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RESEARCH ARTICLE

Repatriating leopards into novel landscapes of a South African province

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Abstract

1. Leopards are often translocated away from where they are caught as non-lethal human-wildlife conflict mitigation. It is alleged that leopards fail to settle where they are translocated to, owing to territoriality. We address the need to publish more accounts of successful repatriation of leopards, but also include novel applications aimed at orphans and confiscated leopards.

2. We satellite collared 16 leopards which included a mixture of relocated and translocated leopards, of which the latter included conventional damage causing animals (DCAs, viz 'problem animals'), orphans and confiscations. We determined standard home-range metrics and assessed home-range stabilization as a means of determining site fidelity. Premature mortality and site infidelity, that is homing back to origins, were considered failures. We looked at range stabilization by examining successive monthly ranges against that of the preceding month, that is utilization distribution overlap indices (UDOIs).

3. Relocations turned out to be residents (~3 km, n = 3), while they were immune to intervention, while translocations resulted in 50% success (n = 12), which were invariably confiscated adults of unknown origin, and simulations of natal dispersals of orphans (~25 km, n = 3). DCAs never settled where released (~90 km, n = 5). Resident leopards showed high monthly UDOIs, and for those translocated a minimum of 0.15 was benchmarked to suggest range stability, which also reflected large spatial ranging.

4. Success in home-range establishment was associated with landscapes which were unsaturated by other leopards, but anthropogenic threats still persisted, such that survival after a year was ~45%, but was not different to the normal background mortality of areas outside protected areas in the country. Operations are costly, particularly that to do with veterinary treatment, immobilization, collars and temporary keeping, but such costs can be carried by public interest groups.

5. All adults (>3 years) of known origin should be relocated (transported distance < home-range diameter), while subadults (1–3 years) can be considered for translocations (transported distance > home-range diameter), while heeding

ecological and genetic considerations, and not exceeding ˜400 km. Other non-lethal mitigation should however be considered before translocation of leopards is contemplated. These findings can be applicable to solitary felids with a similar social organization.

KEYWORDS
asymptotic home range, carnivores, felid conservation, human wildlife conflict, reintroduction, relocation, translocation, utilization distribution overlap indices overlap

1 | INTRODUCTION

Leopards *Panthera pardus* come into conflict with humans over their livestock or game that they keep (Cobb, 1981; Grimbeek, 1992; Mizutani, 1993; Swanepoel, 2008), and thus landowners seek to either destroy them on their properties, or have them removed (Inskip & Zimmermann, 2009). Since attitudes to carnivores have changed in the past decade, landowners may resort to non-lethal approaches (McManus et al., 2014). One of the non-lethal options available is that of translocation, which entails the deliberate movement of an animal from one location to another (Athreya et al., 2007; Fontúrbel & Simonetti, 2011; Linnell et al., 1997), which ostensibly mitigates potential human wildlife conflict at the site (Cobb, 1981; Hamilton, 1981; Linnell et al., 1997; Weise, 2016).

For many years, it has been accepted that translocations of leopard into protected areas (PAs) is futile (Cobb, 1981; Mills, 1991), simply owing to the fact that many of these translocations result in animals returning to an origin or simply continue being a nuisance elsewhere (Hamilton, 1981). Hamilton (1981), however, acknowledged that the failures were simply due to saturated populations in PAs, where it is sometimes forgotten that *some* of the leopards that were translocated by Hamilton (1981) *did* in fact remain on some of the PAs (admittedly only two of seven males), though the technology at the time made for inconclusive outcomes. There has thus been a fixation to purport on failed translocations of leopard (Cobb, 1981; Hamilton, 1981; Mills, 1991), while there have been notable strides in improving translocation success of leopards in subsequent years (Briers-Louw et al., 2019; Hayward et al., 2006; Weise et al., 2015).

There has though been negative sentiment on leopard translocations, especially in human-dominated areas (Athreya et al., 2007), where conflicts have even lead to human fatalities (Athreya, 2006), leading to such policies being critically questioned (Athreya et al., 2011). There, satellite-collared individuals have never been directly implicated in conflict, but given high human population densities, the potential is there (Odden et al., 2014), though in Africa, at least, releases of the species are never contemplated in high human use areas.

This study emerged as a need to repatriate leopards which had been confiscated in a law enforcement operation ('Operation Dewclaw'; see Table 1), where we were tasked to examine whether homing to the origin would indeed take place. At the time, there were suspicions that leopard were being illegally caught to be laundered into the trophy hunting industry.

The project was expanded to include other routine translocations of putative problem animals too and to assess whether we can repatriate leopards to novel environments.

This work is important in the context of the oft purported failure of leopard translocations (Hamilton, 1981), which in many cases was related to outdated technology, that is VHF radio-telemetry. In the interim, the use of more advanced satellite technology has allowed better clarification on translocation success and shown mixed success, with certain documented failures (Odden et al., 2014; Weilenmann et al., 2011), while there have been notable successes too (Briers-Louw et al., 2019; McManus, 2009; Weise et al., 2015), where , for example, 66.7% of translocated leopards successfully established home-ranges (HR) in Namibia (Weise et al., 2015).

Defining translocation success has been debated and various criteria have been proposed (Fischer & Lindenmayer, 2000; Fontúrbel & Simonetti, 2011; Linnell et al., 1997), culminating in established standards (IUCN/SSC, 2013). Leopard-specific studies share similar criteria, that is alleviating conflict at source, refraining from conflict at release site, site fidelity, no homing or exploratory behaviour, and to contribute to the gene pool (Briers-Louw et al., 2019; Weilenmann et al., 2011; Weise et al., 2015), importantly in this, is HR stabilization, reproduction and survival past a year (Briers-Louw et al., 2019).

Of published literature for reintroductions of radio-tracked leopards per study using older radio-telemetry there are sample sizes of one (Cristescu et al., 2013; Hayward et al., 2006; Weise et al., 2015), two (Hamilton, 1976; Mondal et al., 2013), and 10 leopards (Hamilton, 1981) from which to examine this. However, in the era of satellite technology, the sample sizes per study have not improved much, and these include reintroductions of one in Botswana (Houser et al., 2011); two into an Eastern Cape PA of South Africa (McManus, 2009); then four into a Botswana PA (Weilenmann et al., 2011); five in India (Odden et al., 2014); and six into PAs of Malawi (Briers-Louw et al., 2019) and Namibia (Weise et al., 2015), respectively.

The premise for deciding upon suitable release sites for this species in South Africa's North West Province (NWP) was the paucity of leopard occurrence records. Since a province wide mammal-based inventory (2010–2013) used a leopard-specific survey design (Power et al., 2019), it was assumed the species *should* have been detected if present. It is said too that leopard can be declared absent where a camera-trapping effort of at least 500 trap nights is done (Ngoprasert et al., 2012), and some of the vegetation types of NWP had no detections despite > ~1600 trap nights (Figure 1; Power et al., 2019), thus these areas were earmarked as ideal release areas. It was further acknowledged that the species was likely not absent entirely, but thought to be either unsaturated or functionally extinct, as is a well-established hypothesis outside PAs (Balme et al., 2010; Marker & Dickman, 2005; Rosenblatt et al., 2016).

Notwithstanding anthropogenic pressures outside PAs, and the need to mitigate conflict, it was assumed there would be only nominal human disturbance on the edges of smaller PAs (<300 km^2), and these areas would have territorial vacancies (Balme et al., 2010; Hamilton, 1981), such that site fidelity would likely occur, and sufficient conspecifics would ensure site attraction (Hayward, Adendorff et al., 2007a; Smith & Peacock, 1990).

We aimed to assess successful establishment of leopards in release areas, that is site fidelity. Our objectives were to (a) assess whether leopard remained in the proximity of the release area and ascertain that HR stabilization took place.

Given this, we appraised the success of leopard reintroductions by examining (a) reproduction, whether by males or females, which would be a proxy for territoriality, and (b) survival after the first year of monitoring. From this we would address the appropriateness of translocations.

2 | MATERIALS AND METHODS

The NWP is covered by the savanna biome in the northern parts (Figure 1), and it experiences a subtropical to semi-arid climate (Mucina & Rutherford, 2006), and agriculture and mining are prominent economic activities in NWP.

Leopards were either caught using standard walk-in cage traps, or they were confiscated from perpetrators illegally keeping them. Damage causing animals (DCAs) were mostly captured and then collared (Table 1).

Leopards were immobilized using standard chemical immobilization for the species (McKenzie, 1993). A CO_2 powered Dan-inject® dart gun pressure set for ~5 m was used to immobilize leopards with Zoletil (Zoletil 100®, Virbac RSA, Halfway House), with dosages of 5 mg/kg (Bertram & King, 1976), administered by a qualified veterinarian or one of the authors experienced in this (in a veterinarians presence).

Every individual was sexed and aged using both physical appearance (Balme et al., 2012) and tooth wear (Stander, 1997), and we classed adult females and males, as above 2 and 3 years, respectively (*adapted after* Bailey, 1993; Swanepoel, 2008).

Most leopards were collared using dual VHF/GPS/ Iridium satellite collars (African Wildlife Tracking cc, 106 Nuffield Street, Rietondale, Pretoria, South Africa), while one of these had a release mechanism.

One animal was collared with a Sirtrack GSC-275-D GPS Iridium collar (Sirtrack/Lotek, 8A Goddard lane, Havelock North, 4130, New Zealand, provided by Globals Supplies), which was releasable within 15 months. One collar was based on vehicle-tracker technology and registered locations for every movement made (TractGroup, Unit 8,

TABLE 1 The different management categories of the translocated leopards in the NWP

Type	Origin	Definition	Notes
Resident	Known	Leopard captured or not, but indefinitely lives in a specific location as a resident in the population	It may include a relocated/translocated leopard in a given location where it has decided to home back
Damage causing animal	Known	Leopard captured, either by the department or a private individual, and the purpose of capture is related to damage it has done, by killing livestock or game, and landowner wishes for its removal	Conventional 'problem leopard' as known to lay public and most are familiar with this type
Confiscated	Unknown	Leopard obtained, and kept for forensic reasons, as animal has been confiscated from a person illegally keeping them and authorities attempt to release it somewhere	Animal kept temporarily until court order allows for release, and collars are needed to determine origin, as perpetrators often insist on residency of the individual
Orphaned	Known/ Unknown	Leopard obtained/ captured, where it was clear that they were pre-weaned/ not reached independence, and are without doubt proven to be without their mother, who has ostensibly been removed or killed. Natal origin is the location where they were first captured when pre-weaned juveniles (<3 months)	Evidence of orphaning is determined from camera trap footage placed at the individual's location for a period of time that exceeds that which a mother should tend to it. Leopards are released when old enough (>2 years) with a collar
Rehabilitating	Known/Unknown	Leopard obtained/captured, which has endured an injury and undergoes treatment and rehabilitation in temporary captivity, before later release	These include snared individuals, and those which have damaged their teeth, and they are released and monitored

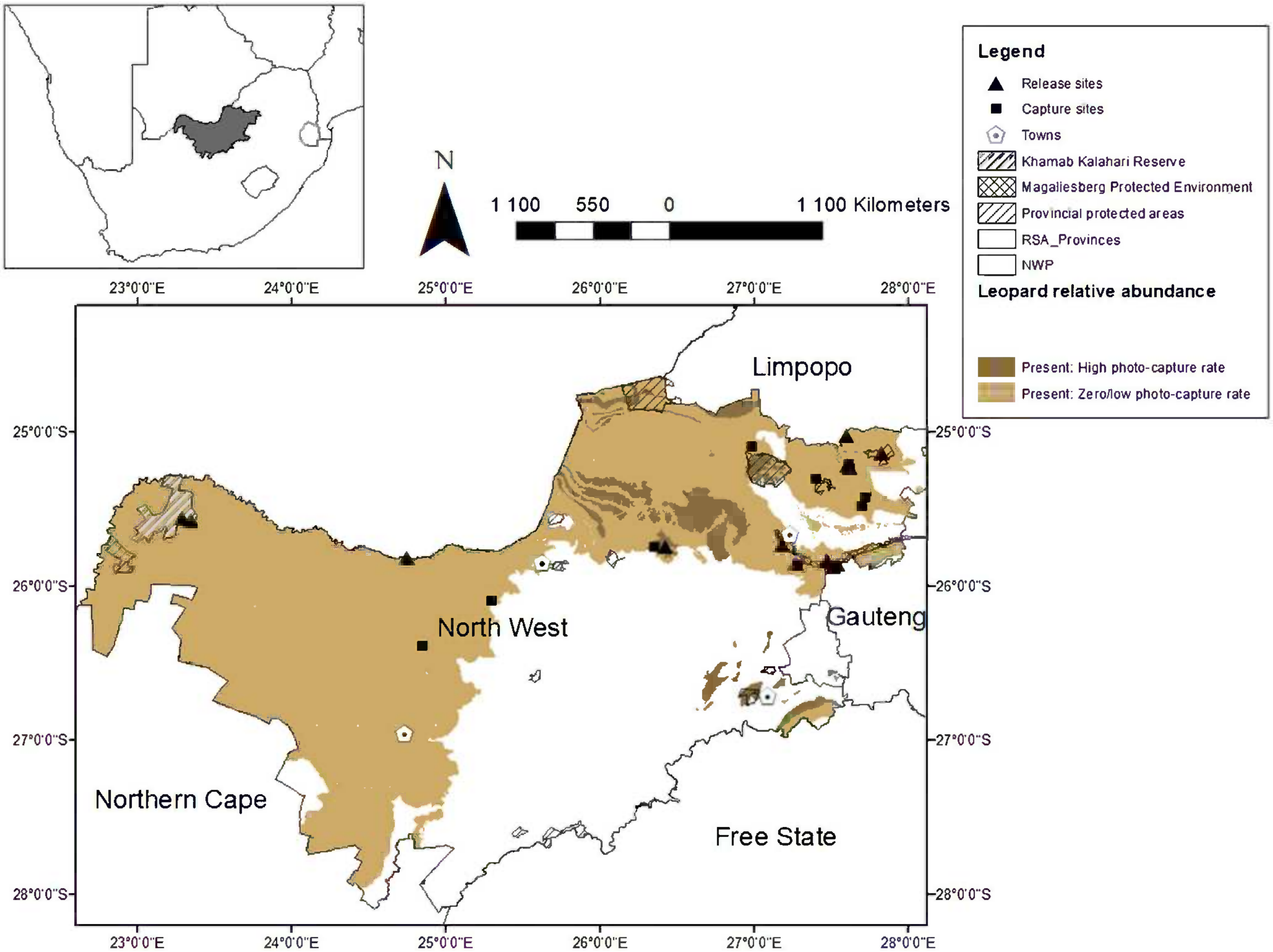


FIGURE 1 The North West province is situated in north-central South Africa

Block A, Blueberry Office Park, Apple street, Honeydew, Johannesburg, 2040, South Africa). No collar exceeded the maximum of 5% of body weight (Amlaner & Macdonald, 1980).

The locations of all animals registered four times per day. The times 00:00, 06:00, 12:00, and 18:00 were selected (*after* Swanepoel, 2008), while the Sirtrack collar registered hourly intervals, and the Tractgroup collar registered multiple points when active, and these were reduced to 6-h intervals for comparability.

Leopards were transported in ventilated transport crates, and if not released immediately, leopards were kept in temporary captivity (McKenzie, 1993), and the South African National Standards (SANS 1884-3:2008) adhered to as policy. If young (<2 years), we awaited for maturity (> 2 years), for release, or the outcomes of court orders for release. Temporary keeping facilities were registered with the province and adhered to the keeping specifications, while the same could not be said of facilities where they were initially kept illegally, where in one situation, the dimensions were the same as that of the animal.

Study animals were of overlapping categories (cf. Weise et al., 2015; Table 1), and categories could be compared against one another.

Sixteen leopards were obtained for collaring, release and monitoring (Table 2). Leopards were released into all PAs where they occur (Figure 1), as reinforcement to existing, but low-density populations (IUCN/SSC, 2013), and for the sake of the monitored individuals we focused on the following release areas: (a) the Magaliesberg and Marico protected environments, (b) North West Parks Board (NWPB) Reserves of Kgaswane Mountain Reserve and Borakalalo National Park and (c) the privately owned Khamab Kalahari Reserve.

The Utilization Distribution (UD) (Van Winkle, 1975) was determined as the kernel density estimate where areas were estimated using the kernelUD function from the adehabitat package in R (R-Core Team 2014).

We calculated HRs in ArcGIS (ESRI, 2019), and where a dispersal or translocation took place discrete areas were examined. We compared across the different categories and grouped confiscated and rehabilitated animals as translocated animals for comparability (cf. Weise et al., 2015).

The nature of translocations followed established protocols (*after* IUCN/SSC, 2013), while a relocation was defined as a translocation less than the maximal diameter of the specific gender's HR, based on ecological or geographic benchmarks.

Success was gauged when (a) HR stabilization took place or that (b) the leopards remained for at least a year on the release area, that is property or reserve.

For relocated or translocated individuals, successful HR establishment was deemed to have occurred when HRs stabilized and were within at *most* one HR diameter away from the release sites.

We worked out monthly Home-Range Overlap Indices (HROIs) and Utilization Distribution Overlap Indices (UDOIs) using the approach of Fattebert et al. (2016), but we used shorter temporal periods, that is 30 days and worked out HR overlap based on the previous month's usage. We benchmarked translocated leopards' HRs against that of residents to determine HR stabilization.

We looked at proximity of the release sites (Norton & Lawson, 1985; Weise et al., 2015), and whether the release area was within the 50% and 95% kernel HRs or not. Scaled HR diameters were measured at distances progressively away from an origin (*after* Fattebert et al., 2015) to a release site. If within this area, this would be seen as a successful establishment, while any scaled HR diameter away from this, progressively less so, until the extreme of returning to the known origin, which would be a certain scaled distance away from the release site.

Success was also evaluated in terms of whether there was survival until HR stabilisation, and whether reproduction had occurred by males or females (*after* Briers-Louw et al., 2019; Weise et al., 2015).

Reproduction was determined by assessing suspected den sites using GPS clusters (cf. Swanepoel, 2008), and we placed camera traps. We used 10 Bushnell (model 119437C, Bushnell Trophy CamTM, USA), two Cuddebacks (Cuddeback® Digital, Model C, Multiple flash, Green Bay, WI, USA) and one Scoutguard camera trap (Scoutguard Digital scouting camera trap, UM562, with MMS via GPRS, 17 Expansion street, Molendinar, Australia), which were also used to determine presence after the satellite component failed, along with radio-telemetry. We used a VHF receiver (R-1000 telemetry, Communications Specialists, Inc, 426 West Taft Avenue, Orange, CA, USA), with a four element yagi-receiving antenna to confirm activity on release areas.

Decollaring was planned for the non-releasable collars, a year after deployment, and longer if there was sufficient battery life on the collar, and GPS clusters of kills were located (Pitman et al., 2013; Swanepoel, 2008), and cage traps were placed for recapture and collar removal, with the same sedation procedure employed.

3 | RESULTS

Two leopards registered no HR data, as one died prematurely, and the other lost its collar. HR sizes were calculated for all remaining leopards (SuppInfo Figures 2–4) and presented (Figures 2–4). All leopards had their collars removed (https://www.youtube.com/watch?v=qlWj9ugBMUQ), except two females which evaded capture even after repeated trap conditioning.

Excluding releases at suspected natal origins (n = 3), and relocations, actual mean translocation distance of known-origin animals was 90.8±65 km (n = 5, range 33-194 km).

Natal area translocations of subadults was 24.7 ± 22 km (2–46 km, n = 3), while relocations were on average 3 ± 4 km (0.1-8 km, n = 3), which invariably turned out to be resident animals (Figures 3 and 4).

Residents which were relocated (Figure 5(b)), and DCAs having returned to their origins (Figure 5(d)), had minimum UDOIs and HROIs of 0.15 (Figure 5(b, d)) and 0.4 (SuppInfo Figure 5), respectively, and so this was used as the benchmark to determine HR stabilization in translocated leopards (Table 3). Translocated leopards of unknown origin had wide variation in HROIs, despite initial stabilizing (Figure 5(a)), which may be due to large HR sizes (Figure 2).

A cost breakdown was determined for each individual (SuppInfo Table 4) and summarized (Table 4).

As for the success of translocations, where stabilized HR is formed within one HR diameter of the release areas, or animals were present on release areas, this was the case for three of five females (n = 5, see Tables 3 and 4), while for males, this was three out of seven (n = 7). Altogether across all leopards this would be a 50% success (cf. Weise et al., 2015), when excluding relocation of residents (Table 3). When looking at survival, this tracked HR stabilization in males, but in the case of females this became two out of five, resulting in survival after a year across all leopards to be 45.4% (n = 11, Table 4).

Leopards kept in temporary captivity >100 days were for the most part successful in establishing HRs (Tables 2 and 3), while also more costly (Table 4). Translocated leopard of unknown origin and rehabilitated orphans successfully established HRs (Table 3, Figures 2 and 3), while translocated DCAs were not successful (Table 3; Figures 3 and 4) as they either homed back to where they came from, or died on the release sites owing to intraspecific competition or from wire snares (Table 3). The least expensive intervention was to relocate leopards, being half that of translocations (Table 4).

4 | DISCUSSION

The *status quo* remains unchanged that translocating (not relocating) problem leopards has limited success – at least in this study, and at a regional level, that is a South African province.

This is not to say that success cannot be garnered elsewhere as there are many agencies that allude to success, while the most convincing documented successes in a province of a similar size are those in the Eastern Cape (Hayward et al., 2006; McManus, 2009). Beyond South Africa, the long distance translocations into Malawian (Briers-Louw et al., 2019) and Namibian reserves (Weise et al., 2015) are resounding successes of what appear to be problem leopards being translocated elsewhere.

We advocate release site fidelity (Briers-Louw et al., 2019; Hamilton, 1981; Weilenmann et al., 2011), though desirable, site fidelity was not considered a prerequisite for translocation success in the Namibian study, as there, free choice of movement was permitted (Weise et al., 2015). It is argued that a carnivore moving out of its recipient area may not necessarily constitute a failure if the animal had little impact on its environment (Weise, 2016). In our case if not exactly in the confines of a PA where the animal was released, we considered relatively nearby to be a good enough proxy using the HR diameter as a yardstick (Table 3). Ultimately, the desired outcome for reintroduction success is for released individuals to exhibit no signs of homing behaviour,

TABLE 2 Summary of the details and origins of the satellite collared leopards from 2014 to 2019 in the NWP

Code	Sex	Age class	Age (years)	Category	Origin	Days in temporary captivity	Collar/Release date	Release site	Translocation distance
LM01	Male	Adult	3–4	Forensic, confiscated	Unknown, illegally kept in Lichtenburg	0	Feb-14	Kgaswane Mountain Reserve, Magaliesberg	
LF02	Female	Adult	3–4	Forensic, confiscated[a]	Unknown, illegally kept in Lichtenburg	103	May-14	Mountain Sanctuary Park, Magaliesberg	
LF03	Female	Adult	7–8	Forensic, confiscated[b]	Unknown, illegally kept in Lichtenburg	182	Aug-14	Mountain Sanctuary Park, Magaliesberg	
LF04	Female	Adult	2–3	Resident	Jabulani Game Ranch, Atlanta	0	Sep-14	Jabulani Game Ranch, Atlanta	0.1
LM05	Male	Adult	3–4	Forensic, confiscated	Unknown, suspected Lephalale, Limpopo?	455	Feb-15	Elandsberg, Assen	
LM06	Male	Adult	3-4	DCA, translocated[b]	Tribal areas, Zandfontein/ Vaalkop dam area	17	Jan-15	Kgaswane Mountain Reserve, Magaliesberg	37
LF07	Female	Adult	2-3	DCA, relocated	Draaifontein, Groot Marico area	0	Aug-15	Bokkraal north, Groot Marico area	8
LM08	Male	Adult	4-5	DCA, translocated[b]	Veekraal, north of Brits, near Sable Ranch	26	Sep-15	Borakalalo National Park	33
LF09	Female	Adult	2–3	DCA, translocated	Kudu hills, Stella	133	Jun-16	Khamab Kalahari Reserve	194
LM10	Male	Subadult	2–3	Forensic, confiscated, rehabilitated	Unknown, suspected Brits	646	Jul-16	Khamab Kalahari Reserve	
LM11	Male	Subadult	2–3	Orphaned and rehabilitated	Olifantspoort, south of Magaliesberg	565	Mar-17	Nooitgedacht, Magaliesberg	26
LM12	Male	Subadult	2–3	Orphaned & rehabilitated	Olifantspoort, south of Magaliesberg	561	Mar-17	Olifantspoort, south of Magaliesberg	2
LM13	Male	Adult	3–4	Resident	Jabulani Game Ranch, Atlanta	0	Oct-17	Jabulani Game Ranch, Atlanta	1
LM14	Male	Adult	6–7	DCA, translocated	Tribal areas, Welgewaagd/ Molorwe, north-west of Pilanesberg	0	Aug-18	Nooitgedacht, Magaliesberg	102
LF15	Female	Adult	2–3	Orphaned & rehabilitated	Klipkop, north of Brits	490	Nov-18	Mountain Sanctuary Park, Magaliesberg	46
LF16	Female	Adult	2–3	DCA, translocated	Mareetsane, west of Mahikeng	0	Sep-19	Molopo river, Mabule, west of Mahikeng	88

[a]Treated for snare wound, 24 September 2014, hospitalized, repatriated on 5 October 2014 (Power et al., 2020).
[b]Dental treatment before release.

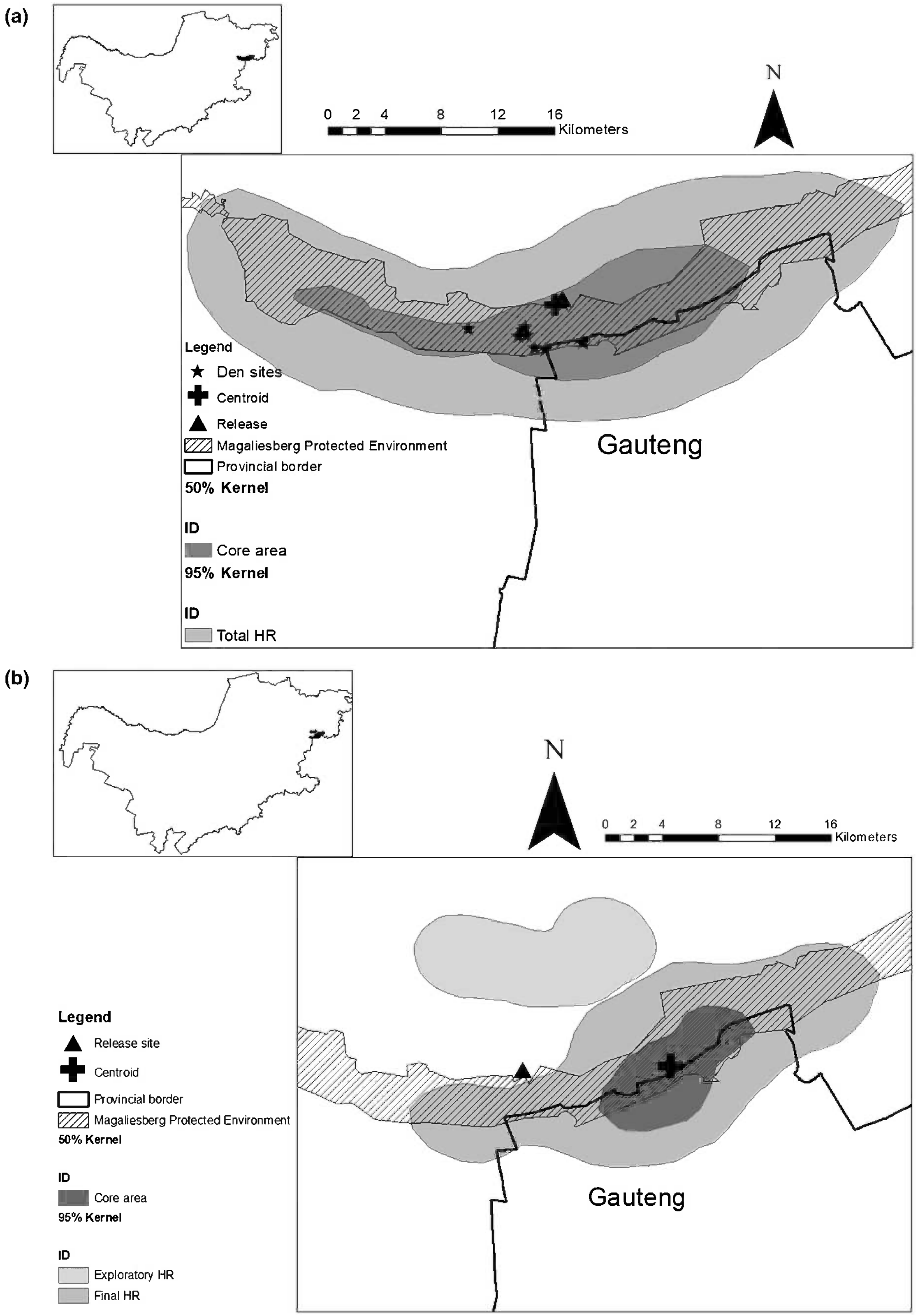
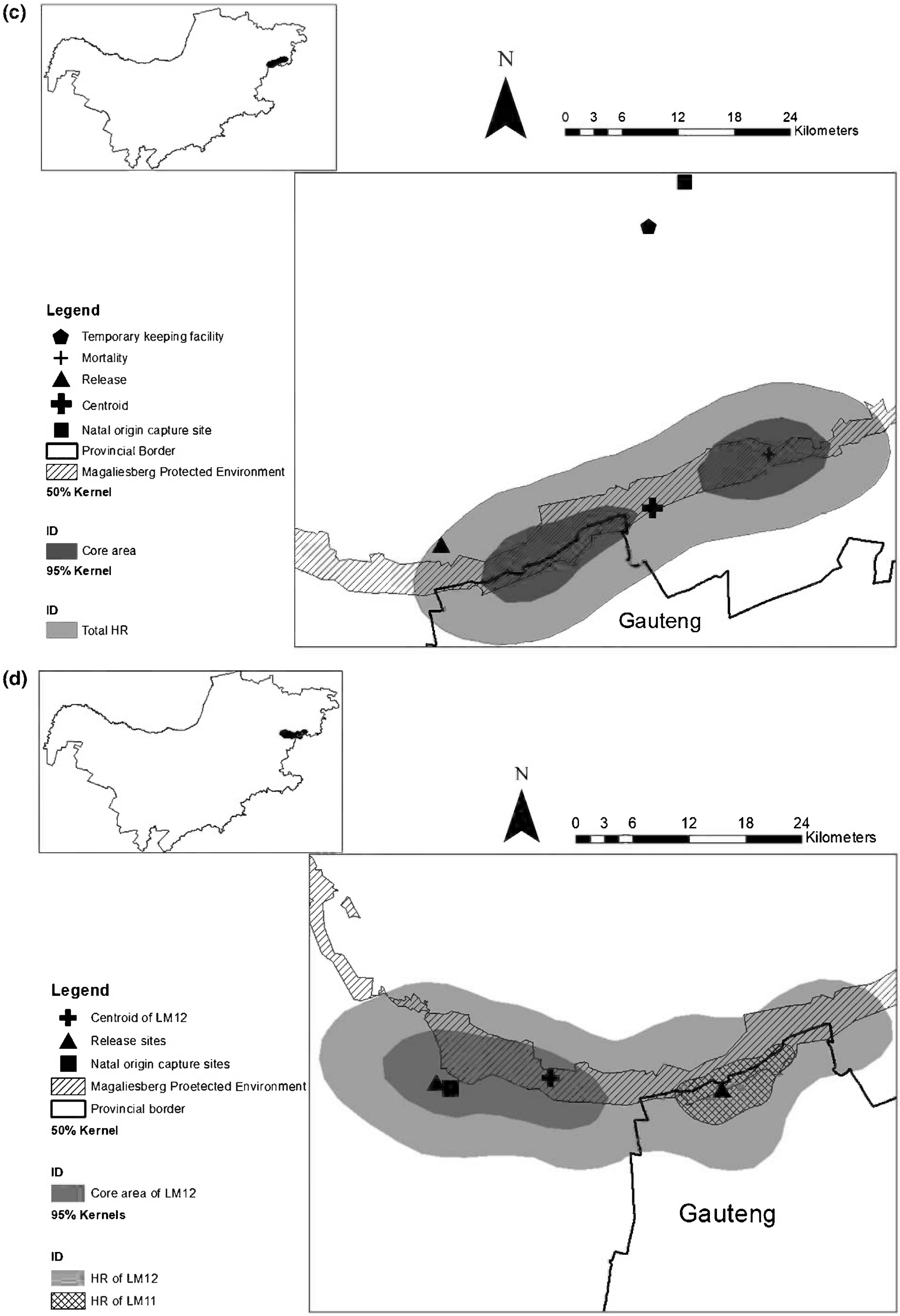


FIGURE 2 HRs of leopards in the Magaliesberg mountain range, with dark (50% kernel), and light grey (95% kernels) for translocations of (a) LF02 (Jun-14 to Nov-15), (b) LF03 (Aug-14 to Jan-15), (c) LF15 (Nov-19 to Jul-20) and (d) two brothers, LM11 and LM12 (Mar-18 to Aug-18). Natal origins, capture and release sites are indicated, as are arithmetic mean centres of HRs and sites of denning and death



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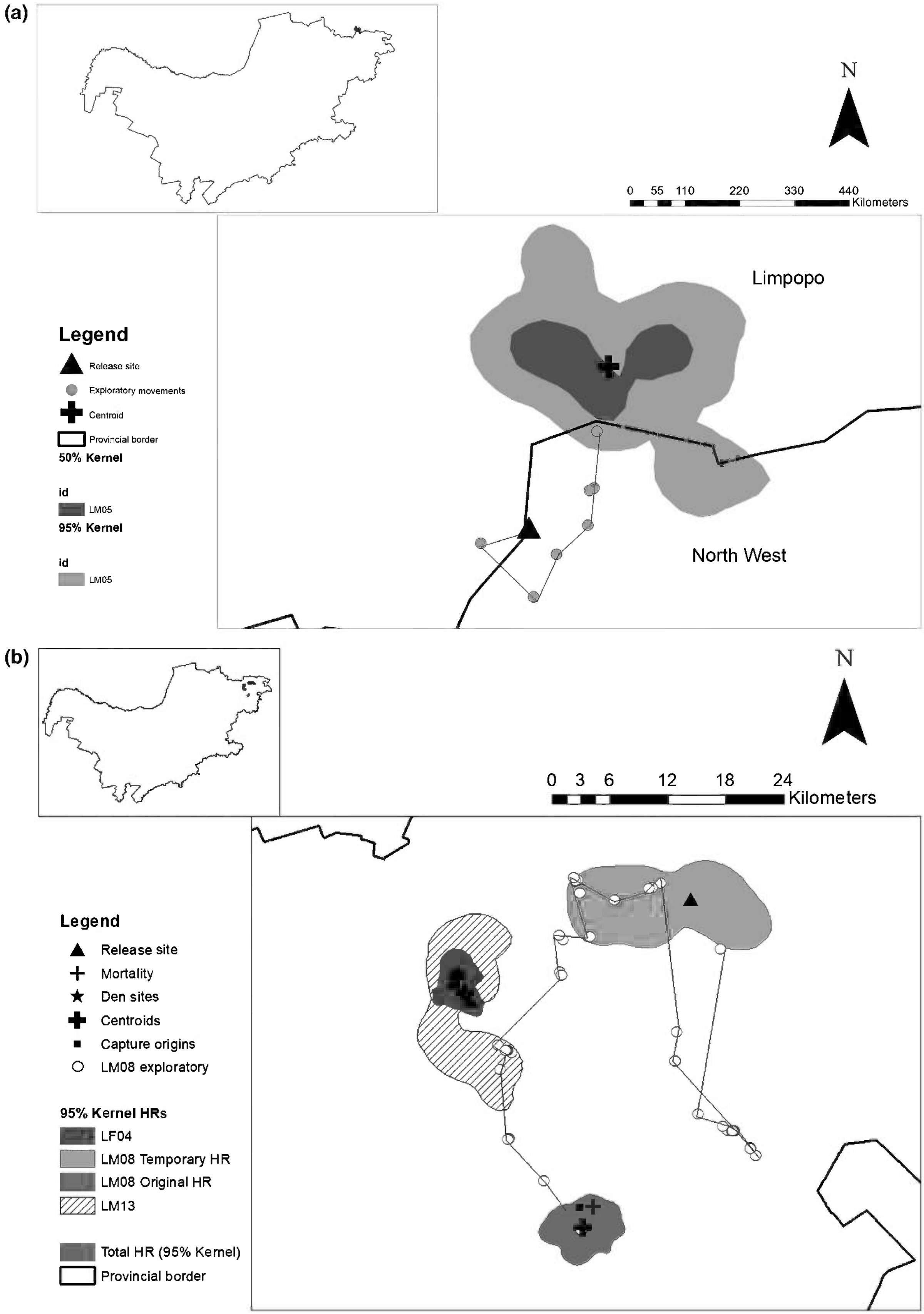

FIGURE 3 HRs of multiples leopards in north-eastern NWP, with dark (50% kernel) and light grey (95% kernels) for translocations of (a) LM05 (Feb-15 to Aug-15), (b) LM08 (Sep-15 to Apr-16), relocations of LF04 (Sep-14 to Aug-15) and LM13 (Oct-17 to Nov-17) and translocations of (c) LM06 (Jan-15 to Apr-15) and LM14 (Aug-18 to Sep-18). Capture and release sites are indicated, as are arithmetic mean centres of HRs and sites of death

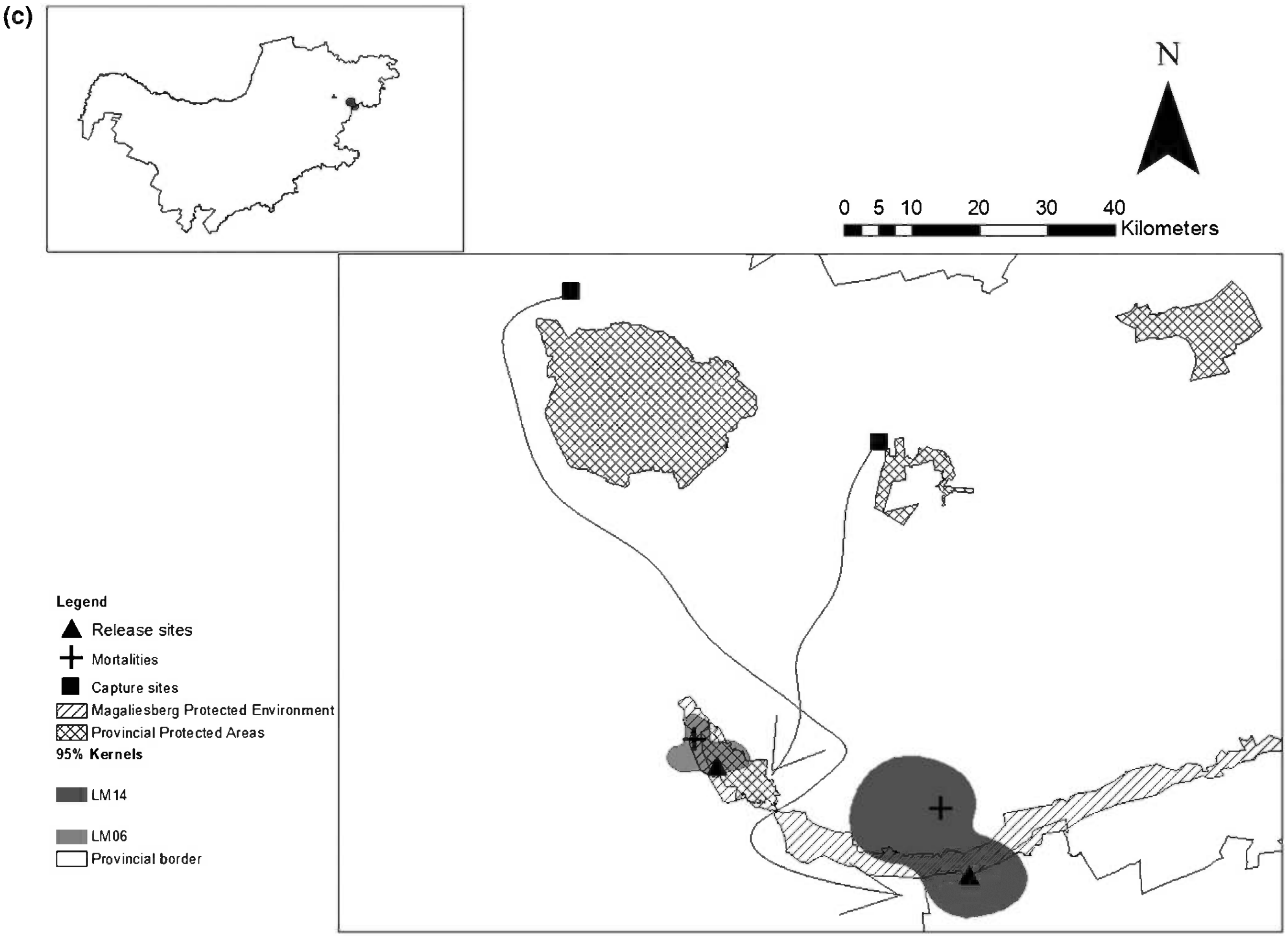

FIGURE 3 (Continued)

display little initial exploratory movements, remain in the release area and ultimately establish a permanent HR as a resident (Briers-Louw et al., 2019; Hunter, 1999; Weilenmann et al., 2011).

Carnivore translocations should exceed 100 km in an attempt to prevent homing behaviour (Fontúrbel & Simonetti, 2011; Hamilton, 1981; Lemeris, 2013), and this is indeed confirmed empirically (Weise et al., 2015), where perhaps the relatively short distance translocations we performed (˜30 to 200 km) permitted homing behaviour (Figures 3(a) and 4(c)). Long-distance translocations, between ˜400 km (Weise et al., 2015) to over ˜1 000 km (Briers-Louw et al., 2019) may be what is required to prevent homing behaviour, while our shorter translocations were constrained by the extent of the NWP (Figure 1), while we also heeded genetic considerations (Ropiquet et al., 2015) and the possible existence of different ecotypes, that is Kalahari and Bushveld.

Dispersing subadult male leopards can move up to 353 km from their natal sites or 195 km when measured in a straight line from the natal origin (Fattebert et al., 2013), so such long distances (˜200-400 km) can be contemplated for translocating subadult animals, and also for genetic reasons, as has been recently discovered in human-influenced landscapes in South Africa where undesirable natal philopatry of males readily occurs (Naude et al., 2020).

In this study, we have demonstrated successful translocations of leopards of both orphaned and unknown origin which were obtained from confiscations, which has also been the case in work in Namibia (Weise et al., 2015) and Botswana (Houser et al., 2011).

It was unclear why confiscated animals were more successfully established in novel HRs than DCA leopards. It could be hypothesized that their longer period of confinement (Table 2) could have been enough to break their homing tendency (Hayward, Adendorff et al., 2007a; Hunter, 1999; Weise et al., 2015), while prior to being seized by authorities these animals may have been in captivity for longer than what we were aware of. Be that as it may, all adults that were obtained in such a manner exhibited success in establishing HRs where they were placed (Figures 2(a), 2(b), 2(d), and 3(a) and Table 3); in one case, the arithmetic mean centre of the HR was ˜1 km from the release site (Figure 2(a)). One theory as to the success of these leopards was that LF02 and LF03 (Figure 2(a) and 2(b)) were coincidentally repatriated to where they were originally obtained from. Though not an impossibility for at least one to be from the release area, this is unlikely, given that a relatedness test was undertaken as part of a forensic examination,

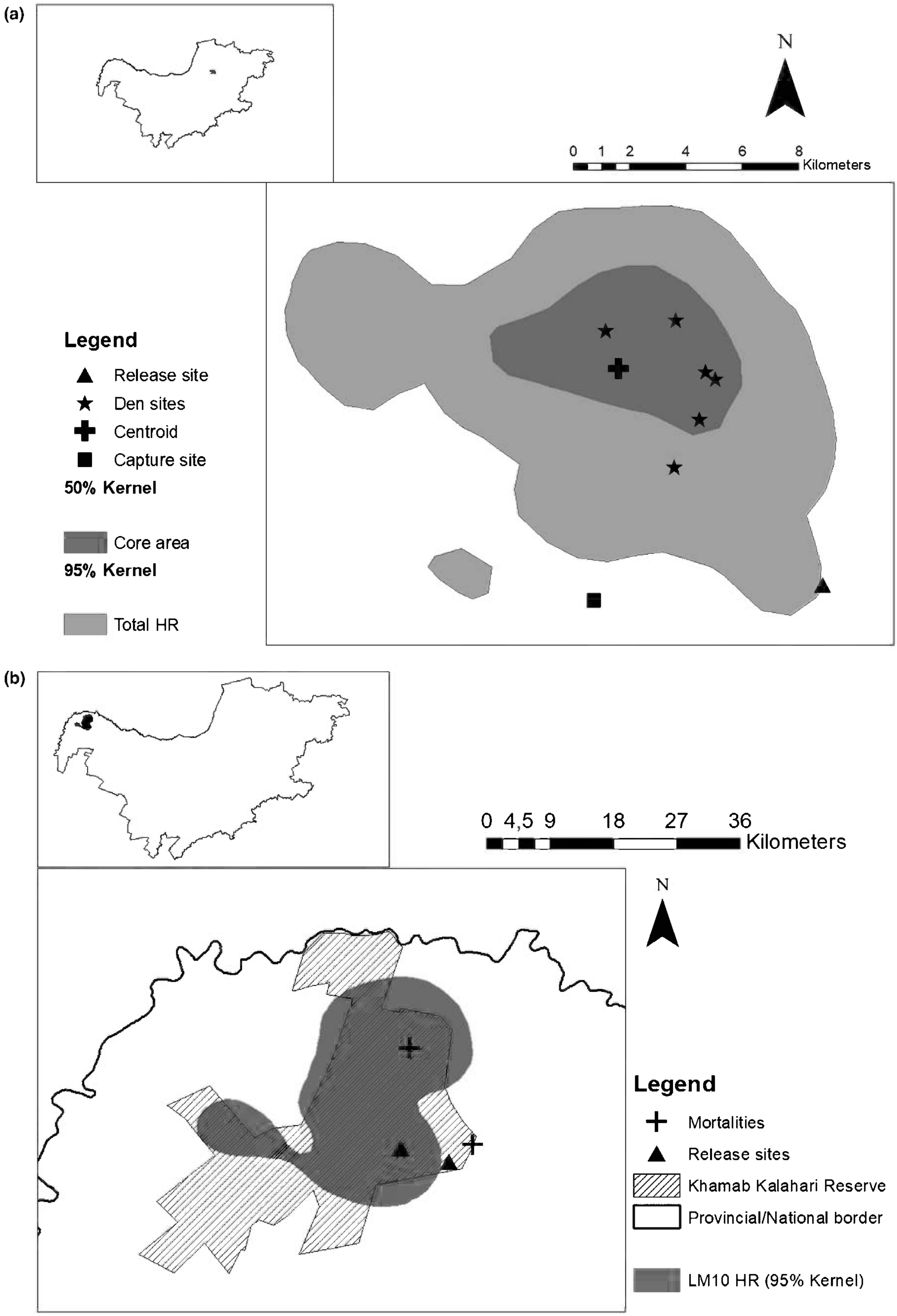

FIGURE 4 HRs of leopards in the western NWP, with dark (50% kernel), and light grey (95% kernels) for (a) relocated LF07 (Aug-15 to Oct-16) and translocations of (b) LF09 and LM10 (Jun-16 to Oct-16) and (c) LF16 (Sep-19 to Apr-20). Capture and release sites are indicated, as are arithmetic mean centres of HRs and sites of death

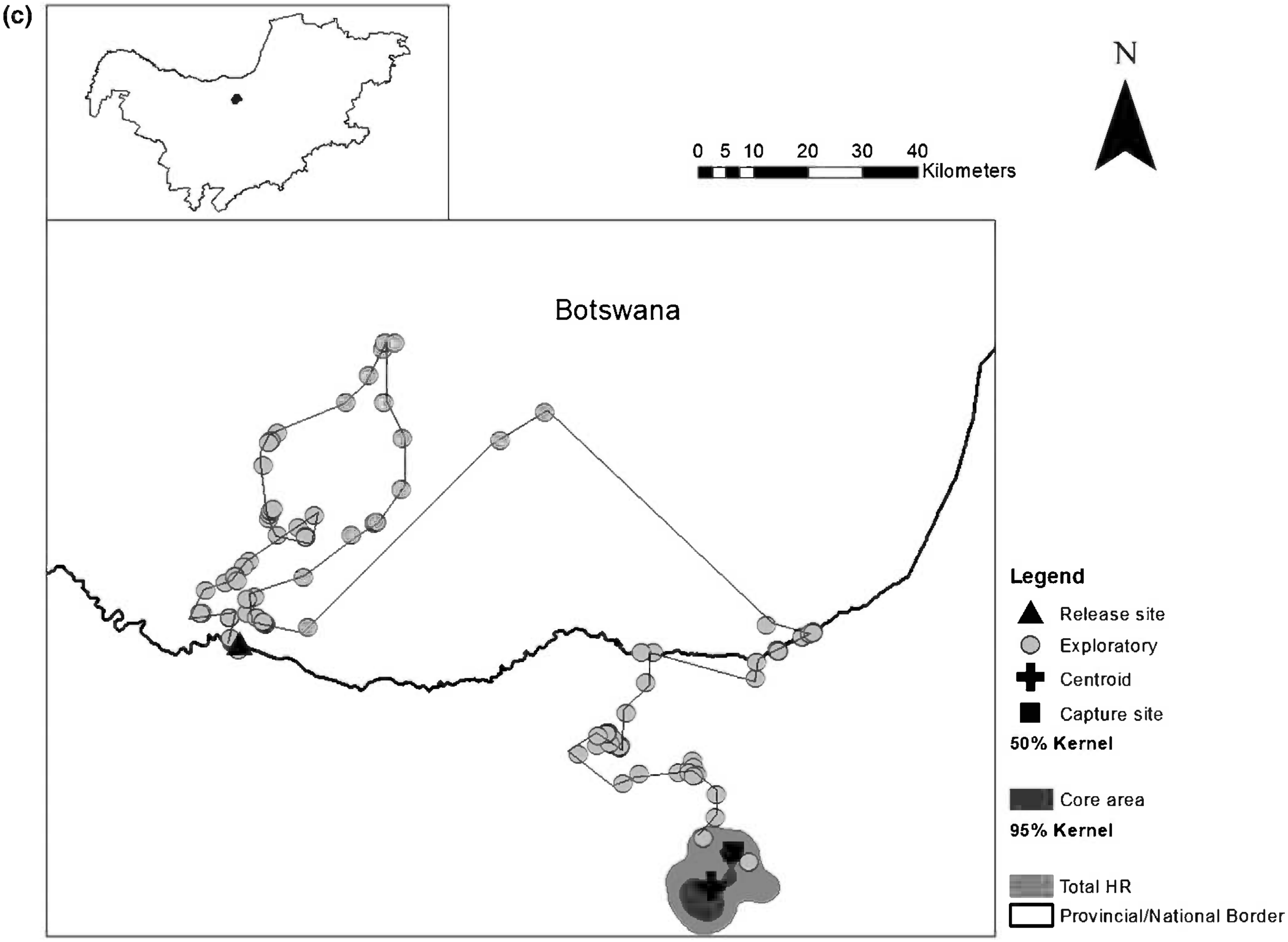

FIGURE 4 (Continued)

and they were found to be unrelated, which would be unusual, given female leopard philopatry (Balme et al., 2013; Fattebert et al., 2015; Naude et al., 2020).

Of the orphaned leopard, there was success for these animals in general, where at least two, a male and female established a stable HR (Figure 2(c) and 2(d)), and the success of these HR establishments was simply due to applying biological knowledge and simulating a dispersal as closely as possible by repatriating these animals relatively near to where they were born, *viz* < 50 km (see also Fattebert et al., 2015).

For the first time, we document a negative impact associated with translocation in that a resident has killed translocated individuals (Table 3), and in the one case the vacated range was filled by another, as is known to occur (Bailey, 1993; Balme et al., 2009). In most cases, the translocated leopards simply home back to their origins (Weilenmann et al., 2011). Failures such as this are important to publish (Fischer & Lindenmayer, 2000), as there tends to be a publication bias towards successful translocations (Fontúrbel & Simonetti, 2011).

The presence of an existing population of conspecifics at a site may affect the success of a reintroduction through attraction or avoidance (Hayward, Adendorff et al., 2007a; Smith & Peacock, 1990). Where resident conspecifics occur, translocated carnivores typically undergo extensive exploratory movements (Briers-Louw et al., 2019; Hamilton, 1981; Odden et al., 2014; Weilenmann et al., 2011;Weise et al., 2015) , which is a prelude to their expulsion, which has been evident in the NWP (Figures 2(d) and 3(a)), which is due to the absence of vacancies in the territorial system of stable leopard populations (Bailey, 1993; Balme et al., 2009; Weilenmann et al., 2011). Similarly, with pumas *Puma concolor*, when translocated they can only establish into the territorial matrix if vacancies are present (Ruth et al., 1998), and in the case of translocated tigers *Panthera tigris*, they are invariably killed by residents (Seidensticker et al., 1976). We were thus guilty of underestimating local leopard occurrence. Lemeris (2013) has produced a spatial model to determine release site suitability for leopards where various ecological parameters are incorporated, and this appears to be a robust approach to be followed in this.

Furthermore, it is not inconceivable that translocated males may even cause social disruptions at recipient sites when challenging established territory holders (Athreya, 2006; Bailey, 1993; Balme et al., 2009; Hamilton, 1976), and they *may* elicit infanticide (Balme & Hunter, 2013), which could induce downward spiralling source-sink like dynamics (Balme et al., 2009). To date this is speculative and there is more empirical support for the converse (Table 3; Seidensticker et al., 1976).

TABLE 3 Details on HR establishment of leopards in the NWP

Animal	Present on release site (> 1 year)	HR Stabilization	Death before HR stabilization	HR diameters from release site	Release site proximity to HR	Causes of mortality and notes
LM01	Yes	NA	NA	<1	Unknown	Camera trapped a year later in release reserve
LF02[a]	Yes	Yes	No	<1	50% Kernel	Rescued <1 year from snare, and has gone on to reproduce twice in each year after release
LF03	Yes	Yes	No	<1	95% Kernel	Present, but later disappearance from study area based on intensive camera trapping searches
LF04[b]	Yes	Yes	No	<1	50% Kernel	Reproduced, and collar removed and located (>2 years later), suggesting harvested, either killed or traded live elsewhere
LM05	Yes	Yes	No	<1	Outside HR	Collar removed and located by LEDET, after 2 years, suggesting harvested, either killed or traded live elsewhere
LM06	No	No	Yes	None	None	Intraspecific aggression, bite marks under neck suggest male conspecific
LF07[b]	Yes	Yes	No	<1	95% Kernel	Produced one litter, and survived beyond 2 years, and camera trap footage confirms
LM08	No	No	Yes	4	None	Intraspecific aggression, bite marks under neck suggest male conspecific, which may have replaced it, as vacated territory, and upon return, this male may have been challenging it on the HR periphery
LF09	No	No	Yes	None	None	Pulmonary/respiratory condition diagnosed from post-mortem, and possibly occurred while in captivity
LM10	No	No	Yes	None	None	Starvation ultimately, but proximately death by either intraspecific or interspecific competition, that is leopard or lion
LM11[b]	Unknown	No	Unknown	None	None	No sign of animal, presumed to have vacated the area entirely, after collar was removed, no camera trap images, so likely dispersed further
LM12[b]	Yes	Yes	No	<1	50% Kernel	No further evidence after decollaring, by way of camera traps and suspected to have dispersed further away
LM13[b]	Unknown	No	Unknown	<1	95% Kernel	Collar removed and recovered and observed from camera traps, but no intensive work done in HR
LM14	No	No	Yes	None	None	Wire snare suffocation
LF15	Yes	Yes	No	<1	95% Kernel	Wire snare suffocation
LF16	No	No	No	4	None	Animal currently alive

[a] Mortality event reversal – rescued from snare (Power et al., 2020).
[b] Relocated individuals.

TABLE 4 Summary of individual leopard specific success in terms of HR stabilization and survival in the NWP, with associated costs, averaged in ZAR, and medians represented for comparison (*after* Weise et al., 2014), which are in bold

			Cost/individual			
Individuals (categories)	**Site fidelity/ HR stabilization in release area**	**Survivorship (1-2 years)**	**Cost (ZAR)**	**Cost (USD)**	**Cost (EUR)**	**Cost (GBP)**
Unknown origin translocations						
LM01	Yes	Yes	30,702,51	1842.15	1535.13	1381.61
LF02	Yes	Yes	69,636,09	4178.17	3481.80	3133.62
LF03	Yes	Yes	112,350,21	6741.01	5617.51	5055.76
LM05	Yes	Yes	138,390.48	8303.43	6919.52	6227.57
Median			**90,993.15**	**5459.59**	**4549.66**	**4094.69**
Mean (± SD)			87,770 ± 47,441			
Translocations of putative DCAs						
LM06	No	No	46,197.98	2771.88	2309.90	2078.91
LM08	No	No	55,375.28	3322.52	2768.76	2491.89
LF09	No	No	41,814.80	2508.89	2090.74	1881.67
LM14	No	No	34,268.00	2056.08	1713.40	1542.06
LF16	No	Yes	52,574.80	3154.49	2628.74	2365.87
Median			**46,197.98**	**2771.88**	**2309.90**	**2078.91**
Mean (± SD)			46,046 ± 8460			
Translocation/Relocation of orphans						
LF15	Yes	No	85,213.50	5112.81	4260.68	3834.61
LM10	No	No	112,809.10	6714.83	5612.39	5013.74
LM11	Unknown	Unknown	65,258.00	3915.48	3262.90	2936.61
LM12	Yes	Unknown	65,114.73	3906.88	3255.74	2930.16
Median			**75,235.75**	**4514.15**	**3761.79**	**3385.61**
Mean (± SD)			820,99 ± 22,545			
relocation of residents						
LF04	Yes	Yes	38,693.37	2321.60	1934.67	1741.20
LF07	Yes	Yes	33,988.00	2039.28	1699.40	1529.46
LM13	Yes	Unknown	11,047.40	662.84	552.37	497.13
Median			**33,988.00**	**2039.28**	**1699.40**	**1529.46**
Mean (± SD)			27,910 ± 14,791			

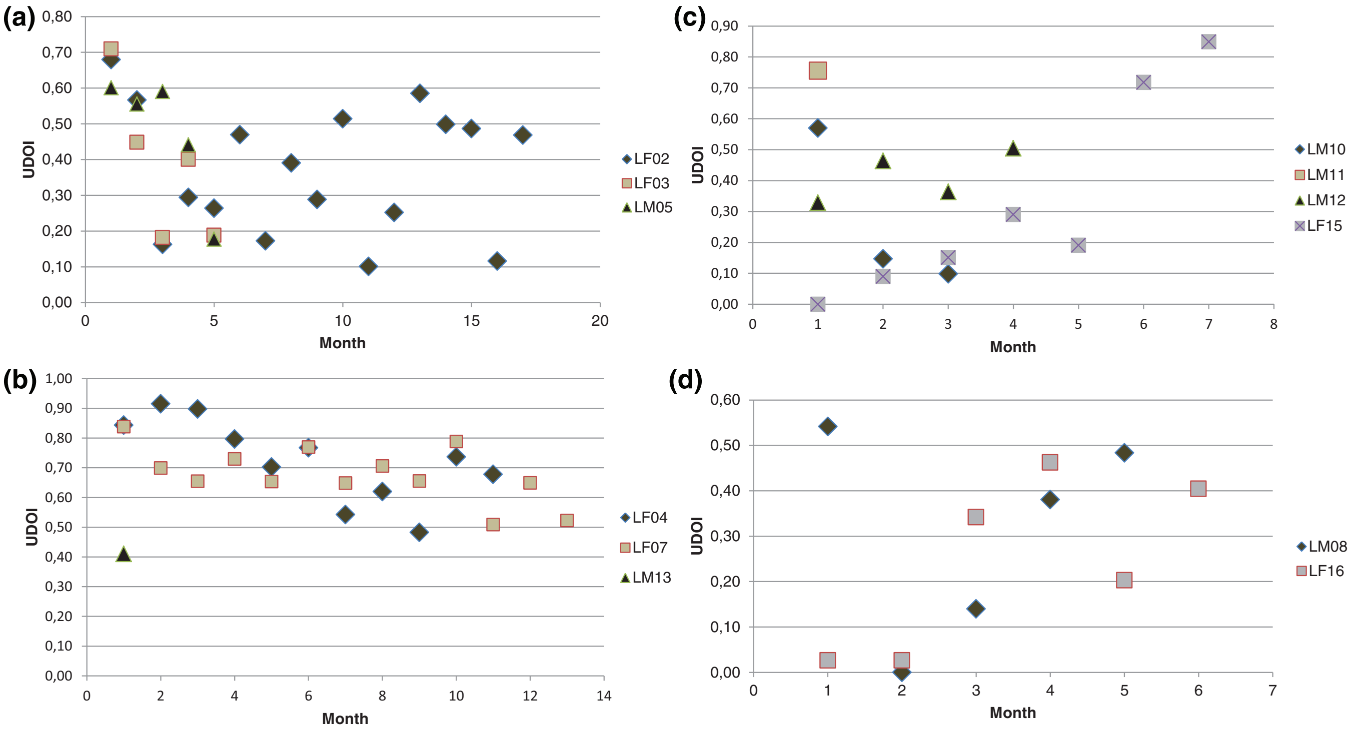

FIGURE 5 Monthly UDOIs of leopards that had been (a) confiscated, (b) relocated and translocated as (c) orphans and (d) DCAs (see SuppInfo data for Figure 5)

Vacant leopard territories are re-colonized by male dispersers within 3 months of a predecessor's death (Balme et al., 2009), and in our example with the death of LM08 (Table 3), this took place after about 6 months when we could speculate of a territory take-over, which was possibly a male leopard that had been residing within its territory (or margins) for a while (cf. Naude et al., 2020).

Where HRs are not asymptotic, and ever increasing in size, this is the case with dispersing subadults (Fattebert et al., 2016; Mizutani & Jewell, 1998), or when animals are engaged in extensive exploratory movements (Briers-Louw et al., 2019; Odden et al., 2014; Weilenmann et al., 2011). Area-observation curves can be analysed by calculating the cumulative monthly HR size change (Briers-Louw et al., 2019), where we found it sufficient to look at monthly-level HR stabilization as to whether asymptotic HR had been attained or not (Figure 5). Comparing translocated animals to that of residents proved worthwhile in this study (see also Weise et al., 2015), but one needed to subjectively decided upon a particular UDOI threshold, and despite clear territoriality (i.e. reproduction), large HRs exhibited by some translocated leopards did confound the UDOI approach a bit, particularly when short temporal periods were examined.

In our study, leopards settled into HRs relatively quickly (Table 3), not unlike attempts made in Namibia (Weise et al., 2015). Translocated leopards were found to establish HRs as early as 2 weeks in Namibia (Weise et al., 2015), 2 months in India (Mondal et al., 2013) and 4 months in Malawi (Briers-Louw et al., 2019). These results (Table 3), and others (Briers-Louw et al., 2019; Weise et al., 2015), contradict Hamilton's (1981) supposition that female leopards cannot establish HRs when translocated.

Interestingly also, Weise et al. (2015) found no significant differences between the survivorship for leopards which were translocated compared to residents (Weise et al., 2015), while we do report lower survival (Table 4). The reality is that it is difficult to tease apart the prevailing mortality rates of any given area, whether natural or anthropogenic (Swanepoel et al., 2015), as one has no sure way of ascribing it to translocation. Hence we did not focus on survival by the end of the first year as it has to be placed in context of what the background mortality rate is.

We have found that young adult females (2-3 years) readily established HRs (Table 3; Figures 2(c), 3(b) and 4(a)), which may be due to unsaturated populations recovering from disturbance (Balme et al., 2009; Fattebert et al., 2016), so perhaps such females outside PAs should simply be relocated nearby. However, in general, young adults may still be suitable candidates for translocation (Weise, 2016). This would explain the success of young orphaned leopards (Tables 2–4), and other translocations where leopards were relatively young (Briers-Louw et al., 2019; Houser et al., 2011; Mondal et al., 2013) and settled readily when compared to older candidates, which showed continuous increases in their cumulative HRs (Briers-Louw et al., 2019). With pumas, the best results came when translocated between 12 and 27 months of age (Ruth et al., 1998), which is when they disperse, and are more likely to accept an unfamiliar area compared to an adult who has spent considerable time in a given place and is adamant upon returning (Ruth et al., 1998).

Young leopard males typically disperse from their maternal HRs (Bailey, 1993; Fattebert et al., 2015), sometimes over considerable distances (Fattebert et al., 2013), resulting in exposure to a range of novel environmental stresses which can resemble effects artificially created through translocation (Weise, 2016). In contrast, subadult females usually take over part of their maternal range (Bailey, 1993; Balme et al., 2013; Fattebert et al., 2015) and are said to be less suited for translocation (Weise, 2016), but this has not been the case in our study (Table 4), just as some of the published case studies would suggest which demonstrate that young adult females can *sometimes* successfully cope with translocation, become self-sustaining and contribute to recruitment in a breeding population (Briers-Louw et al., 2019; Houser et al., 2011; Weise, 2016). Normally, leopard females breed for the first time from ~3 years (Balme et al., 2013), but here, at least two females between 2 and 3 years reproduced (Tables 2 and 3).

Although it ais difficult to assess reproduction in leopards which are very elusive (Hayward, Kerley et al., 2007b; Swanepoel, 2008), as with any felid population when at depressed densities, the opportunity for hastened reproduction arises as a result of a low population density allowing normally subordinate individuals to breed earlier than in established populations (Fattebert et al., 2016; Hunter, 1999).

Like our study (https://www.youtube.com/watch?v=NVWZba96I-c; Table 3), reproduction in translocated female leopards has also been confirmed (Briers-Louw et al., 2019; Weise et al., 2015), and suspected (Houser et al., 2011), while males have been observed copulating (Weise et al., 2015), suggesting a genetic contribution to a population. Reproduction is the ultimate sign of success, particularly where there is the birth of a wild-born generation (Hayward, Kerley et al., 2007b). In our study, a female conceived as early as 3 months after release (Table 3; Power et al., 2020), while other studies purport this to be at 8 months (Weise, 2016) to over a year (Briers-Louw et al., 2019). Confirmed breeding events have important implications as they may eventually compensate for initial mortalities, demonstrating that translocations can locally supplement and support free-ranging gene pools (Table 3; Briers-Louw et al., 2019; Weise, 2016). The rationale of assessing translocation success after 12 months is challenged, as the majority of monitored leopard may have their cubs after 2 years post-release (Briers-Louw et al., 2019; Weise, 2016), all of which points to long-term monitoring being essential (Briers-Louw et al., 2019; Houser et al., 2011).

Monetary compensation for livestock losses has been considered *in lieu* of translocation (Athreya et al., 2011; Fontúrbel & Simonetti, 2011), but the costs of leopard translocation may sometimes be less costly (Weise et al., 2014). In the NWP, given an average estimate of ~ZAR 9000 per heifer (see www.vleissentraal.co.za) this would suggest a break-even point at the loss of five such livestock, or two animals, if no collar is involved with the perpetrating animal (Table 4). There is often no significance in whether translocation or compensation is opted for (Weise et al., 2014). Ultimately, practitioners should decide for themselves what to consider given their available resources. As for non-conflict related leopards, these are generally even more costly (Table 4), but such costs, that is veterinary treatment, satellite collars, temporary keeping, can be recovered from public interest groups (see Power et al., 2020; Weise et al., 2014).

Why some of the translocations of DCA animals failed in the NWP may be due to relatively high human population densities (and anthropogenic mortality), which is said to be the reason for failures in many Indian situations (Athreya et al., 2011), while successes seem to prevail in sparsely inhabited parts of Africa (Briers-Louw et al., 2019; Weise et al., 2015).

The results of this study have been sufficient to dictate a preferred policy of relocation over and above translocation as defined. However, practitioners charged with this on the ground are more inclined to consider translocation, for fear of recurring problems of returning individuals. This is also because local farmers have borne witness to practitioners releasing animals adjacent to capture origins and this has not endeared local farmers to authorities.

Given the largest HR sizes (SuppInfo Figures 2–4), maximal distances for relocation in the NWP would amount to 28 km in the NWP, which is well below genetic threshold distances (Ropiquet et al., 2015).

Outside PAs in South Africa, leopards face threats such as illegal hunting, trapping and snaring (Swanepoel et al., 2015), while they may also be subject to the ills of haphazard translocations (Swanepoel et al., 2016). The outcomes of leopard translocations, particularly if they have failed, are almost never known, and we can speculate that there are numerous failures. Furthermore, practitioners should not regard translocation as a panacea and landowners should rather focus on resolving *in situ* conflict and seek to be tolerant of the species.

Future research should look at survivorship in more detail and consider the probability of successful translocations. While owing to the risks of collaring, and arduous nature of having to decollar satellite collared leopards, further studies should look more to conducting meta-analyses on the published literature.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

RJP and M-VB initiated the work, conceived the ideas and methodology, with LV and PB joining in on successively later occasions. RJP led the writing, and all authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The datasets analysed during the current study are available in the Movebank Data Repository (Power & Venter, 2020).

PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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