

Conservation and behavior of Africa's "Big Five"

Tim CARO*, Jason RIGGIO

Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA

Abstract We examine the conservation status of Africa's "Big Five": lion, leopard, buffalo, black and white rhinoceros and elephant, and the role of behavioral knowledge in their conservation. Efforts to conserve these flagship species consist of *in situ* conservation, captive breeding and reintroductions. With a few exceptions, we find limited evidence that knowledge of behavior informs conservation programs targeted at these species. For management in the wild, knowledge of infanticide and ranging can provide guidelines for realistic hunting quotas and corridors between protected areas, respectively. For *ex situ* and reintroduction programs, behavioral knowledge is chiefly focused on improved animal husbandry. Despite a formidable understanding of these species' behavior, the practicalities of using such knowledge may be diminished because exploitation of these species is so forceful and the bulk of efforts aimed at conserving these species (and indeed most other African species) are primarily *in situ* where behaviorally driven interventions are limited. Our comparative findings suggest that behavior has been of rather narrow use in the conservation of these flagship species [Current Zoology 60 (4): 486–499, 2014].

Keywords African elephant, Black rhinoceros, Buffalo, Flagship species, Leopard, Lion, White rhinoceros

1 Introduction

In Africa, the history of conservation is entwined with European big game hunters who visited large, relatively pristine areas in search of large mammal trophies (Selous, 1881; Roosevelt, 1910; Neumann, 1988). These sportsmen wanted to maintain carnivore and herbivore populations for future hunting trips, their children, and other hunters, and together with colonial administrators were responsible for setting up game reserves before African nations achieved independence. Subsequently, many of the reserves were regazetted as national parks that now form networks of protected areas in Africa today. Big game hunters targeted specific species of mammal and eschewed others (Caro, 2003), but their favorite quarry were the so-called "Big Five", actually six separate species: lion *Panthera leo*, leopard *Panthera pardus*, buffalo *Syncerus caffer*, black rhinoceros *Diceros bicornis*, white rhinoceros *Ceratotherium simum* and elephant *Loxodonta africana* (Williams et al., 2000), some of which have subsequently been split into additional species and subspecies. Since historical times, continental populations of the "Big Five" have dwindled, some of them alarmingly (see Craigie et al., 2010), yet despite their plight these species continue to command very high prices at game sales because of their importance as trophies. Furthermore, they are marketed by governments and the tourism industry to sell tourist

destinations (Lindsey et al., 2007a); are used to raise money by conservation organizations; and are important to zoological institutions in attracting visitors (Caro and Riggio, 2013; Di Minin et al., 2013). In short, they are Africa's quintessential flagship species (Caro, 2010).

In this paper we ask what role aspects of behavior have played in conserving the "Big Five" *in situ*, in captivity and in reintroduction programs. In so doing we are explicitly examining how behavioral information has helped conservation biologists and managers whose ambit is usually concerned with population sizes, subspecies and population genetic differentiation, and anthropogenic threats and who have less knowledge of behavior. The paper is organized as follows: for each species, we briefly outline the conservation status, principal threats and basic behavioral attributes. Next we discuss the ways in which behavioral information has influenced strategies used by managers to conserve the species in three conservation arenas. Our approach is retrospective and therefore differs from that often taken by "conservation behaviorists" who, for example, suggest that specific behaviors such as patterns of dispersal, territory size and mating systems might respectively influence metapopulation structure, density and reintroduction attempts in a prospective and more hypothetical manner.

Although we write this review squarely from the perspective of a conservation practitioner, it is worth

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* Corresponding author. E-mail: tmcara@ucdavis.edu

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noting that conservation success differs according to context. As illustrations, fenced populations are not necessarily regarded as successful in East Africa although they often are in Southern Africa; *in situ* conservation may be preferable to some conservation managers but *ex situ* programs to others; and reintroductions may be viewed as successful for put-and-take hunting but unsuccessful for population sustainability.

Given that these six flagship species have been subject to considerable behavioral study and that our knowledge of their habits is extensive, we believe that this comparative, albeit qualitative attempt to understand whether behavior has informed a broad spectrum of conservation effort is an instructive test case for whether "conservation behavior" contributes to practical conservation.

2 Lion

Over the last 20 years lions have declined by a suspected 30% in sub-Saharan Africa and now total 32–35,000 individuals; they are currently classified by the IUCN as "vulnerable" (Bauer et al., 2012; Riggio et al., 2013). Two subspecies are usually recognized: the African lion *P. l. leo*, and the Asiatic lion *P. l. persica* which is confined to a single population of approximately 400 individuals in India (Singh and Gibson, 2011). Recent genetic evidence suggests, however, that lions in West and Central Africa represent a genetically distinct subspecies, and might be more closely related to the Asiatic lion (Bertola et al., 2011; Dubach et al., 2013) whereas another study suggests five subspecies (Barnett et al., 2014). Lion populations have declined across the African continent and are now restricted principally to East and Southern Africa although a few small, isolated populations still persist in West and Central Africa (Riggio et al., 2013; Henschel et al., 2014). The causes of lion decline are principally habitat destruction (Riggio et al., 2013), lack of an adequate prey base (Ray et al., 2005), retaliatory killing for livestock losses (Hazzah and Dolrenry, 2007; Kissui, 2008; Maclellan et al., 2009), and poor management (see TAWIRI, 2009). Ritual killing (Ikanda and Packer, 2008), a switch from retaliatory to commercial killing (Fitzherbert et al., 2014), tourist hunting (Loveridge et al., 2007; Packer et al., 2009; Croes et al., 2011), inbreeding (Packer et al., 1991; Trinkel et al., 2008), and disease (Roelke-Parker et al., 1996; Packer et al., 1999; Munson et al., 2008) are also contributory factors.

Lions feed on a broad variety of large and medium-sized mammalian prey (Hayward and Kerley, 2005).

Typically they live in stable prides of 2–18 females and coalitions of 2–7 males (Packer, 1986; Pusey and Packer, 1987). Per capita reproductive success of lionesses increases with pride size (Mosser and Packer, 2009) and reproductive success of males increases with coalition size because they are better able to fend off challenges from other males (Packer et al., 1988).

2.1 *In situ*

When a coalition takes over a pride it kills cubs sired by previous male pride holders (Packer et al., 1988). If human hunting of male lions reduces resident coalition size, the chance of a takeover by other coalitions and of associated infanticide increases (Caro et al., 2009). Because hunting has an effect on population growth rates beyond simply removing males, Whitman and colleagues (2004) argued that males under 6 years of age, still capable of pride tenure, should not be hunted and they advanced a field method of assessing lion age through nose coloration (Whitman and Packer, 2007). The policy is now used in the Niassa hunting blocks of northern Mozambique but thus far in few other places. Some have suggested that hunting companies be penalized for shooting males <6 years of age, and that exports of lions <4 years old be prohibited (Begg and Begg, 2008). More generally, male lions should be harvested at a maximum of 3% of the population size (Creel and Creel, 1997) or at 0.5–1.0 male lion/1000 km² to be sustainable (Packer et al., 2011).

Retaliatory killing has been reduced in Maasai areas of Kenya through a well publicized "lion guardians" campaign. This program trains Maasai warriors to track individual lions, giving advanced notice of their whereabouts to those protecting livestock; guardians can attain status and pecuniary rewards through these activities (Hazzah et al., 2009). Acquiring knowledge of ranging behavior is therefore intimately linked to conservation in this region of Kenya.

Lions exhibit sex-biased dispersal with male lions travelling greater distances than females (Pusey and Packer, 1987). Metapopulation models show that the maximum dispersal distance of females is the limiting factor in the recolonization of locally extinct populations; male lions, however, can 'rescue' declining populations at greater distances (Dolrenry et al., 2014). Furthermore, knowledge of lion movement in relation to environmental barriers is useful in understanding the consequences of erecting fences (Cozzi et al., 2013), a topic currently under debate in regards to lions (Hayward et al., 2009; Packer et al., 2013; Creel et al., 2013; Woodroffe et al., 2014).

2.2 Captivity

Lions are bred in captivity principally for entertainment, educational purposes, and “canned hunts” in South Africa, rather than for conservation purposes (Lindsey et al., 2012). Lions breed easily in captivity and attain larger body sizes than wild-caught animals yet have smaller brain sizes (Yamaguchi et al., 2009). Typically, behavioral knowledge is used little in captive breeding, aside from keeping males separated from cubs (e.g., Ncube and Ndagurwa, 2010) or more generally for enriching captive housing. For example, stereotypic behavior in carnivores is directly related to home range size, suggesting that carnivore cages be enlarged (Clubb and Mason, 2003).

2.3 Reintroductions

Reintroduction of lions is commonplace in South Africa with populations restored to at least 44 small fenced reserves (Miller et al., 2013). Most of these translocations use wild lions from other areas because captive-bred reintroductions are not recommended (Hunter et al., 2013). Success rates are high when groups of same-sex lions are introduced together using soft-release methods (Hunter et al., 2007; Trinkel et al., 2008; Trinkel et al., 2010) but groups do not always remain together (Killian and Bothma, 2003) and wandering individuals may bring lions into contact with people (Stander, 1990).

In summary, infanticidal behavior means that hunting male lions has consequences for cub recruitment, whereas ranging and dispersal behavior influences population subdivision and lion-human conflict.

3 Leopard

Leopards are classified as “near threatened” by IUCN and divided into nine subspecies, only one of which is found in Africa; *P. p. pardus*. The continental range of the leopard has decreased by 37% from its historical distribution primarily due to habitat conversion and fragmentation (Ray et al., 2005), poorly managed hunting quotas (Packer et al., 2009; Packer et al., 2011), and persecution through snaring and poisoning as well as a small local trade in skins (Ray et al., 2005; Balme et al., 2009). Nonetheless, leopards live in many habitats including mountainous areas (Chase Grey et al., 2013) and can adapt well to human-dominated landscapes (Nowell and Jackson, 1996; but see Henschel et al., 2011). Consequently they are still found throughout savannah Africa as well as the Congo Basin (Ray et al., 2005; Henschel, 2009).

Leopards have a broad diet of middle-sized and small

prey (Hayward et al., 2006a). They are polygynous with male territories overlapping several solitary female territories (Bailey, 1993; Jenny, 1996). As with lions, males kill offspring sired by other males in order to advance estrus in females and infanticide can account for 49% of cub mortalities; cubs are especially vulnerable during their first 12 months of life (Balme and Hunter, 2013). Therefore, excessive trophy hunting lowers population persistence through reduced cub survival (Balme et al., 2009; Packer et al., 2009).

3.1 *In situ*

Male leopards start to mate at 3 years and enter prime breeding activity between 4 and 6 years of age, showing a decline in reproductive output thereafter. Modeling efforts reveal that if hunters take only males of ≥ 7 years, hunting can be sustainable at a 3.8% level (Caro et al., 2009; Balme et al., 2012). Unfortunately, experimental work with hunters, guides, and even biologists demonstrates that females are often mistaken for ≤ 2 -year-old males, and also that hunters are poor at aging males (Balme et al., 2012). Nonetheless, it may be possible to enhance age estimation of leopards with training.

A reduction in retaliatory leopard killing has been successful around Phinda Private Game Reserve, South Africa where leopard population growth rate increased after a series of interventions including limiting the misuse of destruction permits, corralling livestock at night, assigning guards to herds, disposing of livestock carcasses, and lowering numbers of CITES permits (Balme et al., 2009) none of which involved behavioral information.

Long-distance dispersal data suggest that fragmented leopard populations can be genetically and demographically connected (Fattebert et al., 2013).

3.2 Captivity

African leopards are principally kept in captivity for public enjoyment although some of the critically endangered Asian subspecies are being bred in captivity for planned reintroductions (Shoemaker, 1985; Budd and Leus, 2011). As in most species, enrichment of the captive environment enhances welfare (Markowitz et al., 1995; Clubb and Mason, 2007); for example, leopards exhibit less stereotypic behavior in more complex off-exhibit enclosures and are more active on days with no visitors (Mallapur and Chellam, 2002).

3.3 Reintroductions

Lions notwithstanding, reintroductions of large carnivores are often doomed to failure (Mills, 1991) and limited attempts to reintroduce leopards have rarely

been successful (Hayward et al., 2006b). Reintroductions often involve capture and removal of problem animals with scant regard for soft-release techniques, and these can result in individuals moving large distances out of protected areas to resume stock-raiding (Weilenmann et al., 2010). Interspecific competition with introduced lions can be a problem for this species (Vanak et al., 2013). Nonetheless progress is being made. For example, predicting a reserve's carrying capacity of reintroduced carnivores based on biomass of prey in a predators' preferred prey weight range can give insights into how many animals to reintroduce (Hayward et al., 2007); and training animals to hunt prior to release may be helpful in some contexts (Houser et al., 2011).

In summary, knowledge of behavior has had little influence on conservation measures for this species, save in the case of specifying hunting quotas.

4 Buffalo

With 0.5–1 million individuals, the total African buffalo population is far larger than any of the other "Big Five", and is listed as a species of "least concern" by the IUCN. Three or four subspecies are recognized: forest buffalo *S. c. nanus*; West African savanna buffalo *S. c. brachyceros*; Central African savanna buffalo *S. c. aequinoctialis*; and southern savanna buffalo *S. c. caffer*. The species is still found throughout sub-Saharan Africa in all countries except for Gambia and Eritrea (East, 1999). The principal threats are habitat destruction and illegal hunting - buffalo is favored bush meat (Ndibalema and Songorwa, 2008; Martin et al., 2012). For example, forest buffalo densities are lower outside protected areas and closer to roads providing witness to the effects of illegal hunting (Laurance et al., 2006; Vanthomme et al., 2013). Indeed, the majority of animals are found in protected areas and in areas farther from human settlement (Metzger et al., 2010).

Buffalo live in fission-fusion societies with males making mating visits to large female groups that can exceed 1000 animals; these males live alone or in small bachelor groups (Sinclair, 1977; Prins, 1996). Because of their large numbers and body size, buffalo have a substantial ecological impact in savannah areas (Sinclair, 1977; Winnie et al., 2008). In forests, much smaller herds of buffalo collect in natural clearings (Melletti et al., 2007) suggesting that glades are important for their conservation.

4.1 *In situ*

Buffalo herds historically roamed over large dis-

tances (Epps et al., 2013) with individual buffalo displaying variable migratory behavior (Naidoo et al., 2012). While movement is prevented in fragmented habitats outside of large reserves (Matawa et al., 2012), their behavior suggests that buffalo will readily use corridors between protected areas and will not respond well to fencing (Ryan et al., 2006).

4.2 Captivity

Captive breeding of buffalo is an infrequently used conservation tool and so little behavioral information has been applied to breeding this species in captivity other than recognizing basic physiological knowledge such as captive buffalo give birth predominantly in mid-summer in southern Africa (Skinner et al., 2006).

4.3 Reintroductions

Buffalo reintroductions occur commonly on privately owned wildlife ranches in South Africa and Zimbabwe where shoot-and-sell safari hunting and ecotourism are practiced although these are prohibited in Namibia because of livestock presence (Lindsey et al., 2013). Reintroduction attempts have had variable success: one small group introduced into a nature reserve in South Africa using soft-release broke out of the area while the other remained inside the reserve (Venter, 2004). Additionally, predation can be an important source of mortality of small, introduced herds (Tambling et al., 2013).

In conclusion little behavioral knowledge has been applied to conservation of buffalo in part because little conservation effort has been applied to this still fairly common species.

5 Black Rhinoceros

Less than 5,000 black rhinoceros remain in the wild due to sustained demand for its horn in the Far East, and the species is listed as "critically endangered" by the IUCN. The black rhinoceros has experienced a catastrophic range retraction (Rookmaaker and Antoine, 2012) accompanied by a 98% decline since 1960 to just 2,410 individuals in 1995, but this rose to 4,880 by 2010 (see Emslie, 2008). Four subspecies are recognized: *D. b. bicornis*, *D. b. michaeli*, *D. b. minor* and *D. b. longipes*, the last of which, native to West and Central Africa, was recently declared extinct (Lagrot et al., 2007). Several remaining black rhinoceros populations in East and Southern Africa are now concentrated in fenced sanctuaries or intensive protection zones where law enforcement effort can be focused at effective levels. A few unfenced populations live at very low densities in huge protected areas.

Trade in black and white rhinoceros horn (see below)

is driven by traditional and non-traditional use in Chinese medicine, the latter for treating cancer, and by (a diminishing) use for ceremonial dagger handles in some Middle Eastern countries (Milliken and Shaw, 2012). Civil unrest in several host countries has hampered conservation efforts.

Black rhinoceros are large solitary browsers; they are polygynandrous and sexually monomorphic (Berger and Cunningham, 1995). Males and females separate themselves through scent markings and scrapes and are aggressive when they meet (Owen-Smith, 1988) although they occasionally form temporary associations outside of estrus. Home range size varies enormously between 0.5 km² (Hitchins, 1969) and 500 km² (Loutit, 1984) with male territories overlapping the ranges of several females.

5.1 *In situ*

Conservation of black rhinoceros populations now demands intensive protection involving rangers, local involvement and even helicopters and night vision equipment. Additional strategies to reduce poaching through dehorning can lead to a reduced ability for mothers to defend their calves from spotted hyenas *Crocuta crocuta* (Berger and Cunningham, 1994), but in general behavioral knowledge plays little role in these efforts.

5.2 Captivity

Worldwide, approximately 240 individuals (171 *D. b. michaeli* and 69 *D. b. minor*) resided in captivity in 2005 (Emslie, 2008); offspring sex ratios are skewed towards males in North American zoos (Dennis et al., 2007). Regarding behavioral information, enclosure size is correlated with reproductive performance; zoos with one female have higher breeding success than those with two or more, and aggressive male-submissive female pairings are more likely to be successful (Carlstead et al., 1999). The species exhibits high corticosteroid levels in captivity but shows less stress when housed singly, if fighting is minimized, and when kept away from the public (Carlstead and Brown, 2005). Stereotypic behaviors such as horn rubbing are common (Fouraker and Wagener, 1996). The price of rhinoceros horn is such that captive individuals are in danger of being killed in their enclosures and specimens have been stolen from museums.

5.3 Reintroductions

Black rhinoceros translocations are becoming more common in areas where there is effective protection: free-living individuals are brought in from other countries or from captivity (Fyumagwa and Nyahongo,

2010). There are a number of behavioral issues pertinent to black rhinoceros reintroductions. These include variability in home range size which makes it difficult to predict where new individuals will establish themselves after release (Göttert et al., 2010); worries about small reserves amplifying agnostic interactions between individuals (Linklater and Swaisgood, 2008) and fighting between bulls (Linklater et al., 2011); and the behavior of already established neighbors (Linklater and Hutcheson, 2010). Based on information from 682 releases, both younger animals and larger cohorts fared best in introduction programs where residents are absent (Brett, 1998; Linklater et al., 2012).

In short, knowledge of the behavior of this species has reduced stress in captivity and has improved the likelihood of reintroduction success but *in situ* conservation depends on strict protection more than anything else.

6 White Rhinoceros

Approximately 20,000 white rhinoceros remain in the wild (Emslie, 2012) following intense organized poaching for their horn in Southern Africa. There are two subspecies of white rhinoceros: *C. s. cottoni*, the northern white rhinoceros, and *C. s. simum*, the southern white rhinoceros, although some consider them separate species (Groves et al., 2010). With less than 5 extant individuals, the northern subspecies is listed as “critically endangered” by the IUCN: a population of around 30 individuals persisted in Garamba National Park, Democratic Republic of Congo until a wave of poaching eliminated them in 2006 (Emslie, 2008). In Southern Africa the economic incentives of live sales, sport hunting and ecotourism have led to a significant expansion of range and numbers on private land. Now, however, the southern subspecies is listed as “near threatened” because of continued poaching, increasing illegal demand for horn, and the involvement of international crime syndicates (Milliken et al., 2009). This has lowered live sale prices with increasing numbers of owners seeking to get rid of their animals.

White rhinoceros are large polygynandrous solitary grazers. Females range over much larger areas than males who set up territories in small, high quality forage areas (White et al., 2007) following ritualized fighting (Owen-Smith, 1975). Females mark their territories with dung, urine and broken vegetation, and visit male territories to mate (Owen-Smith, 1975; van Gysegem, 1984). Temporary groups of up to ten rhinoceros sometimes occur (Owen-Smith, 1988) and individuals form

temporary associations when attempting to disperse (Shrader and Owen-Smith, 2002).

6.1 *In situ*

In situ conservation operations center on highly protected fenced sanctuaries. Surplus animals are being translocated to new populations both within and outside the species' former range to increase security. Over 5,500 white rhinoceros across Africa are now managed by the private sector, the majority in South Africa (Emslie, 2012). Since most free-living populations are now fenced (Rachlow et al., 1999), issues of density-dependent reproduction need addressing (Rachlow and Berger, 1998). More and more attempts are being made to integrate local communities into conservation effort of this species.

6.2 Captivity

There are approximately 750 southern white rhinoceros in captivity worldwide. As white rhinoceros are more social than black, they can be kept together although it should be noted that removal of an old cow reduced agonistic behaviors in captive northern white rhinoceros (Cinková and Bičík, 2013). Nonetheless, the species actually breeds poorly due to post-copulatory reproductive failure (Swaigood et al., 2006) that may be related to high levels of corticosteroids (Carlstead and Brown, 2005). Wallows, sand pits, rubbing places, and bulk food are all recommended as standard husbandry tools (Forthman, 1998).

6.3 Reintroductions

In December 2009, the last four northern white rhinoceros were translocated from the Dvur Králové Zoo in Czech Republic to Ol Pejeta Conservancy in Kenya. They face an ever-present threat of poaching and are not viable genetically so will have to be hybridized with the southern subspecies (Emslie, 2012).

Southern white rhinoceros have been reintroduced within the historical range of the species in Namibia, Botswana, Zimbabwe, Swaziland and Mozambique (but reports indicate that this last population was recently driven to extinction due to poaching (<http://news.mongabay.com/2013/0425-rhinos-extinct-in-limpopo.html>)). They have also been introduced outside of their former range to Kenya, Uganda and Zambia (Emslie and Brooks, 1999; Emslie, 2008). Reintroductions effectively saved this species from extinction. The success of reintroductions may depend on keeping the total numbers of individuals low as new animals are prone to dispersing beyond reserve boundaries when population size rises (Støen et al., 2009).

In general, behavioral knowledge has helped to alle-

viate stress in captivity but *in situ* conservation critically depends on very effective policing which demotes the importance of behavior in conservation efforts.

7 Elephant

The African elephant occupies 37 countries in Africa but is quickly being extirpated from many of them (Bouché et al., 2011; Maisels et al., 2013); the rapidly plummeting continental population stands at around 500,000. The species is listed as vulnerable by the IUCN due to an unprecedented wave of ivory poaching driven by an increased demand from China's expanding middle class. Controversial genetic evidence suggests that there may be at least two species of African elephants; the savanna elephant *Loxodonta africana* and the forest elephant *Loxodonta cyclotis* (Roca et al., 2001). A third species, the West African elephant, has also been proposed (Eggert et al., 2002).

Elephants are predominantly found in protected areas but range widely across communal lands (Ahlering et al., 2013; Epps et al., 2011). Formerly, they moved across vast areas in search of feeding areas - in Tanzania (Epps et al., 2013) and Kenya (Okello et al., 2008), for example. In some parts of the continent they continue these movements, 6 km/day in dry landscapes and 3 km/day in wetter ones (Loarie et al., 2009). Elephant corridors still exist in some parts of the continent such as the Sahel (Wall et al., 2013) and in Tanzania, although they are becoming increasingly severed in human-dominated landscapes (Caro et al., 2009; Epps et al., 2011). Elephants are one of the principal players in human-wildlife conflict because of crop raiding (e.g. Barnes, 1996; Naughton-Treves, 1998; Harich et al., 2013).

Savannah elephant behavior is extremely well studied (Moss et al., 2011). They live in fission-fusion societies with stable multi-female (5–10) kin groups (Moss and Poole, 1983); mature bulls are solitary and visit female groups or collect in bachelor male groups infrequently (Moss, 1988). Dominance age-related hierarchies are found in both sexes with individual relationships extending beyond family groups (McComb et al., 2001; Moss et al., 2011). Forest elephants also live in fission-fusion societies (Fishlock and Lee, 2013)

7.1 *In situ*

Savannah elephants require relatively large protected areas free of human activities. Effective protection can work very well for this species because subpopulations breed rapidly (Foley and Faust, 2010). Nonetheless, it can also produce a build-up of locally high elephant

densities which can result in tree damage and the switch from woodland to grassland ecosystems, eventually threatening the elephant population itself (Guldmond and Van Aarde, 2008; Holdo et al., 2009). There is debate as to whether elephants will ultimately exhibit density-dependent population limitation (Gough and Kerley, 2006; Young et al., 2009; Young and van Aarde 2010). Nowadays, successful management interventions are undertaken through contraception (Druce et al., 2011) or translocation; large-scale culling has not been performed for 15 years (van Aarde et al., 1999). Similarly, forest elephants require sacrosanct protected areas far from roads (Blake et al., 2008; Vanthomme et al., 2013).

Given the wide-ranging behavior of savannah elephants, it is important to establish large protected areas such as transboundary reserves while opportunities last (e.g., Parren et al., 2002). Elephant ranging is promoted by the use of waterholes (Loarie et al., 2009). Moreover, elephant corridors can provide the impetus to set up or maintain corridors used by other wildlife: elephants are known to move rapidly along these from one protected area to another (Douglas-Hamilton et al., 2005; Jones et al., 2009).

Sport hunting of elephants, viewed as a tool to protect large hunting blocks, is permitted under the legislation of a number of Range States, and the following countries currently have CITES export quotas for elephant trophies: Botswana, Cameroon, Gabon, Mozambique, Namibia, South Africa, Tanzania, Zambia and Zimbabwe.

Elephants (particularly bulls) raid crops near well-established pathways linking protected areas and waterholes (Von Gerhardt et al., 2014). In place of old measures such as burning, banging drums, and electric fencing, new measures to reduce crop-raiding by elephants include fences with beehives (King et al., 2009; King et al., 2011). Elephants react to the sound of disturbed Africanized honeybees *Apis mellifera scutellata* with head shaking and characteristic rumble vocalizations (King et al., 2010). In addition, chili peppers are being used as a novel deterrent in the form of a cash crop (Parker and Osborn, 2006) or a *Capsicum oleoresin* spray for fields (Osborn, 2002).

Elephants are highly intelligent (Byrne et al., 2009; Greco et al., 2013). To illustrate, old matriarchs have superior discriminatory abilities when it comes to contact calls from other family groups (McComb et al., 2001) and are also very good at assessing the severity of a predatory threat (McComb et al., 2011). Recognizing the threat posed by humans, elephants can distinguish

among voices associated with ethnicities, gender and age, thereby avoiding perceived dangerous groups of people (McComb et al., 2014).

7.2 Captivity

In captivity, individuals show stereotypic behavior and heightened aggression. African elephants breed poorly in captivity and have short longevity. For all these reasons there has been mounting concern about their well-being (Clubb and Mason, 2002; Veasey, 2006) that has led to detailed assessments of captive conditions using behavioral and physiological measures. These include cognitive and behavioral responses, observations of stereotypy, physiological reactions measured as corticosteroid output, and the negative effects of prolonged stress on reproduction and health (Mason and Veasey, 2010). Recommendations include improving living conditions by enlarging enclosure sizes, enriching the environment, reducing exposure to cold conditions, removing hard surfaces and moats, and addressing dietary deficiencies. Although enlarging group sizes to 6–12 animals is suggested for reducing captive stress (Rees, 2009), adding more wild elephants to captive populations is no longer advised (Clubb and Mason, 2002).

7.3 Reintroductions

Translocations are often carried out as an alternative to, or following culling to reduce population densities and have been very successful (Slotow et al., 2005). Yet translocated elephants fail to distinguish the identities of callers on the basis of social familiarity or level of threat suggesting long-lasting behavioral effects following separation from family members (Shannon et al., 2013). Other behavioral difficulties have been noted in young translocated bulls moved without family members that may be ameliorated by the presence of older bulls (Slotow et al., 2000; Bradshaw et al., 2005). Captive-born elephants are sometimes released into wildlife sanctuaries in southern Africa (Evans et al., 2013).

In sum, behavioral knowledge is useful in attempts to design (particularly elephant) corridors between protected areas, to decrease human-elephant conflict, to reduce stress in captive institutions, and in some selected instances to improve translocation efforts.

8 Conclusion

In this review of the conservation challenges facing six flagship species in Africa we have explicitly examined the problems from a conservation biologist's perspective and have challenged animal behaviorists to demonstrate how behavioral knowledge could make a

difference in solving management issues. This is the purview of "conservation behavior" that has inched from examining the potential ways in which behavioral knowledge might benefit conservation programs (Clemmons and Buchholz, 1997) to how it can improve reintroduction and captive breeding programs (Blumstein and Fernandez-Juricic, 2010) and, more recently and vociferously, to documenting how species are changing their behavior in response to anthropogenic pressures in the wild (Candolin and Wong, 2012; Sih, 2013). Investigating the problems faced by the "Big Five" is instructive because it incorporates all three lines of enquiry in "conservation behavior". Our objective was not to list the range of behaviors that could be helpful in promoting conservation of these species but instead to examine how the extensive behavioral information already in existence has aided conservation efforts. Our comparative attempt to examine *in situ*, captive and reintroduction programs systematically leads us to conclude that across 18 different conservation-species arenas behavioral knowledge has had rather little to offer conservation efforts. Nonetheless, in some circumstances, it has informed management activities involving harvesting and possibly reserve design, and has helped to ameliorate the effects of stress for some species in captivity (Table 1).

It is worth noting that the conservation of these six species still occurs, primarily, in the wild. Given that the chief benefits of "conservation behavior" apply to captive and reintroduction programs (Blumstein and Fernandez-Juricic, 2010), it is perhaps unsurprising that behavior has little role to play in the conservation strategies designed for these charismatic species. Moreover, this is broadly true for all species except those that are extremely rare or exist chiefly in captivity (i.e., extinct in the wild).

In situ conservation can benefit from behavioral knowledge in two main ways in regards to the "Big Five". If sport hunting is to be used as a conservation tool *in situ* (Lindsey et al., 2006a; Lindsey et al., 2007b),

and this certainly applies to lion, leopard and buffalo (attempts have been made to list lion and elephant on Appendix I of CITES), then hunting must be sustainable (Kümpel et al., 2010). Knowledge of mammalian breeding systems alters models of sustainable offtake considerably because it changes the number of individuals that can be harvested while maintaining positive or stable population trajectories (Greene et al., 1998; Caro et al., 2009). Second, knowledge of ranging patterns, dispersal, and migration, as well as understanding the factors that influence these movements, informs management about the size of protected areas, the type of protected areas (multiple use or fully protected), and the benefits of corridors for these species. Information on movement patterns is definitely important in elephant conservation.

Ex situ programs can benefit from behavioral knowledge by helping to mitigate the stress of captivity for some species. This knowledge is most important for enriching captive settings and adjusting social conditions (Mason et al., 2013) although zoo managers already use adaptive management and a deep informal knowledge of behavior in captivity to achieve these goals. Reintroductions can benefit from post-release behavioral study and can identify factors affecting stress and movement away from release sites.

We conclude that the relationship between behavioral knowledge and conservation outcome is, at best, mixed when it comes to these charismatic African species. Certainly much is known about the behavior of these species in comparison to the vast majority of threatened species so absence of strong linkage is not due to paucity of behavioral knowledge. Rather, it is either in the lack of application of such knowledge (see Balme et al., 2014), or the relative lack of importance of behavior compared to anthropogenic drivers that is responsible for the weak links between behavior and conservation. In some cases it is the former, for example in the failure to restrict lion hunting offtake to old males, but in general we argue that anthropogenic forces are of such

Table 1 Importance of behavior in efforts to conserve the "Big Five"

	<i>In situ</i>	Captive breeding	Reintroductions
Lion	Infanticide important for hunting quotas	Minimal	Minimal
Leopard	Infanticide important for hunting quotas	Minimal	Minimal
Buffalo	Ranging possibly useful for connectivity	Minimal	Minimal
Black rhinoceros	Minimal	Aberrant behavior indicates stress	Ranging and social behavior helps choose reserve size and release numbers
White rhinoceros	Minimal	Aberrant behavior indicates stress	Minimal
Elephant	Ranging important for connectivity	Behavioral indicators useful for welfare	Aberrant behavior indicates stress

overwhelming magnitude that they make behavioral knowledge of the “Big Five” of minor import to a conservation manager. While the contribution that behavioral studies can make to the conservation of African wildlife is likely to vary on a case-by-case basis, for high profile large African mammals, an understanding of their behavior has had rather little practical conservation application and the best hopes for preventing their extinction require addressing the anthropogenic drivers directly and immediately.

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