12

The Role of Social Behaviour in Carnivore Reintroductions

Michael J. Somers[1] *and Markus Gusset*[2]

[1]Centre for Wildlife Management, Centre for Invasion Biology, University of Pretoria
[2]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford

Summary

Reintroductions are becoming increasingly important in conservation management, particularly for large carnivores. Despite an increase in our understanding of carnivore social behaviour, wildlife managers often disregard this knowledge when reintroducing animals—largely owing to behavioural ecology and reintroduction biology rarely being unified in the literature or in graduate conservation management programmes. Here, we combine these two disciplines and outline the importance of considering aspects of social behaviour when reintroducing large carnivores. We identify two time periods of particular relevance: the time in temporary captivity before release and the period immediately after release. Prior to release, group composition of the animals to be released is important to promote social compatibility. After release, Allee effects arising from difficulty in finding suitable mates emerge as one of the most important constraints in some large-carnivore reintroduction programmes. In our view, incorporating considerations of social behaviour in conservation management would increase the efficiency and effectiveness of costly (carnivore) reintroduction programmes.

Reintroduction of Top-Order Predators Edited by Matt W. Hayward and Michael J. Somers
 ISBN: 978-1-405-17680-4

Introduction

Reintroductions are becoming increasingly important in conservation management, particularly for large carnivores (Reading & Clark, 1996; Breitenmoser *et al.*, 2001; Hayward & Somers, this volume). There has also been a series of recent works on bridging the gap between behavioural research and conservation management (Caro & Durant, 1995; Curio, 1996; Clemmons & Buchholz, 1997; Caro, 1998, 1999, 2007; Martin, 1998; Sutherland, 1998; Anthony & Blumstein, 2000; Gosling & Sutherland, 2000; Festa-Bianchet & Apollonio, 2003; Blumstein & Fernández-Juricic, 2004; Linklater, 2004; Buchholz, 2007; Angeloni *et al.*, 2008). Although the ultimate aims of conservation biology and behavioural ecology are converging, as proponents of both disciplines share the common interest of conserving wildlife (Martin, 1998), the end products do not show this yet (Angeloni *et al.*, 2008). Despite an increase in our understanding of social behaviour, wildlife managers often disregard this knowledge when reintroducing animals. The difference in perspective and approach persists as a mismatch between conservation needs and research practice in behavioural ecology (Caro, 2007). This mismatch perhaps stems from behavioural ecologists having historically focused on basic research, and on ultimate rather than proximate questions, while conservation biologists have focused mostly on applied questions (Linklater, 2004).

Reintroductions have generally proved to be problematic and prone to failure for a multitude of biological and non-biological reasons (i.e. technical, organizational, valuational and even legal) (Fischer & Lindenmayer, 2000). Considering these challenges, would a better understanding of the role of social behaviour promote reintroduction success? This question has received surprisingly little attention to date (but see Kleiman, 1989). Here, we discuss some of the aspects that are of particular importance when reintroducing large carnivores from a social behaviour perspective.

State of knowledge

We conducted a literature search using a database comprising 14,071 papers published on carnivores between 1972 and 2008 (available from http://www.carnivoreconservation.org). We used the search string ("social behaviour" or "social behavior") and ("reintroduction" or "re-introduction" or

"translocation"). We received one result only (Schröpfer & Rohde, 1997), indicating that carnivore behavioural ecology and reintroduction biology have rarely been unified in the literature. Similarly, social behaviour often does not feature prominently in graduate conservation management programmes (van Heezik & Seddon, 2005). However, there has been considerable progress in our understanding of carnivore social behaviour over the past four decades. In addition, reintroduction efforts are being increasingly monitored and evaluated (e.g. Hayward *et al.*, 2007b; Gusset *et al.*, 2008a). We thus set out to identify stages of relevance to improve reintroduction programmes for large carnivores with knowledge from social behaviour.

Stages of relevance

The success of any reintroduction attempt depends on two factors, namely establishing and maintaining a population in the release area (Gusset, this volume). For social species, this suggests that founder group composition is likely to determine establishment success, whereas persistence is likely to depend on the formation of new groups to maintain the population's reproductive capacity. Accordingly, we have identified two time periods of particular importance for applying aspects of social behaviour to large-carnivore reintroductions: the time in temporary captivity before release and the period immediately after release.

Pre-release stage

Maintaining animals in a pre-release enclosure for a period of time has been shown to increase reintroduction success in various species (Fischer & Lindenmayer, 2000). This is termed a "soft release". For carnivores in general, the underlying rationale is to familiarize the animals with the release area and to break homing tendencies (Linnell *et al.*, 1997; Miller *et al.*, 1999). There are numerous examples of translocated carnivores returning to the site of capture (Linnell *et al.*, 1997), a problem related to post-release ranging behaviour (see below) that could be partly overcome by keeping animals in a temporary holding facility before release. This was successfully applied when reintroducing felids (Hunter, 1999), including lions, *Panthera leo* (Hunter *et al.*, 2007;

Trinkel *et al.*, 2008; Slotow & Hunter, this volume); canids (Moehrenschlager & Somers, 2004), including grey wolves, *Canis lupus* (Fritts *et al.*, 1997; Bradley *et al.*, 2005; Smith & Bangs, this volume) and African wild dogs, *Lycaon pictus* (Gusset *et al.*, 2006, 2008a; Davies-Mostert *et al.*, this volume); and other social large carnivores (Hayward *et al.*, 2007a).

Additional benefits of keeping social animals together before release may be social integration of animals into new groups (Kleiman, 1989) and reduction of stress (Texeira *et al.*, 2007). For wild dogs, Gusset *et al.* (2006, 2008a) showed that packs kept in a temporary holding facility for bonding before release were more likely to remain intact when set free and had higher individual post-release survival rates. The same seems to be true for reintroduced wolves, as ensuring social integration prevented pack break-ups after release and increased site fidelity (Fritts *et al.*, 1997; Bradley *et al.*, 2005). Similarly, lions established enduring social relationships before release, which ultimately facilitated the formation of cohesive social groups (Hayward *et al.*, 2007a; Hunter *et al.*, 2007; Trinkel *et al.*, 2008) (Table 12.1).

Table 12.1 **The importance of social integration and management measures to promote social compatibility before release in large-carnivore reintroductions.**

Species	Social integration and management measures
Importance of social integration	
African wild dog	Packs more likely to remain intact when set free and higher individual post-release survival rates[a,b]
Grey wolf	Preventing pack break-ups after release and increased site fidelity[c,d]
Lion	Establishing enduring social relationships and ultimately facilitating the formation of cohesive social groups[e,f,g]
Management measures to promote social compatibility	
African wild dog	Manipulation of social relationships (e.g. through temporary or permanent separation of individuals[a]) based on behavioural observations

[a]Gusset *et al.*, 2006; [b]Gusset *et al.*, 2008a; [c]Fritts *et al.*, 1997; [d]Bradley *et al.*, 2005; [e]Hayward *et al.*, 2007b; [f]Hunter *et al.*, 2007; [g]Trinkel *et al.*, 2008.

If there is a lack of cohesion in a group before release, possibly as a result of its artificial creation, the animals are unlikely to become successful breeders after release and may display intensified post-release ranging behaviour. Creating the opportunity to exercise mate selection before release could increase the likelihood that successful reproductive units will form (Kleiman, 1989). Behavioural observations on social interactions are a suitable means to determine individual preferences manifested in the form of group compatibility, which allows the composition of socially integrated groups for release via artificial selection. For example, management manipulation of social relationships (e.g. through temporary or permanent separation of individuals) was successfully applied to promote bonding in wild dogs (Gusset *et al.*, 2006) and other canids (Moehrenschlager & Somers, 2004) (Table 12.1). Another form of manipulating social relationships is assisted replacement of resident male coalitions in reintroduced lions (Trinkel *et al.*, 2008; Slotow & Hunter, this volume).

Supplying suitable free-ranging animals for reintroduction that mirror natural group composition may be difficult (e.g. Gusset *et al.*, 2006; Slotow & Hunter, this volume), thus posing the challenge of using suboptimally composed groups and also captive-bred animals. At times, there may be no option but to reintroduce animals bred or raised in captivity (Christie, this volume). Reintroductions using captive-bred carnivores are significantly less likely to succeed than those using wild-caught individuals (Jule *et al.*, 2008); yet origin did not affect post-release survival rates of wild dogs in this study. Interestingly, wide-ranging carnivores are particularly prone to stress in captivity (more stereotypic pacing and higher infant mortality) (Clubb & Mason, 2003), which may exacerbate the problem of reintroducing wide-ranging carnivores (e.g. Vickery & Mason, 2003; see below). This may necessitate innovative approaches to preparing captive animals destined for reintroduction (e.g. through pre-release training; Kleiman, 1989), such as conditioning wolves to avoid humans (Badridze, 1999; also see Marnewick *et al.*, this volume). Considering cultural transmission of socially learned behaviour in reintroduction efforts may be essential (Ryan, 2006). For example, as a result of their lacking survival skills (particularly hunting and anti-predatory skills), wild dogs bred or raised in captivity are preferably used for release when they are bonded with wild-caught animals in a pre-release enclosure first (Gusset *et al.*, 2006).

Post-release stage

Wide-ranging carnivores are particularly prone to anthropogenic edge effects at the outside boundaries of protected areas (Woodroffe & Ginsberg, 1998). This can have important implications for the establishment of reintroduced carnivores in terms of mortalities inflicted by post-release ranging behaviour (e.g. Woodroffe *et al.*, 2007; Gusset *et al.*, 2008b). Ranging behaviour was successfully restricted by perimeter fencing in reintroduced lions (Hunter, 1999; Hunter *et al.*, 2007; Slotow & Hunter, this volume), wild dogs (Gusset *et al.*, 2008a; Davies-Mostert *et al.*, this volume) and other social large carnivores (Hayward *et al.*, 2007a). Therefore, ranging behaviour appears to be an important factor to consider in carnivore reintroductions both pre- and post-release (Linnell *et al.*, 1997; Woodroffe & Ginsberg, 1998; Clubb & Mason, 2003). It seems that wide-ranging carnivores, such as wolves and wild dogs, are indeed particularly difficult to reintroduce successfully (Moehrenschlager & Somers, 2004).

If the suitability of a patch of habitat is elevated by conspecific presence, further individuals will settle preferentially in an occupied patch, irrespective of whether an alternative patch of equal quality exists (Dobson & Poole, 1998). From a reintroduction perspective, conspecific attraction as an important factor influencing habitat selection could be useful as a conservation tool that can be employed to encourage preferential recolonization of a given area and to restrict post-release ranging behaviour. For example, the lack of conspecific cues outside the release area possibly increased site fidelity in reintroduced wolves (Fritts *et al.*, 1997). Providing conspecific cues by acoustic stimulation through playbacks was demonstrated to attract wild dogs to the calling station (Robbins & McCreery, 2003). Conversely, such cues could possibly be used to discourage animals from recolonizing an undesired area.

The importance of facilitating conspecific interactions for the persistence of (typically small) re-established populations is illustrated by the occurrence of Allee effects (Deredec & Courchamp, 2007). An Allee effect is defined as a reduction in individual fitness with decreasing size of the aggregation unit considered (e.g. population or social group; Stephens *et al.*, 1999). Difficulty in finding suitable mates at low density probably is the most commonly cited mechanism of the Allee effect (Courchamp *et al.*, 1999; Stephens & Sutherland, 1999). For example, a reintroduced wild dog population studied

over a period of 25 years increased only after it was artificially augmented to a critical minimum number of four packs, which simultaneously produced enough unrelated dispersers for successful pack formation events to occur (Somers *et al.*, 2008). Furthermore, a mate-finding Allee effect at low pack number was inferred to account for the initially slow expansion of reintroduced populations of wolves (Hurford *et al.*, 2006) and wild dogs (Gusset *et al.*, unpublished data) (Table 12.2). Interestingly, Hurford *et al.* (2006) found reintroduced wolves spread faster when pair-bonded before dispersal, reiterating the importance of social integration (see above).

As an Allee effect can be generated by a shortage of interactions among conspecifics at low density, the degree of sociality of a species might reflect the degree of severity of the Allee effect to which it is subject. Allee effects can thus have particularly serious impacts on the population dynamics of obligate

Table 12.2 **Observed Allee effects (i.e. a reduction in individual fitness with decreasing size of the aggregation unit considered) and management measures to mitigate Allee effects in large-carnivore reintroductions.**

Species	Allee effects and management measures
Observed Allee effects	
African wild dog	Allee effect arising from difficulty in finding suitable mates at low pack number[a]
Grey wolf	Allee effect arising from difficulty in finding suitable mates at low pack number[b]
African wild dog	Allee effect arising from difficulty in exercising cooperative activities (e.g. cooperative hunting[c]) at small pack size
Management measures to mitigate Allee effects	
African wild dog	Mate-finding Allee effect mitigated by artificially augmenting a population to a critical minimum number of packs[d]
African wild dog	Allee effect at the pack level mitigated by artificially augmenting a pack to a critical minimum number of individuals[e]

[a]Gusset *et al.*, unpublished data; [b]Hurford *et al.*, 2006; [c]Rasmussen *et al.*, 2008; [d]Somers *et al.*, 2008; [e]Graf *et al.*, 2006.

co-operators, which may rely on a minimum group size for survival and reproduction (Courchamp *et al.*, 1999; Stephens & Sutherland, 1999). For wild dog packs to exceed this potential critical threshold and to capitalize on the benefits provided by a larger size (e.g. in terms of cooperative hunting; Rasmussen *et al.*, 2008), Graf *et al.* (2006) demonstrated that packs destined for reintroduction can be artificially augmented before release (Table 12.2).

Conclusions

In any reintroduction attempt involving social species, founder group composition is likely to determine establishment success, whereas persistence is likely to depend on the formation of new groups to maintain the population's reproductive capacity. The outcome of both these stages can be influenced by aspects of the target species' social behaviour, which was confirmed by an evaluation of both short- and long-term reintroduction successes in wild dogs (Gusset, this volume). Monitoring and managing social behaviour both pre- and post-release is thus well worth the effort from a management perspective.

The study by Graf *et al.* (2006) on testing group augmentation theory within a wild dog reintroduction framework provides an example for how theoretical behavioural ecology and practical reintroduction biology can be mutually beneficial. Measures of behavioural ecology can provide information about how release areas differ in quality, and can identify critical resources in theses areas as well as documenting how re-established species contribute to ecosystem functioning (Lindell, 2008). For example, the ecological effectiveness of reintroduced wolves became evident after triggering a behaviourally mediated trophic cascade (Berger & Smith, 2005; Smith & Bangs, this volume). Therefore, in our view, incorporating considerations of social behaviour in conservation management would increase the efficiency and effectiveness of costly (carnivore) reintroduction programmes.

Acknowledgements

We are grateful to two anonymous referees for helpful comments on this chapter.

References

Angeloni, L., Schlaepfer, M.A., Lawler, J.J. & Crooks, K.R. (2008) A reassessment of the interface between conservation and behaviour. *Animal Behaviour* 75, 731–737.

Anthony, L.L. & Blumstein, D.T. (2000) Integrating behaviour into wildlife conservation: The multiple ways that behaviour can reduce N_e. *Biological Conservation* 95, 303–315.

Badridze, J. (1999) Preparing captive-raised wolves for re-introduction, Georgia, Commonwealth of Independent States (C.I.S.). *Re-introduction News* 18, 5–6.

Berger, J. & Smith, D.W. (2005) Restoring functionality in Yellowstone with recovering carnivores: Gains and uncertainties. *Large Carnivores and the Conservation of Biodiversity*. (eds J.C. Ray, K.H. Redford, R.S. Steneck & J. Berger), pp. 100–109. Island Press, Washington.

Blumstein, D.T. & Fernández-Juricic, E. (2004) The emergence of conservation behavior. *Conservation Biology* 18, 1175–1177.

Bradley, E.H., Pletscher, D.H., Bangs, E.E. et al. (2005) Evaluating wolf translocation as a nonlethal method to reduce livestock conflicts in the northwestern United States. *Conservation Biology* 19, 1498–1508.

Breitenmoser, U., Breitenmoser-Würsten, C., Carbyn, L.N. & Funk, S.M. (2001) Assessment of carnivore reintroductions. *Carnivore Conservation*. (eds J.L. Gittleman, S.M. Funk, D. Macdonald & R.K. Wayne), pp. 241–281. Cambridge University Press, Cambridge.

Buchholz, R. (2007) Behavioural biology: An effective and relevant conservation tool. *Trends in Ecology and Evolution* 22, 401–407.

Caro, T. (ed.) (1998) *Behavioral Ecology and Conservation Biology*. Oxford University Press, Oxford.

Caro, T. (1999) The behaviour-conservation interface. *Trends in Ecology and Evolution* 14, 366–369.

Caro, T. (2007) Behavior and conservation: A bridge too far? *Trends in Ecology and Evolution* 22, 394–400.

Caro, T.M. & Durant, S.M. (1995) The importance of behavioral ecology for conservation biology: Examples from Serengeti carnivores. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*. (eds A.R.E. Sinclair & P. Arcese), pp. 451–472. University of Chicago Press, Chicago.

Clemmons, J.R. & Buchholz, R. (eds) (1997) *Behavioral Approaches to Conservation in the Wild*. Cambridge University Press, Cambridge.

Clubb, R. & Mason, G. (2003) Captivity effects on wide-ranging carnivores. *Nature* 425, 473–474.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* 14, 405–410.

Curio, E. (1996) Conservation needs ethology. *Trends in Ecology and Evolution* 11, 260–263.

Deredec, A. & Courchamp, F. (2007) Importance of the Allee effect for reintroductions. *Écoscience* 14, 440–451.

Dobson, A. & Poole, J. (1998) Conspecific aggregation and conservation biology. *Behavioral Ecology and Conservation Biology*. (ed. T. Caro), pp. 193–208. Oxford University Press, Oxford.

Festa-Bianchet, M. & Apollonio, M. (eds) (2003) *Animal Behavior and Wildlife Conservation*. Island Press, Washington.

Fischer, J. & Lindenmayer, D.B. (2000) An assessment of the published results of animal relocations. *Biological Conservation* 96, 1–11.

Fritts, S.H., Bangs, E.E., Fontaine, J.A. et al. (1997) Planning and implementing a reintroduction of wolves to Yellowstone National Park and central Idaho. *Restoration Ecology* 5, 7–27.

Gosling, L.M. & Sutherland, W.J. (eds) (2000) *Behaviour and Conservation*. Cambridge University Press, Cambridge.

Graf, J.A., Gusset, M., Reid, C., Janse van Rensburg, S., Slotow, R. & Somers, M.J. (2006) Evolutionary ecology meets wildlife management: Artificial group augmentation in the re-introduction of endangered African wild dogs (*Lycaon pictus*). *Animal Conservation* 9, 398–403.

Gusset, M., Maddock, A.H., Gunther, G.J. et al. (2008b) Conflicting human interests over the re-introduction of endangered wild dogs in South Africa. *Biodiversity and Conservation* 17, 83–101.

Gusset, M., Ryan, S.J., Hofmeyr, M. et al. (2008a) Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. *Journal of Applied Ecology* 45, 100–108.

Gusset, M., Slotow, R. & Somers, M.J. (2006) Divided we fail: The importance of social integration for the re-introduction of endangered African wild dogs (*Lycaon pictus*). *Journal of Zoology, London* 270, 502–511.

Hayward, M.W., Adendorff, J., O'Brien, J. et al. (2007a) Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. *The Open Conservation Biology Journal* 1, 1–11.

Hayward, M.W., Adendorff, J., O'Brien, J. et al. (2007b) The reintroduction of large carnivores to the Eastern Cape, South Africa: An assessment. *Oryx* 41, 205–214.

Hunter, L. (1999) Large felid restoration: Lessons from the Phinda Resource Reserve, South Africa, 1992–1999. *Re-introduction News* 18, 9–11.

Hunter, L.T.B., Pretorius, K., Carlisle, L.C. et al. (2007) Restoring lions *Panthera leo* to northern KwaZulu-Natal, South Africa: Short-term biological and technical success but equivocal long-term conservation. *Oryx* 41, 196–204.

Hurford, A., Hebblewhite, M. & Lewis, M.A. (2006) A spatially explicit model for an Allee effect: Why wolves recolonize so slowly in Greater Yellowstone. *Theoretical Population Biology* 70, 244–254.

Jule, K.R., Leaver, L.A. & Lea, S.E.G. (2008) The effects of captive experience on reintroduction survival in carnivores: A review and analysis. *Biological Conservation* 141, 355–363.

Kleiman, D.G. (1989) Reintroduction of captive mammals for conservation: Guidelines for reintroducing endangered species into the wild. *BioScience* 39, 152–161.

Lindell, C.A. (2008) The value of animal behavior in evaluations of restoration success. *Restoration Ecology* 16, 197–203.

Linklater, W.L. (2004) Wanted for conservation research: Behavioral ecologists with a broader perspective. *BioScience* 54, 352–360.

Linnell, J.D.C., Aanes, R., Swenson, J.E., Odden, J. & Smith, M.E. (1997) Translocation of carnivores as a method for managing problem animals: A review. *Biodiversity and Conservation* 6, 1245–1257.

Martin, K. (1998) The role of animal behavior studies in wildlife science and management. *Wildlife Society Bulletin* 26, 911–920.

Miller, B., Ralls, K., Reading, R.P., Scott, J.M. & Estes, J. (1999) Biological and technical considerations of carnivore translocation: A review. *Animal Conservation* 2, 59–68.

Moehrenschlager, A. & Somers, M.J. (2004) Canid reintroductions and metapopulation management. *Canids: Foxes, Wolves, Jackals and Dogs: Status Survey and Conservation Action Plan*. (eds C. Sillero-Zubiri, M. Hoffmann & D.W. Macdonald), pp. 289–297. IUCN, Gland, Switzerland.

Rasmussen, G.S.A., Gusset, M., Courchamp, F. & Macdonald, D.W. (2008) Achilles' heel of sociality revealed by energetic poverty trap in cursorial hunters. *American Naturalist* 172, 508–518.

Reading, R.P. & Clark, T.W. (1996) Carnivore reintroductions: An interdisciplinary examination. *Carnivore Behavior, Ecology, and Evolution*. (ed. J.L. Gittleman), pp. 296–336. Cornell University Press, Ithaca.

Robbins, R.L. & McCreery, E.K. (2003) Acoustic stimulation as a tool in African wild dog conservation. *Biological Conservation* 111, 263–267.

Ryan, S.J. (2006) The role of culture in conservation planning for small or endangered populations. *Conservation Biology* 20, 1321–1324.

Schröpfer, R. & Rohde, A. (1997) The integration of a young female in a male pack of European wolves *Canis lupus* L. *Zeitschrift für Säugetierkunde* 62 (Suppl. II), 209–213.

Somers, M.J., Graf, J.A., Szykman, M., Slotow, R. & Gusset, M. (2008) Dynamics of a small re-introduced population of wild dogs over 25 years: Allee effects and the implications of sociality for endangered species' recovery. *Oecologia* 158, 239–247.

Stephens, P.A. & Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* 14, 401–405.

Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos* 87, 185–190.

Sutherland, W.J. (1998) The importance of behavioural studies in conservation biology. *Animal Behaviour* 56, 801–809.

Teixeira, C.P., De Azevedo, C.S., Mendl, M., Cipreste, C.F. & Young, R.J. (2007) Revisiting translocation and reintroduction programmes: The importance of considering stress. *Animal Behaviour* 73, 1–13.

Trinkel, M., Ferguson, N., Reid, A. et al. (2008) Translocating lions into an inbred lion population in the Hluhluwe-iMfolozi Park, South Africa. *Animal Conservation* 11, 138–143.

van Heezik, Y. & Seddon, P.J. (2005) Structure and content of graduate wildlife management and conservation biology programs: An international perspective. *Conservation Biology* 19, 7–14.

Vickery, S.S. & Mason, G.J. (2003) Behavioral persistence in captive bears: Implications for reintroduction. *Ursus* 14, 35–43.

Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126–2128.

Woodroffe, R., Davies-Mostert, H., Ginsberg, J. et al. (2007) Rates and causes of mortality in endangered African wild dogs *Lycaon pictus*: Lessons for management and monitoring. *Oryx* 41, 215–223.