*A home away from home: insights from successful leopard (*Panthera pardus*) translocations*

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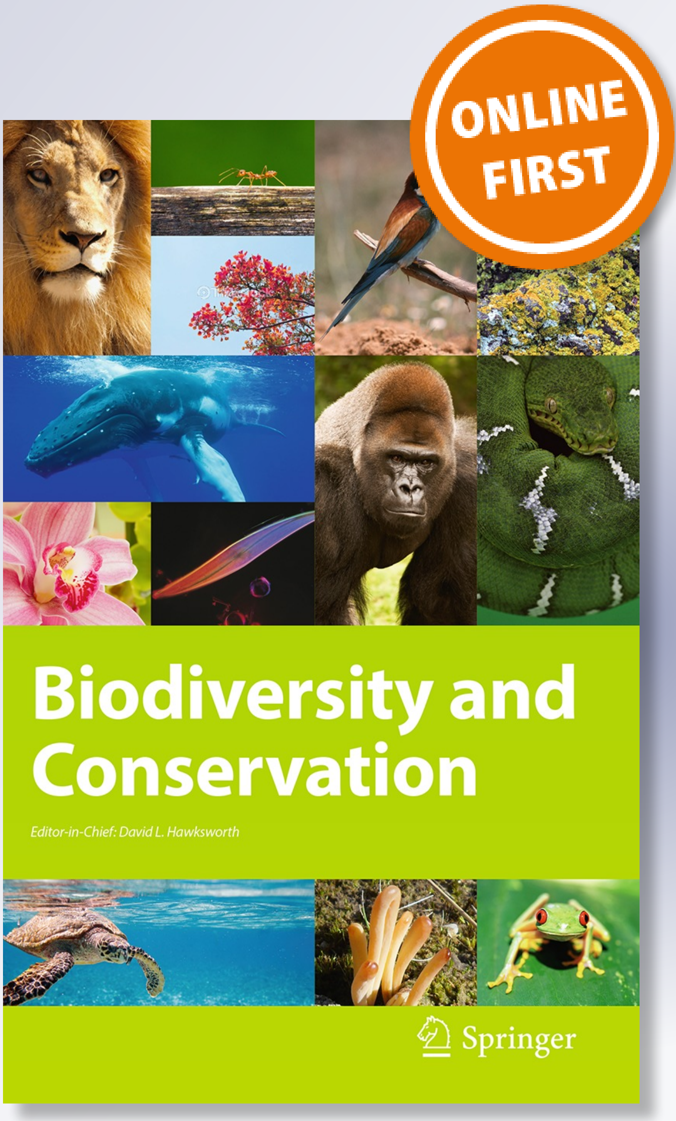

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ORIGINAL PAPER

A home away from home: insights from successful leopard (*Panthera pardus*) translocations

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Abstract When protected carnivores harm people's livelihoods, conservationists often seek non-lethal mitigation strategies. Large carnivore translocation is one such strategy but it has shown limited success. Many reported examples used methods that likely contributed to their failure. We conducted six leopard (*Panthera pardus*) translocations (three males, three females) within Namibia to test specific criteria for improved protocols. We moved leopards 402.7 km (SD = 279.6 km, range 47–754 km). Overall translocation success, using strict criteria, was 67 % and increased to 83 % when post-release conflict was not considered in this assessment. Four individuals successfully established new territories after exploratory periods of <2 months. One female died in a road accident shortly after

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release and a male resumed killing livestock that were illegally herded within a protected area. Both surviving females produced cubs—the ultimate sign of success. When compared with resident leopards (six males, six females), translocated individuals showed no significant difference in range behaviour, survivorship or likelihood of conflict. At their capture sites, livestock depredation ceased for a minimum of 16 months, thus at least temporarily alleviating conflict. We used our successful protocol to develop a translocation suitability model for determining appropriate release sites. For Namibia, this model predicts potential recipient habitat of 117,613 km^2, an area sufficient to support up to 87 leopard translocations. Where alternative conservation strategies have failed and managers decide to proceed with translocations, we recommend the application of our conservative protocol to identify the most suitable recipient locations. Our study demonstrates the potential value of translocation under specific circumstances and as part of a larger conflict management repertoire. Our findings are useful for management of other large carnivores and conflict wildlife.

Keywords *Panthera pardus* · Relocation · Conservation planning · Conflict management

Introduction

Effective wildlife conservation depends on suitable and informed management strategies. This is particularly true for those large carnivores, such as the leopard (*Panthera pardus*), that still occur in large numbers outside of protected areas (Odden et al. 2014; Stein et al. 2012). Here, they may cause conflict with livestock farmers (Inskip and Zimmermann 2009) and are heavily persecuted (Ripple et al. 2014). Wildlife managers need a variety of strategies to mitigate conflicts (Treves and Karanth 2003) and maintain viable free-ranging carnivore populations. We should scrutinise every approach critically to identify its merits and disadvantages, costs and benefits, and its appropriate application.

Where protected large carnivores interfere with human interests, managers and conservationists often seek non-lethal options to reduce such conflicts. One of the available options, translocation, appears to be an unsuccessful strategy, especially for conflict carnivores (Fontúrbel and Simonetti 2011; Linnell et al. 1997; Massei et al. 2010). Although applied to several species (reviewed by Fontúrbel and Simonetti 2011), few studies document translocation outcomes in detail. Moreover, translocation success has been determined on a case-specific basis related to circumstance and with non-standardised objectives (cf. Bradley et al. 2005; Goodrich and Miquelle 2005; Purchase 1998; Riley et al. 1994). Reviewers caution that biased reporting towards successful events may potentially skew conservation decisions in favour of undesirable practices (Fischer and Lindenmayer 2000; Fontúrbel and Simonetti 2011; Massei et al. 2010).

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The leopard is the most widely distributed of all large felids (Nowell and Jackson 1996) and inhabits areas close to people (Athreya et al. 2013). The species poses a threat to livestock (Schiess-Meier et al. 2006; Stander et al. 1997a) and human safety (Athreya et al. 2007; Hamilton 1981; Shepherd et al. 2014). Previous studies of conflict leopard translocations reported very limited success due to poor release site fidelity, homing behaviour and continued livestock depredation (e.g. Stander et al. 1997a; Weilenmann et al. 2010). In extreme cases, leopards caused increased human fatalities around release sites (Athreya et al. 2007, 2011). It appears that saturating isolated conservation areas through continued releases into habitat with established conspecifics can give rise to undesirable outcomes and hence promote conservation failures (Athreya et al. 2011; Hamilton 1981). Conversely, when only few individuals were released into specific areas, the results were more encouraging (Hayward et al. 2006; Houser et al. 2011; Mondal et al. 2013). The importance of release protocol and the intrinsic ability of a local population to accommodate an unknown immigrant have rarely been considered as one of the primary determinants of success (Hamilton 1981; Houser et al. 2011).

Our cumulative understanding of leopard post-translocation behaviour and success is based on the monitoring of merely two dozen individuals (combined from Hamilton 1981; Hayward et al. 2006; Houser et al. 2011, Mondal et al. 2013; Odden et al. 2014; Stander et al. 1997a; Weilenmann et al. 2010) and variable circumstances as well as small sample sizes complicate conclusions for this highly adaptable and opportunistic species. Intensive post-release monitoring often is difficult, time consuming and costly (see tracking costs in Weise et al. 2014) but necessary to improve conservation practice (Hamilton 1981; Houser et al. 2011) because leopard translocations still happen in many African and Asian countries, and we can expect them to continue into the future. It is therefore imperative that we continue to define the parameters and factors that enhance translocation success.

In this Namibian study, we critically evaluate the outcomes of another six leopard translocations, in terms of leopard ecology and conflict mitigation. The objectives of translocations were: (a) to return perceived or confirmed "problem leopards" into free-ranging environments with minimum potential for post-release conflict, (b) to enable these leopards to contribute to the wild gene pool, (c) to alleviate conflict at the source site in cases where livestock depredation had occurred, and (d) to research the factors that influence the success of leopard translocations for future conservation planning. We assess our results by comparing them with monitoring information from 12 resident conspecifics. We investigate translocation protocols to improve the efficacy of this strategy. We use a pragmatic, replicable modelling approach to determine suitable leopard habitat across Namibia. We identify specific release locations and estimate the potential number of leopard translocations.

Methods

Resident leopards

With permission from the Ministry of Environment and Tourism (MET), we trapped resident leopards for research purposes in different bio-geographical areas of Namibia (Fig. 1). Trapped leopards were attended to within 24 h of capture and were subsequently immobilised by licensed veterinary personnel using intramuscularly administered darts containing suitable combinations of Ketamine with $\alpha 2$-agonists or Tiletamine with Zolezepam (Stein et al. 2011). We carried out intensive health assessments and fitted residents

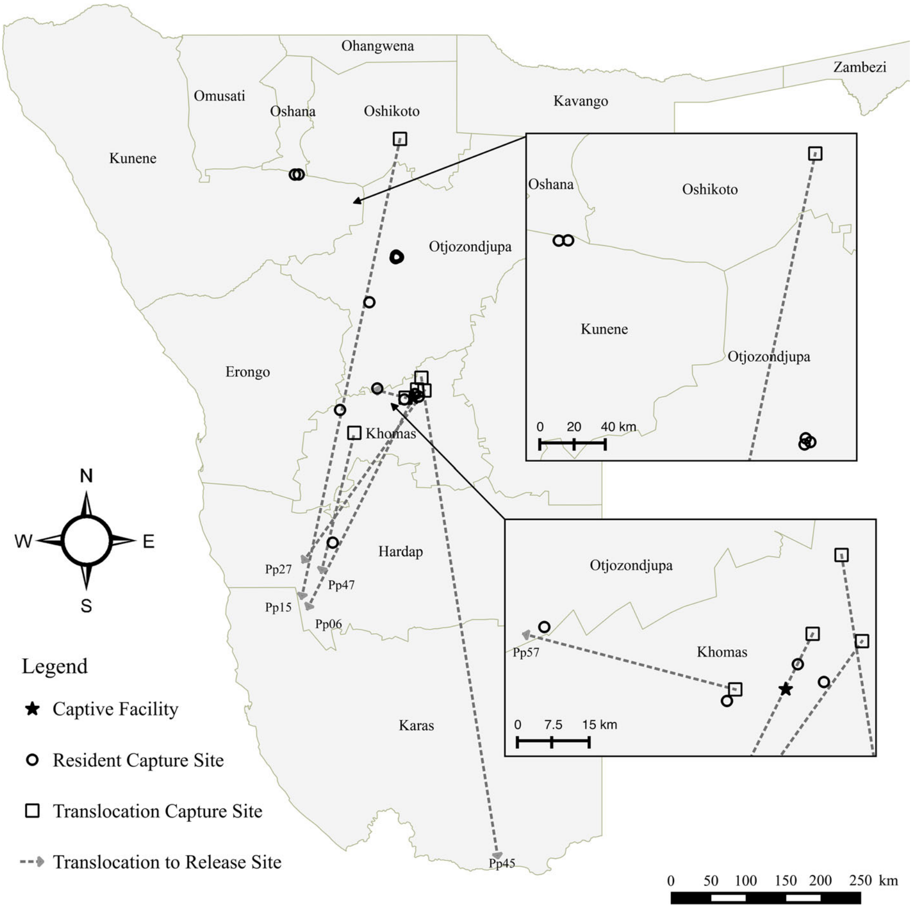

Fig. 1 Sample distribution of translocated and resident study leopards across Namibia, 2004–2014

with tracking collars (details in Table 1) adhering to weight ratios recommended for use of external transmitters (<2 % body weight; Kenward 2001). In pre-prime leopards, we fitted collars to accommodate expected neck growth. All animals fully recovered from capture and immobilisation before release at or close to their capture sites.

We collected monitoring data using standard GPS and VHF telemetry. Positional data occasionally permitted direct observations, and camera-trap photos supplemented information at the different study sites. We attempted to locate VHF-tagged individuals at least once per week (range 1–7 days). If we did not observe a leopard during either ground or aerial VHF telemetry, we calculated the animal's location through triangulation using LOCATE II (Nams 1990). GPS satellite transmitters recorded between one and six daily locations reflecting specific research and management objectives. For example, we adjusted GPS schedules to provide commercial livestock ranchers with the most current leopard locations to improve husbandry practices. All private and public landowners allowed access to their properties for monitoring purposes.

Table 1 Biological and technical details of resident and translocated study leopards in Namibia, 2004–2014

ID	Sex	Estimated age	Weight (kg)	Capture region (release region)	Year[a]	Capture reason	Captivity (days)	Translocation distance (km)	Release mode	Transmitter type
Resident										
PPA51	F	3–5	31	Otjozondjupa	2004	Research	n/a	n/a	Hard	VHF[c]
PPA54	M	5–7	54	Otjozondjupa	2004	Research	n/a	n/a	Hard	VHF[c]
PPA56	F	3–5	34	Otjozondjupa	2005	Research	n/a	n/a	Hard	GPS[d]
Pp04	F	3–5	30	Khomas	2008	Research	n/a	n/a	Hard	GPS[e]
Pp05	M	9–12	63	Khomas	2008	Livestock raider	n/a	n/a	Hard	VHF[c]
Pp48	M	2–4	unknown	Khomas	2010	Research	n/a	n/a	Hard	GPS[e]
Pp62	M	6–8	61	Khomas	2012	Livestock raider	n/a	n/a	Hard	GPS[e]
Pp63	M	3–5	54	Khomas	2012	Indiscriminate	n/a	n/a	Hard	GPS[e]
Pp71	F	4–6	38	Hardap	2013	Indiscriminate	n/a	13[b]	Hard	GPS[e]
V10938	F	3–5	31	Kunene	2013	Research	n/a	n/a	Hard	GPS[d]
V11387	M	5–6	48	Kunene	2013	Research	n/a	n/a	Hard	GPS[d]
Pp77	F	4–6	36	Otjozondjupa	2014	Indiscriminate	n/a	n/a	Hard	GPS[e]
Translocations										
Pp06	M	4–5	44	Khomas (Hardap)	2008	Livestock raider	16	369	Hard	VHF[c]
Pp15	F	4–6	35	Oshikoto (Hardap)	2009	Confiscation—rehab	168	715	Hard	GPS[f] and VHF[e]
Pp27	F	2	31	Khomas (Hardap)	2009	Orphan—rehab	639	313	Hard	GPS[e] and GPS[e]
Pp45	M	2–4	52	Khomas (Karas)	2011	Livestock raider	206	754	Hard	GPS[e]
Pp47	M	2–4	42	Khomas (Hardap)	2011	Livestock raider	183	218	Soft	GPS[e]
Pp57	F	4–6	39	Khomas (Khomas)	2012	Livestock raider	4	47	Hard	GPS[e]

[a] Year of release

[b] Removed from a livestock enclosure but released within expected home range

[c] Advanced telemetry systems, Insanti, USA

[d] Vectronics Aerospace, Berlin, GER

[e] Africa Wildlife Tracking, Pretoria, SA

[f] Sirtrack, Hawkes Bay, NZ

Translocations

Translocated leopards were trapped by private landowners and reported as potential or confirmed conflict animals, or confiscated by the state wildlife agency (Table 1). All individuals were placed into a captive facility providing government-approved standards for their keeping (MET 2012) and with the purpose of subsequent release into public and private conservation areas. Weise et al. (2014) described captivity and translocation protocols—leopards were conscious during transport in grass-padded, closed transport cages. The reinforced, ventilated cages allowed safe transportation whilst limiting the possibility of injury. Anaesthesia and monitoring protocols were similar to those of resident leopards. For intensive post-release monitoring, we fitted translocated individuals with combined GPS satellite—VHF transmitters or VHF transmitters (Table 1). Where possible, we monitored leopards by spoor and experienced San trackers confirmed identification following Stander et al. (1997b).

Release considerations

We define translocation distance as the linear distance from capture site to release site. We translocated leopards at varying distances (Table 1) that were influenced by the case-specific availability of release sites. In this study, we selected candidate release sites according to the following criteria: (i) be within extant leopard range below the estimated carrying capacity and at an approximate density of <2 leopards/100 km^2 (low density in Stein et al. 2012); (ii) contain documented intra-guild competition and adequate prey species; and (iii) have land uses with minimum potential for post-release conflict. We maintained >6 months interval between subsequent releases to minimise negative effects of repeat translocations into the same area (cf. Hamilton 1981; Athreya et al. 2011). Leopards were either hard-released directly from transport cages or soft-released from an acclimatisation pen.

To address previously described biases in translocation reporting (Fischer and Lindenmayer 2000; Fontúrbel and Simonetti 2011; Massei et al. 2010), we define translocation success to include all of these criteria: (i) survival for at least 1 year post-release; (ii) no livestock conflict beyond five stock units per year; and (iii) no homing to the capture site. Based on average landowner tolerance towards leopard predation in Namibia (F. J. Weise unpubl. data; Stein et al. 2010), we determined five livestock units per year per leopard as an acceptable conflict threshold. Despite this threshold, we agreed to compensate landowners for any damage from translocated leopards on properties bordering release areas to prevent immediate persecution of released individuals when conflict occurred. In contrast with other studies (e.g. Hamilton 1981), we do not consider site fidelity as a prerequisite for translocation success, as all leopards were released into free-range environments permitting choice of movement. Reproduction, although considered the ultimate indication of success, was also not a minimum success condition as mating events were difficult to confirm for male leopards in these environments.

Data analysis

Following the conclusion of our study period, we calculated annual Kaplan–Meier survival estimates using a staggered entry design (Pollock et al. 1989). We standardised positional data across all individuals by selecting one location (closest to 12:00 GMT) in every 24 h cycle. We analysed all leopard movements with ArcGIS v.10.1 (ESRI 2013) and calculated

Minimum Convex Polygons (MCP) with the movement ecology tools extension (Wall 2014). We used R v. 3.1.0. (R Core Team 2014) to calculate inferential statistics.

Starting from the day of release, we calculated 100 % MCP values for 10 day periods to determine the duration of exploratory movements of translocated leopards. We moved this 10 days window repeatedly by 1 day, creating a progressive estimate of range area for the first 9 months post-release. We used percentage overlap of daily locations with the release reserve (and connected complexes of protected areas) as a measure of site fidelity for the first 12 months. We assessed homing behaviour using package 'circular' in R (Agostinelli and Lund 2013) by calculating bearing angles and distances between an individual's last known location and release location relative to their capture site. We adjusted bearing angles to set an individual's 'home' direction to 0°. All distances were normalized on a scale from zero to one (the circle's centre to its edge), representing the distance between its capture and release sites. We defined a leopard as 'homing' if it had moved its entire translocation distance towards its capture location, within 22.5° on either side of true 'home' direction (Fies et al. 1987).

Carnivore translocation suitability tool (CaTSuiT)

To determine area suitability for future leopard translocations throughout Namibia, we used a novel ArcGIS-based geospatial modelling tool, *Carnivore Translocation Suitability Tool* (Lemeris 2013), which we modified using national leopard density (Stein et al. 2012) and distribution (P. Gerngross, pers. comm. 2014), government protected areas and private reserves (The EIS 2014; IUCN/UNEP 2014), and designated urban settlements (Namibia Statistics Agency 2012) as inputs. This toolbox is continuously being developed and new iterations are produced for each species to account for variable ecological requirements and conservation goals. As long as input variables are provided in raster format standardised to the same scale, a user may enter any relevant ArcGIS-compatible datasets and the tool eliminates or favours specific areas based on these parameters. The user also defines the relative influence (out of 100) of each input variable. Therefore, conservation managers have maximum flexibility to inform the selection process according to species- or area-specific conditions. The leopard-iteration of *CaTSuiT* is available for download as a geo-processing package (Lemeris 2015).

Within the tool, we selected potential release locations only within public and private protected areas, and where leopard densities are low to moderate—we then excluded areas with high or zero leopard density (Stein et al. 2012). We further constrained any remaining areas by designating a 50 km safety buffer around urban centres. Finally, we excluded any remaining habitat patches smaller than the square of our furthest-travelling translocated individual (before settling into a range) unless they connect with other suitable areas. For our estimate of potential leopard translocations, and to avoid overspill from continued translocations (Athreya et al. 2007), we defined a conservative minimum inter-release interval of 18 months for each suitable area.

Results

Between 2004 and 2014 we studied 12 resident leopards (six males, six females) across four regions of Namibia, and investigated the outcomes of six leopard translocations (three males, three females) (Table 1; Fig. 1). At the time the study was concluded (12/07/2014), one translocated individual and two residents were still being monitored, giving a total of

5614 monitoring days for residents, and a total of 4309 monitoring days for translocated individuals. Of the six leopards we translocated, four were opportunistic livestock raiders and two were rehabilitation cases (one orphan and one confiscated long-term captive). The average captive time for translocated leopards was 203 days (range 4–639 days) and the animals were released at an average distance of 403 km (range 47–754 km) from their original capture sites. All resident leopards and five of the six translocated leopards were hard released. Female Pp57 was released into a private reserve with an estimated density of 3–4 leopards/100 km^2. Five of the translocations were into areas where those individuals experienced novel intra-guild competition from spotted hyaena (*Crocuta crocuta*). Although female Pp71 was moved 13 km from her capture site in a livestock enclosure, she was classed as a resident as she was not moved from her expected home range.

We fitted translocated leopards with combined GPS satellite—VHF transmitters ($n = 5$) or VHF transmitters ($n = 1$). When their original transmitters were depleted, the GPS unit of female Pp15 was replaced by a VHF transmitter, and female Pp27 was fitted with a second GPS unit. Male Pp06 was also monitored using his unique spoor resulting from an old front-foot injury enabling discrete identification.

None of the 18 study leopards was directly persecuted by landowners during monitoring but we recorded four mortalities for different reasons (Table 2). The mean annual survival estimate for translocated leopards (0.929 SD = 0.122, $n_y = 7$, one mortality) was not significantly different from that of residents (0.846, SD = 0.219, $n_y = 10$, 3 mortalities; Mann–Whitney U-Test: $W = 41$, $P = 0.295$). Two of three translocated females (Pp15 and Pp27) reproduced and successfully raised young in their novel environments. Considering a gestation period of up to 106 days (Skinner and Smithers 1990), females conceived as soon as 8 months post-release. Similarly, two of six resident females raised litters and we suspected breeding for two other females (Table 2). In addition, we observed two of three translocated males (Pp06 and Pp45) during courtship behaviour with wild females and Pp45 mating on two occasions. We confirmed courtship 5 months after release. One resident male was observed mating during this study.

We documented 40 and 52 wildlife kills for translocated and resident leopards respectively (Table 3). Prey selection and preference were different between the two groups although at least 75 % of all wildlife kills for each group were kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus africanus*), oryx (*Oryx gazella*) and springbok (*Antidorcas marsupialis*). Male Pp47 hunted as early as 12 h after release. Of the six translocated leopards only Pp45 was involved in post-release conflict by killing 13 sheep that were illegally herded into his new home range on the release reserve. It remains speculative whether he (an opportunistic cattle raider) would have resumed conflict behaviour if stock had not been moved into the protected area—the damage was fully compensated. We are confident that no other translocated leopard killed livestock because we shared positional data with landowners on a regular basis. In comparison, three resident leopards killed livestock opportunistically (between one and three animals per year). To assess the effectiveness of moving conflict leopards we interviewed the four farmers where livestock depredation had occurred prior to translocation of raiders. Pre-translocation livestock losses to leopards (an average of five calves per property in the last 12 months) stopped for at least 16 months on all farms, suggesting that the responsible raiders had been removed. According to landowners, translocated individuals were replaced by 'new' leopards within 6 weeks after removal. On three farms repeat conflict with leopards occurred 16, 25 and 29 months after translocation events but was tolerated because only one to three calves were killed per year. The fourth farmer has not experienced repeat conflict although leopards still occur on the property.

Table 2 Movement and range values for resident and translocated study leopards in Namibia, 2004–2014

ID	Sex	Monitoring duration (days)	No. of daily locations used	MCP-km^2 100 % (50 %)	Kernel 95 % (50 %)	Distance of home range centroid to release site in km	Mean monthly movement in km (locations used)	Weeks until home range was established	Percentage overlap with release area	Comments
Resident										
PPA51	F	586	131	66.3 (16.6)	51.4 (9.8)	–	85.4 (51)	n/a	n/a	1 successful litter during monitoring
PPA54	M	797	94	127.9 (20.9)	81.4 (17.6)	–	137.7 (28)	n/a	n/a	–
PPA56	F	140	140	36.2 (12.6)	44.6 (12.6)	–	115.8 (133)	n/a	n/a	–
Pp04	F	1,923	497	178.1 (27.1)	138.9 (29.8)	–	74.5 (468)	n/a	n/a	2 successful litters during monitoring
Pp05	M	15	insufficient data	insufficient data	insufficient data	–	insufficient data	n/a	n/a	Death from gastro-intestinal inflammation
Pp48	M	202	117	580.8 (57.9)	306.8 (31.5)	–	93.0 (107)	n/a	n/a	Dispersed from capture area
Pp62	M	600	411	184.4 (39.5)	111.9 (29.5)	–	132.3 (393)	n/a	n/a	Increased home range when territorial neighbours were removed
Pp63	M	442	398	205.9 (71.1)	198.4 (82.7)	–	143.8 (366)	n/a	n/a	Shot after monitoring due to cattle predation
Pp71	F	134	132	170.4 (26.5)	109.6 (20.8)	–	60.5 (130)	n/a	n/a	Reproduction suspected. Maintained resident range despite short distance translocation–death in wire snare

Table 2 continued

ID	Sex	Monitoring duration (days)	No. of daily locations used	MCP-km^2 100 % (50 %)	Kernel 95 % (50 %)	Distance of home range centroid to release site in km	Mean monthly movement in km (locations used)	Weeks until home range was established	Percentage overlap with release area	Comments
V10938	F	346	344	120.9 (19.2)	68.7 (10.5)	–	65.7 (341)	n/a	n/a	Reproduction suspected
V11387	M	238	42	132.1 (50.9)	149.2 (25.8)	–	116.1 (36)	n/a	n/a	Mating observed
Pp77	F	152	151	53.7 (14.4)	47.2 (15.0)	–	80.0 (366)	n/a	n/a	–
Translocations										
Pp06	M	377	27	300.9 (53.3)	161.1 (21.7)	6.7 km	insufficient data	insufficient data	100.0	Courtship behaviour observed
Pp15	F	825	174	54.3 (8.8)	38.4 (3.3)	25.7 km	57.2 (167)	25	43.3	1 successful litter during monitoring
Pp27 (first range)	F	1,675	205	147.3 (45.8)	127.5 (11.1)	23.7 km	61.1 (201)	4	1.7	Range shift observed due to road construction – 2 successful litters during monitoring
Pp45	M	815	355	481.1 (15.7)	245.6 (17.3)	13.1 km	66.3 (351)	3	82.4	Courtship behaviour observed twice
Pp47	M	505	385	453.7 (58.3)	255.6 (29.8)	13.3 km	114.3 (335)	5	6.7	–
Pp57	F	110	57	75.2 (16.4)	78.0 (13.1)	29.4 km	97.3 (56)	7	4.1	Death in road accident

Table 3 Known prey items of translocated and resident leopards in Namibia (2004–2014) as identified from carcasses located through GPS and VHF telemetry

Prey	Resident	Translocated
Wildlife		
Greater kudu—*Tragelaphus strepsiceros*	17	6
Warthog—*Phacochoerus africanus*	17	3
Oryx—*Oryx gazelle*	8	9
Common duiker—*Sylvicapra grimmia*	4	0
Springbok—*Antidorcas marsupialis*	3	16
Plains and Mountain Zebra (combined)—*Equus quagga* and *E. zebra hartmannae*	1	2
Common eland—*Taurotragus oryx*	1	0
Steenbok—*Raphicerus campestris*	1	0
Red hartebeest—*Alcelaphus caama*	0	1
Blesbok—*Damaliscus pygargus phillipsi*	0	1
Porcupine—*Hystrix africaeaustralis*	0	1
Aardwolf—*Proteles cristata*	0	1
Livestock		
Cattle—*Bos primigenius*	9	0
Sheep—*Ovis aries*	0	13[a]
Total	53	60

[a] All killed by male Pp45

Based on our definitions, four of six translocations were successful—these leopards established themselves in novel environments with resident conspecifics, they refrained from livestock depredation and reproduced successfully. Pp45 resumed conflict behaviour and Pp57 did not survive. The total cost for these translocations was USD $13,999, giving an Individual Conservation Cost of $3140 (Weise et al. 2014).

Movements

In this study, none of the translocated individuals homed to their original capture site or back to the captive facility (Fig. 2). All translocated leopards displayed exploratory movements and at least temporarily left release areas, but three animals showed some degree of release site fidelity (Fig. 3; Table 2). Female Pp57 (released into the highest density area with the shortest translocation distance) displayed the largest degree of post-release exploration (Fig. 4). She moved further than the distance between capture and release location but did so at over 100° from the true home (Fig. 2). Conversely, soft-released male Pp47 showed least roaming behaviour. The mean linear distance travelled by translocated individuals between their release sites and last known locations was <22 % of their average translocation distance. The mean direction travelled in all cases was over 100° from true home. Site fidelity varied between 1.7 and 100 % in year one and the lowest values were recorded for individuals released into reserves <400 km^2 (Table 2).

All translocated individuals successfully established home ranges in areas with resident conspecifics and with a preference for mountainous terrain. Progressive MCPs showed that four leopards established new ranges within 2 months after release, and as early as 2 weeks, while female Pp15 established a range 6.5 months post-release (Fig. 4). We

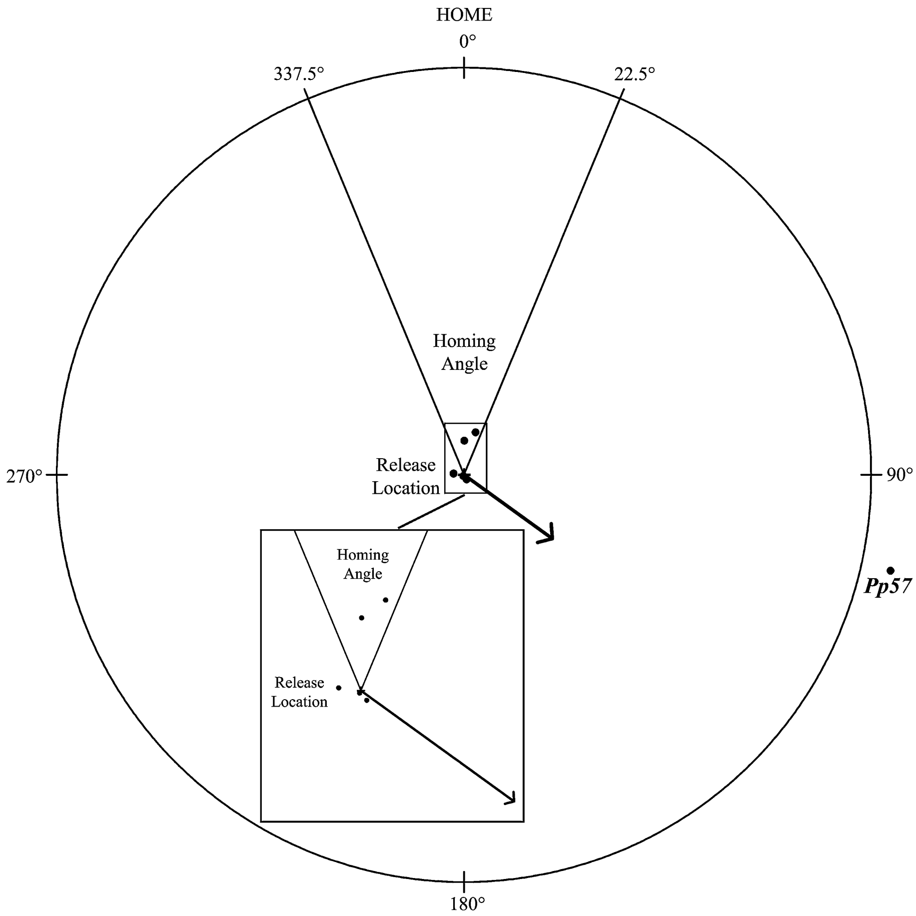

Fig. 2 Angular direction for translocated leopards ($n = 6$) relative to their capture location. The distance from the circle's centre (individual's release location) to outer edge represents an individual's distance travelled relative to its capture location. Data points around the centroid are magnified for clarity

observed a range shift for Pp27 (Fig. 3) that coincided with the beginning of road construction in the core area of her first range. Female Pp15 was accidentally trapped 10 months post-release and returned to her original release area from where she immediately resumed her new range. After removal of exploratory movements, there was no significant difference between the home range estimates for residents and those for translocated leopards for any of the metrics we used (Mann–Whitney U-Tests: 100 % MCP ($W = 91$, $P = 0.451$), 50 % MCP ($W = 101$, $P = 0.880$), 95 % kernel ($W = 92$, $P = 0.514$) and 50 % kernel ($W = 108$, $P = 0.366$)). We did not observe interactions between the four leopards translocated into the same bio-geographic area (Fig. 1) or detrimental effects from novel intra-guild competition with hyaenas. Except for male Pp48, who dispersed from the capture area, all residents maintained stable home ranges throughout the study, or until death was recorded (Fig. 5). Resident male Pp62 increased his range in response to removal of two neighbouring territorial males. Female Pp71 returned into the vicinity of her capture area within 24 h of release.

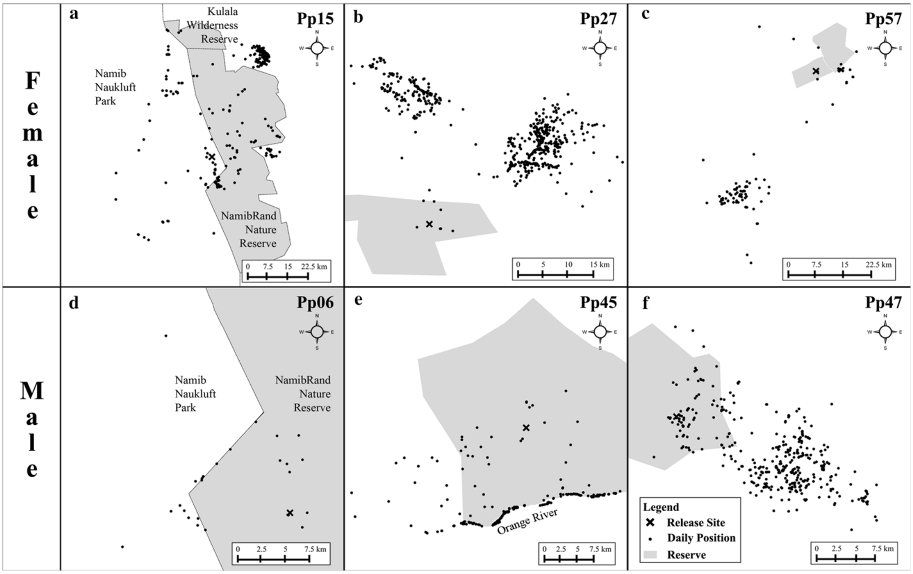

Fig. 3 Movement plots for six translocated leopards, three females (**a**–**c**), three males (**d**–**f**), studied in Namibia between 2008 and 2014. Positions represent pruned daily locations

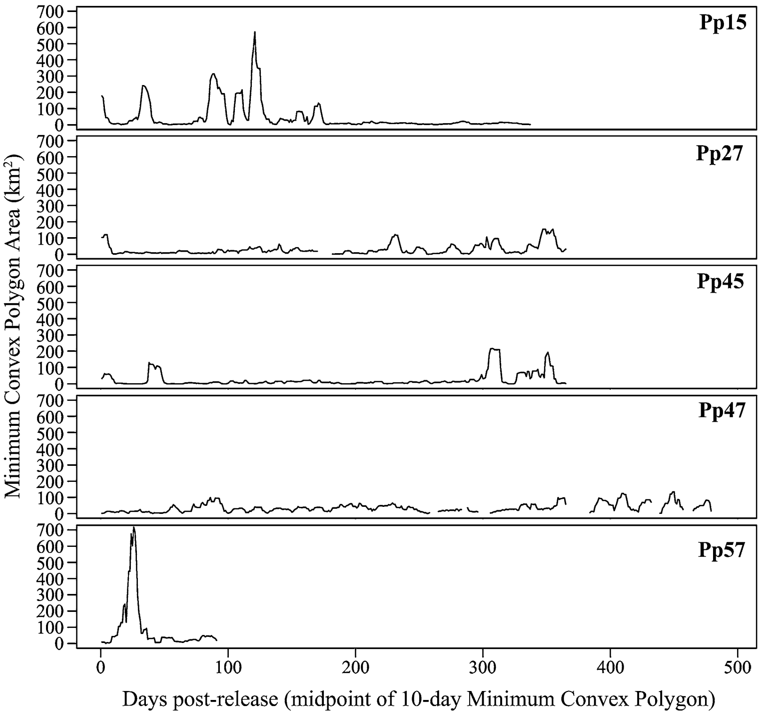

Fig. 4 Progressive 10-days post-release minimum convex polygon area assessments for five translocated leopards. Polygon values were calculated with pruned daily locations. Male Pp06 is excluded for lack of sufficient data

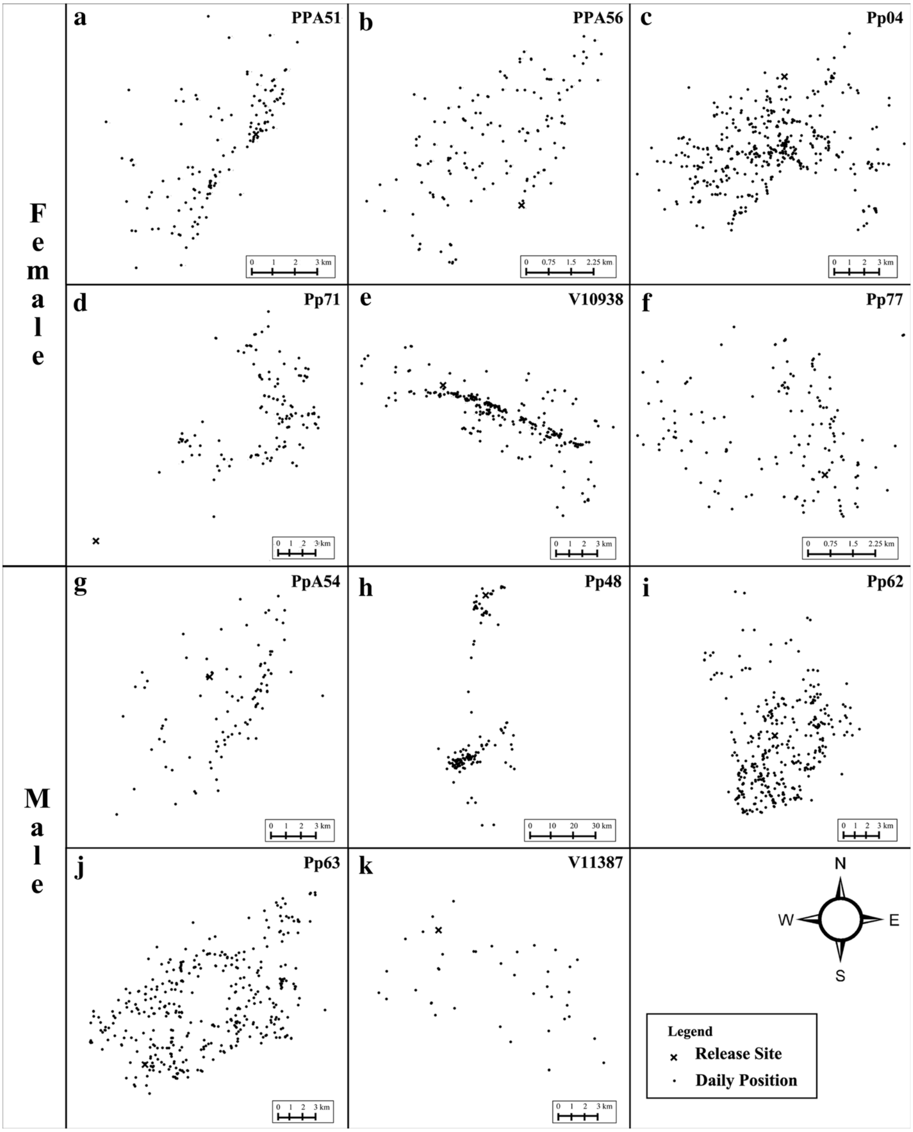

Fig. 5 Movement plots for 11 resident leopards, six females (**a**–**f**), five males (**g**–**k**), studied in Namibia between 2004 and 2014. Positions represent pruned daily locations. Male Pp05 is excluded due to early mortality

Potential release areas in Namibia

CaTSuiT identified approximately 117,613 km^2 of available leopard translocation habitat (equivalent of approximately 14.2 % of Namibia's landscape) within ten government-protected areas (81,016 km^2), 54 communal conservancies (33,147 km^2) and 5 private reserves (3450 km^2) in Namibia (Fig. 6 and Online Resource 1). This value decreased to approximately 103,000 km^2 if smaller reserves (<875 km^2) were removed from results.

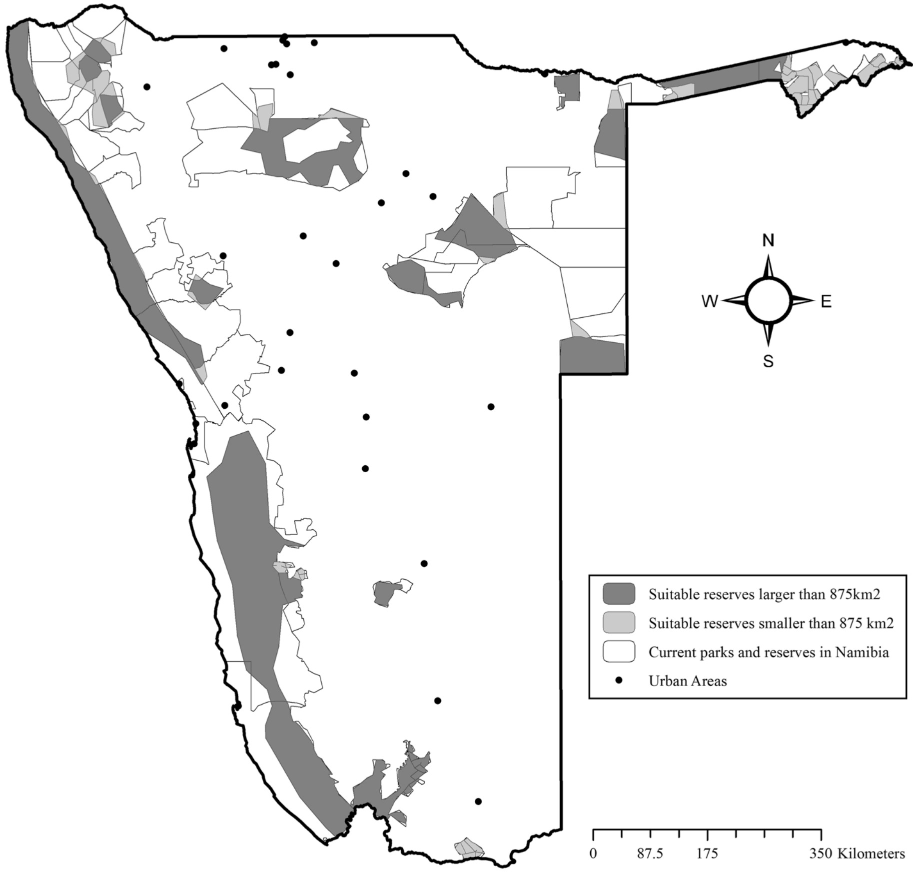

Fig. 6 Leopard recipient area output from carnivore translocation suitability tool. Using the described model inputs, *CaTSuiT* identified a total suitable recipient habitat of 117,613 km^2 across 69 designated conservation areas in Namibia and the potential for approximately 87 leopard translocations

Assuming that leopards can be released into a suitable area and not come under threat if they move into adjacent suitable habitat, our model predicts that at present up to 87 leopard translocations can be supported.

Discussion

Carnivore translocation has generally been criticised as an ineffective tool to achieve desirable levels of conflict reduction (e.g. Fontúrbel and Simonetti 2011; Linnell et al. 1997; Massei et al. 2010). Our study contradicts previous publications in which translocated conflict leopards resumed depredation (Hamilton 1981; Stander et al. 1997a; Weilenmann et al. 2010). Here, the selective live-removal of opportunistic livestock raiders stopped conflict for at least 16 months, and subsequently only one translocated individual continued raiding when livestock were illegally herded into the release area. As hypothesized by Treves and Karanth (2003), the management of few conflict animals also increased tolerance of local conspecifics that caused no conflict or acceptable levels of damage. However, other leopards soon replaced translocated offenders and continued removal of perceived conflict leopards by landowners may induce local source-sink dynamics. The viability of leopard populations may be compromised if removal (dead or alive) includes significant proportions of reproductive females (Caro et al. 2009; Packer et al. 2009). Kerth et al. (2013) demonstrate the reality of this risk because stock-raiding leopards are often misidentified, resulting in unintended persecution of females. On-going or indiscriminate translocation therefore is not a viable long-term conservation option (Athreya et al. 2011; Hamilton 1981) highlighting the need to develop country-specific translocation criteria that reflect population status and characteristics, and increase selectivity. Considering that livestock depredation did eventually resume on three of four source properties, we argue that conflict mitigation should predominantly be focussed on improved livestock protection and husbandry (Ogada et al. 2003; Woodroffe et al. 2007) to reduce the need for translocation or lethal control. Furthermore, the high economic and recreational potential of leopards (Maciejewski and Kerley 2014; Stein et al. 2010) should be promoted to increase their value beyond that of livestock losses (Stander et al. 1997a).

In the present study, leopard translocations were remarkably successful with individuals exhibiting similar ecological traits when compared with residents. They predominantly fed on wildlife and were equally successful in terms of reproduction, resulting in a positive contribution to the free-ranging gene-pool in year two after release. Most importantly, our translocated leopards had similar survival rates to residents, thus differing from studies that reported reduced survivorship for translocated carnivores (e.g. Bradley et al. 2005; Ruth et al. 1998). In addition, released leopards did not cause higher levels of conflict, nor did they home to their capture sites. After short periods of exploration they established ranges in areas with, and similar to those of, resident conspecifics. Contrary to other studies (Stander et al. 1997a; Weilenmann et al. 2010), three translocated leopards displayed encouraging degrees of release site fidelity, and in agreement with Hayward et al. (2006), soft-release appeared to reduce exploratory movements. We speculate that female Pp57 showed the highest degree of post-release dispersal because she was released into high-density leopard range and therefore was likely displaced by established residents. Male Pp48, who had been trapped on the same reserve two years earlier, was the only resident dispersing from its capture site, thus supporting the notion that this area was indeed "saturated" with residents. We provide supportive evidence that long-term rehabilitation of individual leopards can be successful (cf. Houser et al. 2011; Mondal et al. 2013) and overall translocation success was 67 %, or 83 % if livestock had not been herded into Pp45's new range.

Our success in releasing four individuals into the same bio-geographic region demonstrates that repeat releases into areas with a low to medium density of conspecifics may not compromise conservation objectives (cf. Hamilton 1981; Weilenmann et al. 2010). Pp57's case evaluation, in combination with previous efforts (Athreya et al. 2011; Hamilton 1981; Weilenmann et al. 2010), illustrates that leopards should not be released into areas with high density of conspecifics. We also point out that recipient populations need to be allowed an appropriate period to assimilate an intruder. We propose a conservative minimum inter-release interval of 18 months—this mimics natural dispersal of sub-adults in the species (Fattebert et al. 2013; Skinner and Smithers 1990). Consistent post-release dispersal of translocated leopards (Hamilton 1981; Houser et al. 2011; Mondal et al. 2013; Stander et al. 1997a, Weilenmann et al. 2010 and this study) shows that release site fidelity cannot be expected, and even resident individuals may disperse over considerable distances (Fattebert et al. 2013 and Pp48). We propose long distance translocations (>200 km) to prevent homing and suggest a minimum recipient area size of approximately 875 km^2 to improve site fidelity. Based on our experience, we provide protocol recommendations for effective leopard translocations (Online Resource 2).

Looking forward, the identification of appropriate release areas remains one of the most crucial challenges of responsible carnivore translocations. Strategic approaches to determine release area suitability, as demonstrated here using model *CaTSuiT*, should be a priority in countries where translocation is a legal management option. Due to its very low human density, Namibia still provides large areas with suitable leopard habitat. When using conservative input parameters, *CaTSuiT* identified approximately 117,613 km^2, allowing for 87 leopard translocations initially. This estimate represents only a small proportion of Namibia's free-ranging leopard population—approximately 0.004–0.007 % (Stein et al. 2012), and we do not suggest that this potential be utilised to its maximum capacity in a haphazard fashion. It offers an opportunity to alleviate conflict for a considerable number of the country's 3500 livestock producers in cases where opportunistic depredation can reliably be attributed to specific leopards. In addition, the country's leopards belong to the genetically diverse sub-species *P. p. pardus* (Uphyrkina et al. 2001) and form part of a panmictic population (Stein and Hayssen 2013). Sub-Saharan leopards may naturally move across several countries (e.g. Fattebert et al. 2013) and negative effects from translocation-induced genetic drift are therefore unlikely.

However, the conditions influencing habitat suitability will be significantly different in other leopard range countries (or for other carnivores—see Lindsey et al. 2004 for African wild dogs (*Lycaon pictus*)) and require independent modelling and assessment. Asiatic leopards occur in recognised sub-species (Stein and Hayssen 2013) with lower genetic diversity (Uphyrkina et al. 2001) and maximum care should be taken during translocation planning to prevent deleterious effects from artificial genetic (Storfer 1999) or pathogen transfer (Leighton 2002) into distinct natural populations. Where translocations are implemented, we suggest repeating habitat suitability assessments every two years to incorporate new information from translocation events as well as updated data of model input parameters. *CaTSuiT* is freely available (Lemeris 2015) and equipped with an interface that allows users to determine suitable areas based on the selection of an individual's capture location and a desired minimum translocation distance. The software provides a simple and replicable approach to define leopard recipient areas at any required scale. We strongly encourage its use prior to future translocations for conservation purposes, including other large carnivores and conflict wildlife.

Owing to a small sample, our observations are preliminary, but we argue that well-designed translocations can be successful for conserving leopards and possibly other asocial carnivores with similar ecological characteristics. The strategy has already been useful in the conservation of various threatened large carnivores (Goodrich and Miquelle 2005; Gusset et al. 2010; Purchase 1998) and may in future be required (or become essential) for reintroduction of the critically endangered Amur leopard (*P. p. orientalis*) in order to promote reproduction, range expansion and population recovery (Hebblewhite et al. 2011; Uphyrkina and O'Brien 2003). Although we reiterate that it should not be a standard response to carnivore conflict and other non-lethal conservation measures need to be considered beforehand, we emphasise the potential value of translocation when preventive conflict mitigation strategies have failed. In these situations, we recommend the application of conservative translocation protocols in conjunction with prior identification of the most suitable recipient locations.

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