



**HUMANE SOCIETY  
INTERNATIONAL**

# Black Rhino

*(Diceros bicornis)*



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*This factsheet is part of a series highlighting species vulnerability to trophy hunting and lethal offtake.*

## IMPACTS OF TROPHY HUNTING

- Offtakes are not biologically sustainable
- Decreased genetic diversity
- Social disruption

## POPULATION

The population size of the black rhinoceros (also known as the black rhino) is estimated as 3,142 mature individuals as of 2017.<sup>1</sup> The population declined by 85% in the last three generations (43.5 years), 1973 to 2017.<sup>2</sup>

The black rhino has experienced steep long-term population declines with recent small increases (Figure 2).<sup>2</sup> During the 20th century, regional populations were hunted to low numbers or extinction.<sup>3</sup> By 1960, only 100,000 remained due to 'relentless hunting' and habitat loss.<sup>1</sup> From 1973 to 1983, black rhino declined from 37,807 to 9,444 due to heavy poaching.<sup>2</sup> Overall, from 1960 to 1995, large-scale poaching caused a 98% collapse in population numbers.<sup>1</sup>

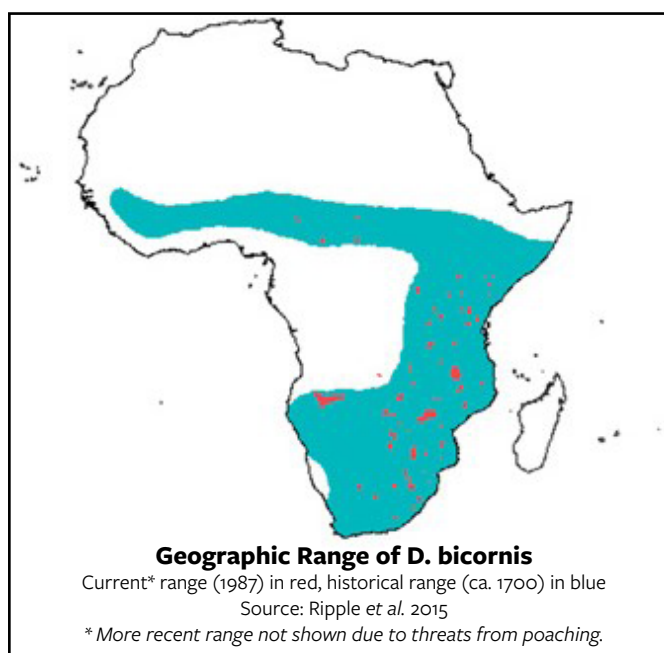
The black rhino has been classified as Critically Endangered by IUCN since 1996, which was recently reconfirmed in the species' 2020 assessment, highlighting long-term concerns about the conservation status of this species. Species are classified as Critically Endangered if they face an extremely high risk of extinction in the wild in the immediate future.

## RANGE

The black rhino has lost more than 98% of its historical range (ca. 1700).<sup>1,4,5</sup> The majority (94%) of black rhinos reside in four range States: South Africa, Namibia, Kenya, and Zimbabwe (in order of population size).<sup>6</sup> They are also extant in three other

## QUICK FACTS:

<b>Population Size:</b>	3,142 mature individuals, estimated decline of 85% in last three generations (43.5 years)
<b>Range:</b>	More than 98% of historical range lost
<b>IUCN Red List:</b>	Critically Endangered (2020)
<b>CITES:</b>	Appendix I (since 1977)
<b>International Trade:</b>	80 black rhino trophies traded internationally from 2009-2018
<b>Threats:</b>	Poaching for horns, habitat loss



native range States: Angola, Mozambique, Tanzania, and have been reintroduced to Botswana, Eswatini, Malawi, Rwanda, and Zambia.<sup>1</sup> Due to habitat loss

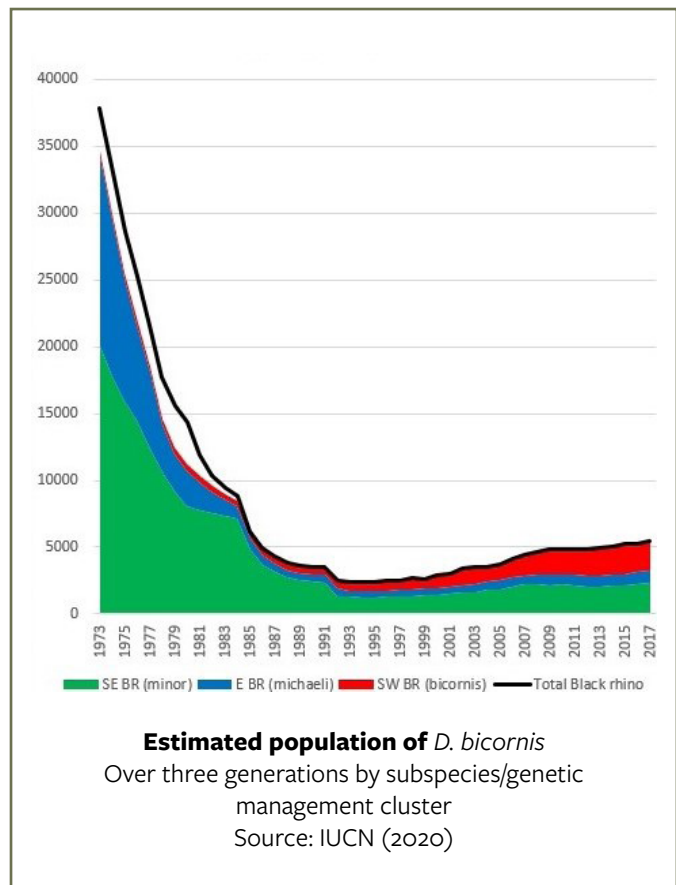
and fragmentation, black rhino have lost 69% of the species' mitochondrial genetic variation.<sup>3</sup>

There has also been an effort to translocate black rhino to areas outside their historic range in order to establish new populations.<sup>1</sup> Translocations have been important to the recovery of the black rhino, especially in South Africa; however, translocations vary in success.<sup>7</sup> Many factors determine the success of translocations, including rhino age,<sup>7</sup> reserve size,<sup>8</sup> habitat quality,<sup>9</sup> and group size.<sup>9</sup> In addition, population growth may be slow as it can take at least three years following a translocation for a male to establish a home range.<sup>10</sup> Due to the complexities of spatial and social interactions, removing black rhinos from their range can disrupt social interactions and adult male-female breeding relationships.<sup>11,12,13,14</sup> Therefore, both social and ecological conditions must be favorable for successful translocation.<sup>9</sup>

Translocation comes at a biological cost to black rhinos, as indicated by increased stress after capture and during captivity in preparation for translocation.<sup>15</sup> Post-mortality rates vary but can be as high as 18%.<sup>7</sup> Translocation is associated with post-release distress, suppressed gonad function, and delayed reproduction, consistent with poor reproductive output observed in captive and translocated rhino.<sup>15</sup> Stress from translocation is believed to be the cause of reduced breeding performance of mothers and low survival rates in young rhinos.<sup>7,16</sup> Stress experienced during immobilization, capture, translocation, and dehorning can have immunosuppressive effects and increase susceptibility to disease.<sup>17</sup> Repeated mobilizations greatly reduce growth rates by negatively affecting multiple fertility parameters.<sup>18</sup> Translocations, especially to restock existing populations, are associated with high rates of male-male conflict and mortality.<sup>7</sup>

## LIFE HISTORY AND REPRODUCTION

Black rhino population growth is slow due to low reproductive rates, long generation times, and high calf mortality. Females give birth for the first time at 7-9 years old, but can be as late as 12 years for some populations.<sup>19,20</sup> Males do not hold home ranges necessary for mating until 9 years old.<sup>21</sup> Gestation lasts approximately 15 months, and females produce one calf at a time.<sup>19</sup> The average calving interval is 2.25-4 years, depending on the population<sup>19,20,22</sup> but can be up to 6 years with poaching pressure.<sup>23</sup>



Calves are weaned around two years old but remain in contact with their mothers for an additional 2-3 years until their mothers give birth again.<sup>22</sup> During this time, mothers have been observed maintaining close proximity to their calves and protecting calves from predators.<sup>22</sup>

Female reproduction is influenced by a number of environmental factors, such as season, vegetation, rainfall, and resource availability.<sup>24,25,26</sup> This research has shown that there are clear links between female nutritional condition and reproduction. Peak calving occurs during the wettest months,<sup>25</sup> and shorter inter-calf intervals are correlated with higher rainfall.<sup>26</sup> Both of these measures indicate that black rhino females reach greater reproductive potential during wetter seasons when resources and vegetation are more abundant. Females are sensitive to heat stress, and reproduction is lower during the hottest time of the year.<sup>25</sup> This is especially concerning as climate change will lead to warmer and drier periods in the future.

In the wild, maximum lifespan is approximately 42 years.<sup>2</sup> Older black rhinos, both male and female, have higher reproductive hormone levels.<sup>27</sup> There is no evidence of a post-reproductive period for females, as they continue to give birth late into life.<sup>20,25,28</sup> In females, the only significant predictor of

reproductive success is age, with older females producing more calves.<sup>29</sup> This highlights the importance of older females for population growth. There is little available research on male reproduction. There is no scientific evidence that males stop reproducing at older ages. One study found that the majority of calves were fathered by a male 25-37 years old.<sup>30</sup> In addition, males 25 years and older produce androgens, important reproductive hormones, at concentrations comparable to younger males.<sup>31</sup>

Black rhinos are polygynous, and males exhibit high variance in reproductive success.<sup>29,19,30</sup> Males compete for home ranges that overlap with the home ranges of several adult females. Once males reach the age of nine, they begin to hold home ranges necessary for mating.<sup>21</sup> Males compete with one another for the best home ranges and access to females. Male-male competition is intense and can be fatal.<sup>7</sup> Among males, horn mass is positively correlated with higher rank.<sup>32</sup> Therefore, trophy hunting that targets males with the largest horns threatens to eliminate the most prolific male and can negatively affect reproduction. For males, home range size is correlated with greater heterozygosity (indicating lower levels of inbreeding), which is the strongest predictor of reproductive success.<sup>29</sup> Reproductive success is highly skewed among males, meaning that a few individuals are responsible for the majority of matings.<sup>19,30</sup> Population declines across their range have resulted in decreases in genetic diversity.<sup>3</sup> Therefore, the removal of males due to poaching or trophy hunting could have detrimental effects on population growth if those males are highly successful or genetically important. In captivity, testosterone concentrations are higher with an increasing number of female rhinos present.<sup>33</sup> In addition, isolated males had lower testosterone concentrations than males housed with other males.<sup>33</sup> This indicates that the presence of neighbors, especially many female neighbors, is important for stimulating reproduction.

Population age structures reveal low numbers of subadults and juveniles, which is problematic for future population growth.<sup>20</sup> There is also evidence that females experience spontaneous natural abortions, which would further slow growth rates.<sup>25</sup> Natural deaths occur due to illness, male-male fighting, accidents (such as falls), and predation.<sup>21</sup> Injuries and mortalities from fighting are more common in smaller reserves.<sup>8</sup> Scientists say that social disruption due to removal (e.g., relocation, trophy hunt-

ing, poaching) will likely increase social conflict.<sup>34</sup>

## **SOCIAL STRUCTURE**

Black rhinos were once believed to be mostly solitary; however scientists suggest that was a misconception due to intense population declines.<sup>33,19</sup> Instead, black rhinos exhibit social structure based on spatial organization, where females have overlapping home ranges, and males defend home ranges encompassing many females.<sup>33</sup> There is also evidence of loose family structures.<sup>30</sup>

Social interactions are largely based on the degree of home range overlap, which is heavily influenced by age, sex, and neighboring rhinos.<sup>11,12,13,14</sup> Social groupings of black rhinos are typically referred to as clusters.<sup>11,14</sup> Female home ranges typically overlap and occur in clusters of three or more females.<sup>11</sup> Female clusters may consist of both related or unrelated individuals,<sup>11</sup> and mothers may share part of their home ranges with adult female offspring.<sup>12,23</sup> Female home ranges also overlap male home ranges, consistent with adult male-female breeding relationships.<sup>11,12,13,14</sup> While adult males do not share home ranges with other adult males; young males frequently overlap ranges of males nine years and older.<sup>11,14</sup> This suggests that young males roam and regularly associate with older males.

Black rhinos exhibit varying levels of social complexity. At the simplest level, temporary aggregations form in habitats with low-lying vegetation and preferred forage species.<sup>11</sup> Neighboring adult males and adult females form longer breeding relationships, which determine individual habitat use and spatial overlap.<sup>13</sup> There is also some added complexity to these relationships in the form of social dominance based on sex and horn size.<sup>32</sup> Among males, larger horns are associated with higher dominance.<sup>32</sup> Between the sexes, females exhibit dominance over males, regardless of horn size.<sup>32</sup> Scientists also believe that olfactory communication plays an important role in social relationships.<sup>27</sup>

In addition, social relationships clearly play some beneficial role, as evidenced by the importance of group size for relocation success.<sup>9</sup> Scientists suggest that social peers could play an important role in resource acquisition, especially in unfamiliar low quality habitats.<sup>9</sup> Navigating the social environment is also important for establishing new home ranges and must be considered in management decisions.<sup>35</sup>

## HABITAT AND ECOLOGY

Black rhinos are herbivorous browsers and prefer small acacias and other palatable woody species, as well as herbs and succulents.<sup>1</sup> However, many woody species are unpalatable due to high levels of plant chemicals.<sup>1</sup> Black rhinos are highly selective foragers, and while they may eat over 80 species, a small number of species account for the majority of their diet.<sup>36</sup> Previous calculations have over-estimated carrying capacities due to failure to acknowledge this.<sup>1</sup> Carrying capacity is driven by rainfall, soil nutrient status, fire histories, levels of grass interference, extent of frost, and densities of other large browsers.<sup>1</sup>

Black rhinos are found in a wide variety of habitats, although the highest densities reside in savanna habitats.<sup>1</sup> Home ranges are highly variable, shift over time, and depend on several factors, such as season, resource availability, habitat type, human disturbance, and neighboring rhinos.<sup>11,14,37</sup> Surface water may be the primary limiting factor for female black rhino habitat use.<sup>37</sup> Home ranges not only reflect resource availability, but black rhinos tend to shift and reconfigure their home ranges to avoid human disturbances.<sup>14</sup> Mean home range sizes vary from 12 km<sup>2</sup> to 89.9 km<sup>2</sup> and are highly dependent on location, methodology, season, and resource availability.<sup>11,38</sup> Home ranges are also important predictors of social interactions and adult male-female breeding relationships.<sup>11,12,13,14</sup> In males, home range size is also correlated with greater genetic heterozygosity, which is the strongest predictor of reproductive success.<sup>29</sup>

Many remaining black rhinos reside in fenced reserves and intensive protection zones.<sup>1</sup> Fenced reserves may also limit future population genetic diversity due to isolation of subpopulations. In addition, injuries and mortalities from male-male fighting are more common in smaller reserves.<sup>8</sup> Therefore, reserve size and location are critical for survival and reproduction.

Black rhinos play an important role in the ecosystem as grazers, which shapes the local landscape. Megaherbivores, such as rhino, are unique in their ecosystem in their ability to alter nutrient cycles, soil properties, fire regimes, and primary production.<sup>5,39</sup> These roles cannot be taken over by smaller herbivores. Due to their importance, scientists recommend a global government-funded scheme for

rare large herbivores, like black rhino.<sup>5</sup> Black rhinos are also economically important. They bring in significant revenue in the photo safari industry.<sup>5</sup> Black rhinos are highly sought by tourists who will pay high prices to observe a black rhino in the wild.<sup>40,41</sup>

## DIRECT ANTHROPOGENIC THREATS

The greatest human-caused, or anthropogenic, threat is illegal killing for the rhino horn trade.<sup>1</sup> African rhino horns are one of the most expensive goods in the world.<sup>42</sup> In 2013-2014, the price of rhino horn ranged between US\$25,000 and US\$65,000 per kilogram.<sup>43</sup> As of 2017, the price of rhino horn had increased to US\$45,000 and US\$120,000 per kilogram.<sup>42</sup> Since rhino horn has long been a highly valued good, there is a history of unregulated and excessive hunting.<sup>42</sup> Between 1960 and 1995, large-scale poaching caused a dramatic 98% collapse in population numbers.<sup>1</sup> Although black rhino poaching peaked in 2015 and has declined, poaching has continued to slow population growth.<sup>1</sup> Poaching also threatens black rhino conservation efforts because many private landowners find it too costly and risky to maintain the species.<sup>1</sup>

There are multiple corrupt networks involved in black rhino poaching.<sup>42,44</sup> Poaching networks range in sophistication and include organized crime syndicates that use high tech methods to poach rhinos and smuggle horns.<sup>44</sup> Pseudo-hunting networks involve a scheme where people apply for trophy hunting permits as a cover for obtaining and trading rhino horns.<sup>44</sup> Pseudo-hunting is a regulatory loophole where ‘hunters’ from atypical countries for trophy hunting, such as Viet Nam, trophy hunt for the sole intent of obtaining rhino horn. This is one way in which seemingly legal products end up in illegal markets. South Africa is currently the primary supplier of illegal rhino horn through poaching and pseudo-hunting.<sup>45</sup> Pseudo-conservation networks are where groups obtain live rhinos and trade them domestically under the guise of conservation, only to kill and dehorn the animals for illegal trade.<sup>44</sup> Theft networks are also common, where black rhino horns are stolen from both private and government stockpiles, as well as institutions and museum collections.<sup>44</sup>

The Groenewald gang or the “Musina group” is a well-known rhino poaching syndicate that was charged with 1,736 counts of racketeering, money laundering, fraud, intimidation, illegal hunting, and

dealing in rhino horns in South Africa.<sup>42</sup> Working at the interface of legal and illegal markets, they were also accused of selling fake trophy hunting permits and illegal dehorning of rhinos.<sup>42</sup> The Groenewald gang allegedly was socially well-connected with the African wildlife industry, and Dawie Groenewald allegedly obtained rhinos and rhino horns from other farmers, as well as illegally hunted rhinos on his own land.<sup>42</sup> The privatization of rhinos allowed for the Groenewald gang, and others, to appear legitimate and go undetected.

Black rhinos have two prominent horns, which grow throughout their lifetime and naturally vary in size.<sup>32</sup> Males and females have similarly sized horns; therefore, both are targeted by poachers. In fact, poachers target all age and sex classes.<sup>46</sup> However, males are disproportionately targeted by poachers, which significantly alters sex ratios.<sup>47</sup> Populations protected from poaching exhibit more equal sex ratios than those with heavy poaching pressure.<sup>47</sup> Males are constrained in the distance they are able to flee from poachers due to the importance of established home ranges, which leaves them at greater risk of being killed.<sup>47</sup> Females travel further than males, up to 40 km a day, in response to poaching pressure,<sup>47</sup> which may be energetically costly, result in loss of resources, and negatively affect survival. Poaching also decreases future population growth by altering age structures and reproductive rates.<sup>23,48</sup> In Kruger National Park, South Africa, a stronghold for black rhinos, the poaching rate is double the recruitment rate.<sup>48</sup> Poaching can also decrease population growth through suppressed recruitment, increased calving intervals, and leaving orphaned calves.<sup>23</sup> After only four years of heavy poaching pressure, the black rhino population in Kruger National Park exhibited a significantly different age structure and a decrease in the proportion of calves.<sup>23</sup> Poaching creates ecological traps, where prime habitat is also associated with a high risk of poaching.<sup>49</sup> These ecological traps, in combination with poor recolonization behavior, means that poaching is likely to cause local extinctions of black rhinos.<sup>49</sup>

Due to drastic population declines and small fragmented populations, each black rhino is important for maintaining genetic diversity, which is essential for reproductive success.<sup>29</sup> In addition, because reproductive success is highly skewed, where select males are responsible for the majority of breeding, offtake of these successful males would have deleterious impacts on population growth.<sup>19</sup>

Hunting organizations argue that individuals must be removed from the population in order to reduce density and stimulate population growth, although there is also no evidence that manipulation of age or sex structures stimulates population growth.<sup>17</sup> Black rhinos exhibit similar birth rates at different population densities.<sup>50</sup> Further, rhinos are poor dispersers and are unlikely to colonize recently vacated home ranges. Following the removal of a neighbor for translocation purposes, rhinos are slow to recolonize the habitat that was occupied by their former neighbor.<sup>13</sup> Female and male rhinos form breeding relationships that influence habitat use; therefore, removal of an individual results in the loss of a breeding relationship that is not immediately replaced. Decreased home range overlap also reduces interactions between the sexes, which is especially concerning in populations with low density. Scientists say that social behavior of black rhino must be considered when removing individuals from a population; otherwise, an unbalanced social structure could shift home ranges and reduce reproductive rates because rhinos are expending more energy on establishing new home ranges rather than on reproduction.<sup>34</sup> Trophy hunting random individuals in the population does not consider these impacts and can further slow population growth.

In addition, hunting organizations also argue that “excess” older males can be removed as they no longer contribute to reproduction; however, there is no evidence that males stop reproducing in old age. Hunting organizations argue that removing males from a population decreases injury or death due to male-male fighting. Yet, scientists say social disruption that is not specifically planned based on rhino social networks will *increase* conflict.<sup>34</sup> In addition, scientists worry that lower population densities will result in fewer breeding opportunities and higher calf predation.<sup>23</sup> Thus, trophy hunting can actually have the opposite effect of what they claim. Genetic diversity is the most important predictor of male reproductive success; therefore, every individual is important to the population. Low levels of genetic diversity across much of the black rhino’s range can be explained by the onset of trophy hunting in the latter half of the 19<sup>th</sup> century.<sup>3</sup> Relentless hunting throughout the 20<sup>th</sup> century also contributed to large population declines.<sup>1</sup> Further, trophy hunters are likely targeting the most important males given their preference for large horns, which belong to the most dominant males.<sup>32</sup> According to experts, “[c]urrent understanding of black rhino-

eros (*Diceros bicornis*) demography and population dynamics remains poor.”<sup>51</sup> Therefore, allowing trophy hunting without adequate evidence and understanding of how offtake will affect the species could be detrimental to future survival.

Due to their rarity, black rhino trophies fetch one of the highest prices of any species.<sup>52</sup> However, considering the small population size and potential negative impacts, there are serious concerns about whether such a rare and Critically Endangered species should be hunted as a trophy. Further, the rarity of the black rhino, and the high trophy fees, may incentivize unsustainable trophy hunting.

Black rhinos may also be used in ‘put-and-take’ hunting, where animals from highly managed areas are released onto a property for the sole purpose of being immediately shot and then restocked again.<sup>45,53</sup> This often occurs in very unnatural settings, where wildlife production units are too small to support self-sustaining wildlife populations.<sup>53</sup> Offtake from ‘put-and-take’ is excessive and feeds into illegal trade.<sup>45</sup> ‘Put-and-take’ hunting threatens biodiversity due to disease transmission, genetic mixing, and releasing subpar individuals.<sup>53</sup> Experts say that this practice should be prohibited as it “compromise[s] the principles of fair chase and the humane treatment of animals.”<sup>53</sup> By way of pseudo-hunting, ‘put-and-take,’ and other loopholes, trophy hunting can provide an avenue for illegal trade.<sup>42</sup>

## MANAGEMENT IMPLICATIONS

Black rhino populations have drastically declined over the last 50 years, primarily due to illegal hunting for their horns and habitat loss. Poaching rhino for their horns is an organized crime problem, which is very difficult to address without full government support within and between range States.<sup>6</sup> Prosecution of those engaged in rhino horn trafficking is improving; however, there are still problems with trial postponements, granting bail, and light sentences for poachers and traffickers.<sup>6</sup>

Pseudo-hunting and ‘put-and-take’ hunting are at the nexus of legal and illegal markets.<sup>45</sup> Both involve corruption by multiple agents that exploit regulatory loopholes and “belong to influential and transnational social networks with links to political and economic elites in supply, transit and consumer countries.”<sup>45</sup> Beyond that, South African court cases indicate that “rhino breeders, professional hunters,

veterinarians, nature conservation officials, and others are involved in the illicit ‘production’ and trafficking of rhino horn.”<sup>42</sup> Wildlife professionals have also been involved in poaching rhinos.<sup>45</sup>

Critically Endangered species should not be trophy hunted, especially when facing ongoing and increasing threats, such as poaching and habitat loss. With such high levels of poaching and slow population growth, no levels of hunting offtake can be considered sustainable, especially given such a poor understanding of demography and population dynamics.<sup>51</sup> Management plans aim for 5% annual population growth; however, due to poaching, some of those targets have been lowered to 1%.<sup>54,55,56</sup> If such low population growth targets are not feasible, then trophy hunting should not be allowed to contribute to the problem. In addition, maintenance of genetic diversity is critical in the face of severe population declines and habitat fragmentation. Trophy hunters and poachers target rhinos with the largest horns, which are also the most dominant males. Males reproductive success is highly variable, meaning that the most important breeding males could be removed, leaving less successful breeders. A long history of trophy hunting has been linked to loss of vital genetic diversity.<sup>3</sup> Removal of dominant males with large horns removes important genetic diversity from the population that may be detrimental to future population growth.

Yet, some countries are *increasing* their trophy hunting quotas for black rhinos. South Africa recently increased its quota from 5 individuals to 0.5% of the population. Based on the most recent (2017) population estimates, that would double the number of black rhinos hunted from 5 to 10 annually. This system requires extremely precise and current population counts, which are not available. In addition, management based on population size should also consider demographic factors. For example, a high percentage of older individuals or a skewed sex ratio would indicate slowed future population growth, which would not be captured by simply counting individuals in the population. Therefore, there are concerns about how this system will impact black rhino populations in the future.<sup>57</sup>

Despite arguments from hunting organizations, there is no evidence that older males or females are redundant in the population. In fact, hunters are likely targeting the most important males for population growth, given their large horn size, social

dominance, and variability in reproductive success. Trophy hunting fees have not provided protection for black rhinos as populations are still plummeting, even in protected areas. Given that black rhino trophy fees are among the highest of all species, there should be some evidence of population protection and recovery if trophy hunting were contributing to conservation. There is also concern that trophy hunting provides a legal pathway for trafficking black rhino horns and encouraging further poaching.

## REFERENCES

- Emslie R. (2020) *Diceros bicornis*. The IUCN Red List of Threatened Species. 8235, e.T6557A152728945.
- Emslie R. (2020) *Diceros bicornis*. The IUCN Red List of Threatened Species - Supplemental.
- Moodley Y. et al. (2017) Extinctions, genetic erosion and conservation options for the black rhinoceros (*Diceros bicornis*). *Sci. Rep.* 7, 1–16.
- Ceballos G. & Ehrlich P.R. (2002) Mammal population losses and the extinction crisis. *Science*. 296, 904–907.
- Ripple W.J. et al. (2015) Collapse of the world's largest herbivores. *Sci. Adv.* 1, e1400103.
- Emslie R.H. et al. (2019) African and Asian Rhinoceroses – Status, Conservation and Trade: A report from the IUCN Species Survival Commission (IUCN/SSC) African and Asian Rhino Specialist Groups and TRAFFIC to the CITES Secretariat pursuant to Resolution Conf. 9.14 (Rev. CoP17). In *CoP18 Doc. 83.1 Annex 2. CITES Secretariat, Geneva, Switzerland*.
- Linklater W.L. et al. (2011) Guidelines for large herbivore translocation simplified: black rhinoceros case study. *J. Appl. Ecol.* 48, 493–502.
- Linklater W.L. & Swaisgood R.R. (2008) Reserve size, conspecific density, and translocation success for black rhinoceros. *J. Wildl. Manage.* 72, 1059–1068.
- Linklater W.L. et al. (2012) Translocations as experiments in the ecological resilience of an asocial mega-herbivore. *PLoS One* 7.
- Adcock K. et al. (1998) Lessons from the introduced black rhino population in Pilanesberg National Park. *Pachyderm* 26, 40–51.
- Lent P.C. & Fike B. (2003) Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. *African J. Wildl. Res.* 33, 109–118.
- Hitchins P.M. (1971) Preliminary findings in a radio telemetric study on the black rhinoceros in Hluhluwe Game Reserve, Zululand. *Proc. a Symp. Biotelemetry, Pretoria*, 79–100.
- Linklater W.L. & Hutcheson I.R. (2010) Black rhinoceros are slow to colonize a harvested neighbour's range. *African J. Wildl. Res.* 40, 58–63.
- Odendaal-Holmes K. et al. (2014) Disturbance and habitat factors in a small reserve: space use by establishing black rhinoceros (*Diceros bicornis*). *African J. Wildl. Res.* 44, 148–160.
- Linklater W.L. et al. (2010) Declining and low fecal corticoids are associated with distress, not acclimation to stress, during the translocation of African rhinoceros. *Anim. Conserv.* 13, 104–111.
- Patton F. et al. (2008) Biological management of the high density black rhino population in Solio Game Reserve, central Kenya. *Pachyderm* 44, 72–79.
- Balfour D. et al. (2019) *Concise best practice guidelines for the biological management of African rhino*. WWF-SA. 123pp.
- Alibhai S.K. et al. (2001) Effects of immobilization on fertility in female black rhino (*Diceros bicornis*). *J. Zool.* 253, 333–345.
- Freeman E.W. et al. (2014) Impacts of environmental pressures on the reproductive physiology of subpopulations of black rhinoceros (*Diceros bicornis bicornis*) in Addo Elephant National Park, South Africa. *Conserv. Physiol.* 2, 1–13.
- Nhleko Z.N. et al. (2017) The reproductive success of black rhinoceroses in the Hluhluwe–iMfolozi Park, KwaZulu-Natal, South Africa. *Koedoe* 59, 1–10.
- Hitchins P.M. & Anderson J.L. (1983) Reproduction, population characteristics and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/Corridor/Umfolozi game reserve complex. *South African J. Wildl. Res.* 13, 78–85.
- Owen-Smith R.N. (1988) *Megaherbivores: the influence of very large body size on ecology* Cambridge University Press.
- le Roex N. & Ferreira S.M. (2020) Age structure changes indicate direct and indirect population impacts in illegally harvested black rhino. *PLoS One* 15, e0236790.
- Okita-Ouma B. et al. (2020) Relationships of reproductive performance indicators in black rhinoceros (*Diceros bicornis michaeli*) with plant available moisture, plant available nutrients and woody cover. *Afr. J. Ecol.*, 1–15.

25. Garnier J.N. *et al.* (2002) Non-invasive assessment of oestrous cycles and evaluation of reproductive seasonality in the female wild black rhinoceros (*Diceros bicornis minor*). *Reproduction* 123, 877–889.
26. Hrabar H. & du Toit J.T. (2005) Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Anim. Conserv.* 8, 259–267.
27. Linklater W.L. *et al.* (2006) Preliminary analyses of the free-release and scent-broadcasting strategies for black rhinoceros reintroduction. *Ecol. J.* 7, 26–34.
28. Schenkel R. & Schenkel-Hulliger L. (1969) *Ecology and Behaviour of the Black Rhinoceros (Diceros bicornis L.)*. A Field Study. Paul Parey, Parey, Hamburg.
29. Cain B. *et al.* (2014) Sex-biased inbreeding effects on reproductive success and home range size of the critically endangered Black rhinoceros. *Conserv. Biol.* 28, 594–603.
30. Garnier J.N. *et al.* (2001) Mating system and reproductive skew in the black rhinoceros. *Mol. Ecol.* 10, 2031–2041.
31. Brown J.L. *et al.* (2001) Comparative analysis of gonadal and adrenal activity in the black and white rhinoceros in North America by noninvasive endocrine monitoring. *Zoo Biol.* 20, 463–486.
32. Berger J. & Cunningham C. (1998) Natural variation in horn size and social dominance and their importance to the conservation of black rhinoceros. *Conserv. Biol.* 12, 708–711.
33. Christensen B.W. *et al.* (2009) Effects of socio-sexual environment on serum testosterone in captive male African rhinoceros. *Theriogenology* 71, 1105–1111.
34. Reid C. *et al.* (2007) Habitat changes reduce the carrying capacity of Hluhluwe-Umfolozi Park, South Africa, for Critically Endangered black rhinoceros *Diceros bicornis*. *Oryx* 41, 247–254.
35. Morgan S. (2010) Black rhinoceros (*Diceros bicornis*) habitat selection and movement analysis. (Doctoral Thesis). University of KwaZulu-Natal.
36. van Lieverloo R.J. *et al.* (2009) A comparison of faecal analysis with backtracking to determine the diet composition and species preference of the black rhinoceros (*Diceros bicornis minor*). *Eur. J. Wildl. Res.* 55, 505–515.
37. le Roex N. *et al.* (2019) Seasonal space-use and resource limitation in free-ranging black rhino. *Mamm. Biol.* 99, 81–87.
38. Göttert T. *et al.* (2010) Habitat use and spatial organisation of relocated black rhinos in Namibia. *Mammalia* 74, 35–42.
39. le Roux E. *et al.* (2018) Megaherbivores modify trophic cascades triggered by fear of predation in an African Savanna Ecosystem. *Curr. Biol.* 28, 2493–2499.
40. Di Minin E. *et al.* (2013) Understanding heterogeneous preference of tourists for big game species: implications for conservation and management. *Anim. Conserv.* 16, 249–258.
41. Lindsey P.A. *et al.* (2007) Wildlife viewing preferences of visitors to protected areas in South Africa: implications for the role of ecotourism in conservation. *J. Ecotourism* 6, 19–33.
42. Hübschle A. (2017) Contested Illegality Processing the Trade Prohibition of Rhino Horn. In *The architecture of illegal markets* (Beckert J. & Dewey M., eds.), pp. 177–197. Oxford University Press.
43. Hübschle A.M. (2017) The social economy of rhino poaching: Of economic freedom fighters, professional hunters and marginalized local people. *Curr. Sociol.* 65, 427–447.
44. Ayling J. (2013) What sustains wildlife crime? Rhino horn trading and the resilience of criminal networks. *J. Int. Wildl. Law Policy* 16, 57–80.
45. Hübschle A. (2016) A Game of Horns: Transnational Flows of Rhino Horn. (Doctoral Thesis). Universität Köln.
46. Leader-Williams N. (1988) Patterns of depletion in a black rhinoceros population in Luangwa Valley, Zambia. *Afr. J. Ecol.*
47. Berger J. (1995) Predation, sensitivity, and sex: Why female black rhinoceroses outlive males. *Behav. Ecol.* 6, 57–64.
48. Ferreira S.M. *et al.* (2018) Realization of poaching effects on rhinoceroses in Kruger National Park, South Africa. *African J. Wildl. Res.* 48, 013001.
49. le Roex N. *et al.* (2020) Poaching creates ecological traps within an iconic protected area. *Anim. Conserv.* 23, 250–259.
50. Ferreira S.M. *et al.* (2019) Species-specific drought impacts on black and white rhinoceroses. *PLoS One* 14, 1–11.
51. Law P.R. *et al.* (2019) Intriguing density dependence but problematic birth rates in Greaver *et al.*'s study of a black-rhinoceros population. *bioRxiv* 039453.
52. Palazy L. *et al.* (2012) Rarity, trophy hunting and ungulates. *Anim. Conserv.* 15, 4–11.
53. *Report to the Minister of Environmental Affairs*



- and Tourism*. (2005). Panel of experts on professional and recreational hunting in South Africa.
54. Emslie, R. & Brooks, M. (1999). *African rhino: status survey and conservation action plan*. Gland, Switzerland: IUCN.
  55. Knight, M.H., Balfour, D. & Emslie, R.H. (2013). *Biodiversity management plan for the black rhinoceros (Diceros bicornis) in South Africa 2011–2020*. Government Gazette (South Africa), 36096, 5–76.
  56. SANParks. (2020). *Strategic Plan: 2020/21–2023/24*. Pretoria, South Africa: SANParks.
  57. Save the Rhino. (2019). *CITES permits changes to South Africa’s black rhino trophy hunting quota*. Available at: <https://www.savetherhino.org/africa/south-africa/cites-permits-changes-to-south-africas-black-rhino-trophy-hunting-quota/>.