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Abstract: Biodiversity in southern Africa is globally extraordinary but threatened by human activities. Although there are considerable biodiversity conservation initiatives within the region, no one has yet assessed the potential use of large carnivores in such actions. Surrogate approaches have often been suggested as one such way of capitalizing on large carnivores. Here we review the suitability of the large carnivore guild (i.e., brown hyaena *Hyaena hyaena*, spotted hyaena *Crocuta crocutta*, cheetah *Acinonyx jubatus*, leopard *Panthera pardus*, lion *Panthea leo* and African wild dog *Lycaon pictus*) to act as surrogate species for biodiversity conservation in southern Africa. We suggest that the guild must be complete for the large carnivores to fully provide their role as ecological keystones. The potential for large carnivores to act as umbrella and indicator species seems limited. However, self-sustaining populations of large carnivores may be useful indicators of unfragmented landscapes. Moreover, diversity within the large carnivore guild may reflect overall biodiversity. Although the global appeal of the large African carnivores makes them important international flagships, we stress that international conservation funding must be linked to local communities for them to be important also locally. In summary, we suggest that the flagship value of these large carnivores should be used to promote biodiversity conservation in the region, and that the suggested relationship between large carnivore diversity and overall biodiversity is empirically tested. Finally we suggest that direct conservation activities should focus on enhancing the keystone values of large carnivores through complete guild conservation and restoration.

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ORIGINAL PAPER

The potential for large carnivores to act as biodiversity surrogates in southern Africa

Fredrik Dalerum · Michael J. Somers · Kyran E. Kunkel · Elissa Z. Cameron

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Abstract Biodiversity in southern Africa is globally extraordinary but threatened by human activities. Although there are considerable biodiversity conservation initiatives within the region, no one has yet assessed the potential use of large carnivores in such actions. Surrogate approaches have often been suggested as one such way of capitalizing on large carnivores. Here we review the suitability of the large carnivore guild (i.e., brown hyaena *Hyaena hyaena*, spotted hyaena *Crocuta crocutta*, cheetah *Acinonyx jubatus*, leopard *Panthera pardus*, lion *Panthea leo* and African wild dog *Lycaon pictus*) to act as surrogate species for biodiversity conservation in southern Africa. We suggest that the guild must be complete for the large carnivores to fully provide their role as ecological keystones. The potential for large carnivores to act as umbrella and indicator species seems limited. However, self-sustaining populations of large carnivores may be useful indicators of unfragmented landscapes. Moreover, diversity within the large carnivore guild may reflect overall biodiversity. Although the global appeal of the large African carnivores makes them important international flagships, we stress that international conservation funding must be linked to local communities for them to be important also locally. In summary, we suggest that the flagship value of these large carnivores should be used to promote biodiversity conservation in the region, and that the suggested relationship between large carnivore diversity and overall biodiversity is empirically tested. Finally we suggest that direct conservation activities

F. Dalerum (✉) · E. Z. Cameron
Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, 0002 Pretoria, South Africa
e-mail: fredrik.dalerum@zoology.up.ac.za

F. Dalerum · M. J. Somers
Centre for Wildlife Management, University of Pretoria, 0002 Pretoria, South Africa

M. J. Somers
Centre for Invasion Biology, University of Pretoria, 0002 Pretoria, South Africa

K. E. Kunkel
World Wildlife Fund, Gallatin Gateway, Montana, USA

should focus on enhancing the keystone values of large carnivores through complete guild conservation and restoration.

Keywords Africa · Biodiversity conservation · Predators · Predation · Substitute species

Introduction

Southern Africa is a region rich in biodiversity, much of which is threatened by human activity. Although numerous conservation initiatives within the region focus on biodiversity, most of these are specifically targeted at plants (e.g., Cowling et al. 2003) and there is a surprising lack of attention to large mammals (but see Kerley et al. 2003). Surrogate species approaches have been suggested as one avenue to involve large mammals in biodiversity conservation efforts (Favreau et al. 2006). Although surrogate species approaches have recently been criticized (Andelman and Fagan 2000; Lindenmayer et al. 2002; Brooks et al. 2004), they hold an innate appeal to conservation practitioners and the general public since they offer a defined terminology to frame conservation issues around.

The large carnivore guild is an important group of animals for the African continent. It includes some of the most charismatic and well-known species in the world. Although sometimes a source of human wildlife conflict (e.g., Woodroffe et al. 2007a; Gusset et al. 2008), large carnivores have important economic implications through ecotourism and commercial trophy hunting (Lindsey et al. 2005a, 2007). Large carnivores are also proposed to be keystone species for their ecosystems, and provide important ecosystem services maintaining biodiversity and ecosystem processes (e.g., Sinclair et al. 2003; Owen-Smith and Mills 2008; see also Terborgh et al. 1999). However, despite recent attention to large carnivores in a biodiversity context (Ray et al. 2005) and a regional assessment of priorities for conservation of African carnivore diversity (Mills et al. 2001), there has been no formal assessment of the potential function of the large carnivore guild for conservation of overall biodiversity in southern Africa.

In this paper we review the potential role of large carnivores for biodiversity conservation in southern Africa using a surrogate terminology framework. We regard the southern African region to be the countries south of the Zambezi River, i.e. Namibia, Botswana, Zimbabwe and South Africa. Firstly we review the function of the large carnivore guild as ecological keystone species (sensu Paine 1966) for southern African ecosystems. We further review the potential for large carnivores to act as umbrella (sensu Noss 1990) and focal (sensu Lambeck 1997) species, as biodiversity indicator species (sensu Landres et al. 1988, see also Niemi and Macdonald 2004), and as flagship species (sensu Simberloff 1998) for biodiversity conservation in the region.

Surrogate species terminology

Although surrogate species approaches offer a defined terminology on which to base conservation efforts, the use of surrogate terms has often been loose with a great confusion of the terminology as a result (Caro and O'Doherty 1999). To clarify our review, we summarize the general definitions of surrogate terminology.

A keystone species is defined as a species that has larger ecosystem impacts than their relative biomass would predict (Paine 1966; see Table 1). They should not be confused with 'dominant' (or 'foundation') species, which may regulate lower trophic levels but are

Table 1 Definitions of surrogate species terminology used in conservation biology

Term	Formal definition	Conservation function
Keystone species	*'A species that has impacts on other species or processes beyond what might be expected based on their abundance'*[a]	Species that provide ecosystem services that maintain biodiversity patterns, i.e. species whose removal from a system leads to massive changes in community dynamics
Umbrella species	*'A species with large area requirements, which if given sufficient protected area will bring many other species under protection'*[b]	Species on which to focus biodiversity conservation efforts, i.e. if large areas are preserved for their conservation, presence of other species will be preserved
Focal species	*'A suite of species, each of which is used to define different spatial and compositional attributes that must be present in a landscape'*[c]	Species on which to focus biodiversity conservation efforts
Indicator species	*'A species whose characteristics are used as an index to attributes too difficult, inconvenient or expensive to measure for other species or environmental conditions'*[d]	Species on which to focus biodiversity monitoring efforts
Flagship species	*'A charismatic species that can be used to anchor conservation actions because it receives public interests and sympathy'*[a]	Species to focus on in public campaigns and fund-raising efforts

[a] Simberloff (1998)

[b] Noss (1990)

[c] Lambeck (1997)

[d] Landres et al. (1988)

doing so by numerical dominance alone (Steneck 2005). Hence, the keystone species concept does not have a true surrogate function, despite often being mentioned in a surrogate species context. Rather, ecological keystones are species that provide ecosystem services that act in creating and maintaining the biodiversity that is targeted by biodiversity conservation (Simberloff 1998). Species can cause top-down effects in ecosystems either by directly causing structural change in the environment or by altering community structure through competition, predation, or as disease vectors (Power et al. 1996). However, since the keystone concept stipulates great impact at low abundance, most top-down effects of carnivore keystones are due to predation processes (Steneck 2005).

To date, two general categories of true surrogate approaches have been used in conservation biology. Surrogate species have either been used to identify appropriate areas for conservation action, or to monitor the effects of disturbance or conservation actions on other species in a system (Caro et al. 2005). The first category consists of the 'umbrella species' and the 'focal species' concepts (Table 1), both of which assume that the conservation of a species, or a suite of species, will render protection to other species in the system. Consequently, these concepts are specifically designed to identify measures for conservation action. The second category consists of the 'indicator species' concept, in which a species is used to monitor the effects of management actions or disturbance on other species or components of a system that are too difficult or costly to monitor directly (Table 1). This second category thus contrasts from the first one in that it targets biodiversity monitoring rather than identifying appropriate conservation action.

Finally, the 'flagship species' concept is often used in a surrogate framework. A flagship species is a charismatic species that is used to anchor conservation efforts in strategic terms such as fund raising and publicity. It is worth noting that the flagship species concept does not necessitate large ecosystem impacts, nor appropriate surrogate function according to either of the two conceptual categories described above (Caro and O'Doherty 1999). Nonetheless, they provide an important focus for the general public, thereby enhancing conservation efforts less directly.

The large carnivore guild in southern Africa

We have defined large carnivores as species that attain an adult body mass of above 20 kg. This definition is a functional one, since species that fall above this size commonly kill prey larger than their own body mass (Carbone et al. 1999).

Using this definition, the large carnivore guild of southern Africa contains two of the world's four hyaena species (the spotted hyaena *Crocuta crocutta* and the brown hyaena *Hyaena brunnea*), three of the world's six large felid species (the lion *Panthera leo*, the cheetah *Acinonyx jubatus* and the leopard *Panthera pardus*), as well as the African wild dog (*Lycaon pictus*). It is thus the most diverse assemblage of sympatric large carnivores in the world, both from a phylogenetic and functional perspective.

Large carnivores as keystone species in southern Africa

While the relative importance of bottom-up versus top down control of terrestrial ecosystems is a heavily debated topic (e.g., Power 1992; Schmitz et al. 2000), there is an emerging consensus that large predators are crucial components of functional terrestrial ecosystems (Terborgh et al. 1999, 2005). For instance, a drastic decline in cougar (*Felis concolor*) numbers in Zion National Park in Utah, USA was shown to cause a trophic cascade with structural effects on both terrestrial and aquatic ecosystems within the park (Ripple and Bechta 2006). In southern Africa, such direct quantifications of top-down effects on community structure of herbivores and plants have never been done. However, predation processes seem to be an important component in pristine southern African ecosystems as well (Mills 2005), although the relative ecological impact of top down and bottom up forces seems to be variable and depending on a number of ecological factors (Owen-Smith and Mills 2006).

While there are substantial diet overlaps between the species within the guild, there are also contrasts in terms of potential prey and diet breadth (Table 2). Both the lion (prey range size 190–550 kg; Hayward and Kerley 2005) and the spotted hyaena (56–182 kg; Hayward 2006) primarily hunt medium sized and large ungulates and also overlap in prey preferences (Hayward 2006), whereas cheetah and leopards rely on hunting somewhat smaller prey (cheetah: 23–56 kg, Hayward et al. 2006a; leopard: 10–40 kg, Hayward et al. 2006b). Both the spotted and the brown hyaena can sustain themselves on carrion (Mills 1982; Skinner and Chimimba 2005), and particularly the brown hyaena has been shown to feed extensively on plants and invertebrates (Mills 1982). Furthermore, while the African wild dog often has been suggested as an ungulate specialist (Creel and Creel 2002), recent data show that wild dog populations can sustain themselves exclusively on small mammals (Woodroffe et al. 2007b). However, this is likely to be a sub-optimal feeding strategy based on energetic requirements (Hayward et al. 2006c).

Table 2 Occurrence of prey categories in diets of the large carnivores in southern Africa

	Large ungulates (>100 kg)	Medium sized ungulates (100–50 kg)	Small ungulates (>50 kg)	Small mammals	Birds and reptiles	Invertebrates	Scavenge
Brown hyaena		X	X	X	X	X	X
Spotted hyaena	X	X	X	X	X		X
Cheetah		X	X				
Leopard		X	X	X	X		
Lion	X	X	X				
Wild dog		X	X	X			

Table is based on information in Skinner and Chimimba (2005); Hayward and Kerley (2005); Hayward (2006); Hayward et al. (2006a); Hayward et al. (2006b); Hayward et al. (2006c); Owen-Smith and Mills (2008)

It has been suggested that the wider prey size range of large carnivores results in dietary niches of smaller carnivores that are nested within the dietary niches of larger species (Sinclair et al. 2003; Radloff and Du Toit 2005). However, a recent study in Kruger National Park, South Africa, contradicted this pattern (Owen-Smith and Mills 2008). Rather, it indicated that despite a substantial overlap in prey size range, predators showed distinctly different preferences among prey, and had different hunting success while attempting to hunt prey of different sizes. This suggests that a single species from the guild is not necessarily substitutable in the effects on prey populations with another species from the guild (see also Woodroffe and Ginsberg 2005). Moreover, the effect that each carnivore species has on prey communities is most likely affected by sympatric occurrences of other species within the guild, since intraguild competition often alters diet breadth (Keddy 2001; see also Sih et al. 1998). Intraguild predation can also affect the structure of the large carnivore guild itself (Palomares and Caro 1999; Creel et al. 2001), and consequently its effects on lower trophic levels (Vance-Chalcraft et al. 2007). Although the largest carnivore species tend to dominate the relative predation impact of the guild (Woodroffe and Ginsberg 2005; Owen-Smith and Mills 2008), the additive effects of multi-species predator assemblages suggest that the ecological keystone role through predation processes are greatly enhanced by occurrences of taxonomically complete guilds compared to single species occurrences.

Large carnivores as umbrella and focal species for biodiversity conservation in southern Africa

In its most basic form, the umbrella species concept relies on the assumption that protection of a species with large home ranges will render protection to sympatric species with smaller home ranges (Roberge and Angelstam 2004). Since large carnivores have among the largest home range requirements among terrestrial mammals (Carbone and Gittleman 2002), they are natural candidates for suitable umbrella species (Noss et al. 1996; Ray 2005). However, although large mammal umbrellas have been efficient in delineating East African reserves (Caro 2003), there is limited empirical support for protection of biodiversity by large carnivore umbrellas in general (Roberge and Angelstam 2004).

Each of the five species within the guild in southern Africa has large home range requirements and often occurs at low population densities (Table 3). Based on this, they would intuitively be ideal umbrella species according to the formal definition of the

Table 3 Approximate ranges for home range sizes and population densities for the large carnivores in southern Africa

	Home range size (km^2)	Population densities (individuals/100 km^2)
Brown hyaena	20–500	1.5–5[a]
Spotted hyaena	25–1,000	0.5–46
Cheetah	50–1,500	0.05–2[b]
Leopard	20–1,400	0.1–5[b]
Lion	20–4,500	0.1–18
Wild dog	150–2,500	0.2–7[a]

Table is based on reviews in Mills (1982), Haas et al. (2005) and Skinner and Chimimba (2005)

[a] Density range estimated from home range sizes and observed group sizes

[b] Density range estimated from home range sizes

Table 4 Use of major biomes by the large carnivores in southern Africa

	Dense woodland	Open woodland	Savannah	Grassland	Desert and semi-desert	Outside reserves
Brown hyaena		X	X	X	X	X
Spotted hyaena		X	X	X	X	X
Cheetah		X	X	X	X	X
Leopard	X	X	X	X	X	X
Lion	X	X	X	X	X	
Wild dog	X	X	X			

Table is based on information in Skinner and Chimimba (2005)

concept (Table 1). Sergio et al. (2005, 2006) showed that a suite of raptors was excellent umbrella species for plant, invertebrate and avian biodiversity in the European Alps. However, although the suite of species used by Sergio et al. (2005, 2006) covered a wide range of habitat types, each species had specific habitat requirements and only occurred in segments of the landscape. In contrast, the large carnivores in southern Africa are non-specific in their habitat requirements (Table 4) and occur widely throughout the region (Fig. 1). Emerging data from game reserves and various carnivore conservation programmes in the region indicates that large carnivore populations mainly are food limited (Hayward et al. 2007a; Hayward et al. 2007b) or limited by human persecution (Woodroffe and Ginsberg 1998). As long as these population constraints are released, for instance by continuous introductions of potential prey or by reduced hunting, and there is sufficient reintroduction effort to overcome possible Allee effects (e.g., Hurford et al. 2006), carnivore populations can thrive even in heavily disturbed systems (e.g., Bothma 2002). Therefore, species sensitive to disturbance or linked to specific habitat types may not be protected under areas specifically managed to host large carnivores, and so the use of large carnivores as biodiversity umbrellas in southern Africa is likely to be limited. A similar conclusion was reached for the boreal forest in Scandinavia (Linnell et al. 2000), and the wide tolerance to disturbance and habitat alteration exhibited by many large carnivores suggests that they may not be as suitable as umbrellas as their large home range requirements imply.

Lambeck (1997) suggested an extension of the umbrella concept, which includes a suite of species with complementary habitat requirements (the ‘focal species’ concept). This concept has been used to include habitat requirements of an assemblage of carnivores into a

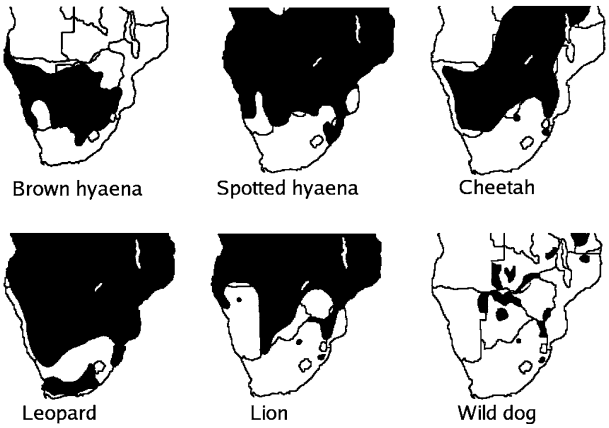

Fig. 1 Distributions of large carnivores in southern Africa. Distribution maps are based on Skinner and Chimimba (2005)

regional conservation plan for the Rocky Mountains in North America (Carroll et al. 2001). However, the large overlap in acceptable habitat within the large carnivore guild in southern Africa (Table 4) probably causes the guild to be an unsuitable assemblage of species also for a focal species approach to the umbrella concept.

Large carnivores as indicator species for biodiversity in southern Africa

Large carnivores are unsuitable biodiversity indicators for the same biological reasons that render them unsuitable as conservation umbrellas. Their broad habitat tolerance as well as their ability to sustain populations in disturbed systems means that they are generally not good indicators for fragile components of ecosystems (Linnell et al. 2000, Kunkel 2003). However, large carnivores are sensitive to fragmentation (e.g., Crooks 2002), and could thus function as good indicators for unfragmented landscapes. In line with this, most of the viable populations of large carnivores in southern Africa persist in large protected areas, such as the Etosha National Park in Namibia, the Kruger National Park in South Africa and the Central Kalahari Game Reserve in Botswana. However, occurrences of large carnivore populations cannot be used directly as indicators of unfragmented landscapes because of game ranching and conservation practices in the region. In southern Africa, large carnivores are often kept in networks of smaller reserves with heavily managed populations with artificial migration (e.g., translocations) between them (Mills 1991; Akçakaya et al. 2006). Thus, large carnivores are often found in areas too small and isolated to sustain viable populations without human intervention, and these areas are therefore not particularly suitable as indicators of unfragmented landscape segments. Therefore, they only serve as indicators of unfragmented landscapes where populations are not intensively managed.

Woodroffe and Ginsberg (2005) suggested that occurrences of complete guilds of large carnivores could function as indicators of undisturbed ecosystems, since intraguild competition would make it unsustainable for weaker species to co-exist with dominant ones in heavily disturbed systems. While the dietary plasticity exhibited by many of the large carnivores makes co-existence with other members of the guild possible, the potential diet overlap between species within the guild indicates that interspecific competition will increase with

declining prey diversity. This supports the findings of Woodroffe and Ginsberg (2005) in that areas that sustain sympatric occurrences of dominant and subordinate species probably also contain a minimum level of prey heterogeneity. Therefore, the diversity of the large carnivore guild, and particularly sympatric occurrences of the subordinate species (cheetah and wild dog) with the dominant ones (lions and spotted hyaenas) is probably reflecting overall prey diversity within the area concerned. We suggest that this hypothesis is tested empirically, since it may add an important indicator tool to conservation programs.

Large carnivores as flagships for biodiversity conservation in southern Africa

The public appeal, particularly in industrialized countries, of the large carnivores in southern Africa is almost unprecedented among any assemblage of sympatric mammals in the world. Therefore, their potential role as flagships for conservation programs is important. Indeed, several of the major conservation organizations focus many of their conservation campaigns on large carnivore species (e.g., the Endangered Wildlife Trust: http://www.ewt.org.za; the Wildlife Conservation Society: http://www.wcs.org/international/africa). However, it is important to notice that much of this public appeal often is not present among local communities that are in direct contact, and often in conflict, with these animals (Sillero-Zubiri and Laurenson, 2001). Therefore, for large carnivores to function as flagships to conservation programs it is necessary to make globally raised funding beneficial to local communities.

In southern Africa, in contrast to many other parts of the world (e.g, Scandinavia: Linnell et al. 2000; the European Alps: Breitenmoser 1998; North America: Kunkel 2003), there is a market for local communities to directly benefit from large carnivores through ecotourism. Although conflict with ranchers exists, people generally appreciate the economic potential, even on private land (Marker et al. 2003; Lindsey et al. 2005b; Gusset et al. 2008). Such financial opportunities come mainly through two avenues, game tourism (Lindsey et al. 2005a) and trophy hunting (Lindsey et al. 2007). We suggest that these activities are further encouraged to ensure sustainability of large carnivores as well as predation processes even outside official national parks and nature reserves.

Conclusions

Despite a lack of direct quantifications of top-down effects by large terrestrial carnivores, there are strong indications that predation is an important component in shaping southern African ecosystems. However, to fully provide their roles as ecological keystones, we stress that sympatric assemblages of large carnivores need to form taxonomically complete guilds. The broad habitat tolerance and general population regulation through food limitation exhibited by large carnivores makes their use as biodiversity conservation umbrellas and biodiversity indicators limited. However, self-sustaining populations may function as good indicators of un-fragmented landscape segments, and diversity within the large carnivore guild is likely a good indicator of prey diversity. Large African carnivores are important flagships on an international level, but we highlight that international conservation funding must be thoroughly funnelled into local communities for them to be important also on a local scale. Furthermore, direct financial benefits to local communities through ecotourism should be encouraged, since this will ensure long-term viability of carnivore populations and predation processes outside national parks and agency managed reserves. In summary, we suggest that biologists and policy makers capitalize on the flagship value of

large carnivores to promote conservation and management of biodiversity in southern Africa. We also suggest that the relationship between carnivore diversity and overall biodiversity is empirically tested, and that direct conservation activities should focus on enhancing the keystone value of large carnivores through complete guild conservation and restoration.

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