Factors affecting the success of artificial pack formation in an endangered, social carnivore: the African wild dog

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Abstract

Social integration is an important factor when reintroducing group-living species, but examples of the formation of social groups before reintroduction are largely lacking. African wild dogs (*Lycaon pictus*) are endangered, and reintroductions have become a routine part of range expansion in South Africa. Wild dogs form packs that are essential to their reproduction and survival, and artificial pack formation is often required before reintroduction. We examined the proximate (i.e. social integration) and ultimate (i.e. reproduction) success of 43 artificial pack formation attempts in the South African managed metapopulation, between 1995 and 2018. The top (and dominant) model for proximate success included an interaction between total group size and an initial separation fence. Larger groups took longer to integrate, irrespective of initial separation, whereas smaller groups brought together immediately integrated faster than those that were initially separated. The top models for ultimate success included an interaction between the proportion of males and number of days spent in the pre-release enclosure, the total number of days in the enclosure, and an interaction between the proportion of captive-sourced individuals and the total number of days in the enclosure. Ultimate success increased when packs spent less time in the enclosure, especially if those packs has a low proportion of males (i.e. female biased) or included > 25% captive-sourced individuals. Neither the size of the artificially created pack or the season in which the pack was released affect ultimate success. The success of social integration and reproductive success of artificially formed packs in this study was higher than for natural pack formations. We provide guidelines for optimising future artificial pack formation in wild dogs for reintroduction success. Our results serve as an example of the practical importance of social behaviour in successfully implementing conservation measures for group-living species.

Keywords group formation, *Lycaon pictus*, pre-release enclosure, separation, social integration, reproduction

Introduction

Animal translocations and reintroductions have become widespread and effective conservation tools (Seddon *et al.*, 2007). The main factors to consider when reintroducing animals include the selection of a suitable release site, a suitable founder population, and removing the original cause of local extirpation (Fischer & Lindenmayer, 2000). However, when it comes to reintroducing group-living species, there is the additional consideration of social behaviour (Somers & Gusset, 2009). Although the IUCN's Species Survival Commission Reintroduction Specialist Group provides universal standards and guidelines for reintroductions (IUCN/SSC, 1998; Seddon *et al.*, 2007; IUCN/SSC, 2013), examples of reintroducing social groups are largely lacking. Furthermore, the importance of social structure is noted, but no advice is provided regarding the creation of viable social groups for reintroductions (Soorae, 2008; 2010; 2011; 2013). It is suggested that holding carnivores before reintroduction helps to break their homing tendencies, and allows acclimatisation (Linnell *et al.*, 1997; Miller *et al.*, 1999; Briers-Louw *et al.*, 2019). But, for group-living carnivores, this is also an important time for social integration when artificial social groups are being formed (Gusset *et al.*, 2006). Despite understanding the importance of social behaviour when reintroducing animals, guidelines are unavailable for managers implementing reintroductions of social species. Consequently, many decisions regarding group reintroductions are based on personal knowledge and experience, and the success of such an approach is variable.

African wild dogs (*Lycaon pictus*) were historically distributed throughout sub-Saharan Africa (Creel & Creel, 1998), but they have since disappeared from much of their historical range and, as a result, are listed as Endangered on the IUCN Red List of Threatened Species (Woodroffe & Sillero-Zubiri, 2012). Wild dogs display a complex social structure, forming packs with a nearly obligate cooperative breeding system (Creel & Creel, 2002). Thus, they rely on being part of a socially integrated pack for survival (Gusset *et al.*, 2006) and, in general, larger packs tend to be better at hunting, raising pups, and avoiding threats (Courchamp & Macdonald, 2001; Creel & Creel, 2002; Buettner *et al.*, 2007; Rasmussen *et al.*, 2008; Davies *et al.*, 2016). Within South Africa, small and isolated populations are managed collectively as a metapopulation (Davies-Mostert *et al.*, 2009). This involves the reintroduction of wild dogs through the translocation of a single-sex group (usually siblings) to a release site, joining them with an unrelated opposite-sex group, and ultimately releasing them together as a newly formed pack (Gusset, 2010). This approach mimics natural dispersal processes (Creel & Creel, 2002) as, most often, the groups used in this study comprise individuals identified as dispersing and searching for mates. The managed metapopulation approach is required in South Africa, where no sufficiently large contiguous patches of suitable habitat remain aside from Kruger National Park, and it has been successful in increasing the wild dog population since its implementation in 1998 (Davies-Mostert *et al.*, 2015).

Wild dogs disperse from their natal pack (primary dispersal) during their first year of sexual maturity (i.e. two to three years old (McNutt, 1996; Davies-Mostert *et al.*, 2015)) in search of unrelated opposite-sex dispersal groups with which to form a new pack. Although not always the case (Davies-Mostert *et al.*, 2015), males tend to disperse in larger groups than females (average of four individuals compared to an average of two for females (McNutt, 1996; Creel & Creel, 2002)) and, when dispersal groups meet, aggression can occur within the sexes due to an unestablished dominance hierarchy (Creel *et al.*, 1997a). The creation of social bonds during this time is crucial for the formation of a stable and breeding pack (McCreery, 2000). Furthermore, the associations between dispersing same-sex siblings are strong, and the presence of same-sex unrelated individuals may impede pack formation (de Villiers *et al.*, 2003).

During artificial pack formation for reintroduction, wild dogs are kept in a pre-release enclosure to facilitate social integration of the two unrelated, opposite-sex groups, before release into the new area (Gusset *et al.*, 2006). Time spent together in the pre-release enclosure has a positive effect on wild dog survival post-release (Gusset *et al.*, 2010). Additionally, this pre-release enclosure time increases the social integration of wild dogs (Gusset *et al.*, 2008), and wild dogs kept in a pre-release enclosure are more likely to remain together after release (Gusset *et al.*, 2006). However, management records show that wild dogs are kept in different types of pre-release enclosures (one vs two compartments) and for vastly different lengths of time (WAG-SA, 1998–2018; KZN-WAG, 2004–2018). Pre-release resting group dynamics are an indicator of social integration, where a decreasing resting distance to a separating fence indicates successful pack formation when using a dual-compartment enclosure (Potgieter *et al.*, 2015). Pre-release enclosure guidelines for wild dogs are available (Potgieter *et al.*, 2012) but, due to resource constraints, many pre-release enclosures in South Africa comprise only one compartment (i.e. no separating fence), and two groups of wild dogs are often joined within the same enclosure from the start. Resource availability (e.g. pre-release enclosure) is, therefore, an important factor to consider when attempting to form a wild dog pack, especially when financial and human resources are limited. It is essential that we understand the dynamics of artificial pack formation under varying scenarios, to aim for optimal success of pack formation, and to reach conservation goals. Historically, captive-sourced wild dogs have also been used in reintroductions, but this was only successful when captive individuals were joined with wild-sourced individuals before release (Frantzen *et al.*, 2001; Gusset *et al.*, 2010). Although wild dog reintroductions have been relatively successful in South Africa (Gusset *et al.*, 2010; Davies-Mostert *et al.*, 2015), and the importance of social integration is recognised (Gusset *et al.*, 2006), no formal assessment regarding the factors affecting artificial pack formation, and ultimate future reproductive success, has been undertaken.

To address this knowledge gap, we collated data on artificial pack formation attempts with wild dogs in South Africa over the past 23 years (1995–2018), with the aim of investigating the factors affecting the proximate (i.e. social integration) and ultimate (i.e. reproduction) success of artificial pack formation. The relatedness of same-sex individuals affects social integration (de Villiers *et al.*, 2003;

Gusset *et al.*, 2008). Therefore, we predicted that a male-biased sex ratio (to mimic natural dispersal (McNutt, 1996; Creel & Creel, 2002)) and a low proportion of unrelated same-sex individuals, would positively affect proximate success by decreasing the time taken for social integration. Because larger packs are generally more successful than smaller ones (Courchamp & Macdonald, 2001; Buettner *et al.*, 2007; Davies *et al.*, 2016), we also predicted that total group size would affect ultimate success, where larger groups would improve the likelihood of reproduction after release.

Methods

Data collection

We collated data on the protocols followed, and the outcomes of artificial pack formations in wild dogs from the Wild Dog Managed Metapopulation Compendium (Potgieter *et al.*, 2012), and minutes of meetings of the Wild Dog Advisory Group of South Africa (WAG-SA, 1998–2018) and the KwaZulu-Natal Wild Dog Advisory Group (KZN-WAG, 2004–2018). Biannual or quarterly WAG meetings record data on the demographics, translocations, and reintroductions of all wild dogs in South Africa. We extracted information recorded from individual reserve reports regarding artificial pack formations. In instances where details were missing, we made follow-up communications with individual managers, researchers, and wildlife monitors. We were able to extract sufficient data for 43 separate artificial pack formation attempts over 23 years; that is, from the first attempted artificial pack formation recorded to the most recent (1995–2018; Supplementary material Table S1). Of these events, 37 resulted in the formation and release of a pack. For each successful artificial pack formation attempt, we recorded ten factors (Table 1) based on current literature and our subsequent predictions. We defined age classes as pup (< 1 year), yearling (1–2 years), and adult (> 2 years old). If aggression occurred (the occurrence of $\geq$ 1 encounter causing physical injury with visible wounds), we classified it as either inter- (male-female/female-male) or intra-group (male-male/female-female). We calculated the proportion of unrelated same-sex individuals by the number of unrelated same-sex individuals divided by the total number of same-sex individuals. We defined the reproductive season as mating (February–April), denning (May–July), and non-denning (August–January) as per Van den Berghe *et al.* (2012). We considered social integration successful if a dominant pair formed and mixed-sex resting groups were observed within the pre-release enclosure, and counted the days to integration. A dominant pair is identifiable through mating behaviour, over-marking, and mate-guarding (Frame *et al.*, 1979; Creel & Creel, 2002). Spatial relationships mirror the strength of social bonds and, therefore, the social integration between the sexes (McCreery, 2000). Based on McCreery (2000), we defined individuals resting within one adult wild dog length (approximately 90 cm) as resting together, and males and females observed in this manner over the inactive midday period during at least one scan sample, to be resting together. When considering events where wild dogs were initially separated, we used the metric of resting distance to the partitioning fence (Potgieter *et al.*, 2015). Only packs that were considered socially integrated were released and, finally, we considered reproduction successful if a female gave birth in the first breeding season after release.

Table 1. Factors investigated for their potential effect on the proximate and/or ultimate success (see text for details) of artificial pack formation in African wild dogs.

Parameter	**Parameter value**	
	Mean ± SE	**Range**
Total group size	6.72 ± 0.47	2–16
Proportion of males	0.52 ± 0.02	0.30–0.80
Proportion of adults	0.92 ± 0.03	0.40–1.00
Proportion of unrelated males	0.07 ± 0.03	0.00–0.80
Proportion of unrelated females	0.06 ± 0.03	0.00–1.00
Proportion of captive-sourced animals	0.15 ± 0.04	0.00–1.00
Total number of days in pre-enclosure	92.72 ± 19.91	4–629
	Parameter description	
Initial separation	Separation (n = 20), no separation (n = 23)	
Aggression	Inter-group (n = 9), intra-group (n = 2), none (n = 32)	
Reproductive season at release	Mating (n = 8), denning (n = 17), non-denning (n = 18)	

Statistical analysis

Before analysis, we assessed collinearity between explanatory variables using variance inflation factors and Spearman rank correlation tests (Zar, 2010). For proximate success, we found multicollinearity between the proportion of adults and the proportion of unrelated males, and so removed the proportion of adults. We made this decision as Gusset *et al.* (2008) found no effect of age structure on artificial pack formation, and same-sex unrelated individuals are more likely to affect social integration (de Villiers *et al.*, 2003). For ultimate success, we also removed the proportion of adults, as well as separation fence and aggression, due to collinearity with the proportion of unrelated males.

To investigate the factors affecting the time taken to integrate socially (proximate success), we created 36 candidate generalised linear models with a Poisson distribution. We set the number of days until social integration within the enclosure as the response variable. We set the total group size (continuous), proportion of males (discrete), proportion of captive-sourced individuals (discrete), initial separation (categorical), aggression (categorical), proportion of unrelated males (discrete), proportion of unrelated females (discrete), and reproductive season at time of joining (categorical), as explanatory variables. Additionally, as social integration is so complex (Gusset *et al.*, 2006), we also included all possible pairwise interactions as explanatory variables. For this analysis, we were only interested in groups that did socially integrate (n = 37), but also had to subset the data further to include only the events where the exact number of days taken to integrate socially was known (n = 23).

To investigate the factors affecting the ultimate success of artificial pack formation, we created a further 28 candidate generalised linear models with a Binomial distribution. We set denning in the first breeding season after release (yes/no) as the response variable. We then set the total group size, the proportion of males, the proportion of captive-sourced individuals, the proportion of unrelated males, the proportion of unrelated females, the reproductive season at the time of release, and total number of days spent in the pre-release enclosure (continuous), as explanatory variables. We also included all possible pairwise interactions as explanatory variables. For this analysis, all packs that were released, and had the potential to breed, were included (n = 29; six packs that were released died (either entire pack or all of one sex) before their first breeding season and two packs were contracepted, and were thus not included).

To identify the best model(s), we used model selection based on Akaike's information criterion adjusted for small sample size (AIC_c), where models with ΔAIC_c values ≤ 2 are considered important (Burnham & Anderson, 2002) and then assessed model fit using R^2. We performed all statistical analyses and created all figures in R (Core Team, 2008) for Windows, using functions in the packages *lme4* (Bates *et al.*, 2014), *MuMIn* (Bartoń, 2013), *rsq* (Zhang, 2018), and *ggplot2* (Wickham, 2009).

Results

Proximate success

In general, the proximate success of artificial pack formation was high, where 37 of 40 (93%) groups socially integrated. The total group size, the presence of an initial separation fence, and the interaction between total group size and separation fence, affected the time to form artificial packs successfully (Table 2). When dealing with smaller group sizes, social integration occurred more quickly when there was no initial separation fence; however, with larger group sizes, social integration occurred more slowly regardless of the presence of an initial separation fence (Fig. 1). Of the three events that did not result in social integration, it was the result of aggression, and one case of all females escaping from the pre-release enclosure before being united with the males.

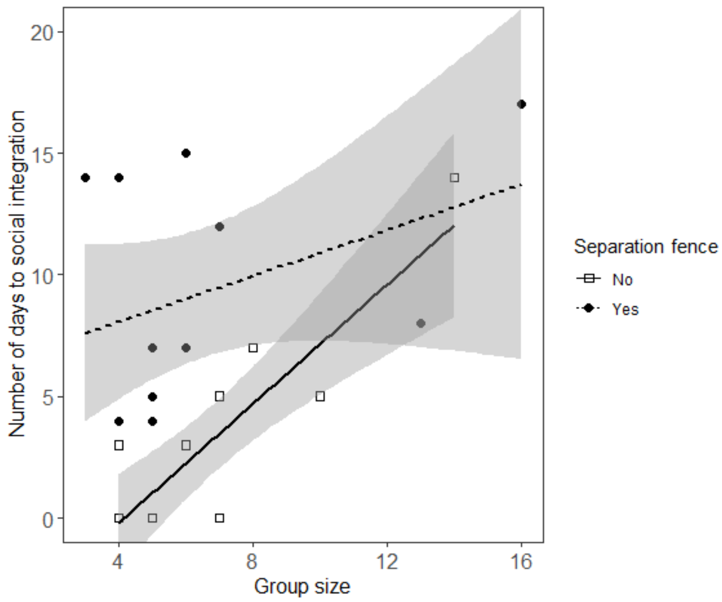

Figure 1. The number of days until social integration in artificially formed African wild dog packs based on total group size and the presence of an initial separation fence. The shaded region represents the 95% confidence interval.

Table 2. The five highest-ranking candidate models used to investigate factors affecting the proximate success of artificial pack formation in African wild dogs. The top model is indicated in bold, where $\Delta AIC_c \leq 2$. For a full table of all 36 candidate models, see supplementary material Table S2.

Rank	Model	Coeff*	Std error*	ΔAIC_c	Weight	R^2
1	**Group size + separation + groups size*separation**	**-0.21**	**0.05**	**0.00**	**> 0.99**	**0.60**
2	Prop unrelated males + separation + prop unrelated males*separation	-0.01	0.18	11.03	< 0.01	0.50
3	Group size + season joined + group size*season joined	0.00	0.01	15.43	< 0.01	0.60
4	Prop captive + separation + prop captive*separation	0.00	0.00	24.81	< 0.01	0.38
5	Separation	2.85	0.52	29.43	< 0.01	0.31

**Refers to model interaction term only*

Ultimate success

The ultimate success of artificial pack formation was also high, with 26 of 29 (90%) packs breeding in the first season post-release. Three models were highlighted as important (Table 3). First, the proportion of males, the total number of days in the pre-release enclosure, and the interaction between the two affected ultimate success. Female-biased packs (i.e. male proportion < 0.5) had a higher probability of reproduction with decreased time in the enclosure (Fig. 2). Male-biased packs had a higher probability of reproduction with increased time in the enclosure; however, as the confidence interval surrounding male-biased packs is large, it is unlikely that this has a strong effect on reproductive success (Fig. 2, Table 3). Second, the total number of days in the enclosure affected ultimate success, where packs were more likely to reproduce with reduced time in the enclosure (Fig. 3). Third, the proportion of captive-sourced individuals, the total number of days in the enclosure, and the interaction between the two affected ultimate success. Packs containing a higher proportion of captive-sourced individuals (i.e. > 0.25) had a higher probability of reproduction with decreased time in the enclosure (Fig. 4). Packs containing no or a small proportion of captive-sourced individuals (i.e. < 0.25) had a higher probability of reproduction with increased time in the enclosure. However, as the confidence interval is large, it is unlikely that this has a strong effect on reproductive success (Fig. 4, Table 3). Size of the newly formed packs and the season of release of the newly formed packs had little effect on the probability of reproduction in the first year post-release.

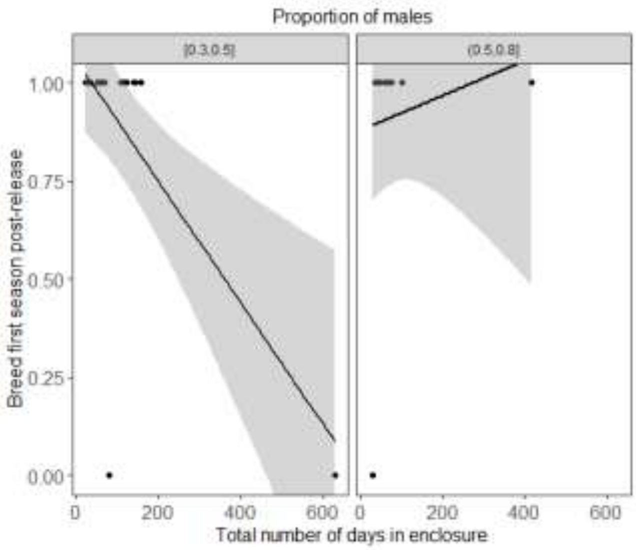

Figure 2. The proportion of artificially formed African wild dog packs reproducing based on the proportion of males and the total number of days in the enclosure pre-release. The shaded region represents the 95% confidence interval.

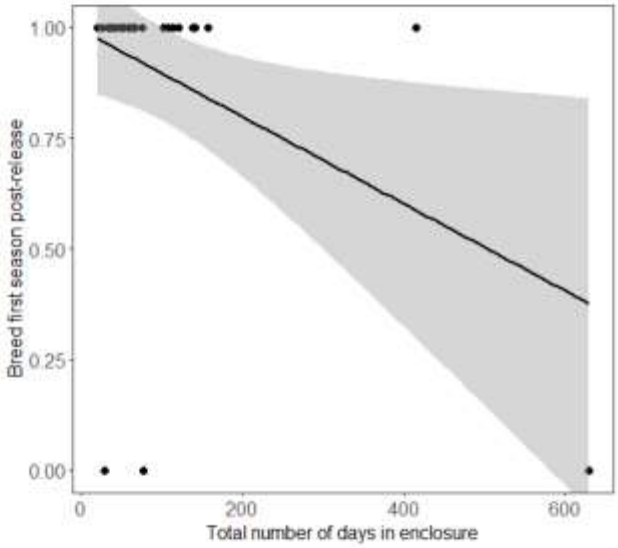

Figure 3. The proportion of artificially formed African wild dog packs reproducing based on the total number of days in the enclosure pre-release. The shaded region represents the 95% confidence interval.

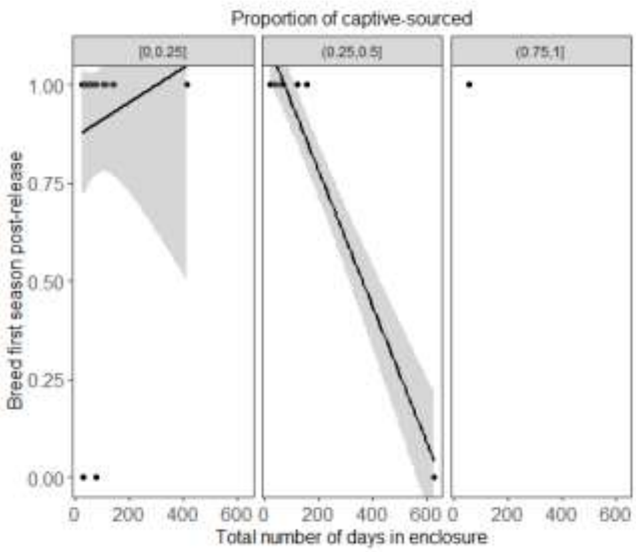

Figure 4. The proportion of artificially formed African wild dog packs reproducing based on the proportion of captive-sourced individuals and the total number of days in the enclosure pre-release. The shaded region represents the 95% confidence interval.

Table 3. The five highest-ranking candidate models used to investigate factors affecting the ultimate success of artificial pack formation in African wild dogs. The top models are indicated in bold, where $\Delta AIC_c \leq 2$. For a full table of all 28 candidate models, see supplementary material Table S3.

Rank	Model	Coeff*	Std error*	ΔAIC_c	Weight	R^2
1	**Total days + prop males + total days*prop males**	**0.25**	**0.63**	**0.00**	**0.22**	**0.44**
2	**Total days**	**0.44**	**652.10**	**0.79**	**0.15**	**0.20**
3	**Prop captive + total days + prop captive*total days**	**-0.03**	**84.72**	**1.93**	**0.08**	**0.35**
4	Season + total days + season*total days	-0.54	652.10	2.24	0.07	0.66
5	Prop males	-11.35	28.40	2.53	0.06	0.03

**Refers to model interaction term only*

Discussion

Holding animals in an enclosure before release may increase reintroduction success (Fischer & Lindenmayer, 2000; Devineau *et al.*, 2011; Briers-Louw *et al.*, 2019). For carnivores, this allows animals to familiarise themselves with their new environment and to break homing tendencies (Linnell *et al.*, 1997; Miller *et al.*, 1999). For group-living carnivores, it is also an important time for social integration in artificially formed groups (Hunter *et al.*, 2007; Gusset *et al.*, 2008). However, the optimal structure and integration of social groups used in the artificial formation of wild dog packs were not fully understood. Here, we defined two levels of success for artificial pack formation in wild dogs; namely pre-release social integration and post-release reproduction. With 37 of 40 events resulting in successful social integration, our results show that artificial pack formation in wild dogs has, in general, been very successful (93%). Gusset *et al.* (2009) calculated a natural pack formation probability of 64%, indicating that artificial pack formation in the managed metapopulation is greater than in free-roaming populations. Our results also show high ultimate success (90%), with 26 of 29 artificially created packs denning in the first breeding season after release, regardless of the season in which they were released. Gusset *et al.* (2009) calculated that the probability of a litter being produced by a newly formed pack (i.e. in the first breeding season after formation) was 33%, increasing to 66% for all subsequent years, indicating that ultimate success of artificially formed packs in the present study was also very high.

Social integration has been highlighted as essential for wild dog reintroduction success (Gusset *et al.*, 2010), and wild dogs kept in a pre-release enclosure are more likely to remain together after release (Gusset *et al.*, 2006). Time spent in a pre-release enclosure increases social integration of wild dogs (Gusset *et al.*, 2008), and has also been found to facilitate the social integration of unrelated lions

(*Panthera leo*) into viable social groups that go on to reproduce (Hunter *et al.*, 2007). Time spent together in a pre-release enclosure also has positive effects on wild dog survival upon release (Gusset *et al.*, 2010), and Gusset *et al.* (2006) suggested a pre-release enclosure period of up to 91 days for wild dogs (based on three case studies). Our results show that larger groups took longer to integrate than smaller ones, and therefore this factor should be considered when planning artificial pack formations. In addition, our analyses revealed that social integration was delayed when an initial separation fence was used with smaller groups but the presence of a separation fence did not affect larger groups. Gusset *et al.* (2006) report that there were insufficient data to conclude whether a separating fence facilitates social integration in wild dogs. Although it has been suggested that dispersal groups naturally come together over several days (Frame *et al.*, 1979), Hofmeyr (2001) suggested that opposite-sex groups should be introduced into the same enclosure immediately. Our results support the suggestion of joining opposite-sex groups immediately. It is suggested that the intrinsically rewarding physical properties of social behaviours, such as grooming and resting together, facilitates pair-bonding (Ågmo *et al.*, 2012). Such an approach would support the idea that groups should be placed together from the start to facilitate social bonding and the formation of a dominant pair. As the establishment of dominance hierarchies is extremely complex (Chase *et al.*, 2002), we propose that larger groups simply require more time to form a dominant pair and construct a hierarchy with more competing individuals.

With regard to ultimate success, packs were less likely to reproduce with increased time spent in the pre-release enclosure, suggesting there may be negative consequences of continuing to hold newly formed packs in captivity after signs of cohesive social integration are observed. Confinement-specific stressors, such as restricted movement, reduced retreat space, and forced proximity to humans, can adversely affect animals in captivity (Morgan & Tromborg, 2007). Although temporary, the pre-release enclosure period is a form of captivity, where the aforementioned stressors exist. Prolonged confinement of wild animals has been shown to cause stress; for example, translocated wild eastern bettongs (*Bettongia gaimardi*) have higher faecal glucocorticoid metabolite concentrations when their release is delayed (Batson *et al.*, 2017). Ultimately, prolonged high levels of glucocorticoids (i.e. chronic stress) can be detrimental to reproduction (Pottinger, 1999). In contrast to the hypothesis that chronic stress causes reproductive suppression, dominant wild dogs have higher basal corticosterone levels than subordinates (Creel *et al.*, 1997a; Creel, 2001), meaning that reproductive suppression in wild dogs is not driven by prolonged glucocorticoid elevation (i.e. chronic stress). However, this evidence relates only to free-roaming and stable packs. In addition to confinement stress, unfamiliar wild dogs brought together in a pre-release enclosure must also construct a dominance hierarchy. During this time, aggression can be severe (Creel *et al.*, 1997a) and individuals have limited space to avoid this aggression. Although capture and handling do not cause chronic stress in wild dogs (Creel *et al.*, 1997b), no physiological data exist regarding the impact of confinement on free-roaming wild dogs, especially groups of unfamiliar wild dogs brought together for artificial pack formation. We suggest that prolonged confinement, coupled with the joining of unknown groups, may cause chronic stress to such a level that it has a subsequent detrimental effect on reproduction. Nevertheless, such research is clearly needed for free-roaming wild dogs in confinement of different durations.

We also show that the pattern of decreased likelihood of reproduction with increased time in the enclosure is highlighted for female-biased packs. The hippocampus in females responds to stress differently to that in males, where females with high levels of oestrogen are especially sensitive (Shors *et al.*, 2001). Female tigers (*Panthera tigris*) are more sensitive to the stress of anthropogenic disturbance than males, resulting in higher faecal glucocorticoid metabolite concentrations (Bhattacharjee *et al.*, 2015). Also, captive female wild dogs have higher faecal cortisol metabolite concentrations than free-roaming females (Van der Weyde *et al.*, 2016). If a pack contains a high proportion of females, then there are more females competing for dominance and aggression can be severe when a dominance hierarchy has not yet been established (Creel *et al.*, 1997a; Creel, 2001). As such, the construction of a dominance hierarchy with more competing individuals may cause higher and prolonged levels of stress in these females. This, compounded with a long confinement period, may amount to chronic stress, which may have a subsequent detrimental effect on reproduction upon release. When packs contain a low proportion of females, there may be less stress in defining dominance amongst females and, thus, with confinement as the only stressor, it may be less likely to have such a detrimental impact on reproduction post-release. We suggest that confinement, coupled with female wild dogs potentially being more susceptible to chronic stress, can lead to female-biased packs being less successful post-release after a long confinement period.

Packs containing only captive-sourced individuals are not successful when it comes to reintroductions (Frantzen *et al.*, 2001). This was considered in subsequent reintroductions, where captive-sourced individuals were only used when joined with wild individuals when forming new packs (Gusset *et al.*, 2010). Some captive-sourced individuals were used in this study, and our results show that, for packs containing more than 25% captive-sourced individuals, their likelihood of reproduction significantly reduces with time spent in the enclosure. We suggest that the low ability of captive-sourced wild dogs to adapt to their environment (e.g. avoid lions, disease immunity) and contribute to the pack (e.g. communal hunting), coupled with the detrimental effect of prolonged confinement on the wild-sourced individuals with which they are joined, leads to packs being less likely to reproduce in their first season post-release.

Contrary to our expectations, total group size did not have a significant effect on ultimate success, at least not in the first breeding season following release. In general, larger packs are more successful hunters (Creel & Creel, 2002; Rasmussen *et al.*, 2008), have higher pup and juvenile survival (Buettner *et al.*, 2007; Davies *et al.*, 2016), select better den sites (Davies *et al.*, 2016), and are better at avoiding threats (Courchamp & Macdonald, 2001). Gusset & Macdonald (2010) reported a mean pack size for the managed metapopulation of 6.2 $\pm$ 3.4 (range = 2–17), similar to the present study (6.6 $\pm$ 0.5, range = 2–16). This is lower than in larger, unmanaged populations (Creel *et al.*, 2004). However, metapopulation reserves tend to have low densities of competitors and high availability of suitable prey

(Davies-Mostert *et al.*, 2009). Consequently, in line with previous research (Gusset *et al.*, 2008; Somers *et al.*, 2008; Gusset & Macdonald, 2010), our results suggest that pack size may not strongly affect the ultimate success of wild dog packs within the managed metapopulation, at least shortly after release.

The factors highlighted as important were not able to strongly predict the ultimate success of packs in this study (refer to model weights in Table 3). This is likely due to large variation in external variables at each site and each year, such as lion density, prey density, and wild dog density. Unfortunately, these data were unavailable for our study, but our results support the notion that external factors are likely to be important when it comes to the ultimate success of reintroductions (i.e. reproduction). Another caveat to note is that although the lineages of the wild dogs involved in our study were known, and relatedness was considered when choosing opposite-sex groups for artificial pack formation, genetic data were not available. We acknowledge the potential effect that genetic diversity and mate choice may have on both proximate and ultimate success, as wild dogs do show inbreeding avoidance (Becker *et al.*, 2012). However, recent genetic evidence pertaining to the last 10 years within the managed metapopulation suggests no inbreeding and high levels of heterozygosity (Tensen et al. *In prep*). We must also acknowledge the small samples sizes retained in our analyses, meaning we must be cautious in our conclusions.

As the first comprehensive study of artificial group formation in a social carnivore, our results provide a robust evaluation of current methods used for wild dog pack formation and provide practical guidelines for optimising the formation of future packs. Currently, only ~600 wild dogs remain in South Africa, ~250 (42%) of which reside in the managed metapopulation (WAG-SA, 2018). As such, optimising actions and outcomes within the conservation strategy of the South African managed metapopulation is of high priority. In addition to providing important information for the reintroduction of wild dogs, our results show that it is possible to socially integrate unrelated individuals of social animals, which has applications for the reintroduction and restoration of many species. Within the Carnivora, this knowledge could be applied to artificial pack formation of endangered dholes (*Cuon alpinus*) and grey wolves (*Canis lupus*). Outside of the Canidae, this could also be applied to creating coalitions of unrelated male cheetahs (*Acinonyx jubatus*) for reintroduction (Marnewick *et al.*, 2009; Boast *et al.*, 2018), as well as adding to the knowledge of creating viable lion prides (Slotow & Hunter, 2009). Our results can also provide a platform for the pair bonding or group formation of primates. In conclusion, our results highlight the necessity to incorporate species' social behaviour into reintroductions, and the subsequent impact on conservation success that it can produce. Ultimately, these results can be used to positively impact wild dog populations, range expansion, and recovery, as well as to stimulate thinking for the reintroduction of other threatened social species in fragmented landscapes, where dispersal corridors are becoming limited due to extensive anthropogenic pressure.

Implications for management

Reducing the number of pre-release enclosure days is vital at sites where resource restrictions mean that enclosures are multi-purpose, and the cost of provisioning wild dogs is high. For example, many protected areas in South Africa use pre-release enclosures for multiple species reintroductions, or for holding animals for game auctions, or temporary veterinary care. In addition to reducing resource costs, limiting the number of days in the pre-release enclosure also increases the probability of pack ultimate success. So, effort must be made to reduce the time packs spend in pre-release enclosures. Our results indicate that a separation fence is not necessary for artificial pack formation in wild dogs, as it delays social integration of small groups and has no effect on large groups. A preliminary study has investigated the use of odour familiarity to increase social integration when two groups of unrelated, opposite-sex wild dogs are joined in one enclosure (Marchal et al. unpublished data). The method involves body rubbing of all individuals while still sedated, before waking together as one group, and preliminary results show rapid social cohesion, where eight out of nine events using this method resulted in rapid social integration (in once instance the females escaped from their enclosure before social integration could occur). We highlight the necessity for pre-release enclosure observations of inter-group social dynamics to assess social integration.

To optimise the process of artificial pack formation, we suggest that smaller groups be given at least five days to integrate socially if in one enclosure, and at least ten days if in a double-compartmented enclosure. For large groups, we suggest that the wild dogs be given at least 14 days to integrate socially, regardless of enclosure type (see decision framework in Supplementary material Figure S1). In order to reduce the stress experience within the pre-release enclosure, we advise that, in accordance with WAG-SA pre-release enclosure guidelines (Potgieter *et al.*, 2012), stressful events (such as feeding days and enclosure checks) be kept regular, as predictable stressful events are less stressful than those occurring irregularly (Bassett & Buchanan-Smith, 2007). We also suggest that when captive-sourced individuals are to be used, they comprise < 25% of the pack. Finally, we caution the long-term placement of packs in enclosures, as it is detrimental to their ultimate success.

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Supplementary material

Table S1. Location and year of each attempted artificial pack formation in African wild dogs included in the study.

Event ID	Site	Province	Year
1	Madikwe Game Reserve	North West	1995
2	Hluhluwe-iMfolozi Park	KwaZulu-Natal	1997
3	Madikwe Game Reserve	North West	1998
4	Madikwe Game Reserve	North West	1998
5	Pilanesberg National Park	North West	1999
6	Venetia Limpopo Nature Reserve	Limpopo	2000
7	Karongwe Game Reserve	Mpumalanga	2000
8	Hluhluwe-iMfolozi Park	KwaZulu-Natal	2000
9	Karongwe Game Reserve	Mpumalanga	2001
10	De Wildt Cheetah and Wildlife Centre	Gauteng	2001
11	Karongwe Game Reserve	Mpumalanga	2001
12	Pilanesberg National Park	North West	2001
13	Marakele National Park	Limpopo	2002
14	Hluhluwe-iMfolozi Park	KwaZulu-Natal	2003
15	Shamwari Game Reserve	Eastern Cape	2003
16	Tswalu Kalahari Reserve	Northern Cape	2004
17	Mkhuze Game Reserve	KwaZulu-Natal	2004
18	Balule Private Game Reserve	Mpumalanga	2005
19	Thanda Private Reserve	KwaZulu-Natal	2006
20	Madikwe Game Reserve	North West	2006
21	Venetia Limpopo Nature Reserve	Limpopo	2006
22	Hluhluwe-iMfolozi Park	KwaZulu-Natal	2006
23	Venetia Limpopo Nature Reserve	Limpopo	2007
24	Limpopo-Lipadi Private Game Reserve	Limpopo	2010
25	Tembe Elephant Park	KwaZulu-Natal	2010
26	Manyoni Private Game Reserve	KwaZulu-Natal	2010
27	Mkhuze Game Reserve	KwaZulu-Natal	2011
28	Hluhluwe-iMfolozi Park	KwaZulu-Natal	2011
29	Khamab Kalahari Reserve	North West	2011
30	Hluhluwe-iMfolozi Park	KwaZulu-Natal	2012
31	Hluhluwe-iMfolozi Park	KwaZulu-Natal	2013
32	Khamab Kalahari Reserve	North West	2014
33	uMphafa Private Nature Reserve	KwaZulu-Natal	2014
34	uMphafa Private Nature Reserve	KwaZulu-Natal	2014
35	Zimanga Private Game Reserve	KwaZulu-Natal	2014
36	Hluhluwe-iMfolozi Park	KwaZulu-Natal	2015
37	Somkhanda Game Reserve	KwaZulu-Natal	2015
38	Blue Canyon Conservancy	Mpumalanga	2016
39	Balule Private Game Reserve	Mpumalanga	2016
40	Tswalu Kalahari Reserve	Northern Cape	2017
41	Mkhuze Game Reserve	KwaZulu-Natal	2017
42	Kruger National Park	Mpumalanga	2017
43	Hluhluwe-iMfolozi Park	KwaZulu-Natal	2018

Table S2. The 36 candidate models used to investigate factors affecting proximate success of artificial pack formation in African wild dogs. The top model is indicated in bold, where $\Delta AIC_c \leq 2$.

Rank	Model	Coeff*	Std error*	ΔAIC_c	Weight
1	**Group size + Separation + Group size*Separation**	**-0.21**	**0.05**	**0.00**	**>0.99**
2	Separation + Prop unrelated males + Separation*Prop unrelated males	-0.01	0.18	11.03	<0.01
3	Group size + Season joined + Group size*Season joined	0.00	0.01	15.43	<0.01
4	Prop captive + Separation + Prop captive *Separation	0.00	0.00	24.81	<0.01
5	Separation	2.85	0.52	29.43	<0.01
6	Separation + Aggression + Separation*Aggression	0.00	0.00	30.31	<0.01
7	Separation + Prop unrelated females + Separation*Prop unrelated females	0.00	0.00	31.57	<0.01
8	Separation + Season joined + Separation*Season joined	0.00	0.00	32.21	<0.01
9	Prop males + Separation + Prop males*Separation	0.00	0.00	33.23	<0.01
10	Group size + Prop captive + Group size*Prop captive	0.00	0.00	33.54	<0.01
11	Prop captive + Aggression + Prop captive *Aggression	0.00	0.00	35.41	<0.01
12	Group size + Prop males + Group size*Prop males	0.00	0.00	36.32	<0.01
13	Prop captive	0.00	0.00	39.17	<0.01
14	Prop captive + Prop unrelated males + Prop captive *Prop unrelated males	0.00	0.00	39.62	<0.01
15	Prop captive + Prop unrelated females + Prop captive *Prop unrelated females	0.00	0.00	39.71	<0.01
16	Prop males + Prop captive + Prop males*Prop captive	0.00	0.00	42.17	<0.01
17	Prop captive + Season joined + Prop captive *Season joined	0.00	0.00	43.64	<0.01
18	Group size	0.00	0.00	45.72	<0.01
19	Group size + Prop unrelated females + Group size*Prop unrelated females	0.00	0.00	46.62	<0.01
20	Group size + Aggression + Group size*Aggression	0.00	0.00	47.90	<0.01
21	Prop unrelated females*Season joined + Prop unrelated females + Season joined	0.00	0.00	48.46	<0.01
22	Prop unrelated males + Season joined + Prop unrelated males*Season joined	0.00	0.00	49.22	<0.01
23	Group size*Prop unrelated males	0.00	0.00	49.25	<0.01
24	Season joined	0.00	0.00	53.74	<0.01
25	Prop unrelated males + Prop unrelated females + Prop unrelated males*Prop unrelated females	0.00	0.00	54.88	<0.01
26	Aggression + Season joined + Aggression*Season joined	0.00	0.00	55.18	<0.01

27	Prop males + Prop unrelated females + Prop males*Prop unrelated females	0.00	0.00	56.19	<0.01
28	Aggression + Prop unrelated males + Aggression*Prop unrelated males	0.00	0.00	56.25	<0.01
29	Aggression + Prop unrelated females + Aggression*Prop unrelated females	0.00	0.00	56.71	<0.01
30	Aggression	0.00	0.00	56.97	<0.01
31	Prop unrelated males	0.00	0.00	57.47	<0.01
32	Prop males + Prop unrelated males + Prop males*Prop unrelated males	0.00	0.00	57.83	<0.01
33	Prop unrelated females	0.00	0.00	57.84	<0.01
34	Prop males	0.00	0.00	58.62	<0.01
35	Prop males + Aggression + Prop males*Aggression	0.00	0.00	59.61	<0.01
36	Prop males + Season joined + Prop males*Season joined	0.00	0.00	60.41	<0.01

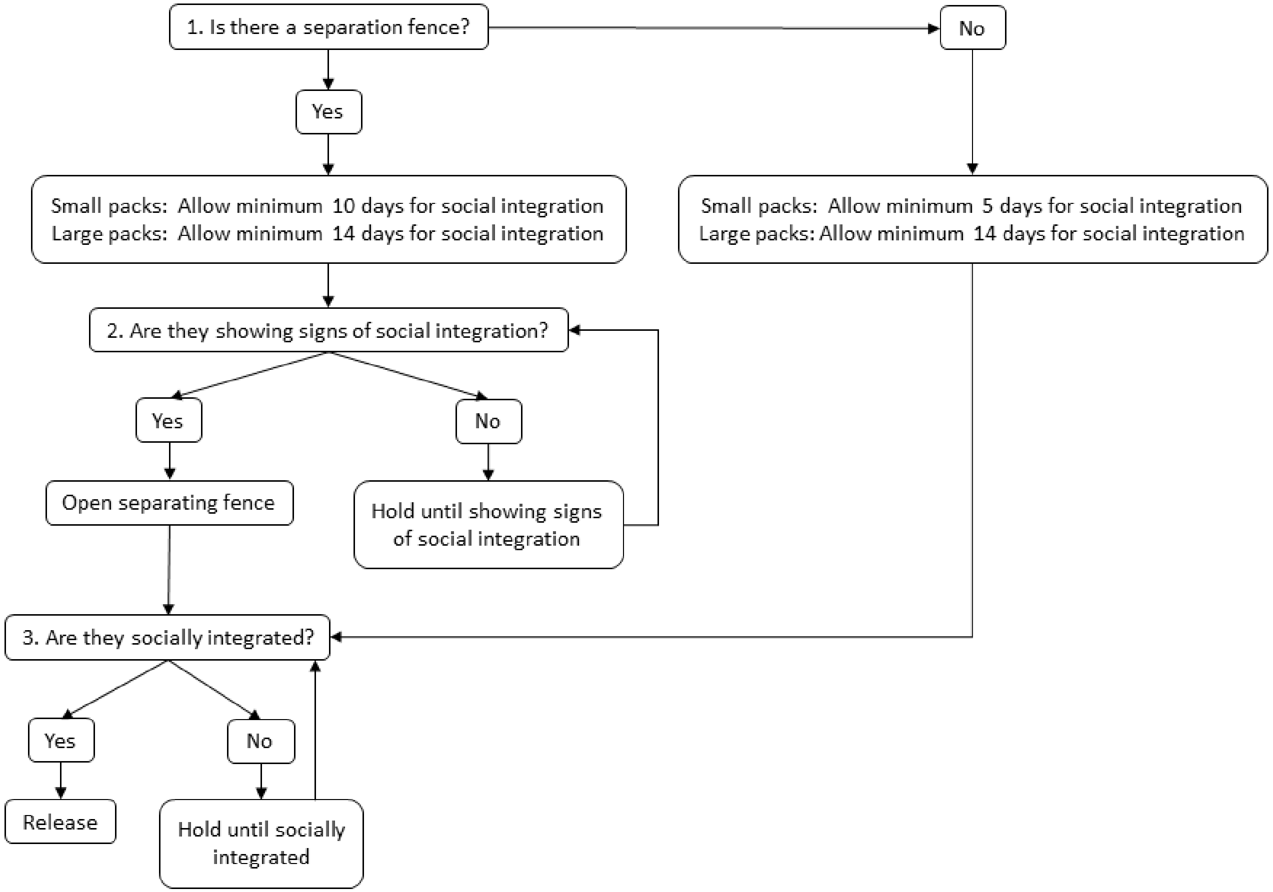
**Refers to model interaction term only*

Table S3. The 28 candidate models used to investigate factors affecting ultimate success of artificial pack formation in African wild dogs. The top models are indicated in bold, where $\Delta AIC_c \leq 2$.

Rank	Model	Coeff*	Std error*	ΔAIC_c	Weight
1	**Prop males + Total days + Prop males*Total days**	**0.25**	**0.63**	**0.00**	**0.22**
2	**Total days**	**0.44**	**652.10**	**0.79**	**0.15**
3	**Prop captive + Total days + Prop captive*Total days**	**-0.03**	**84.72**	**1.93**	**0.08**
4	Season released + Total days + Season released*Total days	-0.54	652.10	2.24	0.07
5	Prop males	-11.35	28.40	2.53	0.06
6	Prop unrelated males + Total days + Prop unrelated males*Total days	-0.01	9.87	2.85	0.05
7	Prop unrelated females	5.57	16310.00	2.94	0.05
8	Prop males + Prop unrelated males + Prop males*Prop unrelated males	37.05	36900.00	3.31	0.04
9	Prop unrelated males	-14.01	17630.00	3.40	0.04
10	Prop captive	23.15	18440.00	3.51	0.04
11	Group size	-0.07	102.60	3.58	0.04
12	Group size + Prop males + Group size*Prop males	0.22	1.35	3.60	0.04
13	Group size + Total days + Group size*Total days	0.00	0.00	3.89	0.03
14	Group size + Prop captive + Group size*Prop captive	-1.15	1535.00	4.87	0.02
15	Prop unrelated males + Prop unrelated females + Prop unrelated males*Prop unrelated females	0.00	0.00	5.28	0.02
16	Prop unrelated females + Total days + Prop unrelated females*Total days	0.00	221.30	5.55	0.01
17	Season released	17.21	20890.00	5.84	0.01
18	Prop captive + Prop unrelated males + Prop captive*Prop unrelated males	-1.17	2510.00	6.56	0.01
19	Prop males + Prop captive + Prop males*Prop captive	0.04	2.78	7.16	0.01
20	Group size + Prop unrelated males + Group size*Prop unrelated males	0.08	180.90	7.18	0.01
21	Prop males + Prop unrelated females + Prop males*Prop unrelated females	-1.63	10090.00	7.28	0.01
22	Prop captive + Prop unrelated females + Prop captive*Prop unrelated females	0.16	17170.00	7.96	<0.01
23	Group size + Prop unrelated females + Group size*Prop unrelated females	0.00	744.50	8.10	<0.01
24	Prop males + Season released + Prop males*Season released	0.49	2514.00	8.96	<0.01
25	Group size + Season released + Group size*Season released	-0.02	102.60	10.38	<0.01
26	Prop unrelated males + Season released + Prop unrelated males*Season released	0.00	0.00	10.64	<0.01

27	Prop unrelated females + Season released + Prop unrelated females*Season released	0.00	0.00	10.88	<0.01
28	Prop captive + Season released + Prop captive*Season released	0.02	696.80	13.42	<0.01

**Refers to model interaction term only*



2. Signs of social integration

Both male and female groups are resting within one dog body length of the separating fence

(Potgieter *et al.* 2015)

3. Social integration

An alpha pair has formed

i. A male-female pair resting together, often separate from the rest of the group
ii. The male is mate-guarding the female (i.e. chasing other males away from her)
iii. One is over-marking the others urine/faeces.
iv. Mating is observed

(Creel & Creel 2002; Frame *et al.* 1979)

There are mixed-sex resting groups

i. Resting groups containing both sexes over the midday inactive period, for four days in a row.
ii. Dogs are considered resting together if they are within one dog body length apart

(McCreery 2000; Marchal *et al.* unpublished)

NB. Keep disturbing events (e.g. feeding/enclosure checks) regular and predictable to reduce stress

Figure S1. Decision-making framework for optimising the pre-release enclosure social integration process for African wild dog reintroductions.