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Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa

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Summary

1. We evaluated one of the most extensive efforts to date to re-introduce an endangered species: attempts to establish an actively managed meta-population of African wild dogs *Lycaon pictus* in South Africa.

2. Using an information-theoretic approach, known-fate modelling in program MARK was employed to estimate the survival of re-introduced wild dogs and their offspring, and to model covariate effects relative to survival. Multiple a priori hypotheses on correlates of re-introduction success were tested (collated from extensive individual experiences) using different re-introduction attempts as natural quasi experiments.

3. Survival analyses revealed that the determinants of re-introduction success can be reduced to two factors relevant for management, suggesting that wild dog re-introductions should be attempted with socially integrated animals that are released into securely fenced areas, unless measures are implemented to mitigate human-related mortalities outside protected areas.

4. *Synthesis and application.* This study illustrates that monitoring and evaluation of conservation efforts, complimented with expert knowledge, forms the foundation of informed decision-making to underpin management recommendations with scientific evidence, particularly if the proposed actions are controversial.

Key-words: African wild dog, evaluation, evidence-based conservation, *Lycaon pictus*, MARK, meta-population, monitoring, re-introduction, survival analysis.

Introduction

Re-introductions are a commonly used and potentially powerful tool for ecological restoration and endangered species recovery (Van Wieren 2006). There may even be legal obligations to re-establish a species within its historical range following extirpation or extinction (Rees 2001). According to the IUCN (1998), the principal aim of any re-introduction is to establish a self-sustaining population that requires minimal long-term management. When this criterion for success has been used, however, the majority of past re-introduction attempts have failed (Griffith *et al.* 1989; Beck *et al.* 1994; Wolf *et al.* 1996; Wolf, Garland & Griffith 1998; Reading, Clark & Griffith 1997; Fischer & Lindenmayer 2000). It might thus be unrealistic

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to expect survival and persistence without periodic interventions, thereby creating actively managed meta-populations (Moehrenschlager & Somers 2004; Akçakaya, Mills & Doncaster 2007).

Past failures demonstrate that the science of re-introduction biology is still in its infancy, which prompts us to learn from earlier experiences. Re-introduction success has not increased over time (Fischer & Lindenmayer 2000) and many re-introduction attempts are heavily based upon subjective beliefs (Hein 1997), as conservation efforts in general are not always based upon a critical appraisal of the available evidence (Pullin *et al.* 2004). The absence of rigorous evaluations has been identified as a major obstacle in promoting conservation biology as a scientific discipline (Kleiman *et al.* 2000; Stem *et al.* 2005; Ferraro & Pattanayak 2006). The emerging field of evidence-based conservation holds promise for predicting which management actions are likely to be most effective in achieving conservation goals (Pullin & Knight 2001, 2003; Sutherland *et al.* 2004). With the assumption that objective evaluation may lead to informed decision-making, we evaluated one of the most extensive efforts to date to re-introduce an endangered species, namely the establishment of an actively managed meta-population of African wild dogs *Lycaon pictus* (Temminck) in South Africa.

Wild dogs are an intensely social species in danger of extinction if nothing is done to halt their decline (Creel & Creel 2002; Woodroffe, McNutt & Mills 2004). In South Africa, in an effort to restore wild dog numbers in increasingly fragmented landscapes and to complement the single viable population occurring in Kruger National Park, a plan was launched to manage separate subpopulations of wild dogs in several small, geographically isolated conservation areas as a single meta-population. This intensive management approach, which was derived from a population and habitat viability assessment (Mills *et al.* 1998), involves the re-introduction of wild dogs into suitable conservation areas and periodic translocations among them to mimic natural dispersal and maintain gene flow. This conservation strategy is largely based upon expert opinion (Wild Dog Advisory Group of South Africa) and there is no predictive framework available to quantify which re-introduction techniques are the most efficient, despite the initial failures (Woodroffe & Ginsberg 1997, 1999) and high costs (Lindsey *et al.* 2005a) associated with wild dog re-introductions and translocations.

This comprehensive evaluation involved the participation of a broad group of conservationists, whose expertise on wild dog re-introductions was accumulated, synthesized and translated into quantitative data, in order to base future management actions upon a consensus interpretation of the available evidence. The spatial and temporal extent of monitoring data available from all wild dog re-introduction attempts in South Africa since 1995 provided a rare opportunity to evaluate simultaneously the ecological, behavioural, socio-political and management-related determinants of re-introduction success within an endangered species, thereby using different re-introduction attempts as natural quasi experiments (Sarrazin & Barbault 1996).

We sought to elucidate those factors that have affected the survival of re-introduced wild dogs and their offspring. Survival of and breeding by the release generation were proposed as two pragmatic key measures of re-introduction success (Seddon 1999) and represent the cumulative outcome of multiple forces, both biological and non-biological. Long-term persistence of re-introduced wild dogs is assessed by means of population viability modelling elsewhere (Gusset 2006). Lessons learnt from this case study should be applicable to other re-introduction programmes facing similar challenges.

Materials and methods

Data were collected by post-release monitoring from 12 re-introduction sites and 18 release events (Table 1), resulting in a total of 256 individual records (127 released wild dogs that produced 129 pups). We quantified the survival of re-introduced wild dogs 6, 12, 18 and 24 months after release and that of pups produced to 6 and 12 months of age. These pups were invariably followed for fewer 6-month intervals than the initially released animals. We hypothesized that re-introduction success was potentially related to one or more of the factors listed in Table 2.

Table 1. Wild dog re-introductions and translocations in South Africa (up to 2005)

Release site	Province	Geographic position	Release date(s)
Balule Nature Reserve	Limpopo	24°13′ S/30°59′ E	2005
Hluhluwe-iMfolozi Park	KwaZulu-Natal	28°05′ S/31°56′ E	1980/1981 (4×)*, 1986*, 1997, 2001, 2003
Karongwe Game Reserve	Limpopo	24°15′ S/30°35′ E	2001†, 2002
Kgalagadi Transfrontier Park	Northern Cape	25°45′ S/20°15′ E	1975*
Klaserie Game Reserve	Limpopo	24°15′ S/31°15′ E	1991*
Kwandwe Private Game Reserve	Eastern Cape	33°09′ S/26°62′ E	2004
Madikwe Game Reserve	North West	25°00′ S/26°12′ E	1995, 1998 (2×), 2000
Marakele National Park	Limpopo	24°25′ S/27°40′ E	2003
Pilanesberg National Park	North West	25°15′ S/26°85′ E	1999, 2001
Shambala Private Game Reserve	Limpopo	24°19′ S/27°58′ E	2002
Shamwari Game Reserve	Eastern Cape	33°27′ S/26°03′ E	2003
Tswalu Kalahari Reserve	Northern Cape	27°12′ S/22°31′ E	2004
uMkhuze Game Reserve	KwaZulu-Natal	27°40′ S/32°15′ E	2005
Venetia Limpopo Nature Reserve	Limpopo	22°20′ S/29°20′ E	1992*, 2004

*Not included in survival analysis because of a lack of data.
†Excluded from analysis because all animals were recaptured 4 months after release.

Table 2. Factors hypothesized to influence the survival of re-introduced wild dogs

Parameter	Parameter value (percentages or mean ± SE)
Individual aspects	
Age of released wild dogs	Pup 24% (30/127), yearling 9% (12/127), adult 67% (85/127)
Sex of released wild dogs	Male 54% (68/127), female 46% (59/127)
Origin of released wild dogs	Wild-caught 61% (79/127), wild-caught but captive-raised 13% (16/127), captive-bred 13% (16/127), mixed (pups only) 13% (16/127)
Aspects of release areas	
Human population density (km^{-2}) in surroundings of release area	72 ± 16 (range 9–197, n = 12)
Main land use practised in surroundings of release area	Livestock farming 50% (6/12), communal land 25% (3/12), game ranching 25% (3/12)
Public high-speed road traversing release area	17% (2/12) of release areas
Release area entirely fenced or contiguous to large protected area	92% (11/12) of release areas
Length of perimeter fence (km) around release area	115 ± 9 (range 64–160, n = 12)
Protection status of release area	Private 67% (8/12), government 33% (4/12)
Release area located at international border	8% (1/12) of release areas
Size of release area (km^2)	380 ± 75 (range 84–900, n = 12)
Number of release events per release area	1·9 ± 0·6 (range 1–8, n = 12)
Number of wild dogs released per release area	12·8 ± 3·0 (range 3–42, n = 12)
Disease aspects	
Domestic dogs occurring outside release area	75% (9/12) of release areas
Rabies vaccination programme for domestic dogs	75% (9/12) of release areas
Infectious diseases in other carnivores in release area	83% (10/12) of release areas
Rabies vaccination programme for released wild dogs	72% (13/18) of release events
Ecological aspects	
Prey (> 10% in wild dog diet) density (km^{-2}) in release area	15 ± 3 (range 1–38, n = 18)
Competitor (lion and spotted hyaena) density (km^{-2}) in release area	0·13 ± 0·03 (range 0·01–0·40, n = 18)
Management reduction of competitor density in release area	75% (9/12) of release areas
Aspects of release events	
Number of wild dogs released per release event	7·1 ± 0·9 (range 2–16, n = 18)
Wild dogs resident in release area	33% (6/18) of release events
Season of release	Mating 22% (4/18), denning 45% (8/18), other 33% (6/18)
Supplementary feeding upon release	44% (8/18) of release events
Group splits upon release	22% (4/18) of release events
Wild dogs breaking out of release area	56% (10/18) of release events
Conservation education programme	33% (6/18) of release events
Birth of offspring upon release	94% (17/18) of release events
Aspects of social integration	
Time wild dogs kept in boma (days)	Individually 212 ± 17 (range 15–634, n = 127), together 181 ± 18 (range 15–634, n = 127), apart 6 ± 2 (range 0–86, n = 127)
Sequence of bonding wild dogs in boma	In same boma from beginning 83% (15/18), initially separated by fence 17% (3/18)
Aggression in boma	50% (9/18) of release events
Death in boma	17% (3/18) of release events
Pregnancy in boma	44% (8/18) of release events
Birth of offspring in boma	17% (3/18) of release events
Emergence of dominant pair in boma	89% (16/18) of release events
Removal of wild dogs that interfered with social integration in boma	22% (4/18) of release events
Structure of release group	Existing packs 11% (2/18), packs result of bonding groups in boma 83% (15/18), single-sex groups 6% (1/18)
Composition of release group	Naturally composed groups (existing packs/groups or packs result of bonding single-sex groups in boma) 61% (11/18), artificially composed groups (packs result of bonding non-single-sex groups in boma) 39% (7/18)
Age ratio of released wild dogs (proportion adults)	0·75 ± 0·07 (range 0·33–1·00, n = 18)
Sex ratio of released wild dogs (proportion males)	0·56 ± 0·04 (range 0·17–1·00, n = 18)

An information-theoretic approach (Lebreton *et al.* 1992; Burnham & Anderson 2002) was used to assess the influence of these factors on the survival of re-introduced wild dogs and their offspring. Because of the large variety of management strategies used and factors potentially impacting survival, six a priori hypotheses were developed based upon our experiences in wild dog re-introductions (English *et al.* 1993; Maddock 1995, 1999; Hofmeyr 1997; Andreka *et al.* 1999; Krüger, Lawes & Maddock 1999; Somers & Maddock 1999; Hofmeyr *et al.* 2000, 2004; Van Dyk & Slotow 2003; Davies & Du Toit 2004; Lindsey, Du Toit & Mills 2004a,b, 2005; Lindsey *et al.*

2005a,b; Graf *et al.* 2006; Gusset, Slotow & Somers 2006; Gusset, Graf & Somers 2006). Each hypothesis was expressed as a suite of candidate models, comprising a subset of the factors listed in Table 2 relating to individual characteristics of the released animals, aspects of re-introduction sites, disease-related and ecological influences, circumstances of release events, and aspects affecting social integration before release.

Known-fate modelling in program MARK (White & Burnham 1999) was used to estimate the survival of re-introduced wild dogs and their offspring, and to model covariate effects relative to survival. Known-fate models imply that the fates of individuals are independent (Cooch & White 2006). This was unlikely to be the case (Gusset, Slotow & Somers 2006); however, we assumed that the covariates operated similarly on individual survival probabilities.

Violating the assumption of independent individual fates may not cause biased parameter estimates but can lead to bias in the variance estimates, because of overdispersion in the data (Cooch & White 2006). The conservative approach, and current convention (G. White, personal communication), to correcting this potential problem is to select a global, most general model from the set of candidate models, and calculate the amount of overdispersion (i.e. the variance inflation factor, c) as the ratio of the chi-square goodness-of-fit statistic to its degrees of freedom (Cooch & White 2006). This value was used to modify variance estimates and the model selection criterion, yielding a quasi-likelihood adjusted version of Akaike's information criterion ($QAIC_c$; Burnham & Anderson 2002). $\Delta QAIC_c$ (i.e. the difference between the model with the lowest $QAIC_c$ value and the $QAIC_c$ values from all other models) was used to rank models and select the best-fit model for inference. In addition, normalized $QAIC_c$ weights were used to evaluate the strength of evidence for each model considered.

In a first step, the effect of time since release or birth on survival was examined. In a second step, a global model was created to quantify overdispersion and to ensure that there was more structure in the data than merely as a result of time transitions in survival estimates. In a third step, linear constraint models were developed to assess the relationship between the six suites of covariate models and survival, by modifying the design matrix and thus using the logit link function in MARK (White & Burnham 1999). A stepwise reduction approach was applied, sequentially eliminating factors from the full model (i.e. the model containing all covariates in one suite) according to their individual reduction of fit until the top-ranked model showed sufficiently stronger support than the base model ($\Delta QAIC_c > 2$). The precision of the slope coefficient (β) estimates in the logistic regression models was used as evidence of a significant effect based on the degree to which confidence intervals (CI) overlapped zero.

Results

EFFECT OF TIME ON SURVIVAL

To understand some of the potential heterogeneity in survival estimates, the first model examined was survival by time, $S(t)$ (t = 6-month interval), which was compared to a model of survival independent of time, S^*. $S(t)$ had a much better fit than S^* ($\Delta QAIC_c = 567{\cdot}05$) and carried 100% of the model weight. The β estimates for the four time transitions had a 95% CI not overlapping zero ($\beta_{t1} = 1{\cdot}73$, SE = 0·04, 95% CI = 1·66–1·80; $\beta_{t2} = 1{\cdot}92$, SE = 0·04, 95% CI = 1·83–2·00; $\beta_{t3} = 2{\cdot}30$, SE = 0·05, 95% CI = 2·20–2·40; $\beta_{t4} = 2{\cdot}40$, SE = 0·08, 95% CI = 2·24–2·55), suggesting a significant effect of time transition on survival. The survival estimates from the reconstituted models are indicated in Fig. 1. This pattern was not surprising given that the first two time transitions included the pups produced by the re-introduced wild dogs, with pups having lower survival rates than yearlings and adults.

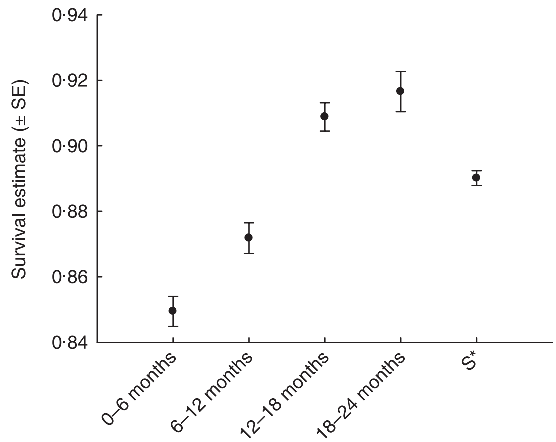

Fig. 1. Survival estimates for re-introduced wild dogs over the four time transitions covered by the study (i.e. 0–6, 6–12, 12–18 and 18–24 months after release or birth) and the corrected overall 6-month survival estimate for the time-independent base model, S^*.

GLOBAL MODEL

A global model of time + covariates was created, where the covariates were modelled as group attributes. This global model had a much better fit than $S(t)$ ($\Delta QAIC_c = 143{\cdot}21$) and carried 100% of the model weight. This implied that there was more structure in the data than simple effects of time. The global model showed a moderate degree of overdispersion ($c = 2{\cdot}12$).

As a time-dependent model describing each covariate and transition would produce more parameters than there were data, simply examining a saturated model would not be productive. Therefore, to assess whether model fit was improved with the addition of the six suites of time-invariant covariates, a simple S^* model, survival of all individuals over one interval, independent of time, was used as the base model. All models were corrected for overdispersion based on $c = 2{\cdot}12$ derived from the global model. The base model gave a corrected overall 6-month survival estimate of $S = 0{\cdot}89$ (SE = 0·003) (Fig. 1).

EFFECT OF COVARIATES ON SURVIVAL

Individual aspects

The first suite of models addressed the potential effects of individual characteristics of the re-introduced wild dogs (Table 2). The top-ranked and only model showing stronger support than the base model ($\Delta QAIC_c = 50{\cdot}22$), carrying 40% of the model weight, contained the factors age, sex,

Table 3. Slope coefficient (β) estimates of parameters included in the top-ranked logistic regression models. Parameters with 95% confidence intervals (CI) of β estimates not overlapping zero (indicated in italics) had a significant influence on the survival of re-introduced wild dogs

Parameter	β estimate	SE	Lower 95% CI	Upper 95% CI
Individual aspects				
Intercept	2·10	0·04	2·03	2·17
Pup	0·35	0·20	–0·75	0·05
Yearling	13·81	557·89	–1079·65	1107·26
Adult	0·20	0·28	–0·34	0·74
Male	0·38	0·28	–0·17	0·92
Female	*0·69*	*0·34*	*0·03*	*1·35*
Unknown sex	*–2·10*	*0·32*	*–2·72*	*–1·48*
Wild-caught origin	*–0·38*	*0·19*	*–0·75*	*–0·01*
Mixed origin	0·95	0·50	–0·03	1·93
Aspects of release areas				
Intercept	2·09	0·03	2·03	2·16
Human population density	4·69	3·48	–2·12	11·51
Fence length	*–7·80*	*3·22*	*–14·11*	*–1·50*
Size of release area	1·23	0·81	–0·36	2·82
Disease aspects				
No top-ranked model				
Ecological aspects				
Intercept	2·10	0·03	2·03	2·17
Prey density	–1·23	0·82	–2·82	0·37
Aspects of release events				
Intercept	2·07	0·03	2·01	2·14
Group split	*0·91*	*0·43*	*0·07*	*1·76*
Break-out	0·31	0·23	–0·14	0·76
Conservation education	0·21	0·30	–0·37	0·79
Aspects of social integration				
Intercept	2·08	0·03	2·02	2·15
Time in boma together	*2·18*	*1·04*	*0·13*	*4·23*
Death	–0·57	0·30	–1·16	0·02
Pregnancy	0·19	0·24	–0·28	0·66
Birth	*1·09*	*0·47*	*0·16*	*2·01*
Existing pack	0·43	0·54	–0·62	1·48
Single-sex group	–1·17	1·22	–3·56	1·22
Age ratio	0·55	0·56	–0·54	1·64
Sex ratio	–1·26	0·73	–2·69	0·17

wild-caught origin and mixed origin. Three parameters were individually significant: female, unknown sex and wild-caught origin (Table 3). Back-transformations to survival estimates (S_{female} = 0·94, SE_{female} = 0·02; S_{unknown} = 0·49, SE_{unknown} = 0·08; $S_{\text{wild-caught}}$ = 0·85, $SE_{\text{wild-caught}}$ = 0·02) suggested that wild dogs of unknown sex and wild-caught origin had a lower survival, and females a higher survival, relative to the overall estimate.

Aspects of release areas

A second suite of models was developed to assess the potential effects of covariates pertaining to aspects of the individual release sites (Table 2). The top-ranked model contained the factors human population density, fence length and size of release area, but did not show much stronger support than the base model ($\Delta QAIC_c$ = 0·43), carrying 25% of the model weight. Fence length was the only individually significant parameter (Table 3). Substituting the observed values of fence length into the constrained model and back-transforming to survival estimates suggested that increasing fence length reduced survival.

Disease aspects

In a third suite of models, the potential effects of disease and disease management were evaluated (Table 2). Of this model suite, none exceeded the fit of the base model, indicating that none of these covariates influenced survival.

Ecological aspects

The fourth suite of models addressed potential ecological influences (Table 2). The top-ranked model contained the factor prey density but did not show much stronger support than the base model ($\Delta QAIC_c$ = 0·10), carrying 26% of the model weight. Prey density was not individually significant (Table 3).

Aspects of release events

A fifth suite of models was developed to assess the potential effects of covariates pertaining to the circumstances of the individual release events (Table 2). The top-ranked and only model showing stronger support than the base model ($\Delta QAIC_c = 2{\cdot}25$), carrying 48% of the model weight, contained the factors group split, break-out and conservation education. Group split was the only individually significant parameter (Table 3). Back-transformation to survival estimate ($S = 0{\cdot}95$, SE = 0·02) suggested that the occurrence of group splits improved survival.

Aspects of social integration

All wild dogs in the meta-population were kept in pre-release holding (boma) facilities to facilitate bonding, as wild dogs rely on a socially integrated pack for survival and reproduction (Gusset, Slotow & Somers 2006). Therefore, in a sixth suite of models, covariates that potentially influence social integration before release were evaluated (Table 2). The top-ranked and only model showing stronger support than the base model ($\Delta QAIC_c = 3{\cdot}27$), carrying 48% of the model weight, contained the factors time spent together in boma, death, pregnancy, birth, existing pack, single-sex group, age ratio and sex ratio. Two parameters were individually significant: birth and time spent together in boma (Table 3). Back-transformation to survival estimate ($S_{birth} = 0{\cdot}96$, $SE_{birth} = 0{\cdot}02$) suggested that the occurrence of birth while in the boma improved survival. Substituting the observed values of time spent together in boma into the constrained model and back-transforming to survival estimates suggested that increasing boma time improved survival.

Significant covariates

To assess the effective importance of the individually significant covariates in the top-ranked logistic regression models, a last model was developed with these seven parameters (Table 3). Of all time-independent models, this model had the best fit. This implied that these seven covariates indeed most strongly influenced the survival of re-introduced wild dogs and their offspring.

Discussion

The re-introduction of wild dogs into several small conservation areas in South Africa has been successful, with high survival rates of the released animals and their offspring (Fig. 1) and with offspring produced at all release sites. The initial target size of nine packs for the meta-population (Mills *et al.* 1998) was achieved in just half of the allotted 10 years (Lindsey *et al.* 2005a). Another achievement of this conservation strategy was a better understanding of what makes re-introductions successful, although factors constraining wild dog re-introductions in South Africa probably do not fully encompass the set of limiting factors that operate in large protected areas elsewhere in Africa.

Understanding and mitigating previous causes of population decline should be a prerequisite for considering a re-introduction (Kleiman, Stanley Price & Beck 1994; Fischer & Lindenmayer 2000). The eradication of carnivores is often the result of conflicts with humans, and the failure of past wild dog re-introductions can be attributed, in part, to human persecution of the released animals (Childes 1988; Van Heerden 1993; Scheepers & Venzke 1995; Kock *et al.* 1999; Davies & Du Toit 2004). Deliberate and accidental killing by people also accounts for the majority of fatalities in the meta-population. Interestingly, however, the existence of conservation education programmes did not influence the survival of re-introduced wild dogs. There is a general understanding that re-introduction success, especially of carnivores, is strongly dependent on public support (Yalden 1993; Reading & Clark 1996; Breitenmoser *et al.* 2001), yet the empirical evidence for this claim is equivocal (Beck *et al.* 1994; Wolf *et al.* 1996; Reading *et al.* 1997). A critical appraisal of the available evidence may help resolve this controversy.

A probable reason why re-introductions have been successful despite negative public perceptions (Lindsey, Du Toit & Mills 2005; Gusset 2006) is that in South Africa conservation areas are generally fenced, with fences being regularly patrolled. Perimeter fences can at least partly prevent wild dogs from straying onto neighbouring land and thus coming into potentially fatal contact with humans. Accordingly, fence length, as our surrogate for the level of fence maintenance (i.e. the longer the fence, the less likely it is to be maintained), was negatively related to the survival of re-introduced wild dogs, with larger release areas being enclosed by longer fences and having more recorded break-outs. Furthermore, the only re-introduction site that was not entirely fenced experienced the most problems with snaring of wild dogs. While fencing is expensive (Lindsey *et al.* 2005a) and may not be the most desirable conservation measure, our interpretation of the results suggests that fences can be scientifically justified. This holds until measures are implemented to mitigate human-related mortalities of wild dogs outside protected areas.

Another important aspect in re-introductions is habitat quality and quantity at the release site (Griffith *et al.* 1989; Wolf *et al.* 1996, 1998). Our data and those from a previous assessment of the ecological suitability of wild dog re-introduction sites (Lindsey *et al.* 2004a) suggest that, within the range of parameter values examined (Table 2), these habitat requirements are fulfilled for a suite of conservation areas in South Africa. However, some conservation areas containing wild dogs periodically restock their prey base, at considerable costs (Lindsey *et al.* 2005a). These additional expenses can, at least partly, be made up with financial benefits derived from wild dog-based ecotourism (Lindsey *et al.* 2005b; Gusset 2006). Accordingly, Beck *et al.* (1994) found that the availability of long-term funds is a strong determinant of re-introduction success, also to sustain the monitoring efforts indispensable for evaluating conservation measures (see below).

Predation on released animals can hamper re-introduction attempts (Fischer & Lindenmayer 2000), and mortality inflicted by lions *Panthera leo* has been invoked to account for past failures to re-introduce wild dogs (Scheepers & Venzke 1995). Lion-caused mortalities have also been recorded in the meta-population; however, within the range of parameter values examined (Table 2), lion and spotted hyaena *Crocuta crocuta* densities did not influence the survival of re-introduced wild dogs. This was not because of the existence of predator control measures, which has been found to enhance re-introduction success in other species (Fischer & Lindenmayer 2000). Controversial interventions such as predator control may be justified only if their positive effects can be unambiguously demonstrated.

A hazard to re-introductions can be disease, with disease outbreaks having thwarted past re-introduction attempts in wild dogs (Scheepers & Venzke 1995). In the meta-population, canine distemper and rabies transmitted from black-backed jackals *Canis mesomelas* (Hofmeyr *et al*. 2000) were the only natural causes wiping out two entire re-introduced subpopulations, while timely vaccination attenuated a further rabies outbreak (Hofmeyr *et al*. 2004). However, the presence of infected sympatric wild carnivores or domestic dogs *Canis familiaris*, and the existence of rabies vaccination programmes for either domestic or wild dogs, did not influence the survival of re-introduced wild dogs. This illustrates one of the limitations of evaluating conservation efforts in endangered species, as a proper control for the intervention in question is often absent.

Maintaining animals in a boma for a period of time has been shown to increase re-introduction success in various species (Fischer & Lindenmayer 2000), which has been corroborated by our study. For carnivores in general, the underlying mechanisms discussed are to familiarize the animals with the release area and to break homing tendencies (Linnell *et al*. 1997; Miller *et al*. 1999). Our data suggest that an additional function of keeping group-living animals together in a boma before release is social integration (Kleiman 1989). The positive effect of the occurrence of birth while in the boma underlines this suggestion, as reproduction can be viewed as the result of successful bonding (Gusset, Slotow & Somers 2006), with packs reportedly splitting into single-sex groups in past wild dog re-introduction attempts that have failed (Childes 1988; Kock *et al*. 1999). A probable reason why pack splits improved survival in our study is that most of the splits observed in the meta-population (75%) were pack fissions. Most packs that underwent fission after release (67%) gave birth in the boma; these packs were invariably kept in a boma for longer because of the newborn pups, which may explain the positive relationship between boma time and survival. These findings suggest a link between successful bonding, occurrence of birth in boma and pack fission after release, resulting in the benefits derived from an increased number of packs in a subpopulation (Gusset 2006). Building boma facilities and maintaining wild dogs in a boma is costly (Lindsey *et al*. 2005a) but our interpretation of the results suggests that these expenses can be scientifically justified.

Wild-caught animals generally fare better in re-introductions (Griffith *et al*. 1989; Ginsberg 1994; Fischer & Lindenmayer 2000) and past failures to re-introduce wild dogs have been linked to the release of captive-bred animals (Childes 1988; Scheepers & Venzke 1995). However, wild dogs bred or raised in captivity can be used for re-introduction as well, if necessary, when first bonded with wild-caught individuals in a boma (Gusset, Slotow & Somers 2006). A probable reason why wild-caught animals in our study had a lower survival is related to most pups (64%) being produced by wild-caught parents, with pups having lower survival rates than yearlings and adults (Fig. 1). This would also explain why wild dogs of unknown sex and males had a lower survival, as these were pups that often died before they could be sexed, with a male bias (55%) in the production of pups.

CONCLUSIONS

In our case study, the determinants of re-introduction success can be reduced to two factors relevant for management, suggesting that wild dog re-introductions should be attempted with socially integrated animals that are released into securely fenced areas, unless measures are implemented to mitigate human-related mortalities outside protected areas. These aspects are therefore likely to be a productive focus of future conservation research and management, together with continued monitoring to elucidate further indicators of re-introduction success. In this regard, behavioural monitoring becomes essential both pre- and post-release, for example to identify and remove individuals that interfere with the socialization process (Van Dyk & Slotow 2003; Gusset, Slotow & Somers 2006).

Our study highlights the merit of systematic review of the available evidence (Pullin & Stewart 2006), thereby maximizing both the impact of scientific findings upon conservation practice and the efficiency of limited conservation funding. Making the most of the available evidence provides a foundation not only for informed decision-making but also for communicating policy to a wider public, especially if management actions are controversial (e.g. allocation of limited funding, fencing, vaccination and predator control). Furthermore, as demonstrated here, such evaluations can help integrate expert opinions into a scientific framework, thereby recognizing the importance of experience-based knowledge for conservation (Fazey *et al*. 2006).

Evaluating conservation efforts, however, is generally hampered by a lack of monitoring and documentation (Nichols & Williams 2006). We thus encourage long-term monitoring of re-introduced animals and effects of management practices, whereby monitoring should be targeted at disentangling competing hypotheses regarding which management actions are likely to be most effective in achieving conservation goals. We also urge the authorities in charge to disseminate their findings and suggest integrating guidelines and mechanisms for regular evaluations into endangered species recovery programmes. Without monitoring and evaluation, the possibility of adaptive management is severely limited.

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