = 1.09$; $P = 0.297$; CI = -0.06, 0.17).

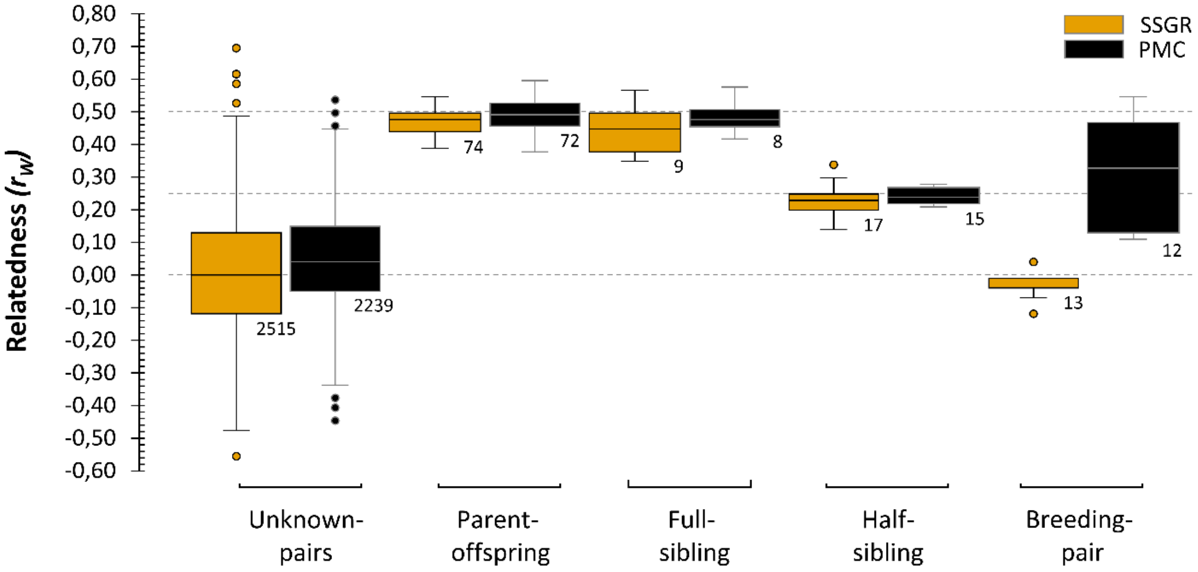


Figure 27. Pairwise relatedness estimates (r_w) of confirmed kinship categories. Expected theoretical relatedness coefficients for parent-offspring or full siblings (0.5), half-sibling (0.25), and unrelated or random pairs (0) are indicated by dashed lines. The distribution for each kinship category and number of pairs (below boxes) is indicated for Sabi Sand Game Reserve (gold; SSGR) and the Phinda-uMkhuze Complex (black; PMC).

Pedigree reconstruction provided no evidence of direct inbreeding in SSGR, whereas in PMC, one father-daughter and two half-sibling mating events were identified. The inbreeding coefficient (F_{IS}) was significantly greater in PMC than in SSGR (Table 23; $\bar{x}_{SSGR}$ = -0.08 ± 0.02 [SE], $\bar{x}_{PMC}$ = 0.06 ± 0.03; t_{40} = 4.93; P <0.001; CI = -0.20, 0.08), with evidence of significant outbreeding in SSGR with F_{IS} scores significantly less than zero ($\bar{x}_{SSGR}$ = -0.08 ± 0.02; t_{20} = 5.27; P <0.0001; CI = -0.11, -0.05), and significant levels of inbreeding in PMC with F_{IS} scores significantly greater than zero ($\bar{x}_{PMC}$ = 0.06 ± 0.03; t_{20} = 2.58; P <0.05; CI = 0.01, 0.12).

4.4.4. Spatio-genetic structure

The mean proportion of home range overlap (Table 25) among all individuals was higher in PMC than SSGR ($\bar{x}_{SSGR}$ = 0.16 ± 0.01 [SE], $\bar{x}_{PMC}$ = 0.20 ± 0.01; t_{2088} = 2.90; P <0.001). While the proportion of home range overlap was not significant between populations for female-female and male-male dyads, female-male home range overlap was significantly higher in PMC than in SSGR ($\bar{x}_{SSGR}$ = 0.15 ± 0.01, $\bar{x}_{PMC}$ = 0.20 ± 0.01; t_{1036} = 3.22; P = 0.001). Home range overlap between kin-related pairs was not significant, with the exception of mother-son pairs in PMC being twice that of SSGR ($\bar{x}_{SSGR}$ = 0.31 ± 0.10, $\bar{x}_{PMC}$ = 0.61 ± 0.06; t_9 = 2.49;

$P = 0.034$), and breeding pair home range overlap being nearly 20% greater in SSGR than PMC ($\bar{x}_{SSGR} = 0.63 \pm 0.05$, $\bar{x}_{PMC} = 0.45 \pm 0.07$; $t_{18} = 2.11$; $P = 0.049$). Home range overlap between mother-daughter pairs was slightly greater than mother-son pairs in SSGR ($\bar{x}_{FD} = 0.55 \pm 0.06$, $\bar{x} = 0.31 \pm 0.10$; $t_9 = 2.03$; $P = 0.073$).

Table 25. Pairwise home range overlap of 95% autocorrelated kernel density estimates. Described are the utilisation density (UD) per dyad, confirmed kin-relationships, and breeding pairs across all individuals for 142 known leopards within the Sabi Sand Game Reserve (SSGR) and Phinda-uMkhuze Complex (PMC), South Africa from 2002–2018. Parameter estimates are presented as the percentage of population pairs with overlap (%), mean proportion of home range utilization overlap ($\bar{x}$), standard errors (SE), and associated *P*-values based on the t-statistic for independent variables (two-tailed), with Welch-correction for unequal variance, where confidence intervals are presented (CI).

Category	SSGR		PMC		**Comparison**		
	%	$\bar{x}$ (±SE)	%	$\bar{x}$ (±SE)	t_{df}	*P*-value	CI
All Individuals	45.51	0.16 (0.00)	43.22	0.20 (0.00)	4.54_{2088}	<0.001***	-0.07, 0.03
Dyads							
Female-Female	48.13	0.15 (0.00)	44.52	0.18 (0.02)	1.48_{334}	0.140^{ns}	-0.07, 0.00
Female-Male	44.47	0.15 (0.01)	44.14	0.20 (0.01)	3.22_{1036}	0.001**	-0.08, -0.02
Male-Male	38.79	0.18 (0.02)	40.83	0.22 (0.01)	1.27_{200}	0.203^{ns}	-0.09, 0.02
Kin-relationships							
Father-Daughter	63.16	0.49 (0.08)	76.47	0.34 (0.06)	1.61_{18}	0.124^{ns}	-0.04, 0.33
Father-Son	33.33	0.32 (0.14)	39.13	0.39 (0.11)	0.41_{6}	0.694^{ns}	-0.51, 0.36
Mother-Daughter	70.37	0.55 (0.06)	92.86	0.59 (0.07)	0.44_{27}	0.666^{ns}	-0.24, 0.15
Mother-Son	48.73	0.31 (0.10)	81.15	0.61 (0.06)	2.49_{9}	0.034*	-0.55, -0.05
Breeding Pairs	100	0.63 (0.05)	83.33	0.45 (0.07)	2.11_{18}	0.049*	0.00, 0.37
SSGR							
Father-Daughter | Father-Son			(*n* = 19/12)		1.07_{4}	0.344^{ns}	-0.27, 0.61
Mother-Daughter | Mother-Son			(*n* = 27/16)		2.03_{9}	$0.073^{\cdot}$	-0.03, 0.52
PMC							
Father-Daughter | Father-Son			(*n* = 17/23)		0.39_{10}	0.706^{ns}	-0.31, 0.22
Mother-Daughter | Mother-Son			(*n* = 14/18)		0.14_{25}	0.893^{ns}	-0.21, 0.18

Significance (^{ns} = non-significant; $^{\cdot}P \leq 0.10$; $^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$)

Of the 27 daughters (Figure 28A) and 16 sons (Figure 28C) assigned in SSGR, 37% of daughters and no sons established home range centroids within their mean maternal home ranges, 30% of daughters and 25% of sons within the 1st order mean peripheral home range, 3% of daughters and 19% of sons within the 2nd order, and 30% of daughters and 56% of sons beyond. In contrast, of the 14 daughters (Figure 28B) and 18 sons (Figure 28D) assigned in

PMC, 43% of daughters and 22% of sons established home range centroids within their mean maternal home ranges, 43% of daughters and 50% of sons within the 1st order mean peripheral home range, 14% of daughters and 11% of sons within the 2nd order, and no daughters and 17% of sons beyond.

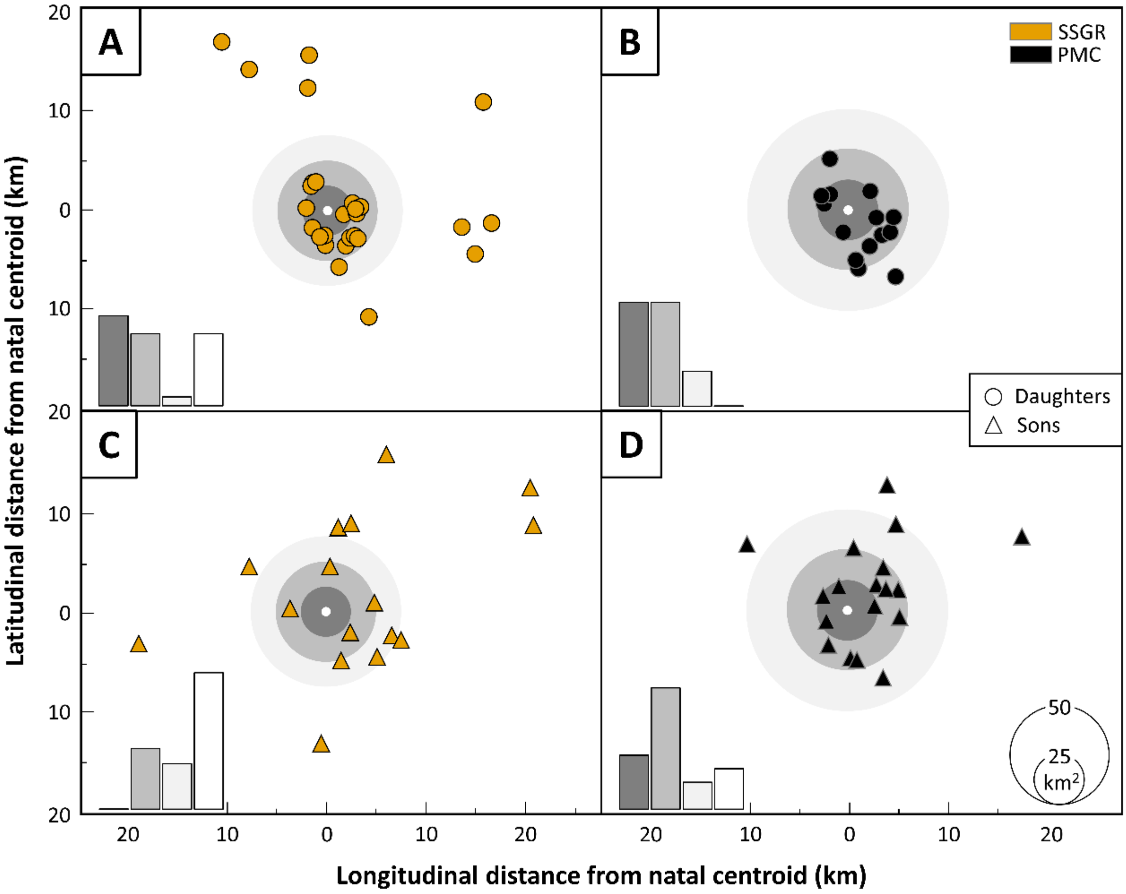


Figure 28. Spatial distribution of post-dispersal offspring relative to their natal home range. Post-dispersal centroids for daughters (circles) and sons (triangles) are shown relative to their superimposed maternal centroids (white circles) for Sabi Sand Game Reserve (gold; SSGR) and Phinda-uMkhuze Complex (black; PMC). Rings of grey indicate the area of successional mean female home range (95% Autocorrelated Kernel Density Estimate) radii around the natal centroid. Three levels are shown: the maternal home range (dark grey), the 1st order peripheral home range (grey), and the 2nd order peripheral home range. A linear summary of the proportion of individuals in each category is provided (bar graph bottom left).

Mantel tests showed population-level spatio-genetic structuring in both populations (Figure 29). Pairwise relatedness (r_W) decreased significantly as the proximity (km) between individuals increased within female-female dyad pairs in SSGR ($R^2 = -0.16$; $P < 0.001$) and within female-female ($R^2 = -0.23$; $P < 0.001$), female-male ($R^2 = -0.25$; $P < 0.001$), and male-male ($R^2 = -0.12$; $P = 0.025$) dyad pairs in PMC (Figure 29; Table 26). Auto-correlograms revealed fine-scale spatio-genetic structure by pairwise proximity between individuals in each dyad. Female kin-clustering was observed in both populations (Figure 29A), where significantly positive autocorrelation occurred over three female home range radii in SSGR (0–6 km) and four in PMC (0–8 km). This female kin-clustering effect was stronger over these distances in the PMC. Significant clustering of females that were less related than expected at random occurred for a range beyond this distance in both populations (SSGR= 16–24 km, PMC = 14–24 km) while the spatio-genetic structure of all dyads showed no significant autocorrelation (spatio-genetic independence) beyond 24 km in both reserves. While this relationship was stronger in PMC than SSGR, significantly positive female-male kin-clustering occurred over five home range radii in SSGR and four in PMC (Figure 29B). Significant clustering of unrelated individuals then occurred for a range beyond this distance in both populations (SSGR = 12–26 km, PMC = 12–34 km), while all spatio-genetic structure attenuated beyond 24–28 km in both reserves. The spatio-genetic structure of male-male dyad pairs was largely independent throughout both populations (Figure 29C), with some isolated incidents of significant autocorrelation. Spatio-genetic structure in SSGR was independent, while bimodal structure occurred in PMC (8–14; 21–25 km) which attenuated beyond 26 km.

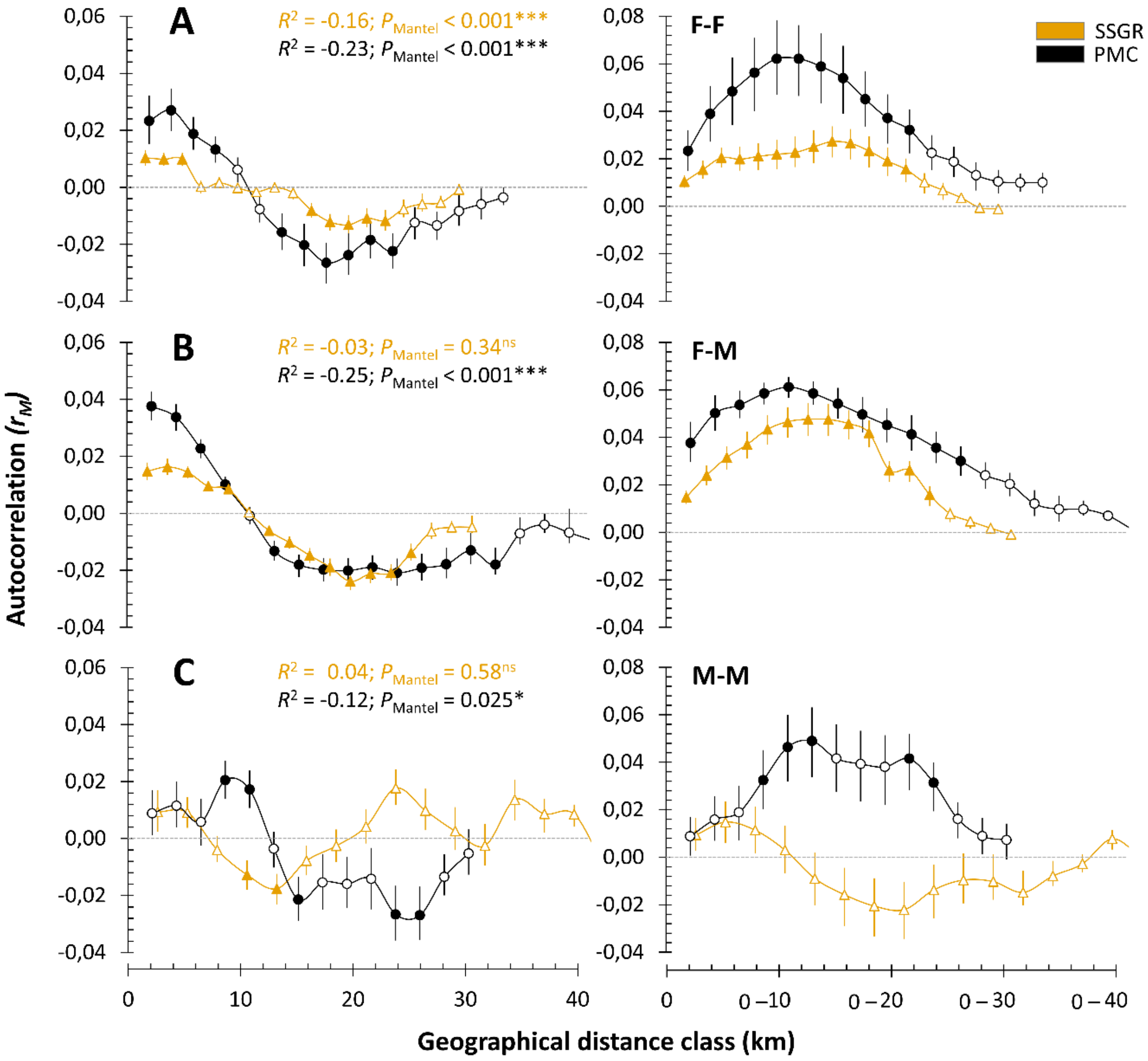


Figure 29. Spatial autocorrelation of pairwise relatedness estimates. Geographical distances (km) are indicated for the Sabi Sands Game Reserve (gold triangles; SSGR) and the Phinda-uMkhuze Complex (black circles; PMC) by (A; F-F) female-female, (B; F-M) female-male, and (C; M-M) male-male dyads. These are depicted as a function of geographic distance (left) and as the effect of different distance class sizes on the extent of genetic autocorrelation (right). Significant spatio-genetic autocorrelation is indicated by solid shapes and its direction indicated above or below the dashed zero-line. Hollow shapes indicate non-significance or an independent spatio-genetic pattern within the distance class.

Table 26. Pairwise distances (km) between home range centroids. Shown are the pairwise distances between 95% autocorrelated kernel density estimate centroids per dyad, confirmed kin-relationships, confirmed breeding pairs, and all individuals for 142 known leopards within the Sabi Sand Game Reserve (SSGR) and Phinda-uMkhuze Complex (PMC), South Africa, from 2002–2018. Parameter estimates are presented as the total number of pairs (*n*), mean distance in kilometres ($\overline{x}$), standard errors (SE), and associated *P*-values based on the t-statistic for independent variables (two-tailed), with Welch-correction for unequal variance, where 95% confidence intervals are presented (CI).

	Category	**SSGR**		**PMC**		**Comparison**		
		n	$\overline{x}$ (±SE)	*n*	$\overline{x}$ (±SE)	t_{df}	*P*-value	CI
	All Individuals	2,628	13.40 (0.13)	2346	13.23 (0.16)	0.81_{4719}	0.420^{ns}	-0.24; 0.58
Dyads	Female-Female	1,176	12.90 (0.19)	465	13.70 (0.35)	1.94_{775}	$0.053^{\cdot}$	-1.56; 0.00
	Female-Male	1,176	13.73 (1.99)	1178	13.09 (0.22)	2.15_{2327}	0.032*	0.06; 1.23
	Male-Male	276	14.44 (0.43)	703	13.28 (0.30)	2.21_{566}	0.028*	0.13; 2.18
Kin-relationships	Father-Daughter	19	7.72 (2.15)	17	5.61 (0.46)	0.96_{19}	0.348^{ns}	-2.49; 6.72
	Father-Son	12	10.21 (1.58)	23	10.86 (1.76)	0.28_{31}	0.784^{ns}	-5.47; 4.16
	Mother-Daughter	27	4.61 (1.30)	14	3.57 (0.68)	0.71_{36}	0.482^{ns}	-1.93; 4.02
	Mother-Son	16	7.64 (1.64)	18	3.54 (0.81)	2.24_{22}	0.036*	0.30; 7.89
	Breeding Pair	13	2.27 (0.51)	12	9.70 (2.42)	3.08_{23}	0.005**	-12.43; -2.43
SSGR	Father-Daughter | Father-Son					0.93_{28}	0.359^{ns}	-7.95; 2.97
	Mother-Daughter | Mother-Son					1.45_{32}	0.158^{ns}	-7.30; 1.24
PMC	Father-Daughter | Father-Son					2.90_{24}	0.008**	-9.00; -1.51
	Mother-Daughter | Mother-Son					0.03_{29}	0.979^{ns}	-2.13; 2.19

Significance (^{ns} = non-significant; $^{\cdot}$P ≤ 0.10; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001)

4.5. Discussion

In this chapter, I contrast leopard populations from SSGR (a well-protected population at carrying capacity) and PMC (a post-harvest population in recovery) to reveal the fine-scale genetic consequences of disrupted dispersal due to these markedly different histories of anthropogenic mortality. As predicted, mothers shared >50% of their home ranges with their daughters in both populations. A consequence of this female philopatry is the spatial formation of adult female kin-clusters, a phenomenon evidenced by the strong spatio-genetic autocorrelation in female-female dyads for both SSGR and PMC. Matrilineal assemblages are typical among large, solitary carnivores, having been observed in brown bears (*Ursus arctos*; Støen *et al.*, 2005), pumas (Logan & Sweanor, 2000; Sweanor *et al.*, 2001), and tigers (Smith, 1993; Goodrich *et al.*, 2010; Gour *et al.*, 2013). Strategies to deal with the costs of increased resource competition (for food and mates) implicit in this conservative dispersal by females are assumed to have evolved because of the increased inclusive fitness benefits that accrue — the so-called 'resident fitness hypothesis' (Anderson, 1989; Lambin *et al.*, 2001). This is clearly evident in the recovering PMC, where daughters do not establish beyond the 2nd order mean peripheral home range of mothers. Here, historical anthropogenic mortality may have created 'gaps' in the spatial matrix, allowing mothers to accommodate daughters within their home ranges (Balme *et al.*, 2017a). Female kin-clustering and natal philopatry are evident in SSGR, however unexpectedly, 30% of daughters appear to have dispersed beyond their maternal home ranges. As this population is considered to be at capacity (Balme *et al.*, 2017b), this may be novel evidence of density-dependent female dispersal, as postulated by Fattebert *et al.* (2015a).

Sub-adult males disperse from their natal range at sexual maturity (~3 years old) to avoid conflict with resident adult males (Fattebert *et al.*, 2015b; 2016) and inbreeding with related females (Balme *et al.*, 2019). While kin-recognition mechanisms have evolved in many species to limit close inbreeding, sex-biased natal dispersal is the primary outbreeding mechanism of most polygynous mammals and is essential to maintaining gene flow within and among populations (Greenwood, 1980). Sexually mature male leopards in SSGR conformed to this inbreeding avoidance or mate competition paradigm with no sons establishing within their maternal home ranges. However, in PMC, 22% of sons established home ranges overlapping with their maternal home range, suggesting a disruption in the proximate drivers of male dispersal, leading to reduced dispersal and opportunistic philopatry, in congruence with Fattebert *et al.* (2015b). This is further supported by a strong negative correlation between relatedness and distance among female-male dyads in PMC, resulting in population-level male kin-clustering similar to that of females. While this phenomenon of disrupted dispersal has been reported in large carnivores with cooperative breeding strategies (Loveridge *et al.*, 2007a), it has rarely been documented in solitary species (Riley *et al.*, 2014), and to my knowledge, this is the first evidence of population-level male kin-clustering in a large solitary felid.

Male kin-clustering in polygynous mammals increases the likelihood of opportunistic mating events with close female relatives (sisters, mothers, aunts, and cousins) which, without kin-recognition (Støen *et al.*, 2005), may result in local inbreeding (Perrin & Mazalov, 2000; Matocq & Lacey, 2003). In this chapter, mean relatedness scores among confirmed breeding pairs in SSGR were essentially random (Figure 27), with low population-level F_{IS} scores indicative of significant outbreeding. This result was expected, as there is likely outbreeding and effective gene flow throughout the contiguous Kruger National Park landscape. The high degree of relatedness (half-sibling) among breeding pairs in PMC, however, suggests that historically high levels of anthropogenic mortality promote opportunistic male philopatry and kin-clustering which translates into significant population-level inbreeding (high F_{IS} scores). While behavioural avoidance alone does not seem to be a strong enough driver of dispersal, as local inbreeding was observed (father-daughter and half-sibling) in PMC, it may be muting even stronger population-level inbreeding signals. Similar findings of reduced dispersal and outbreeding benefits linked to sustained harvest have been documented in pumas (Sweanor *et al.*, 2001), bobcats (Johnson *et al.*, 2010), and black bears (*Ursus americanus*; Moore *et al.* 2014). While the PMC leopard population is currently recovering from high levels of anthropogenically-linked mortality (Rogan *et al.*, 2019), demographic-based metrics alone do not reveal the loss of genetic diversity and the consequences this may have for the future health and viability of the population (Kendall *et al.*, 2009). It may be that this 'genetic scarring' effect on the PMC population just represents temporary issues while the population recovers to carrying capacity, rather than a long-term feature of the population. If so, heterozygosity and inbreeding would recover quite rapidly if and when male leopards are forced to disperse further, as long as other unrelated males are immigrating into the PMC from surrounding reserves. The lack of immigration is, therefore, perhaps a bigger problem than male philopatry to the medium-term genetic diversity of the PMC population. My results thus further highlight the importance of population connectivity to ensure gene flow and genetic diversity through immigration (Frankham, 2003; Fattebert *et al.*, 2015b; Hauenstein *et al.*, 2019).

Potential alternative explanations for this observed pattern include within-reserve habitat fragmentation and typical density-dependent dispersal contributing to the differences between these populations because they are at different stages of 'development'. The former posits that high levels of human-caused mortality (such as in the PMC) are correlated with anthropogenic barriers to movement (Tucker *et al.*, 2018). However, there is no evidence to suggest that anthropogenic barriers limit leopard dispersal in either of these populations (Figure 26), and if this were the primary force behind limited dispersal, it would still not explain why these barriers are sex-specific (Figure 29). The latter suggests that the SSGR has been stable for some time, while the PMC is recovering and has only recently stabilised, such that increasing density to parity with SSGR (+2.3 leopards per 100 km^2) might correct male dispersal and ultimately outbreeding. Though demographic recovery is plausible, this does not mitigate the 'genetic scaring' (evident in reduced heterozygosity and increased inbreeding) accrued by the PMC population (and likely many other small reserves) when having undergone fluctuations of extreme harvest. Without immigration and effective connectivity between these reserves (an increasingly scarce alternative), genetic recovery through drift alone may not be rapid enough, as the ongoing genetic resilience of these populations is compromised and at risk of stochastic effects. Moreover, mortality need not be unsustainable to induce these effects, as it is not known whether 'sustainable mortality' by humans would necessarily eliminate the patterns observed. Certainly, less mortality would have a mitigating effect, but it is not known to what degree. This study is limited by the comparison of only two reserves along the wide spectrum of anthropogenic mortality and its impacts. Unfortunately, the fine-scale genetic structure of African leopard populations remains understudied. This hinders the use of heterozygosity, relatedness scores, and conventional inbreeding coefficients as a means of interpreting population-level effects, as there are no baseline data on allelic frequencies and diversity of 'natural' (outbred or panmictic) populations. Despite this, I am encouraged that multiple lines of evidence derived from both spatial and genetic data provide consistent support for anthropogenic mortality driving limited dispersal in males which in turn results in kin-clustering and ultimately inbreeding.

Given time and adequate protection, territorial turnover among male leopards in PMC may slow and stabilise, re-establishing male-biased dispersal and restoring the typical *in situ* outbreeding effect of genetic drift as capacity is reached (Couvet, 2002; Fattebert *et al.*, 2015b). An alternative is leopard translocation under a metapopulation management approach; however, translocations have been largely unsuccessful to date, as leopards are wide-ranging, have complex social dynamics, and are costly to contain (Weilenmann *et al.*, 2010; Athreya *et al.*, 2010; Weise *et al.*, 2014; Ropiquet *et al.*, 2015). Genetic recovery and ultimate sustainability could more likely be managed and fast-tracked by formally maintaining connectivity between PMC and its surrounding reserves (e.g., Makhasa Nature Reserve, Ubombo Mountain Nature Reserve, Isimangaliso Wetland Park, Manyoni Private Game Reserve, Thanda Safari Game Reserve, and Hluhluwe-iMfolozi Park). Wildlife corridors have proven successful in maintaining functional gene flow between populations in large, solitary felids like jaguar (Wultsch *et al.*, 2016) and tiger (Sharma *et al.*, 2013), despite the political (e.g., land ownership and conservation priorities) and logistical (e.g., road networks and suitable habitat) challenges.

Few PAs sufficiently encompass the wide range of these species and large, solitary carnivores effectively confined to small reserves often suffer edge effects and even localised extinction (Woodroffe & Ginsberg, 1998). This chapter demonstrates novel genetic consequences underlying this process and emphasises the importance of managing and mitigating the effects of increasingly threatened PAs and fragmented corridors of structurally suitable habitat that could maintain effective connectivity (Kaiser, 2001; Fattebert *et al.*, 2015a; Hauenstein *et al.*, 2019).

CHAPTER 5

SYNTHESIS AND CONCLUSIONS

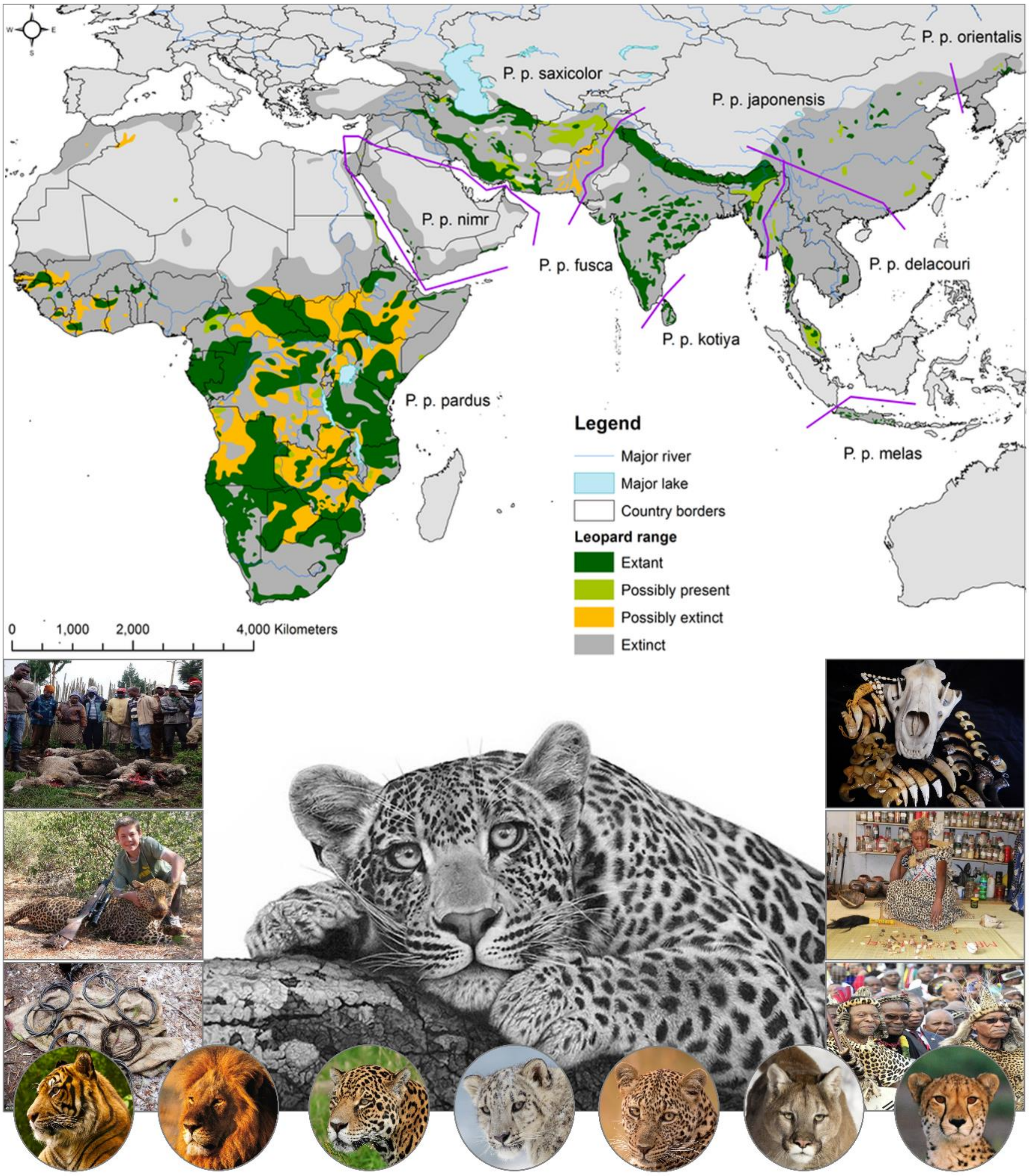


Figure 30. Leopards encompass the global challenges faced by large felids in the Anthropocene. Much of their broad geographic range falls outside of formally protected areas, exposing them to the full suite of anthropogenic threats facing large felids. Moreover, leopard derivatives are readily traded for traditional use. Images are used with permission or under the creative commons license.

I have contextualised the main findings of each of the data chapters in this thesis within the broader literature as it pertains to traditional use, illegal trade, and impacts on wildlife in general. In this chapter, I consolidate the three data chapters by placing them in a broader context of global leopard conservation and the challenges of illicit wildlife trade. I advocate for the reassessment of traditional use as a significant regional threat to leopards, emphasising the importance of revised sustainable use policy, continuous monitoring of trade, and effective PA connectivity. I highlight the unique value of integrating multidisciplinary research (socio-cultural engagement, molecular geographic assignment techniques, and population-level ecological monitoring) in the global strategy for the conservation of leopards with implications for the conservation of all large carnivores.

5.1 Summary of key findings

Followers of the Shembe Church in South Africa represent the foremost culturo-religious users of illegal leopard skins in southern Africa (Marinovich, 2018). Understanding the factors associated with leopard skin possession in Shembe followers is thus essential to understanding the drivers of illegal leopard exploitation in service of traditional use throughout southern Africa. In Chapter 2, I used questionnaire data from an extensive survey of Shembe followers (n = 8,600) to reveal that variation in possession of and desire for an authentic leopard skin was almost entirely explained by employment and follower age, respectively. Given the importance of wearing a leopard skin to Shembe followers, Panthera has sought to provide *faux* alternatives at no cost to the individual in the hope that this will reduce the demand for authentic skins. By comparing a subset of followers before and after receiving their *faux* alternative (n = 2,300), I was able to assess the overall success of this intervention in addition to identifying the factors associated with the subsequent acquisition of or desire for authentic skins despite having a *faux* alternative.

Encouragingly, most followers were satisfied with the alternative, having retained and used it at gatherings, with little noticeable damage or perceived societal judgement. Furthermore, while some followers who had been given a *faux* skin still acquired authentic leopard skins, desirability-driven demand had decreased significantly in the three years since the intervention began with attitudinal shifts favouring *faux* skin alternatives. Similar to possession amongst followers both acquisition and desirability for a skin after being provided with a *faux* alternative were best explained by improved employment status, *faux* skin satisfaction, and increasing age. Notably, the positive influence of education or awareness concerning leopard conservation status and the illegality of possessing an authentic skin suggests that targeted education and enforcement programs would do much to reduce demand for leopard skins amongst this community.

The persistent demand for leopard skins within the Shembe Church likely still exceeds South African capacity of only 1,688–6,979 leopards (Swanepoel *et al.*, 2011), and informal interviews with traders at traditional wildlife markets suggest that material is becoming increasingly scarce, compelling traders to source from surrounding range states. To investigate the geographic extent of the trade and identify likely source countries of locally traded leopard skins, I used DNA-based assignment tests in Chapter 3. Skin samples of illegally traded leopards were sourced from a police raid, Shembe Church followers, and *muti* markets. By first developing a genetic reference database of leopards across southern Africa, I was able to successfully validate the origins of known samples and assign the origins of seized leopard samples to their most likely source areas across southern Africa. My results showed that illegal leopard skin trade for traditional use in South Africa is transnational and syndicated, with poaching 'hotspots' identified in southwestern Zimbabwe, along the eastern borders of South Africa, and in southern Mozambique. *Muti* markets had a more localised genetic footprint than Shembe and Raid samples which were larger and multinational. Notably, there was a significant male-bias in the samples across all three forms of trade sources with evidence for both counterfeits and duplication of individuals in *muti* markets. Techniques developed here can be used to identify the origins of seized leopard products and monitor trade routes across the region, potentially allowing for the redirection of resource-limited efforts towards targeted intervention and leveraging of transnational policy to increase anti-poaching enforcement. Arguably, the greatest impact could be made by focusing more closely on the Transnational Criminal Organisations (TCOs) themselves. DNA-based methods can make these TCOs easier to find and define. It is important to know who the leopard poachers are, but it may be even more important to know who is distributing their product, as this is a particularly high-yield link in the chain. If low-income, subsistence communities are urged into opportunistic harvest by a syndicate of traders (TCOs), for instance, one needs to get at the syndicate of traders, as they are the ones profiting most from the trade and are thus consistent buyers. Therefore finding common features within and among police raids, ceremonial users and cultural traders or markets is essential to understanding and deterring illegal trade.

To further understand the potential impacts and ecological costs of sustained leopard exploitation, I used a combination of spatial and genetic data from adult leopards to contrast the structure of two South African populations with markedly different histories of anthropogenically-linked mortality in Chapter 4 (Naude *et al.*, 2020). Home range overlap, parentage assignment, and spatio-genetic autocorrelation showed that historical exploitation (pre-2012) of leopards has disrupted and reduced sub-adult male dispersal patterns, thereby facilitating opportunistic male natal philopatry, with sons establishing territories closer to their mothers and sisters. The resultant male kin-clustering of this historically exploited population is comparable to that of females in the well-protected reserve and resulted in localised inbreeding. These findings provide novel evidence directly linking unsustainable anthropogenic mortality to inbreeding through disrupted dispersal in a large, solitary felid, and in doing so, reveals the genetic consequences underlying this behavioural change. Thus, I emphasise the importance of managing the effects of sustained exploitation on local leopard populations and mitigating habitat fragmentation between contiguous PAs by promoting *in situ* recovery and providing corridors of suitable habitat that maintain genetic connectivity.

5.2 The economics of wildlife crime, trade policy, and traditional consumerism

5.2.1 The poacher-trader-consumer cycle

Effective intervention strategies in wildlife trade require a holistic understanding of each node along the supply-demand cycle (Moyle, 2009). In its simplest form (Figure 31), illegal trade in leopards includes local consumer demand (e.g., traditional users; see Chapter 2), facilitated by local and regional trade (e.g., traditional markets and smuggling syndicates; see Chapter 3), which stimulates regional supply (e.g., opportunistic and targeted poaching; see Chapter 3 & 4). Ultimately, this cycle represents the criminal organisation of a wildlife crime, with important economic decisions being made and informed by both the production and transaction costs accrued by the organization at each node (Schneider, 2008). Transaction-cost economic theory describes two primary types of cost, namely those of coordination and motivation (Moyle, 2009). The former posits that a completed sale requires interaction, negotiation, and logistics between buyers and sellers, while the transaction cost speaks to the required trust between the buyer, the seller, and their products. While legal markets enforce and regulate such contracts through the fear of court action, illegal markets have no such formal recourse mechanisms. In these illegal markets, there is also a third transaction cost, evasion. The results presented here show that leopard parts are being traded illegally both domestically and internationally (see Chapter 3), and accordingly the participants in this trade should be facing costs associated with evading arrest or prosecution (Moyle, 2009; Pires & Moreto, 2011). As evasion costs escalate, so the likelihood of a completed transaction diminishes and in IWT, these evasion costs should be a significant burden on criminal organisations and traders. The three primary costs discussed here relate to optimal deterrence, as described in the economic theory of crime (Becker, 1968). This theory posits that acts of wildlife crime are rational, economic decisions, occurring more frequently when the cost of the activity is relatively low (McCarthy, 2002).

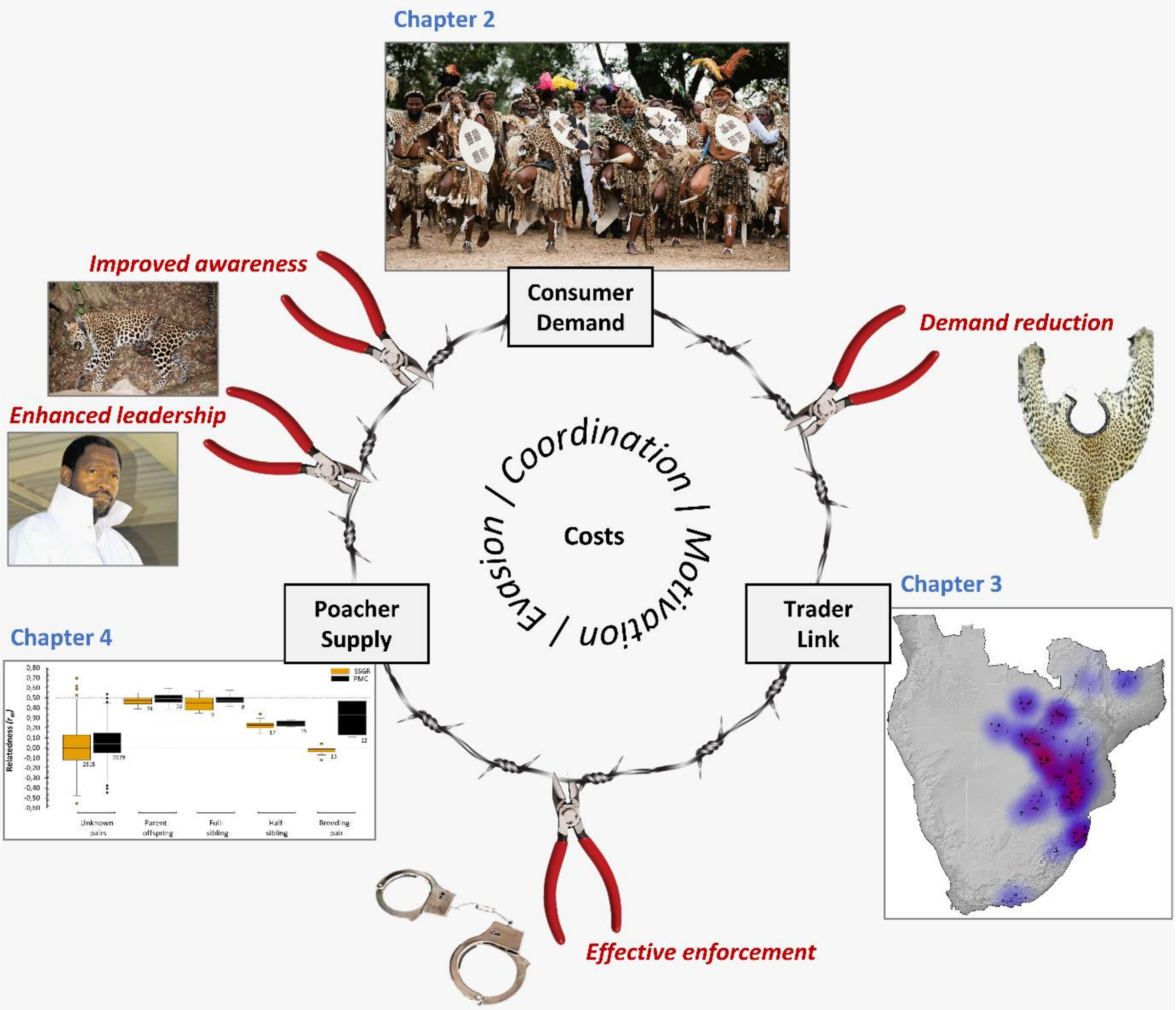


Figure 31. The poacher-trader-consumer cycle. Understanding this cycle connecting the nodes of consumer demand, trader link, and poacher supply and the cost that each link bears is crucial to innovative, successful, and ultimately sustainable intervention. Following this framework, Panthera's multifaceted approach to intervention has focused on demand reduction, effective enforcement, enhanced leadership, and improved awareness. Images are used with permission or under the creative commons license.

In the case of the southern African illegal leopard skin trade for traditional use, it seems likely that small-scale opportunistic poachers may be the main suppliers to a network of traditional markets (Figure 31). These leopards are likely sourced through direct wire-snare poaching and as bushmeat by-catch (see 1.2.3) or through unregulated trophy hunting (see 1.2.2) across unprotected and transformed landscapes, which account for 62% of regional leopard range (see 1.4.2) or within and around poorly managed PAs (see Chapter 4 [Naude *et al.*, 2020]). Knowing who the leopard poachers are and how they obtain their products remains a major challenge to the overall understanding of the illegal trade of leopards in southern Africa and one that I was unable to explore in this thesis. It is widely hypothesised that the major suppliers of this trade are from low-income or subsistence communities who have been urged into opportunistic harvest by a syndicate of traders through traditional markets, likely exacerbated by circumstances of poverty (Hitchcock, 2000).

Given that most extant leopard range is outside of PAs, the difficulties of adequate leopard containment within most PAs, and the high susceptibility of leopards to HWC (see 1.4.2), it is understandable that conservation organisations and anti-poaching agencies are often overstretched and cannot adequately protect leopards across this vast region (Nurse, 2013). Moreover, due to inconsistencies in policy regarding the illegal nature of this form of wildlife use (see 1.4.3) and prosecutorial services already being overburned by high rates of civilian crime in addition to other high profile wildlife crimes (e.g., rhino horn trade), rates of arrest and successful conviction remain relatively low (Nurse, 2015; Runhovde, 2017). Under current conditions, coordination costs are minimal, as the informal trade in leopard skins is clearly syndicated and transnational (see Chapter 3). Both motivational and evasion costs are similarly low as prosecutorial agents remain overburdened, corruption is rife, and actual, as well as perceived, conviction rates remain low (see Chapter 2). Furthermore, contradictions in local possession and trade laws (see 1.4.2) make this illegal transnational trade (see 1.2.4) in leopard derivatives a rational, economic decision with relatively low risks for traders (Figure 31). While a variety of leopard derivative consumers exist (see 1.3.4), I have focussed here on traditional healers and followers of the Shembe Church in South Africa (see Chapter 3). Local consumer demand in the latter will continue to increase (see Chapter 2), which when combined with low coordination, motivation, and evasion costs suggests a failure at both a national and regional level to deter this consumer-driven cycle of IWT (Figure 31).

Each node in the poacher-trader-consumer cycle (Figure 31), and the links between them, represent an opportunity for innovative intervention strategies and to understand the inadequacies of policy or its regional enforcement. Southern African leopard conservation requires a paradigm shift towards clarification of its laws, policies, and social awareness regarding cultural use and the protection of its threatened wildlife species (see 1.4.2). For intervention strategies to be both successful and sustainable (see 5.3), whether driven by civil society organisations (e.g., NGO's such as Panthera, World Wide Fund for Nature [WWF] and Wildlife Conservation Society [WCS]) or the state (e.g., the Department of Agriculture, Forestry and Fisheries [DAFF] and the South African National Biodiversity Institute [SANBI]), they need to optimise trade deterrence through increasing the three costs behind the economic theory of wildlife crime (Figure 31), while clearly designating entitlement and respecting traditional use of protected wildlife.

5.2.2 Undocumented, unregulated, and untraced

A number of substantial challenges exist in tackling the southern African illegal leopard skin trade for traditional use. The first problem is a distinct lack of data, without which there is a failure to understand the scale and impact of the threat. Secondly, the deterrent costs to possession and trade are limited by corruptible and overburdened conservation authorities, who do not have the systemic support to direct and improve enforcement. Thirdly, there is a lack of integrated research tools with which to adequately monitor trade and provide data on the status of leopard populations; these would clearly serve to not only assist in closing the adaptive management loop but also inform future conservation policy on sustainable use.

In this thesis I present the first assessment of illegal leopard skin use in the Shembe Church in South Africa (see Chapter 2), the geographical scale of this trade for traditional use across southern Africa (see Chapter 3) and how this exploitation, if left unchecked, may impact leopard populations (see Chapter 4 [Naude *et al.*, 2020]). I show that there is a persistent demand for authentic leopard skins among the Shembe and that both Shembe and *muti* samples are sourced both locally and transnationally, serving to highlight a hitherto underrepresented threat to leopards across the region. With greater sampling effort at both smaller Shembe gatherings and *muti* markets the true extent of the local and transnational trade may be revealed. In my experience during this study, documenting the cultural use of leopard derivatives in southern Africa has been well received by traditional users and was neither invasive nor offensive. This suggests that effective documentation and sampling clearly requires time and respect, with resources allocated explicitly for social engagement. If approached in this manner, we can continue to explore traditional use of felids unhindered by socio-political sensitivities in southern Africa.

In and of itself, this research and the formal documentation of cultural use are insufficient to elicit change or improve regulation and compliance. South Africa's environmental policies (NEMBA, TOPS, and CITES) are well established, but all lack clarity regarding legal designation of cultural user status and exceptions to these laws (see 1.4.3; e.g., Zulu royalty versus ubiquitous religious use); as a result, researchers, enforcement agencies, and the policymakers themselves remain confused about the realities of implementation. Moreover, many of these enforcement agencies face an internal conflict of interests. For example, in the post-FFL follow-up questionnaires with Shembe followers who had received a *faux* skin (see Chapter 2), 16 of the Shembe followers interviewed were employed by Ezemvelo Wildlife (the statutory authority for conservation in the KwaZulu Natal province) and in possession of illegal leopard skins. This speaks to a systemic lack of awareness among cultural users which is likely a good starting point for intervention. Indeed, the follow-up questionnaires indicated that improved knowledge of leopard population status and possession and permitting legalities significantly reduced authentic skin desirability and subsequent acquisition among Shembe followers (see Chapter 2). Continued public engagement across multiple user platforms will improve awareness; however, addressing corruption and reducing the burden on environmental enforcement agencies will prove more difficult. This can be improved through targeted enforcement in areas most at risk of poaching and trade (see Chapter 3) through the use of adaptive and sophisticated monitoring tools. Research into IWT monitoring tools (see Chapter 3) can provide appropriate technical support for targeted and improved enforcement. Taken together, these highlight poaching hotspots and trace trade routes which can be translated into direct policing and policy-level engagement. The methods developed in this thesis can act as rolling technical support to countering illegal trade in leopard skins for traditional use across southern Africa.

5.2.3 Stages of consumer understanding and regulation

It is unclear whether traditional healers and Shembe followers are aware of their role in this IWT and the impact it has on regional leopard populations. Shembe questionnaire data showed a significant decline in authentic skin desirability with improved awareness of leopard population status and knowledge gained regarding the illegality and permitting of their trade (see Chapter 2). This suggests that social awareness and a sense of responsibility may play a role in demand reduction, but it is important to acknowledge that increasing cultural demand for wildlife products and the commercialisation of this trade may be in a developmental ‘stage’ of societal control in South Africa.

A consideration of the global fur trade in the 1960s and 1970s is illuminating in this regard (see 1.3.1). While undergoing a cycle of rarity demand for newly fashionable felid skins, it grew into a global, transnational, and exploitative trade before research into its impact on wild felid populations spurred concerns over individual welfare, inspiring outrage and ultimately condemnation of this culture. The research into unsustainable rates of felid exploitation also led to the introduction of international trade policy and legislation which, together with social outrage, resulted in the collapse of the fur trade in fashion by the late 1980s.

Though significantly diminished, demand for and trade in felid skins for fashion persists, though it is highly regulated by sustainability laws and stigmatised by societal pressure. Perhaps the current demand for leopard skins and the expansion of its quasi-traditional consumer-base (e.g., Shembe followers and traditional healers) is at the beginning of this attitudinal cycle of consumer understanding and self-regulation. The demand reduction example of declining fur trade of western nations may not be very applicable to the Shembe trade, however, as the former shamed a wealthy, small segment of western culture for killing animals for vanity. In contrast, the latter has a deep cultural foundation, with values shared by many who follow this religion. Increasing societal awareness and knowledge of the impact on wild leopard populations could stimulate societal self-regulation and increased enforcement of environmental trade policy. Though it is a slow motivator of behaviour change, a sense of cultural value and transgenerational equity will be essential. Such examples of cyclical behavioural change are common and have proven effective (e.g., anti-smoking [Steptoe *et al.*, 1995] and single-use plastic [Ritch *et al.*, 2009; Singh & Mathur, 2019] campaigns); however, it is unclear, given global rates of leopard decline, whether there is enough time to effect sufficient behavioural change through these means.

5.3 Towards successful and innovative intervention strategies

While leopard conservation in southern Africa is a national- and provincial-level governmental mandate, in practice, the implementation of monitoring, research, and interventions often rely on the NGO space (e.g., Cape Leopard Trust [CLT], Endangered Wildlife Trust [EWT], and WildlifeACT). Panthera’s approach to leopard conservation across this region has been multi-disciplinary, targeting each of the established nodes of the poacher-trader-consumer cycle

(Figure 31) through demand reduction, effective enforcement, improved awareness, and enhanced leadership.

5.3.1 Demand reduction

The economic theory of wildlife crime dictates that IWT occurs more frequently when the benefit to the criminal is relatively high (Moyle, 2009). The value of an authentic leopard skin stems from its rarity and cultural significance. By providing a culturally acceptable alternative to authentic skins (see Chapter 2), one would not only supplement the individual's immediate demand for an authentic product but also flush the authentic skin market. Together these changes would lessen the long-term rarity value of an authentic skin, thereby reducing the incentive to the criminal or trader driving illegal trade. The FFL programme was designed to provide an alternative that is acceptable and sustainable as a means of shifting demand away from and thereby reducing the value of authentic leopard skins. It has been and will be crucial that these *faux* skins are assimilated into Shembe culture, and my results (see Chapter 2) show some early successes. The FFL programme has distributed over 22,000 *faux* skins to date, with further distribution planned, and the ultimate goal of facilitating a self-sustaining business model within the Shembe church. Already, the *faux* material produced in China is being tailored by a small, entrepreneurial group of Shembe women to make them more aesthetically pleasing to wearers. This business opportunity and its endorsement would secure long-term sustainability and acceptance within the Shembe church.

5.3.2 Effective enforcement

Optimal deterrence of IWT is facilitated by increasing coordination, motivation, and evasion costs (see 5.2.1) for traders (Moyle, 2009). By providing a tool for the assignment of confiscated leopard derivatives to their geographic origin (see Chapter 3), this thesis equips southern African conservation enforcement agencies with the ability to understand and monitor trade from a single seizure to large confiscations and trade dynamics across the region. It is hoped that the data presented in Chapter 3 represent the first of many applications of this geographic assignment tool for leopard trade in the region and that it will garner the support of the South African Democratic Countries (SADC) scientific authority, to whom it has already been presented.

The data presented in this thesis clearly show a large and growing cultural and religious use of leopard derivatives in South Africa (see Chapter 2) and that these are being sourced from throughout southern Africa (see Chapter 3) where it is likely having devastating effects on the genetic integrity of source populations (see Chapter 4 [Naude *et al.*, 2020]). Given the source-sink of the current trade and limited regional enforcement, it is hoped that the SADC community could politically pressurise the South African government into re-evaluating the efficacy of its conservation policy regarding cultural use and local law enforcement activity. Precedent for this approach comes in the form of the domestic ban on tiger trade in China in 1993, following pressure from neighbouring countries who suspected that the demand for tiger bone within China (approximately 4 tonnes a year) exceeded what was available in the country (an estimated 50 tigers at the time) and material was, therefore, being sourced from surrounding range states (Moyle, 2009). It is worth noting that the international ban and China's domestic ban on tiger trade have not been associated with marked declines in poaching across Asia. Instead, poaching efforts were shifted, most notably to India. In order to avoid similar shifts, the southern African conservation community would need to cooperate and monitor trade at a regional scale accompanied by trade route vigilance and policy that addressed poaching regionally rather than by country.

5.3.3 Improved awareness

Monitoring leopard populations and the impact that any threat has on their persistence is particularly challenging due to their elusive nature and range outside of formally PAs (see 1.4.1). Only now through range-wide systematic camera trapping efforts conducted by Panthera and their collaborators in conjunction with illegal trade monitoring (see Chapter 3) are we beginning to understand the severity of southern African threats and how these are impacting population trends. Emerging population trend data collected by Panthera suggest declines in most government PAs with only the best-resourced or naturally isolated reserves supporting stable leopard populations (M. Rogan, in preparation). While survey data reveal that few Shembe followers are cognisant of their role as endpoint consumers in the poaching and trade of leopards assumed to be driving these declines. Communicating the link between use and threats to wildlife populations for traditional users is difficult and complicated by such data being provided by foreign-based NGOs (i.e. Panthera) who are culturally distinct from African users of wildlife. To their credit, Panthera has used diverse mechanisms for communication including face-to-face discussions with questionnaires (see Chapter 2), a targeted video (in English and Zulu) shown at gatherings and schools across the study area, and the formalised ‘To Skin a Cat’ documentary (DropBox link). These multimedia awareness campaigns serve to enhance basic knowledge, clarify the link between consumers, poachers, traders, and leopard status, highlighting the role of alternatives while maintaining an emphasis on the cultural significance and the conservation actions required for the transgenerational persistence of leopards.

The FFL intervention and the awareness it has delivered among *faux* leopard skin owners has elicited a change in knowledge and informed decision-making behaviour around illegal leopard skin trade amongst Shembe followers (see Chapter 2). As this improved awareness has proven effective and is achievable with existing resources, it is an intervention which can be employed by Panthera and other conservation stakeholders across other traditional users with almost immediate effect. While awareness is designed to supplement other interventions, it remains crucial to the long-term sustainability of changed behaviour among consumers. An excellent example of a successful awareness-based behavioural change in conservation intervention strategies is that of the Lion Guardians programme in Kenya. Here, Masaai *morans* (young men) would traditionally practice the killing of lions as part of their ‘coming of age’ (Table 1) ceremony. However, due to interventions regarding awareness of regional lion declines, these very *morans* have now become ‘Lion Guardians’, protecting individual lions and thereby community livestock and reducing HWC (Table 1; Hazzah *et al.*, 2017).

5.3.4 Enhanced leadership

Ultimately, the most effective intervention is one that appeals to a change from within an organisation using the top-down influence of cultural hierarchy to elicit transformation among its practitioners. While respecting cultural authority, such a method utilises existing channels of communication and is self-regulating. A clear example of this is the banned use of illegal skins in cultural adornment among Tibetans by the Dalai Lama (see 1.3.1). Similarly, Panthera’s distribution of *faux* spotted cat skin skirts among the Kuomboka paddlers of western Zambia endorsed by the Lozi king has proven very effective. While we have tried to gain the direct support of Vela Shembe (the current prophet and leader of the largest faction of the Shembe Church), this has thus far proven unsuccessful due to the cultural complexity of access and bureaucracy within the church. Nevertheless, the organisation has established relationships with church leadership which has resulted in the changes seen to date. It is clear, however, that the efficacy and sustainability of any conservation intervention regarding cultural use, requires acceptance, support, and leadership among the existing cultural hierarchy and this remains an ongoing challenge with regards to the Shembe Church and its followers.

5.4 Shifting traditions, values, and symbolism

Historically, much significance was placed on the symbolic value of leopards and other large felids across many cultures around the world (see 1.3.4). Skin, tooth, and claw adornments immediately implied bravery or strength not only for the direct danger faced in their acquisition if through a hunt, but also for the perceived role of these felids in nature as powerful predators symbolising majesty and fear. The possession and right to wear leopard derivatives has persisted as a measure of societal status and royalty from pre-historic times to today (see 1.3.4). In some cases these rights were exclusive, such as the in Zulu kingdom (Harries *et al.* 1993), where leopard skin adornment was reserved for royalty and violation of this edict was punishable by death (Raum, 1973). Given that many members of the Shembe Church are also subjects of the Zulu kingdom it could be argued that the wearing of leopard skins represents a direct challenge to more established Zulu culture. What was once and still is the privilege of a select few among Zulu royalty is now being used by Shembe followers as part of a relatively recent traditional practice, having only been established in the last century (*circa* 1910; Marinovich, 2018). In this regard it is important to note that the Shembe Church believe that every man is the *inkosi* (chief) of his own household and thereby entitled to a wear a leopard skin (see Chapter 2).

Globalisation undoubtedly changes cultural practice and its meaning. In some cases, this may enhance and fortify its value systems, but in most cases, the merging of cultures likely devolves fundamentalism. It may be that leopard skin use, and indeed much of modern cultural use of wildlife, is driven by commercial consumer motivations, such as rarity value and prestige, rather than the deeply entrenched, cultural symbolism it once embodied. This modern culture of money appropriating cultural and religious symbolism is more akin to the fur trade for fashion in the 1960s and 1970s (see 1.3.1). Unfortunately, the commercial versus cultural drivers of value will only become evident as leopard populations decline. It stands to reason that if the usage of leopard derivates is primarily culturally motivated, changing sentiment should turn users toward conservative behaviour whereas, if usage is commercially driven, rarity value with increasing decline will only escalate exploitation despite costs, driving an anthropogenic Allee effect (see 5.2.1; Courchamp *et al.*, 2006; Harris *et al.*, 2017). However, of overall concern is the growth rate of culturo-religious use which has far outstripped use by traditional healers and royalty. This growth alone is grounds for an appeal to the Shembe Church and cultural leaders to change their identities around big cats, identifying themselves as agents of conservation and sustainable use, as well as guardians of transgenerational equity, rather than exploitative consumers in light of the evidence of decline. Moreover, statutory authorities and policymakers in felid range states with cultural users need to address the threats of cultural use head-on, clearly delineating and disseminating entitlement, legality, and consequences from policy to conservation practice.

5.5 Adaptive management, ongoing research, and revised policy

There is a real risk that much of the work presented in this thesis, and associated research on the status of populations within PAs throughout southern Africa (see 1.4.2), is merely ‘documenting the demise’ of leopards. Such is the extent of the current traditional use throughout the entire southern African region that we no longer have the privilege of acquiring baseline data on population level processes and impacts without simultaneously acting to develop interventions and arguing for improved policy. Consequently, ongoing leopard research and management need to be applied and adaptive, respectively; findings need to be rapidly integrated into both improved policy and enforcement of existing laws as they pertain to IWT. It is only through this integrated approach that leopard populations in southern Africa will avoid collapses similar to that recorded for other vulnerable species in Africa and leopards in northern Africa and across much of South-East Asia (see 1.4).

In order to reduce the threat of traditional use to felid conservation, researchers, managers, and policymakers need to address the associated cultural and political sensitivities. In this thesis I show how partnerships between a multitude of stakeholders and users have enabled research on traditional consumers (see Chapter 2), established the required illegal trade monitoring techniques (see Chapter 3), and explored the impacts of sustained exploitation on extant leopard populations (see Chapter 4 [Naude *et al.*, 2020]). This research highlights a closing window of opportunity for strategic intervention with regards to cultural use of all traded felids given that many are in decline across much of their range (see 1.2). We need an integrated research-management-intervention system which firstly respects cultural integrity and secondly promotes the philosophy of sustainable use, while translating directly into clear and contextually appropriate phrasing in policy, enforcement, and social engagement. As conservation agents, we need to recognise leopards as sentinels for free-roaming species and those not adequately conserved by existing PA networks. As threats change and land-use transforms, so we must adapt our management and research towards a multidisciplinary and holistic approach to the conservation of these species (e.g., Figure 31).

5.6 Future research and direction

The data, and the interpretation thereof, presented in this thesis on the FFL programme and engagement with the Shembe Church and other cultural users represent only a portion of a larger intervention strategy by Panthera. In addition to the collection of longitudinal questionnaire data during the distribution of *faux* skins (presented here in Chapter 2), Panthera has been conducting procession and skin ratio counts at major gatherings across South Africa to further assess the efficacy of the intervention. To further investigate and expand on the DNA-based geographic assignment (see Chapter 3), I will continue to monitor Shembe use and further assess the impact of *muti*-markets and traditional healers in South Africa toward the long-term objective of establishing a range-wide assignment and indexing database, not only for leopards but for other felids in trade. These techniques can also be honed to the technical level of true forensic prosecution (e.g., improved forensic sampling, chain of custody, and case security) for use in a criminal investigation, as governed by the legal standards of admissible evidence and criminal procedure, in addition to informing broad-scale patterns of IWT in southern Africa. Additionally, using lessons learnt in our current interventions to identify and customise our approach to intervention with sustainable alternatives to felid derivatives, I am conducting a systematic review of felid use in traditional practices across Africa. This thesis presents an aspect of a larger integrative monitoring approach to leopard conservation which includes systematic camera trapping, counter wildlife crime enforcement, and socio-political engagement. To date, it is this multi-faceted and holistic approach that has garnered support and respect from the individual leopard skin consumer to regional scientific policymakers.

5.7 Conclusion

Traditional use is an under-represented threat to the conservation of felids in Africa and many other species worldwide. In southern Africa, the extensive use of leopard derivatives among traditional healers and burgeoning culturo-religious groups poses a direct threat to the stability of wild populations. This thesis uses a multi-disciplinary approach to describe some of the factors associated with the illegal leopard skin trade among significant traditional users in South Africa. In doing so, it quantifies the extent of this trade across the southern African region, and assesses its impact on local leopard populations. Focusing on the Shembe Church as the foremost culturo-religious users of illegal leopard skins in the world, I showed that demand is driven by economic status and the societal prestige of leopard skin ownership. Without improved awareness and a change in the perceived weaknesses of law enforcement, this illegal demand for ceremonial regalia will continue to threaten regional leopard populations. DNA-based geographic assignment of confiscated skins among the Shembe and traditional traders corroborated the transnationality and syndication of this illegal leopard skin trade. My results also show that unsustainable and male-biased exploitation has direct ecological costs in poorly protected reserves through disruption of natal dispersal, which increases inbreeding potential and compromises the genetic integrity of wild leopard populations. Together these findings address the lack of conservation- and policy-relevant data regarding the impact and scale of the trade for traditional use in South Africa.

These findings can be applied to all felid populations threatened by exploitation, emphasising the importance of long-term monitoring within PAs and improving management interventions to mitigate these effects. Interventions such as antipoaching can be more effectively directed toward the ‘hotspots’ identified in this thesis while PA management should prioritise the maintenance of dispersal corridors to promote *in situ* recovery of already exploited populations. Demand reduction strategies such as the provisioning of suitable alternatives, together with improved awareness and increased enforcement are essential to addressing the growing culturo-religious demand for leopard products that is driving the poacher-trader-consumer cycle which threatens this iconic large predator. Based on these findings, I call for a restructuring of conservation policy on traditional use in southern Africa, which allows for the integration of multidisciplinary monitoring tools, adaptive management, and transboundary prosecution. Success will depend on finding the balance between an improved regional policy which effectively conserves wild felid populations while maintaining a respect for cultural practices.

During the course of my PhD, I have seen more dead leopards than I will ever have the fortune of seeing alive in the wild. That is why I have committed my career to combatting this and other illegal wildlife trade.

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snaring in retaliation for real or perceived livestock losses or caught as by-catch during indiscriminate bushmeat poaching. Beyond the direct and obvious welfare cost to individuals, valuable time, energy, and resources are wasted on the removal of snares by rangers and anti-poaching units.

Figure 6 **Commercial fur trade for fashionable culture devastated wild felid populations.** With growing wealth and globalisation, the insulating functionality, and majestic symbolism of fur gave way to the commercialisation of social prestige and affluence. Moreover, this trend was exacerbated and continues to be led by famous individuals, the cultural and political icons of modern fashion, and evolving traditional practice. Though now largely sustainable, the fur trade underwent a full cycle of overexploitation, societal consciousness, and self-regulation (see 5.2.3). 13

Figure 7 **Tiger and other rare skins have deep culturo-religious significance in Tibetan** culture. Depicted here are the elaborate tiger *skin* chubas worn by affluent Tibetan men at the Litang Horse Festival in the Chinese Province of Sichuan and the famous traditional tent made of 108 tiger skins. After facing much political pressure and cultural shame, the 14th Dalai Lama, Tenzin Gyatso, banned the use of endangered wildlife products in traditional Tibetan attire, burning thousands of skins in moral support of the edict. Nevertheless, there remains resistance to this ‘modernisation’ and loss of tradition among the more conservative followers. 15

Figure 8 **Traditional Asian Medicine (**TAM**) threatens many felid species across South-East Asia.** The practice of TAM is deeply spiritual, relying on centuries of cultural knowledge systems to prescribe alternative and often charm-like remedies alongside conventional Western medicine. Despite much controversy, this is a recognised and legislated form of alternative treatment which still directly challenges international environmental policy and drives illegal trade. 17

Figure 9 **Traditional healing in Africa, when Western religion meets cultural spirituality.** Here traditional healers and diviners are the formal conduits of ancestral guidance and interpreters of divine direction. As such, they often hold dual roles as medicinal healers and spiritual guides. 20

per colour. Included are (A) versus excluded (B) assignments per country from the calculation of geographic-specific allele frequencies. The 100 colour-coded circles per area are random draws from the set of all possible locations weighted according to their probability. The concentration of these 100 circles in any given area gives a guide as to the probability that the sample arose from that area under each condition.

Figure 20 **Sensitivity analyses of leopard reference sampling re-assignment across southern Africa.** Sensitivity analyses were conducted for 1,452 individual leopard reference samples, through systematic removal and the randomised re-assignment of one (A), five (B), and ten (C) individuals. The colour shading indicates the mean distance (km) between the true reference sample location and the re-assignment of that sample under each condition. Sensitivity scores (0–500 km) are smoothed across the assignment landscape. 89

Figure 21 **Examples of DNA-based geographic assignment quality for leopards across southern Africa.** In testing the 237 illegally traded samples, assignment quality (solid line, 95% kernel density; dashed line, 99% kernel density) is represented by: (A, B) showing high-quality assignments (one centre of point densities in both contours); (C, D, and E) moderate-quality assignments (two centres in either 95% or 99% contours); and (F) a poor-quality assignment (multiple centres in either 95% or 99% contours). 90

Figure 22 **Genetic assignment footprints of leopard samples by trade source in southern Africa**. Shown are traded leopard sample geographic assignments (*n* = 237) by (A) raid confiscation, (B) Shembe trade, (C) *muti* markets, and (D) combined. Locations of the large leopard skin raid (A; square; *n* = 96), opportunistic sampling at major Shembe gatherings (B; triangles; n = 81), and various traditional muti markets (*C*; diamonds; n = 60) are indicated. Colour shading and intensity indicate the mean density of assignments calculated as the median point of 100 random draws from the set of all possible locations weighted according to their individual assignment probabilities (under each condition). Assignments are smoothed across the landscape as (A–C) 0–20 and (D) 0–50 assignments per 100 km2. 92

LIST OF ABBREVIATIONS & ACRONYMS

AIC	Akaike information criterion or score
AICc	AIC corrected for small sample size
AKDE	autocorrelated kernel density estimates
ANOVA	analysis of variance
AUC	area under the curve
BC	Bhattacharyya coefficient
BM	Brownian Motion
BSA	bovine albumin serum
CAM	continuous assignment method
CBD	Convention on Biological Diversity
CI	confidence interval
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CLT	Cape Leopard Trust
DAFF	South African Department of Agriculture, Forestry and Fisheries
DCA	damage-causing animals
DNA	deoxyribonucleic acid
EU	European Union
EWT	Endangered Wildlife Trust
FFL	Furs For Life
GAC	genotype accumulation curve
GPS	global positioning satellite
HWC	human-wildlife conflict
HWE	Hardy-Weinberg equilibrium
IOU	Integrated Ornstein-Uhlenbeck
IUCN	International Union for Conservation of Nature
IWT	illegal wildlife trade
HRO	Home range overlap
KDE	kernel density estimations
LD	linkage disequilibrium
LOD	likelihood-of-difference score
MCMC	Markov chain Monte Carlo

min	minutes
NEMBA	National Environmental Management: Biodiversity Act No 10 of 2004
NGO	non-governmental organisation
OR	odds ratio
OU	Ornstein-Uhlenbeck
OUF	Ornstein-Uhlenbeck with Foraging
PA	protected area
PCR	polymerase chain reaction
PMC	Phinda-uMkhuze Complex
RSA	Republic of South Africa
SADC	South African Democratic Countries
SANBI	South African Biodiversity Institute
SCAT	smoothed continuous assignment technique
SE	standard error
sec	seconds
SSGR	Sabi Sand Game Reserve
TAM	traditional Asian medicine
TCM	traditional Chinese medicine
THPASA	Traditional Health Practitioners Act of South Africa No 34 of 2004
TOPS	Threatened or Protected Species
UD	utilisation density
USA	United States of America
VHF	very high frequency
VIF	variance inflation factors
WCS	Wildlife Conservation Society
WFCMS	World Federation of Chinese Medicine Societies
WHO	World Health Organisation
WWF	World Wide Fund for Nature

LIST OF TRANSLATIONS

Ale-mayo	(Swahili) – ritual killing of lions by Maasai youth in coming of age
amadlozi	(Zulu) – ‘ancestors’
amambatha	(Zulu) – Furs For Life *faux* leopard skin
badimo	(Bapedi, Batswana and Basotho) – ‘ancestors’
ba porofeta	(Sotho) - faith healer or prophet
chubas	(Tibetan) – traditional gowns
faux	(French) – made in imitation, ‘fake’ or ‘artificial’
iBheshu	(Zulu) – Nguni (cow hide) back skirts
igqoka	(Zulu) – traditional Zulu Nguni (cow hide) shields
ihawu	(Zulu) – traditional Zulu Nguni (cow hide) shields
iinyanya	(Xhosa) – ‘ancestors’
in situ	(Latin) – ‘on site’ or ‘in position’
isinene	(Zulu) – waist-round skirts of banded animals skins
izimboko	(Zulu) – traditional Zulu fighting sticks
Kuomboka	(Lozi) – the king’s paddling festival in western Zambia
Losar	(Tibetan) – a festival celebrated on the first day of the lunisolar calendar
muti	(Zulu) – from *umuthi* describing traditional medicine in Southern Africa
N’cwala	(Ngoni) – a festival celebrating ritual thanksgiving in eastern Zambia
Paseo Panthera	(Spanish) – ‘the Path of the Panther’
umnazaretha	(Zulu) – holy white surplices worn by Nazerites on church grounds
umqhele	(Zulu) – headbands made of spotted cat skins

APPENDIX

Appendix 1. Questions used for the study on authentic leopard skin possession and desirability through pre-FFL questionnaire surveys (*n* = 8,600) and post-FFL follow-up questionnaires (*n* = 2,300) among Shembe Church followers in South Africa (see Chapter 2).

A) Informed voluntary consent clause to participate in this research study

Study title: Under the skin of a culture: illegal leopard skin trade and longitudinal attitude shifts towards faux alternatives in the Shembe Church.

Invitation to participate and benefits: You are invited to participate in this research study conducted with Shembe Church followers who are interested in receiving *faux* leopard skin alternatives as part of Panthera's 'Furs for Life' initiative. We believe that your experience would be a valuable source of information and hope that by participating you may gain useful knowledge, as well as have an opportunity to share your interests and concerns regarding this species, its trade and the value of *faux* alternatives as a direct consumer.

Procedures: During this study, you will be asked to answer some questions regarding your use of leopard skins as part of cultural/religious ceremonial regalia in the Shembe Church, how Shembe society perceives this species and your knowledge about the trade of leopards.

Recording: We will keen written or audio records as part of the study. If you object, please tell us and we will not keep a formal record of our interaction.

Risks: There are no potentially harmful risks related to your participation in this study.

Withdrawal disclaimer: Your participation is completely voluntary; you may refuse to participate, and you may withdraw at any time without having to state a reason and without any prejudice or penalty against you. Should you choose to withdraw, the researcher commits not to use any of the information you have provided. Note that the researcher may also withdraw you from the study at any time.

Confidentiality: All information collected in this study will be kept private in that you will not be identified by name or by affiliation to an institution. Confidentiality and anonymity will be maintained as pseudonyms will be used. None of the data collected may be used in any legal action against you.

What agreeing means: By agreeing to this consent form, you agree to participate in this research study. The aim, procedures to be used, as well as the potential risks and benefits of your participation have been explained verbally to you in detail, using this form. Refusal to participate in or withdrawal from this study at any time will have no effect on you in any way. You are free to contact us, to ask questions or request further information, at any time during this research.

B) Pre-FFL questionnaire – survey details

Interviewer: ________________________ Date: _YYYY / MM / DD_

Location: ________________________ GPS: S ________________________

E ________________________

C) Pre-FFL questionnaire – Follower personal details and socio-economic information

Full name: ________________________ ID number: _X X X X X X X X X X X X X_

Telephone: +27 _________________ Date of birth: _YYYY / MM / DD_

What is your highest level of formal education? None | Primary | Secondary | Tertiary

What is your general employment status? Unemployed | Temporary | Permanent

D) Pre-FFL questionnaire – Authentic leopard skin possession and desirability

Do you possess an authentic leopard skin? Yes | No

Do you still want an authentic leopard skin now that you have a *faux* alternative? Yes | No

E) Pre-FFL questionnaire – Follower experience, perspective, attitude and opinion

Leopard populations in South Africa are ____ ? Uncertain | Increasing | Stable | Decreasing

Should the South African government protect leopards? Yes | No

Is it legal to own an authentic leopard skin without a permit? Uncertain | Yes | No

Do you know of anyone who has been convicted for possessing a skin? Yes | No

Will you wear the *faux* leopard skin at Shembe gatherings? Yes | No

F) Post-FFL interview – survey details

Interviewer: ________________________ Date: _YYYY / MM / DD_

G) Post-FFL interview – Check of follower personal details and socio-economic information

Full name: ________________________ ID number: _X X X X X X X X X X X X X_

Telephone: +27 _________________ Date of birth: _YYYY / MM / DD_

What is your highest level of formal education? None | Primary | Secondary | Tertiary

What is your general employment status? Unemployed | Temporary | Permanent

H) Post-FFL interview – Authentic leopard skin possession and desirability

Since receiving your *faux* alternative, have you acquired an authentic leopard skin? Yes | No

Would you still acquire an authentic leopard skin if you could? Yes | No

I) Post FFL interview – Follower experience, perspective, attitude and opinion

Leopard populations in South Africa are ___ ? Uncertain | Increasing | Stable | Decreasing

Should the South African government protect leopards? Yes | No

Is it legal to own an authentic leopard skin without a permit? Uncertain | Yes | No

Do you know of anyone who has been convicted for possessing a skin? Yes | No

Will you wear the *faux* leopard skin at Shembe gatherings? Yes | No

J) Post FFL interview – Follower faux skin experience, attitude and satisfaction

Do you still own your *faux* leopard skin *amambatha*? Yes | No

If no, why not? ______________________

Have you been using your *faux* leopard skin *amambatha* at Shembe gatherings Yes | No

If no, why not? ______________________

Have you noticed any damage to your *faux* leopard skin *amambatha*? Yes | No

If yes, what? ______________________

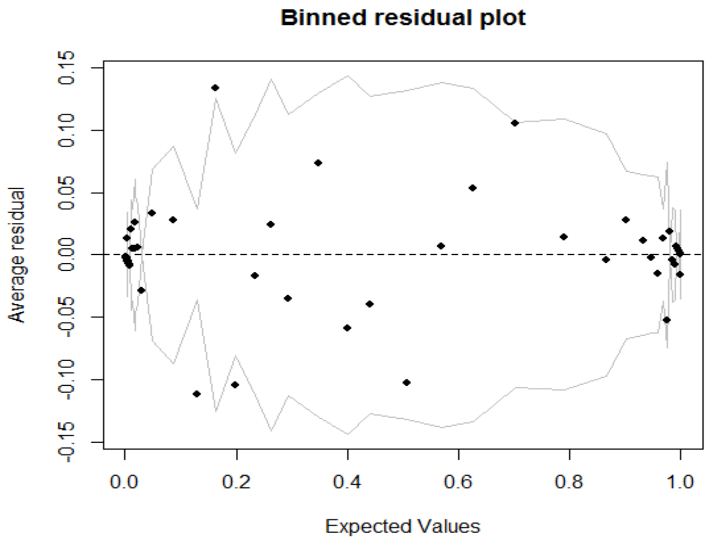
Do you feel judged or ‘looked down on’ for your *faux* leopard skin *amambatha*? Yes | No

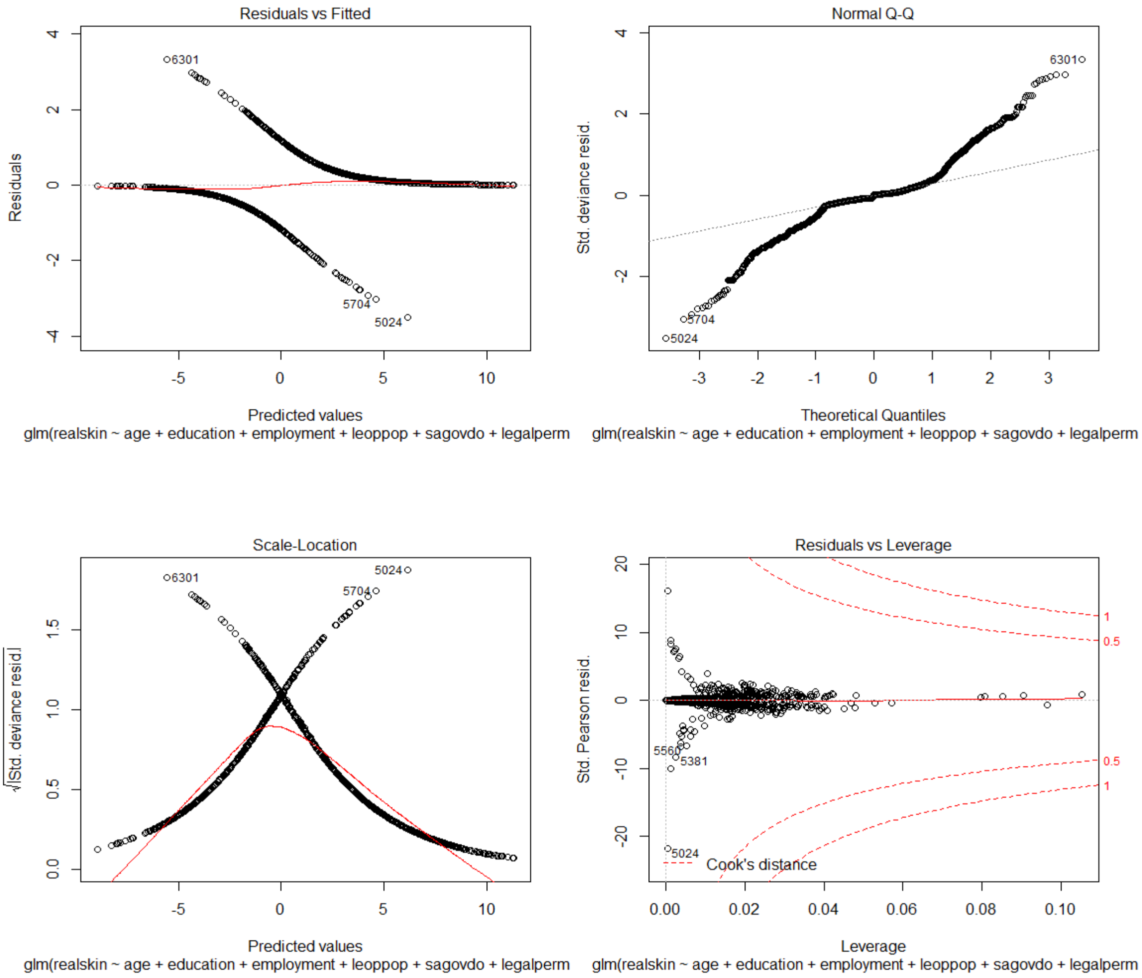
If yes, why? ______________________

How satisfied are you with your *faux* leopard skin *amambatha*?

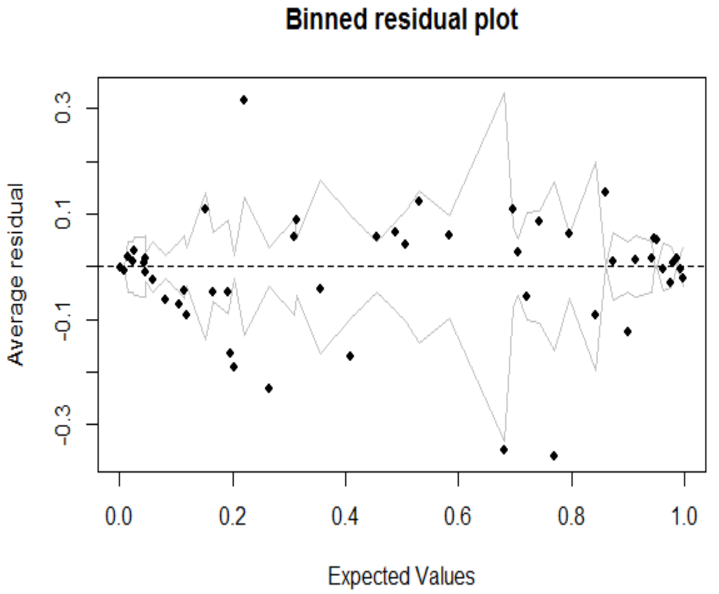
Very unhappy | Unhappy | Indifferent | Happy | Very happy

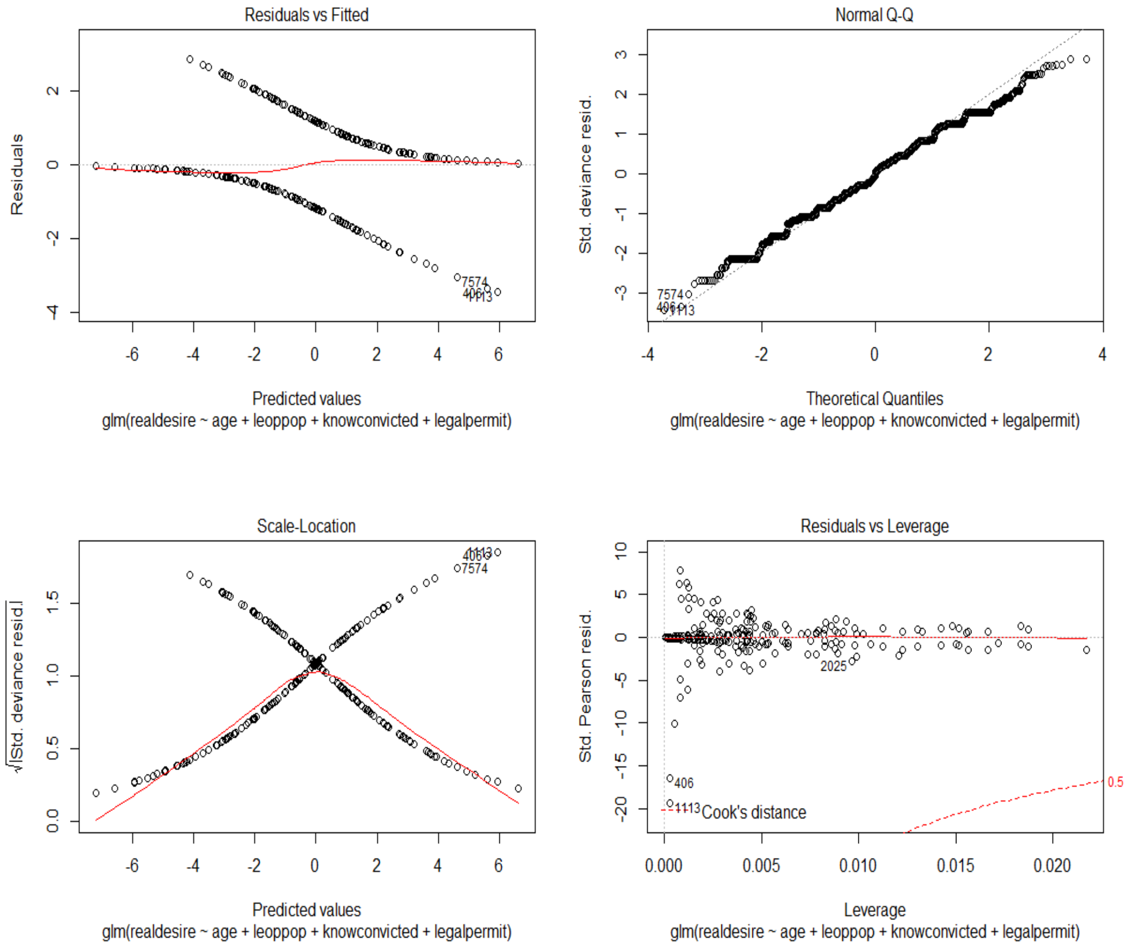
Appendix 2. Diagnostics plots for the best logistic regression models explaining Shembe follower authentic leopard skin possession pre-FFL intervention (entire pre-FFL questionnaire: *n* = 8,600; 2013–2018).



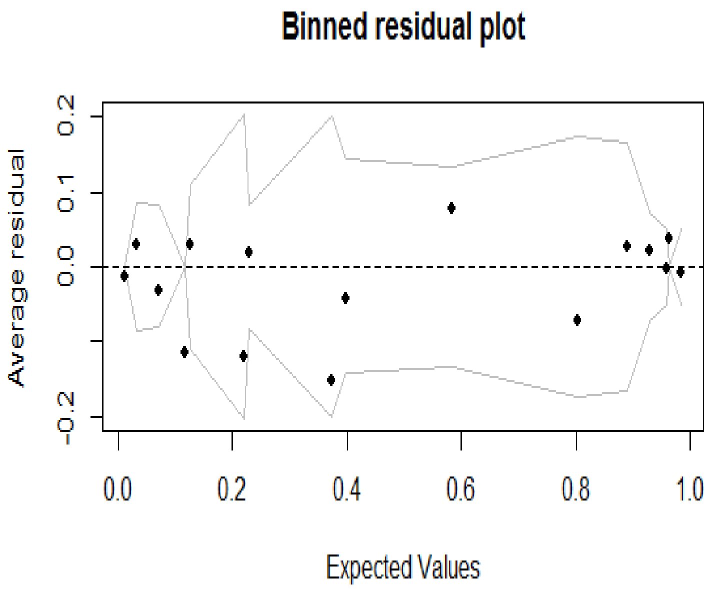


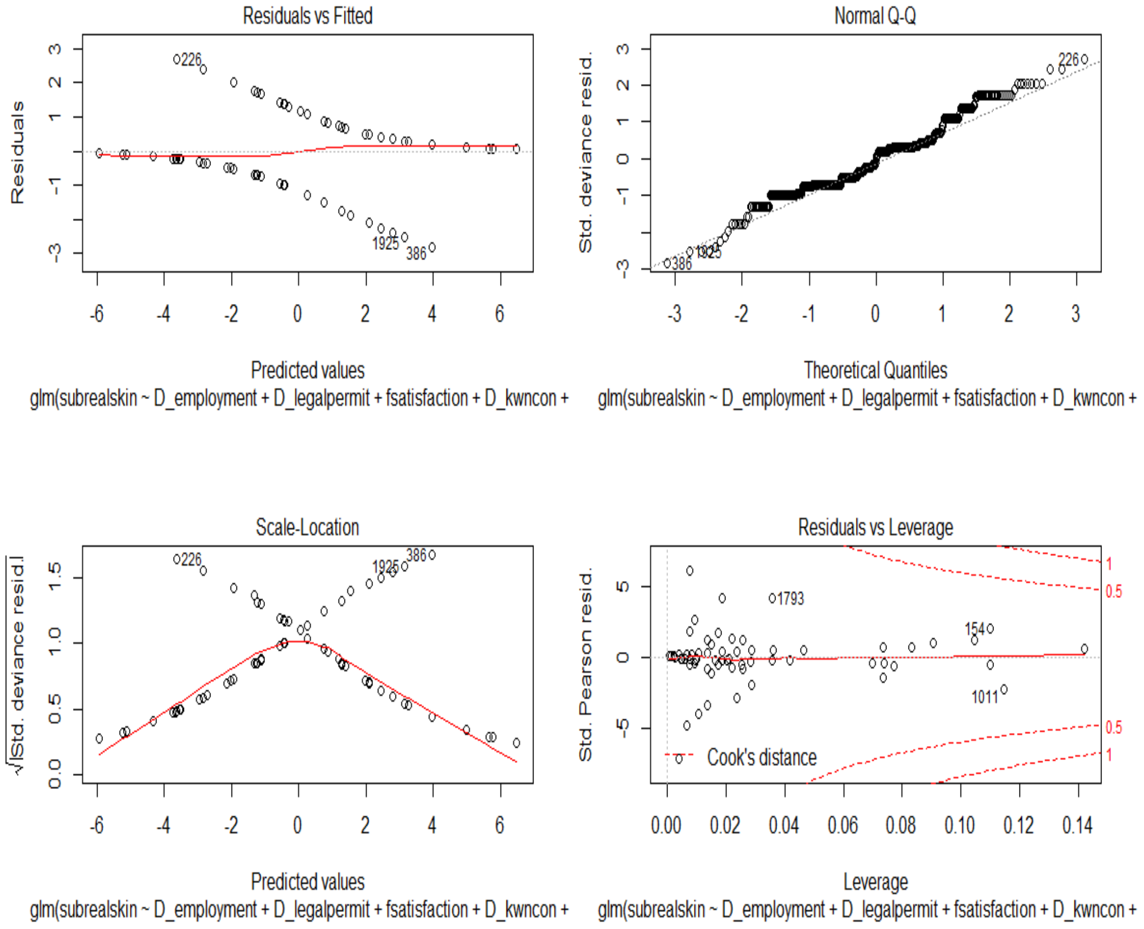
Appendix 3. Diagnostics plots for the best logistic regression models explaining Shembe follower authentic leopard skin desiribility pre-FFL intervention (entire pre-FFL questionnaire: *n* = 8,600; 2013–2018).



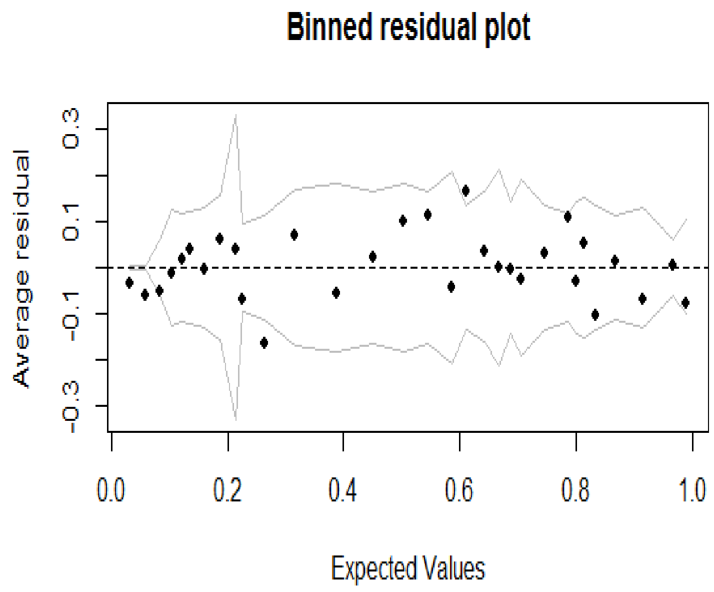


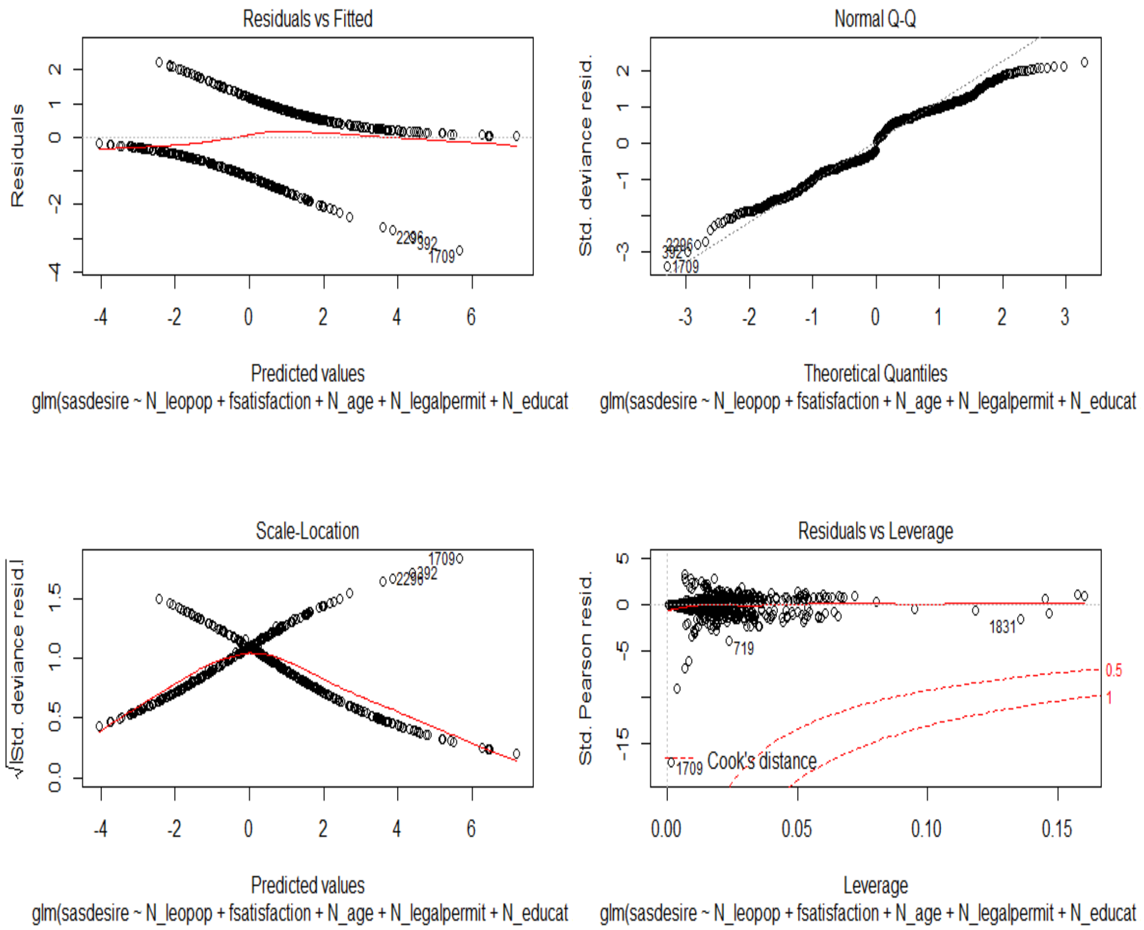
Appendix 4. Diagnostics plots for the best logistic regression models explaining Shembe follower authentic leopard skin aquisition post-FFL intervention (post-FFL follow-up questionnaire: *n* = 2,300; 2013–2018).



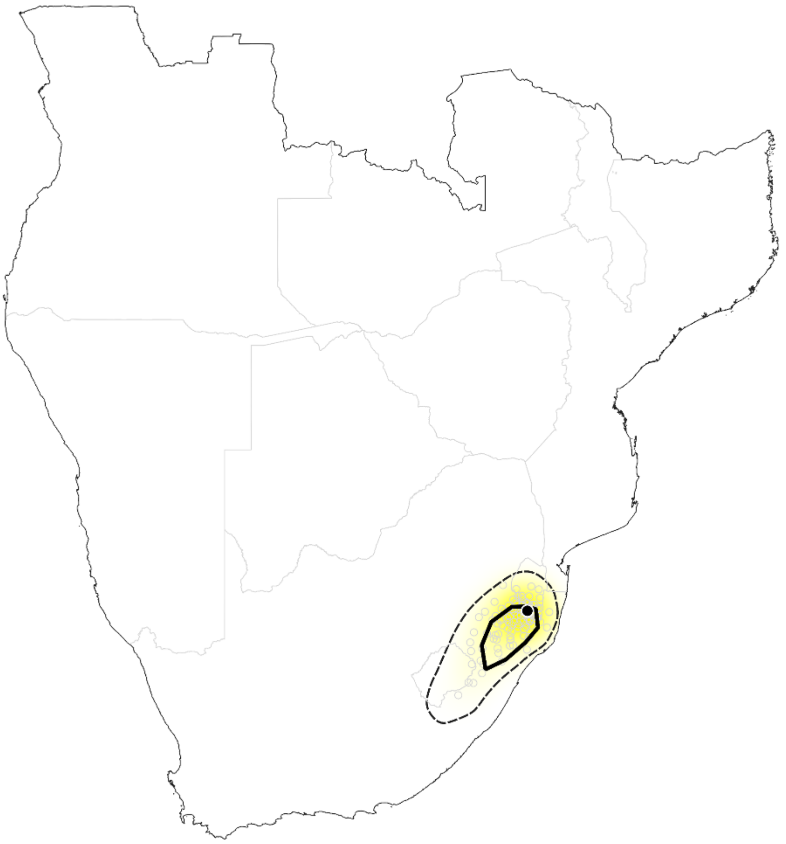


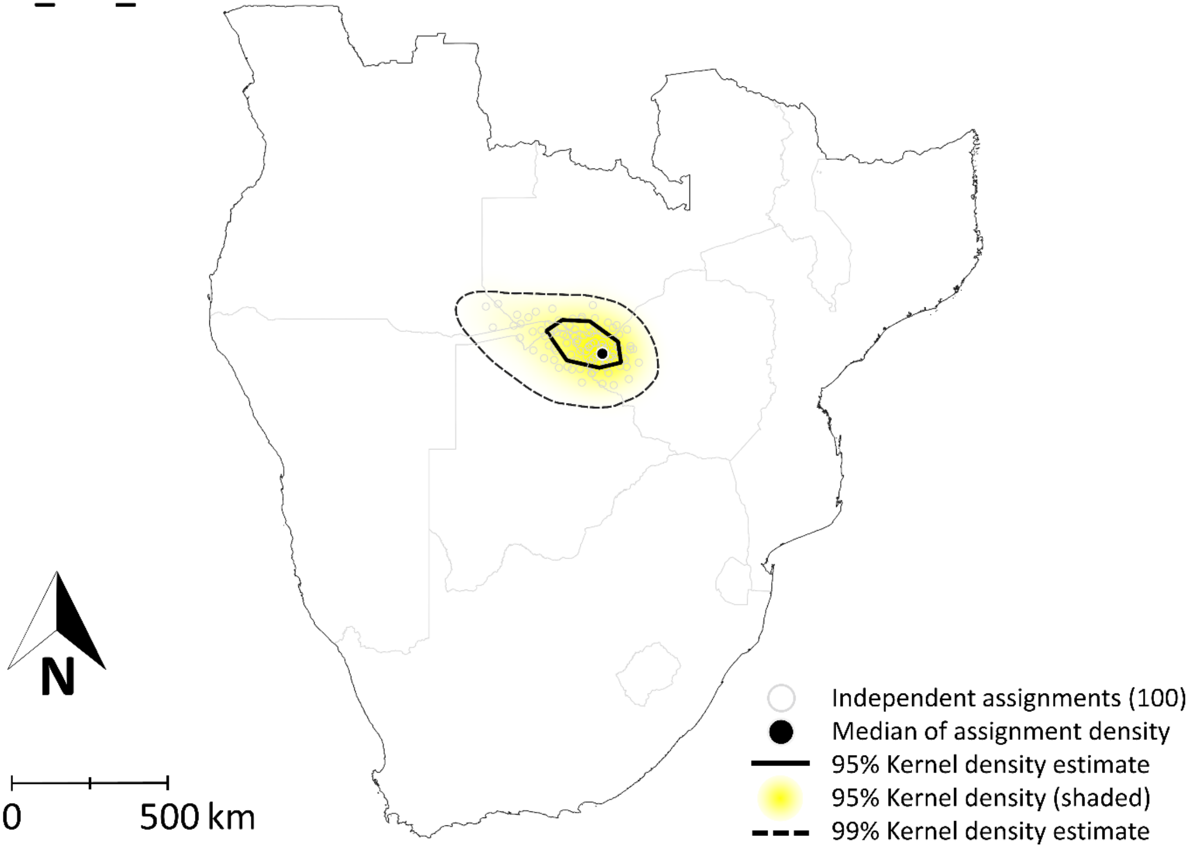
Appendix 5. Diagnostics plots for the best logistic regression models explaining Shembe follower authentic leopard skin desirability post-FFL intervention (post-FFL follow-up questionnaire: n = 2,300; 2013–2018).



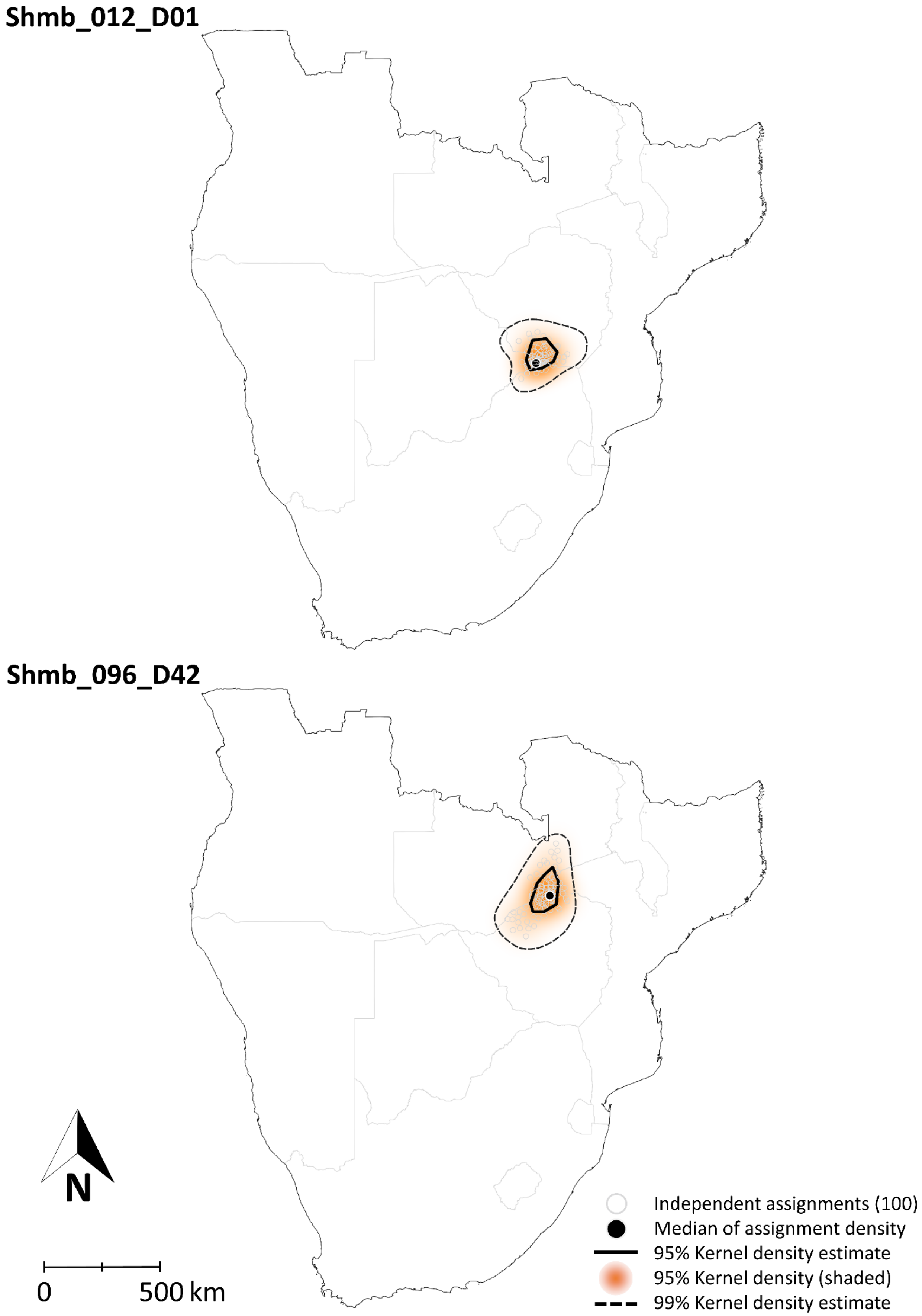


Appendix 6. An example of two assignment plots of Raid samples indicating the 100 assignments sampled from the posterior distribution, the median assignment density, as well as the 95% and 99% kernel densities for each assignment in southern Africa.


Raid_004_D05

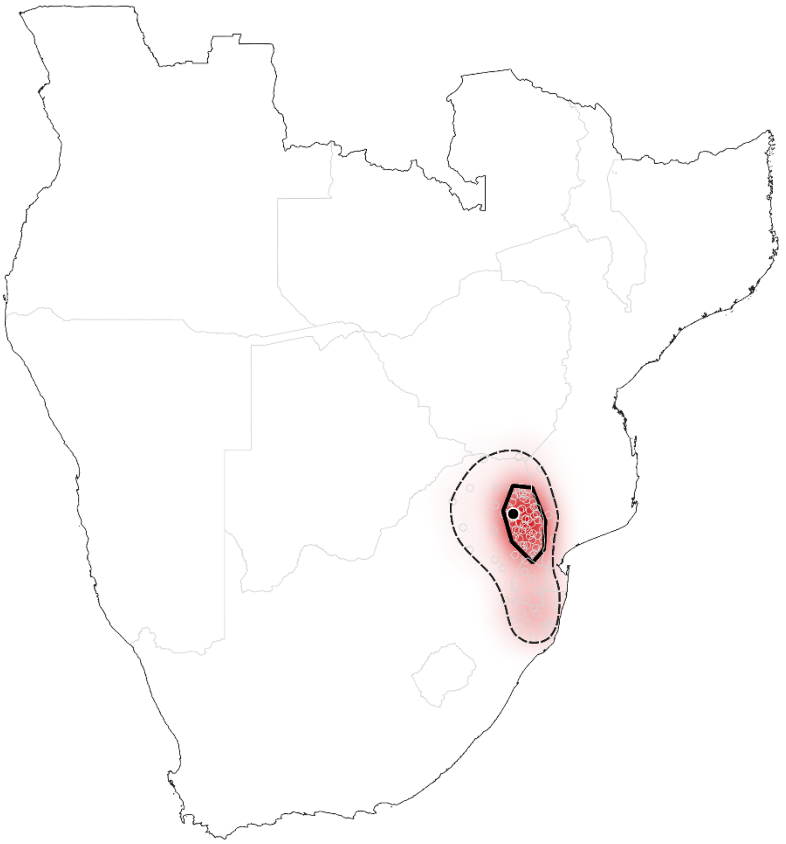

Raid_009_D12

Appendix 7. An example of two assignment plots of Shembe samples indicating the 100 assignments sampled from the posterior distribution, the median assignment density, as well as the 95% and 99% kernel densities for each assignment in southern Africa.

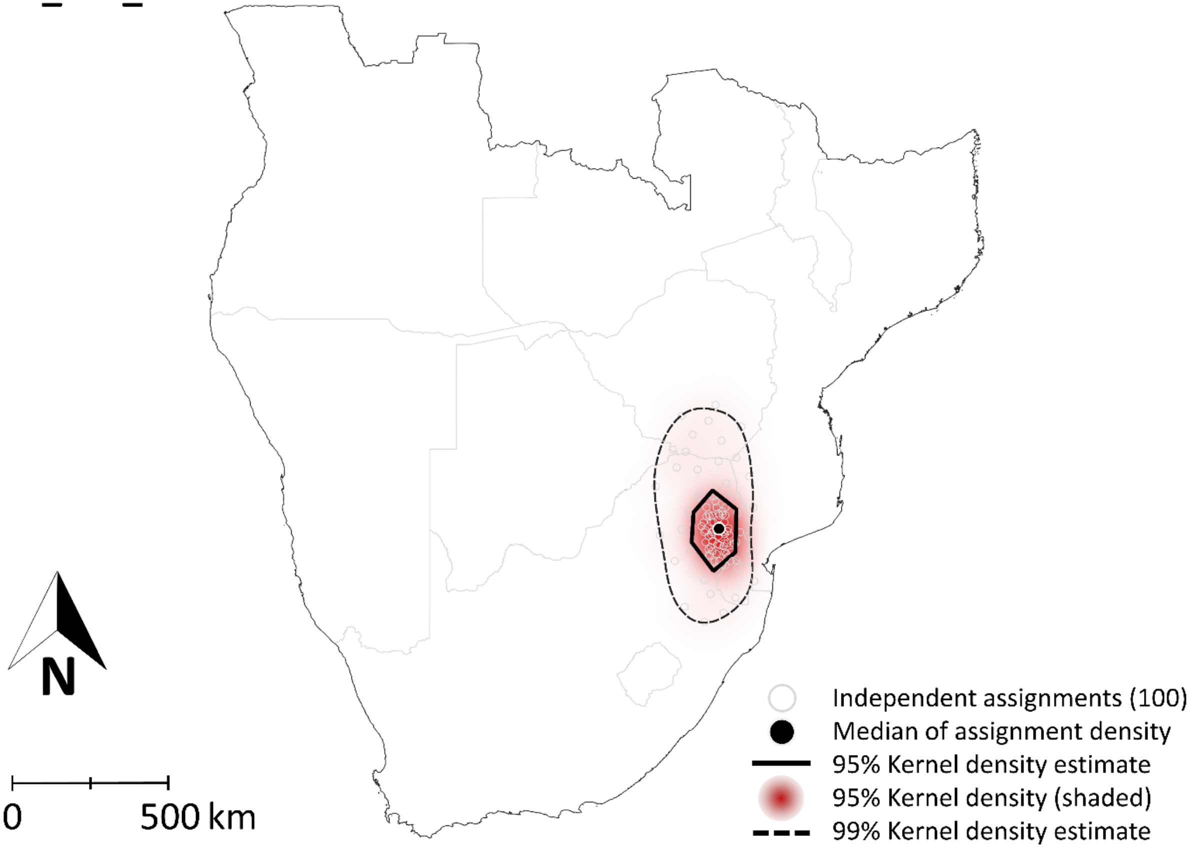


Appendix 8. An example of two assignment plots of *Muti* samples indicating the 100 assignments sampled from the posterior distribution, the median assignment density, as well as the 95% and 99% kernel densities for each assignment in southern Africa.

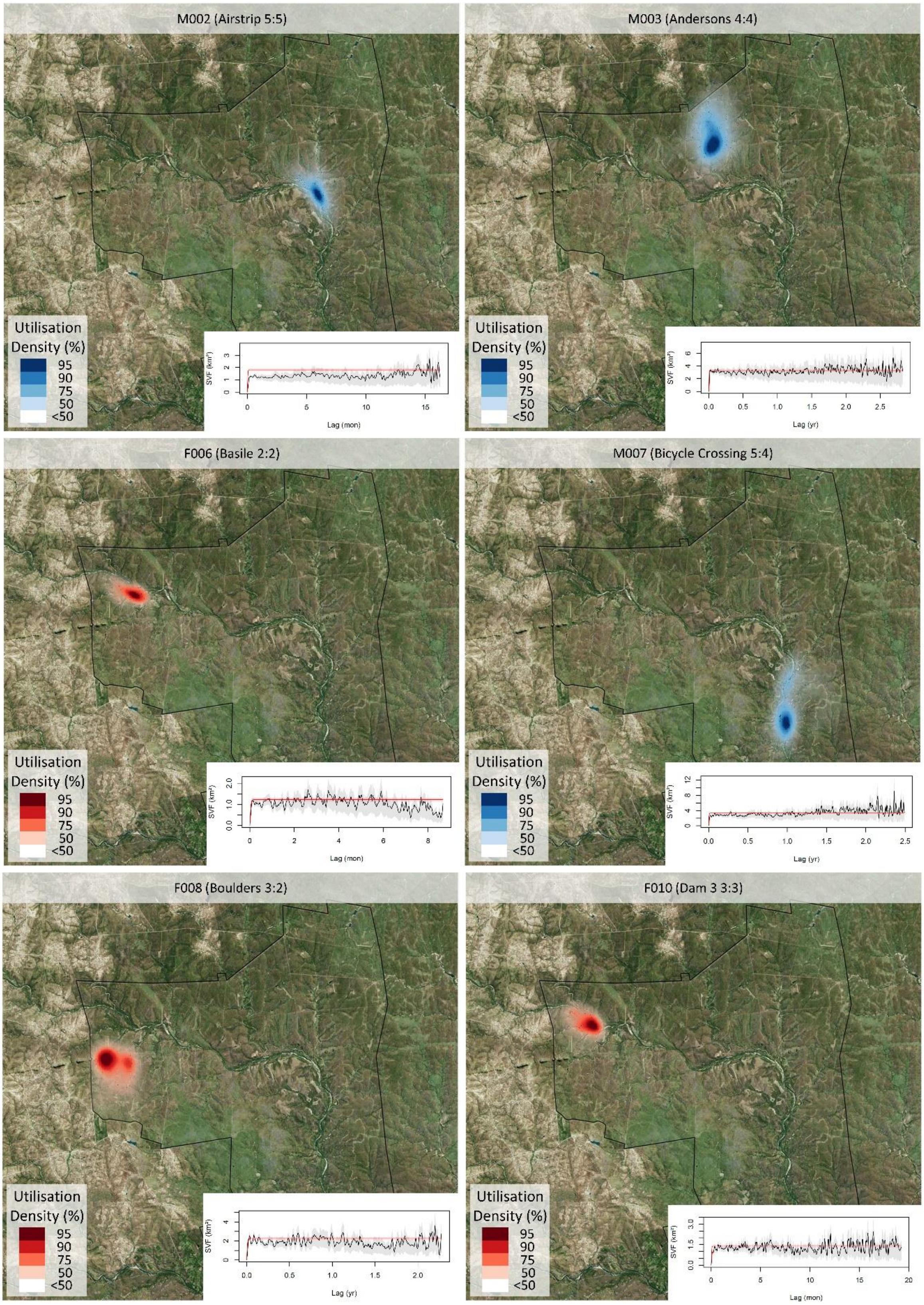
***Muti*_043_D23**



***Muti*_019_D15**



Appendix 9. An example of six autocorrelated kernel density estimates of leopard home range by utilisation density in the Sabi Sands Game Reserve. Indicated are both male (blue) and female (red) utilisation densities, as well as the space-use variograms used to define home range model selection.



Appendix 10. An example of six autocorrelated kernel density estimates of leopard home range by utilisation density in the Phinda-uMkhuze Complex. Indicated are both male (blue) and female (red) utilisation densities, as well as the space-use variograms used to define home range model selection.