Practical Considerations for the Reintroduction of Large, Terrestrial, Mammalian Predators Based on Reintroductions to South Africa's Eastern Cape Province

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Abstract: The expansion of conservation estate in South Africa has seen large predators increasingly reintroduced in order to restore ecological integrity, conserve threatened species and maximise tourism. Reintroductions occurred at fenced, ecotourism sites in South Africa's Eastern Cape Province. Lion *Panthera leo* reintroduction began in 2000 and has been highly successful with a population of 56 currently extant in the region arising from 35 reintroduced individuals. The African wild dog *Lycaon pictus* population has increased to 24 from a founder population of 11. Reintroduction of spotted hyaenas *Crocuta crocuta* also appears successful, although reintroductions of leopards *Panthera pardus* and cheetahs *Acinonyx jubatus* have been less successful. Here we review the successes and failures of the reintroductions that have occurred in the region and describe recommendations to assist future translocations. Ecological attributes of each species affected the success with which they were reintroduced. Soft-release techniques, adequate fencing, appropriate socio-economic environment, the order of predator reintroduction with subordinate species released prior to dominant ones, adequate prey base and adequate monitoring all improved the success of reintroductions. Carrying capacity for large predators is unknown and continued monitoring and, we fear, intensive management will be necessary in virtually all modern day conservation areas.

Keywords: Carnivore conservation management, ecological economics, ecotourism, fencing, range expansion.

INTRODUCTION

Reintroducing species to parts of their former range where they have become extinct is one of the last measures wildlife managers can employ to conserve threatened species. Reintroduction is thus employed after conservation actions at a site have failed. Reintroduction of large predators has had a poor success rate in the past [1-4] and the overall conservation benefits in the long-term are questionable [5]. Despite carnivores being reintroduced more frequently than expected [6], conservation managers around the world are not expending equal amounts of energy and resources attempting reintroductions of top-order predators [1].

Like much of Africa, the agricultural and economic development of South Africa led to such conservation failures through the extinction of large predators in all but the most uninhabitable areas [7], such as the tropical and sub-tropical lowveld (e.g., Kruger National Park and north-east KwaZulu-Natal) and the arid Kalahari. Since the advent of democracy in South Africa, uneconomical pastoralism in marginal lands has given way to game farming and ecotourism ventures leading to a massive increase in estate managed for conservation [8]. Wildlife has been reintroduced to these

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Table 1. Details of the large predator reintroductions that have occurred at each of the study sites. Founder population refers to the number of individuals initially reintroduced and excludes supplementary reintroductions. The 2005 estimate is a result of such supplementary reintroductions and births and deaths

Site	Species	Reintroduction start date	Founder population	2005 population estimate
Addo	Leopard	2004	1	1
	Lion	2003	6	9
	Spotted hyaena	2003	4	10
Amakhala	Cheetah	2004	2	5
	Lion	2004	3	3
Blaauwbosch	Cheetah	2002	3	7
Kariega	Lion	2004	4	4
Kwandwe	Brown hyaena	2002	6	4
	Cheetah	2001	6	12
	Leopard	2005	2	2
	Lion	2001	4	12
	Serval	2005	5	4
	Wild dog	2005	6	14
Lalibela	Cheetah	2005	2	0
	Lion	2003	3	5
Samara	Cheetah	2003	3	8
Scotia	Lion	1996	6	5
Shamwari	Brown hyaena	2001	9	15
	Cheetah	2002	1	6
	Leopard	2001	2	2
	Lion	2000	6	15
	Serval	2001	3	11
	Wild dog	2003	5	10
Pumba	Cheetah	2005	2	2
	Leopard	2005	2	2
	Lion	2004	2	4
	Spotted hyaena	2005	3	3
Great Fish River	Brown hyaena	1986	3	Present
	Leopard	1985	3	Unknown
Eastern Cape	*Brown hyaena*		*18*	*> 18*
	Spotted hyaena		*11*	*13*
	Cheetah		*36*	*41*
	Leopard		*9*	*>7*
	Lion		*34*	*56*
	African wild dog		*11*	*24*

areas and this has culminated in the reintroduction of large predators [9].

It is widely recommended that the results of reintroductions be published and peer-reviewed at frequent intervals to allow other reintroduction attempts to benefit from past experiences [1, 10]. This should be part of a continuous feedback loop with the results of the documented evaluation leading to alterations to the existing reintroduction programme *via* an adaptive management strategy [10]. We selected a five-yearly reporting regime, based on expert recommendations [10], but this short-time period for the initial assessment enforced limitations in our ability to measure the success of the reintroductions [9]. Based on the only assess-

ment criteria that was valid for the initial stages of a reintroduction programme (three year breeding programme with natural recruitment exceeding mortality), lions *Panthera leo* were the most successful species reintroduced to the Eastern Cape with 35 individuals reintroduced since 2000 and 49 cubs having been born leading to a 2005 population of 56 individuals (Table **1**) [9]. African wild dogs *Lycaon pictus* have doubled to 24 by 2005, arising from the 11 founders in 2003 and supplemented with 27 pups [9]. Cheetah *Acinonyx jubatus* reintroductions were less successful with 36 reintroduced and at least 23 cubs being born, but only 41 surviving in 2005 [9]. Spotted hyaenas *Crocuta crocuta* have only been present in the Eastern Cape for two years but their numbers have increased to 13 through the birth of two cubs [9]. Reintroductions of brown hyaenas *Hyaena brunnea* began in 1986 and numbers have remained steady of at least 18 in 2005 [9]. The ability of leopards *Panthera pardus* to persist despite human persecution suggests populations are stable in the Eastern Cape with nine having been reintroduced, mostly from sites within the province, although their secretive nature meant cubs have not been observed [9].

Historically, post-release monitoring of large carnivore translocations has rarely occurred and, where it has, suggests a low success rate with the causes of failures poorly understood [11]. Several authors have concluded that the factors affecting translocation success of large carnivores are too

Fig. (1). Map of the Eastern Cape Province showing the location of the conservation areas discussed in the text.

poorly understood to justify it as a conservation technique [3, 4]. Furthermore, carnivore reintroductions are considered fundamentally more difficult than those of herbivores or omnivores [12, 13]. The reintroduction of predators to South Africa's Eastern Cape Province has generally involved detailed monitoring. We define reintroduction as an attempt to establish a species within its historical range but from where it has been extirpated.

This paper reviews the causes of success and failure of the large (> 10 kg) canid, felid and hyaenid reintroductions that have occurred in South Africa's Eastern Cape Province since 2000 (described in [9]). We report on the rationale behind the reintroductions, where the reintroduced stock was sourced from, pre- and post- release management, monitoring, costs and benefits of the reintroductions, and techniques to manipulate the behaviour of the large predators. Finally we discuss factors affecting our reintroduction success including genetics, habitat, causes of the initial decline, use of captive-bred stock, veterinary assistance, the economics of reintroduction, the value of fencing, the importance of monitoring and understanding a species behavioural ecology, the long-term evolutionary impacts of management, lessons learnt and the need to determine carrying capacity at reintroduction sites for large predators.

Given large carnivores are declining globally [14], identifying the successes and failures of reintroduction attempts is crucial to future conservation management efforts and overall conservation success. Ideally, this would be objectively assessed *via* statistical analysis (e.g., [15]). The short time frame since the reintroductions began in the Eastern Cape, and the small number of sites and species reintroduced restricted such analysis, particularly given Harrell's [16] 'rule of thumb' for regression models that a maximum of $n/10$ explanatory variables can be used where n is the number of observations (in this case 11 sites) [17]. Furthermore, some of the factors that are likely to have influenced the success of the reintroductions exhibited zero variability (e.g., all sites were fenced and all reintroductions were objectively classified as successful). An alternative analytical technique would be a meta-analysis (R. Slotow, *pers comm.*), however this requires the use of statistical effect and sample sizes from published sources, which are lacking. Hence, this review uses the expert opinion of the people charged with implementing or monitoring the reintroductions to identify and discuss the factors they considered to be important for the reintroduction of top-order predators.

REINTRODUCTION SITES

The large carnivore reintroductions reported on here occurred at 11 sites [9, 18] (Fig. **1**). Data were collected from reintroduced animals *via* telemetry at Addo, Shamwari and Kwandwe, and intensive (twice daily) searches and incidental observations at each of these sites and by direct questioning of conservation managers, reserve owners and personal observations.

Like virtually all game reserves and national parks in South Africa, each reserve was enclosed with predator-proof, electrified fencing allowing them to be managed as distinct ecological units. They also each had electric fenced bomas to ensure a pre-release captivity period (soft-release). None of the sites allow hunting of large predators, and all obtain, at least, a large portion of their finances from ecotourism.

REASONS FOR REINTRODUCING PREDATORS

Clearly defined aims are essential for successful reintroduction [19], and in the Eastern Cape reserves these aims varied. The financial benefits arising from ecotourism drove the majority of reintroductions (Addo, Kariega, Kwandwe, Pumba, Scotia, Shamwari). The desire to provide tourists with a unique experience in the face of strong competition from other reserves has even led to captive-bred white lions being released in Pumba [9].

Several sites aimed to restore ecological integrity that would arise with an intact fauna (Addo, Kariega, Kwandwe, Pumba, Shamwari). Predators were also seen as performing a valuable management service by reducing the number of herbivores that were previously culled (Addo, Shamwari). Other sites also sought to actively conserve threatened or conservation-dependent species (Addo, Kwandwe, Shamwari).

SOURCING PREDATORS FOR REINTRODUCTION

The availability of animals to be reintroduced, their disease status and their genetic compatibility were influential in determining the source populations of reintroduced species and when they were released. Addo sourced their lions from the Kgalagadi Transfrontier Park, as the lions of the Kalahari were thought to be the most genetically similar extant population to the lions which originally occurred in the Eastern Cape, although there has been no study to prove this. The six founding lions were captured from widely separated areas and different prides to maximise genetic diversity, with nomadic females or males about to disperse being chosen to avoid disruption of the existing pride structure. Neither female was suckling when captured.

Shamwari sourced their lions from Madikwe and Pilanesberg because they were totally disease (tuberculosis and feline immunodeficiency virus) -free, like the Kalahari lions. As in Addo, each lion was captured from different prides to diversify the genetic base from which the founder population was created.

Kwandwe sourced some of their cheetahs from Phinda, where they occur in sympatry with lions [20]. Other cheetahs came from farmland in Limpopo, where they did not coexist with competitively superior species. The competitor-naïve cheetahs from farmland suffered a high mortality rate compared to the Phinda cheetahs (Fig. **4** in [9]) leading Kwandwe managers to conclude that cheetahs to be reintroduced alongside lions and spotted hyaenas are ideally obtained from areas where they coexist.

Leopards are difficult to successfully reintroduce for ecotourism purposes. Firstly, they tend to return to their original location (see review by [21]). Secondly, their secretive nature means they are rarely seen by tourists and occasionally escape to cause problems in adjacent pastoral areas. Shamwari sourced their leopard from rehabilitation centres where the 'wild edge' had been softened by exposure to veterinarians and carers. This has worked exceptionally well, with frequent sightings by tourists (leopards observed on

50% of days over 8 months to July 2006) [22] and the leopards have hunted independently since release [23].

PRE-RELEASE MANAGEMENT

All sites employed 'soft-release' techniques [24 p 306], where predators were kept in a boma for varying periods (Fig. **2**). Boma construction is fundamental (see technical specifications in [25]) to ensure animals are exposed to electrified fencing, habituated to game viewing vehicles, allowed to settle, become accustomed to collars and other conspecifics within a new social group [25, 26] and ensure territorial bonds are relaxed so they remain at the release location [20, 27]. Bonding is not always successful however, and, in Welgevonden Private Game Reserve, a pride fragmented despite three months pre-release captivity [28].

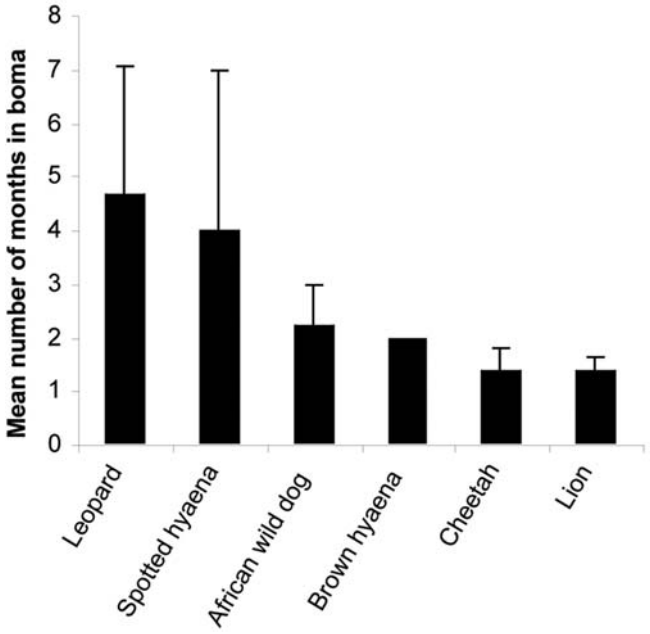

Fig. (2). Length of time each reintroduced carnivore species spent in an on-site, acclimatisation boma (mean months ± 1 S.E.). The large S.E. for leopard stems from the escape of Addo's leopard within 24 hours of its soft release. Similarly, the long boma period for spotted hyaenas was due to disease testing.

Veterinary care can also be provided during the pre-release period, particularly internal and external parasite treatments, as increased parasite loads can occur in such stressful, captive situations [25]. This is also a time when individuals can be uniquely marked. While spot and coat patterns can assist in identifying individuals of several predator species (e.g. [29, 30]), this often requires intensive investigation and close proximity. Consequently, branding with unique line patterns, that end up looking like scars, can be used to identify individuals [20], although such wounds take a long time to heal [19]. Individuals can be marked when they are released or upon attaining independence.

At most Eastern Cape reintroduction sites, once the predators had settled within bomas, vehicles were left nearby with radios on and tourist game drives passed by in order to allow captive individuals to become accustomed to humans. Administering long-lasting sedatives can reduce aggression and speed bonding of non-related individuals in bomas [19, 20], however this strategy was only used at Kariega, where it was considered successful. Younger individuals also habituate faster than older ones [19].

The predators at Shamwari were always fed after a whistle was blown. This meant they associated the whistle with food and this has facilitated subsequent management activities. Cheetah, that were being restricted to a corner of the reserve by lions, were moved to more open habitat by following the whistle and a carcass dragged behind a vehicle. Shamwari's wild dogs and leopards have also been manipulated in this manner. Kwandwe managers also implemented this strategy with their wild dogs but have not had cause to use it.

The length of time individuals were kept in bomas varied amongst species and depended upon numerous factors (Fig. **2**). Lions and cheetahs required the least amount of time in bomas (Fig. **2**), although it is crucial that, like all predators, they develop an aversion to the electric fencing. For example, after two months in a boma, reintroduced lions at Phinda chased a zebra through the electrified boundary fence but failed to continue the chase past the fenceline despite the zebra's continued onward movement [20]. Conversely, driving prey through fences is a frequent cause of wild dog escapes and they place a great deal of pressure on fence infrastructure by using them to increase their hunting success [31, 32]. Cheetah have also been reported using fences to hunt [25].

Leopards tend to require the most time in bomas (Fig. **2**), particularly where they are intended for ecotourism, so as to reduce their fear of humans and become less secretive. Leopards at Kwandwe and Shamwari were only released from the boma when they showed reduced levels of fear and could be manipulated for management activities. This strategy may increase the risk that these leopards could attack humans, as they may lack fear and wariness that would otherwise reduce such attacks.

African wild dogs also required a substantial period interned so that packs bond and develop a dominance hierarchy, particularly when individuals are not known to each other prior to capture. Without this, the pack is likely to fragment upon release and is then unlikely to breed [33, 34]. If unrelated individuals are to be combined into social groups (of wild dogs, lions, spotted hyaena or male cheetah), then the length of time in bomas may increase. Behavioural observations should be utilised to determine when groups are bonded and a dominance hierarchy has developed because the lack of social stability can lead to increased movements and mortality post-release [35, 36].

POST-RELEASE MONITORING AND MANAGEMENT

It is universally recommended that continuing, long-term monitoring occur after reintroductions have taken place [1, 4, 11, 14, 26]. Despite such recommendations, not all reserves had specific monitoring programmes. Addo, Kwandwe and Shamwari have monitoring programmes run by trained ecologists, although not always full-time, permanent or long-term. Universities (Fort Hare, Nelson Mandela Metropolitan, Rhodes and Walter Sisulu) in the Eastern Cape have benefited from the expansion of game reserves with Addo, Kwandwe, Pumba and Shamwari coordinating research pro-

jects through these institutions. In the Eastern Cape, monitoring often involved fitting radio telemetry collars or implants to all or some members of the reintroduced group and it has been suggested that monitoring with telemetry is likely to be necessary for up to 25 years post-release [1]. For those reserves that do monitor reintroduced animals, publication of the results of this research is only now beginning to occur [37, 38].

Reintroducing large predators to small, enclosed reserves is an intensive process and a great deal of management is required once they are released. The most common management activity after the release of lions is their removal after a rapid population increase. No lions were killed as part of these removals, and all removed individuals were used to restock other reserves.

Some animals have occasionally been supplementary fed following release. The lionesses at Addo were provided with culled warthog *Phacochoerus africanus* carcasses whilst they were struggling to keep young cubs alive. A female cheetah at Kwandwe was provided with carcasses when she was malnourished while raising four cubs.

Other interventions have occurred to provide veterinary care for wounded individuals. The alpha female wild dog at Shamwari was mauled by lions and was treated. An adult male lion at Addo had a large, gaping wound to his thigh stitched up while his collar was being removed. Such interventions are generally against the policies of each reserve, however the expenses associated with obtaining and reintroducing replacement animals are such that the survival of individuals is desirable. The wild dogs at Kwandwe were inoculated against rabies when their radio collars were refitted.

COSTS AND BENEFITS OF REINTRODUCING PREDATORS

Purchasing large predators for reintroduction is costly. Based on 2004 wildlife auction prices, when one South African Rand bought 0.16 US$ (exchange rate @ 1/7/2004), buying individual cheetahs cost $2400, hyaenas $800, leopards and lions $4000, and African wild dogs $1280. Consequently, Shamwari housed $5,181,056 worth of all wildlife, including $127,680 in predators, and these predators killed $190,342 worth of wildlife in 2004 of which impala ($60,800) and bushbuck ($29,200) were most costly. In 2004, Addo housed $12,148,600 worth of wildlife of which buffalo *Syncerus caffer* comprised over $9.92 million and predators accounted for $35,200. Lions alone killed $473,984 worth of wildlife in 2004 with buffalo ($441,487) and kudu ($14,235) forming the bulk of these costs. Similar calculations from Zimbabwe showed that ten lions killed US$59,840 per year, but benefits through photographic safaris yielded a 10.4% net benefit in 1995 [39]. Pilanesberg's lions were estimated to cost $160,000 per annum but yielded $4,160,000 in return [40].

This illustrates the value of reintroduction schemes being associated with ecotourism ventures where relocation costs can be rapidly erased. Elsewhere, where government-led programmes are more common, this is not the case and reintroductions involve substantial capital outlays with little opportunity of capital return [41].

Constructing and maintaining the infrastructure required to house large predators is also expensive (Fig. **3**). Each of the Eastern Cape conservation areas has predator-proof boundary fences. The construction specifications of these fences is important (specifications described in [19, 26]). Fences also require daily maintenance, although this can simultaneously fulfil valuable anti-poaching patrols.

Despite these costs, where data were available, it is financially beneficial to reintroduce large predators. Scotia estimated the reintroduction of lion led to a $320,000 - $640,000 increase in turnover per annum. Shamwari saw a 31% increase in occupancy and a 71% increase in revenue following predator reintroduction.

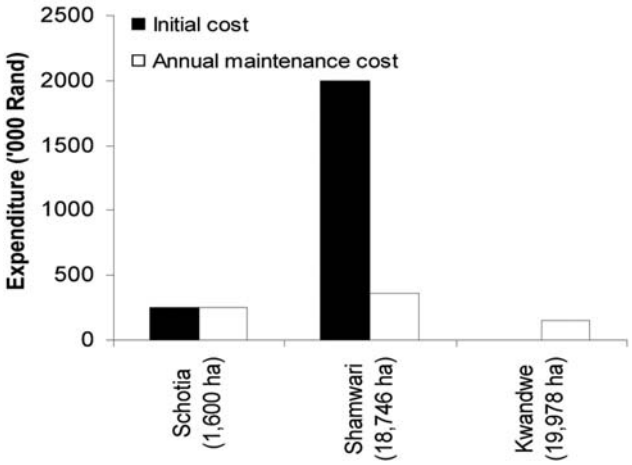

Fig. (3). Construction and maintenance costs of infrastructure necessary to house large reintroduced predators. Note that there were no additional construction costs to upgrade facilities to house predators at Kwandwe because it opened with large predators present.

MANIPULATING PREDATORS

The level of knowledge about the ecology of large predators in Africa is such that managers are now planning for various outcomes during the reintroduction process. Shamwari successfully employed this technique by housing two groups of three lions in separate bomas for two weeks to allow them to bond and create two separate prides upon release. Addo attempted a similar strategy with its lions, although upon release all but the sub-adult female joined together [37]. After six months, the males that were held in bomas together formed coalitions that fought for dominance and eventually established territories, however the females remained separate and non-territorial [37].

The prides at Shamwari, Kwandwe and Lalibela have been kept small, and male coalitions that were born and attained independence were moved to other reserves, to minimise the chances of large and valuable wildlife (buffalo and giraffe *Giraffa camelopardalis*) being killed. This may lead to evolutionary changes in both predator and prey however [42, 43].

REINTRODUCTION SUCCESSES AND FAILURES

Overall the reintroduction of large predators in the Eastern Cape was assessed as successful according to the available, relevant criteria [9] and, with economic forces driving the programme, it is unlikely that the reintroduction of such

charismatic, tourist-attracting species will fail. Young have been observed for all reintroduced species, except leopard, and all populations have increased from the number initially reintroduced. Lions have rapidly become overabundant. Our data suggest that competitively dominant carnivores are more resilient to the reintroduction process than threatened species because they are free from competitive persecution. Despite this success, only lions are above the 50 breeding individuals considered necessary to protect from genetic problems [44] assuming occasional mixing of individuals between reserves. Consequently continued population supplementation and mixing of new genes will be fundamental to the long-term conservation of all species reported on here and therefore continued monitoring and management intervention will be necessary.

FACTORS AFFECTING REINTRODUCTION SUCCESS

Causes of Initial Local Extinction

Another prerequisite for successful reintroduction is the elimination of the factors that initially caused the decline of the species [45, 46]. In the Eastern Cape these were predominately human persecution *via* hunting (both predator and prey), although the reduction of natural habitats through agriculture is also likely to have been important. Reintroduction sites in the Eastern Cape have each had some form of historical habitat disturbance, however their legislated protection as conservation estate affords both habitat and individuals safety. These sites are designed for ecotourism and, as such, have limited levels of hunting, as part of management activities to reduce herbivore overabundance.

Presence of an Existing Population

The presence of an existing population of a species may either positively or negatively affect the success of a reintroduction through attraction to a site or avoidance of it. For example, a lioness in oestrus was used to attract the other lions reintroduced to Matusadona National Park, Zimbabwe [47]. The hypothesized existing leopard populations in many Eastern Cape reserves prior to the reintroductions reported here [9] may supplement mortalities amongst the reintroduced stock. Conversely, breeding individuals in sites surrounding reintroduction sites may lead to escapes as reintroduced individuals seek off-site mating opportunities. The ability of leopards to cross fences suggests they are most susceptible to such problems. Similarly, existing populations of spotted hyaenas at Madikwe Game Reserve, South Africa, killed a clan that were reintroduced [26]. The presence of an existing population is considered a factor contributing to the failure of some reintroduction programmes [12].

Fencing

The success of reintroductions in South Africa is largely due to fencing [15], which minimises negative human-wildlife interactions and provides assured ownership of valuable wildlife capital. In an ideal world, fencing conservation areas would be unnecessary and wildlife could roam wherever it chose, however most conservation areas worldwide today are natural islands in a matrix of disturbed environments [48]. Hence it soon may be necessary to fence all wildlife conservation areas or sections of them where wildlife and humans may interact negatively.

The value of fencing conservation reserves, or even core areas of reserves, to reduce encroachment, negative human-wildlife interactions or the effects of unwanted species (exotics, etc.) cannot be understated. Even in Kenya's Laikipia ranches, where researchers have been devising methods to reduce the impacts of wildlife-human interactions [49], fences have been recommended as ways of reducing negative impacts [50]. Clearly, the placement of fences is critical and must consider the behaviour and ecology of the species present in a reserve rather than human interests (e.g. [51]).

Habitat Features

There are numerous other factors that have previously been identified as important to the success of reintroductions. The principal cause of most species' decline is the loss and alteration of habitat [45, 52]. For large carnivores this is less likely than for other species, as prey availability is more important than the vegetation characteristics of a site [42, 53, 54]. Hence, if there is suitable prey available [23, 55-58], adequate refuges for competitively-inferior predators to escape persecution and kleptoparasitism from larger predators [59] and measures to alleviate human – wildlife conflict [15], then all large predator reintroductions are likely to be successful. Each of the sites in the Eastern Cape has properly reserved habitat and adequate food availability. Furthermore, socio-political factors are directing the reintroductions in the Eastern Cape, because there is a substantial economic benefit to conserve land, protect and improve habitats which is likely to increase wildlife carrying capacity and thereby sustain increased predator density [60, 61].

Captive-Bred Stock

Reintroduction of captive-bred mammals has also been doomed by poor techniques preparing captive animals for survival in the wild [45]. While the reintroduction of captive-bred African wild dogs in Etosha in the 1990s failed because the could not hunt successfully [62], mixing captive-bred and wild caught African wild dogs is a common method today [26, 33] and is highly successful at teaching captive-bred individuals how to hunt and socialise appropriately.

Social Group Composition

An appropriate mix of individuals in a social group is an important consideration in reintroductions [45]. Large social predators seem resilient to interactions with unrelated and unknown individuals when kept for long periods in captive situations [33, 36], particularly when sedatives are given during the initial, high-stress phase of the boma period.

The choice of group composition for the Addo lion reintroduction illustrates the depth of knowledge South African wildlife managers have developed, yet lessons have been learned from this. Four males and two females is atypical in terms of lion pride structure [63], however the size of Addo's Main Camp section (13,400 ha) was considered too small for large numbers of lion [53] and so managers hoped infanticide by unrelated male lions [64] and predation of cubs by spotted hyaenas would slow the population increase. This has worked to date, with three of four litters failing.

Veterinary Assistance

Disease can hamper reintroduction attempts [34, 62], however as few as 24% of reintroduction programs utilise

veterinary screening [12]. Therefore involving veterinarians is crucial. Several of the Eastern Cape conservation areas have such experts on staff (e.g. Addo – South African National Parks; Amakhala; Shamwari) and there is a large industry in South Africa of wildlife relocation companies that also have veterinarians experienced in treating large species.

Economics

Costs can inhibit wildlife reintroduction [45], however in areas where wildlife has an economic value, this value generally drives their reintroduction. This is particularly the case in South Africa where government conservation agencies and private companies have experts in the capture and movement of animals, such that translocation is relatively safe and cheap. Subsequently, the desires of tourists drive the reintroduction of charismatic species, especially large predators [25], which concomitantly protects habitat [60].

Genetics

Carnivore reintroductions typically involve small founder populations so that genetic problems may become an issue. The original lions in the Eastern Cape were thought to be genetically similar to Kalahari lions and only Addo reintroduced these. It may be worthwhile using excess lions from Addo to increase genetic diversity at other sites with the longer-term aim of converting all Eastern Cape lions to something akin to the Kalahari strain. Such hybrid matings among different populations may allow natural selection to produce a 'locally-adapted' genotype [13].

A studbook needs to be created and maintained for this to be successful. Given the likelihood of moving individuals between reserves, this studbook should also direct the shapes of identification brands (if they are used) to avoid duplication of marks between sites. Furthermore, genetic analysis should be conducted to ensure related individuals are identified prior to movement between sites.

Evolutionary Impacts of Management Actions

Another issue that must be considered, with regard to the level of management required in small, enclosed reserves, is that management actions may lead to evolutionary responses. Coalitions of male lions have been removed at several sites, however this may mean that the anti-predator strategy of large prey species, like buffalo and giraffe, becomes redundant and may weaken the herd *via* the retention of genes that would otherwise have been selected out of the population. Conversely it seems unlikely that such management will result in an alteration of the lions' predatory instinct given that those reintroduced to Addo from the buffalo-free Kalahari took less than one year to learn how to hunt buffalo successfully [42]. Even the frequent management practice of maintaining coalitions of male lions is unusual in more natural ecosystems where coalition sizes range up to nine [65]. Consequently, cognisance must be given to allowing evolutionary processes to continue.

LESSONS LEARNT

Competitively subordinate and vulnerable carnivores should be released prior to dominant species. This is probably because these more sensitive species need to locate refugia [59] before the arrival of potential competitors and predators. This rarely happened in the Eastern Cape game reserves and may explain the limited success of cheetah reintroductions [9].

Shamwari managers considered it a mistake, in retrospect, to release cheetahs sequentially. They believe their cheetahs would have adapted better if they were reintroduced simultaneously in larger numbers. Also, the large male cheetah coalition at Kwandwe has been problematic through attacks on conspecifics.

All reserves recognised the importance of soft-release techniques [34]. The location and construction of pre-release housing bomas has caused problems however. These should be constructed so that free-ranging predators cannot harass those awaiting release. Such harassment led to a male cheetah being killed by a female leopard at Shamwari, and was regularly observed at Addo when the dominant lion coalition harassed (roared, charged the fence, scent marked all around the boma) the captive hyaenas.

Whilst in the boma, it is important that lions or leopards do not learn to associate humans with food. Consequently, they were fed either remotely or from concealed positions, such as *via* pulley-systems that deposited carcasses over the boma fence or through a shute while the human operators were concealed from view (see [19] for specifications).

A sound relationship with adjacent land owners is also an important consideration. Consultation and cooperation is crucial in this regard. Educating and training staff is also critical to minimise the chance of accidents.

CARRYING CAPACITY FOR LARGE PREDATORS

There appears to be a deficiency in knowledge about the carrying capacity at each site for each predator. Managers of each reserve have an idea of how many individuals of each species they desire on their reserve (Fig. **4**), but there is no scientific rationale behind this. Recent research may be able to provide estimates however [53]. Overpopulation of a predator can result in escapes [66] and this is a problem even in large conservation areas, like the Kgalagadi Transfrontier Park [67]. Frequent observations of individuals along boundary fences may be indicative that carrying capacity (ecological and/or social) has been exceeded (e.g. [25]).

Currently the reserves are battling with what to do with excess large predators, particularly lions. To date, excess individuals from truly free-range sites have generally been removed to restock newer reserves. This practice has been employed elsewhere and in Phinda excess lions and cheetahs were removed within three years of the reintroduction due to declines in prey species [20]. This option is rapidly running out and new avenues of population control, such as contraception [68] or sterilization of certain individuals, are being sought. Yet this raises May's [13] ethical quandary as to "what extent does this preserve the African lion with its diverse array of individual and group behaviour", even if the species still survives? National parks and many Eastern Cape reserves are averse to incorporating hunting of excess predators into their management regimes because of the bad publicity they will derive from tourists and the animal welfare lobby, despite the potential income benefits [69, 70]. The misdirected power of these groups is evidenced by the cessation of elephant *Loxodonta africana* culling in South African national parks [71].

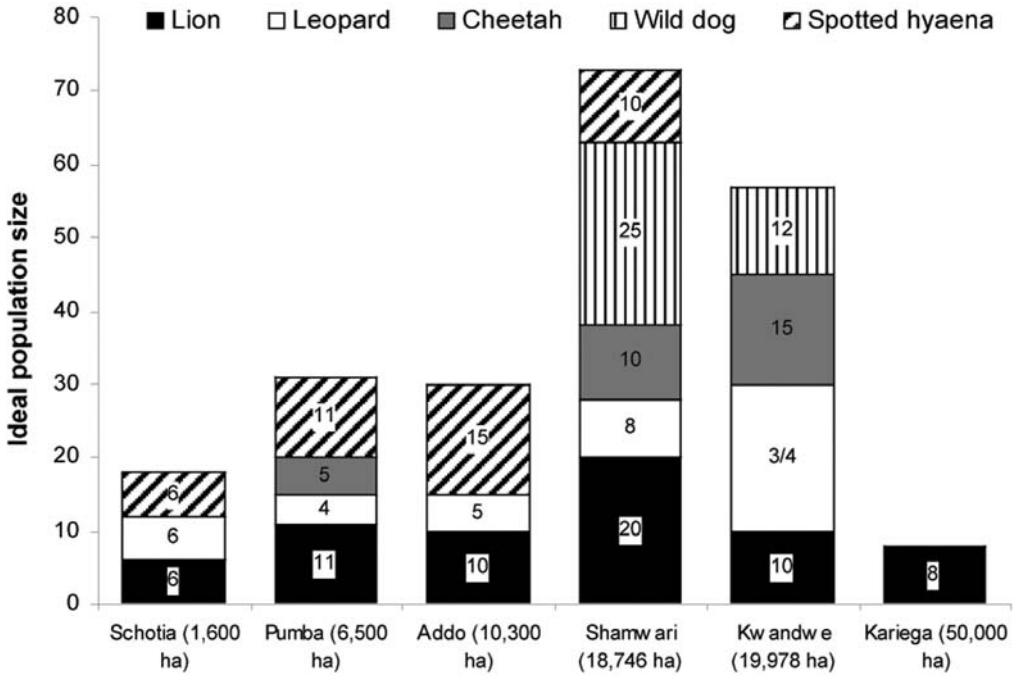

Fig. (4). Estimates of the carrying capacity of large predators at each reserve made by their conservation managers.

CONCLUSIONS

Where reviews a decade ago concluded that reintroductions of large predators were not viable [3, 4], an increase in knowledge and technical improvements since has made it common practice [9]. Management is a permanent requirement for the conservation of large, terrestrial predators in all but the largest conservation areas [9] and for those inherently rare species [72]. The impact of these species on prey populations in small, enclosed areas and the potential for loss of genetic diversity will necessitate frequent monitoring and intervention for the foreseeable future. One option available to clumps of private conservation areas, such as many of those in the Eastern Cape, is to join together as a conservancy, which would retain individual tourist ventures while allowing for the removal of internal fences resulting in one large conservation unit. This would substantially reduce management costs and allow evolutionary processes to continue [9]. Without this, the value of these reintroductions into small isolated reserves for the conservation of threatened species is questionable [5].

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