

# Effective implementation of age restrictions increases selectivity of sport hunting of the African lion

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## Abstract

1. Sport hunting of wildlife can play a role in conservation but can also drive population declines if not managed sustainably. Previous simulation modelling found that large felid species could theoretically be hunted sustainably by restricting harvests to older individuals that have likely reproduced. Several African countries currently use age-based hunting for lions although the outcomes have yet to be evaluated in a wild population.
2. Here we provide the first empirical evidence that a system of incentives sufficiently encouraged age-based hunting and reduced offtake of a wild felid, thereby reducing the potential risk of unsustainable hunting on a threatened species. We examined long-term hunting data and the lion population trend in Niassa National Reserve, Mozambique.
3. To incentivise hunter compliance, a “points” system was developed, which rewards operators that harvest lions older than the 6-year minimum trophy age recommended for sustainable hunting and penalises operators that hunt “underage” lions (<4 years). A key component of this system is the ecological application of key physical traits that predictably change with age in order to estimate (by hunters) and validate (by authorities) trophy individuals’ ages pre- and post-mortem, respectively. Analysis of 138 lion hunts and 87 lion trophies from 2003 to 2015 revealed that after enforcement of age restrictions in 2006, hunters shifted harvests to suitably aged lions (>6 years), from 25% of offtakes in 2004 to 100% by 2014.
4. Simultaneously, the number of lions and percentage of quota harvested decreased, resulting in lower lion offtakes. Following an initial decrease after enforcement of the ageing system, the percentage of hunts harvesting lions stabilised, demonstrating that hunters successfully located and aged older lions.
5. *Synthesis and applications.* Evidence suggests that age restrictions combined with an incentive-based points system regulated sport hunting and reduced pressure on the lion population. We attribute the successful implementation of this management system to: (1) committed, consistent enforcement by management authorities, (2) genuine involvement of all stakeholders from the start, (3) annual auditing by an independent third party, (4) the reliable, transparent, straightforward ageing process and (5) the simple, pragmatic points system for incentivising hunter compliance. Our study demonstrates that the use of age restrictions can increase the selectivity of sport hunting and lower trophy offtakes to reduce the possibility of

unsustainable sport hunting negatively impacting species populations in the absence of reliable estimates of population size. It must be noted, however, that there was no measurable change in the lion numbers over the past decade that could be attributed to the implementation of this policy alone.

#### KEYWORDS

African lion, age-based hunting, age restrictions, minimum age, Mozambique, Niassa National Reserve, *Panthera leo*, sport hunting, sustainability, trophy hunting

## 1 | INTRODUCTION

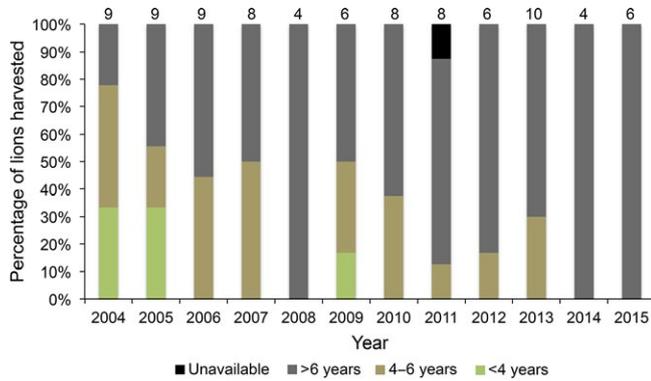
Sport hunting of wildlife can play a role in conservation world-wide by motivating and financing the protection of animals and land (Jorge, Vanak, Thaker, Begg, & Slotow, 2013; Lindsey, Roulet, & Romañach, 2007; Naidoo et al., 2016). However, sport hunting can also play a role in driving species declines in some areas, as has been observed for elephants (Selier, Page, Vanak, & Slotow, 2014), leopards (Pitman, Swanepoel, Hunter, Slotow, & Balme, 2015) and lions (Bauer et al., 2015). An animal's age is a common metric used to guide the sustainable harvest and management of a number of species throughout the world (Berkeley, Hixon, Larson, & Love, 2004; Garel, Cugnasse, Hewison, & Maillard, 2006; Gipson, Ballard, Nowak, & Mech, 2000; Hiller, 2014; Lundervold & Langvatn, 2003). Simulation modelling studies recently identified the implementation of age restrictions on trophy harvests as a promising method for regulating sustainable sport hunting of large carnivores, including African lions (Creel et al., 2016; Packer et al., 2009; Whitman, Starfield, Quadling, & Packer, 2004). A major benefit of age-based hunting (set at appropriate age thresholds) is that the age distribution of age-structured populations naturally ensures sustainable harvest, potentially alleviating the need for quotas based on population monitoring in large landscapes where the exact number of animals present may be impossible to determine. Several African countries have implemented age-based hunting over the past decade yet the outcomes of this method have yet to be measured in the field. Here we provide the first empirical evidence that age restrictions can be effectively implemented at the management level to increase the selectivity of sport hunting and lower trophy offtakes to reduce the risk of unsustainable hunting.

We focus on the African lion because it is a highly threatened species yet is legally sport hunted in nine countries, with roughly 240 wild lions hunted each year in Africa (most from Tanzania, Zimbabwe, Zambia, Mozambique, Namibia, Burkina Faso, Benin and Central African Republic; Bauer et al., 2015; Lindsey et al., 2013). Lions are experiencing rapid population decline, with the global population decreasing 42% over the past 21 years (three generations) to an estimated 20,000 individuals (Bauer et al., 2015). Excessive sport hunting has contributed to lion declines in parts of southern and eastern Africa (Groom, Funston, & Mandisodza, 2014; Loveridge, Searle, Murindagomo, & Macdonald, 2007; Packer et al., 2009, 2011; Rosenblatt et al., 2014). In an attempt to mitigate overexploitation by sport hunting, modelling studies found that sustainable hunting of

large felids could be achieved by restricting harvest to males that have raised at least one litter of offspring to independence, or  $\geq 5$  years in lions (Packer et al., 2009; Whitman et al., 2004; note that very recent modelling suggests that higher age thresholds are required in some populations, e.g. Creel et al., 2016). This accounts for infanticide, which occurs when invading males kill the offspring of males that have been displaced or removed, a phenomenon that makes large felids susceptible to population instability due to sport hunting (Bertram, 1975; Caro, Young, Cauldwell, & Brown, 2009; Packer, 2001). An age-based harvest also reduces the need for precise information on lion numbers, removing the risk of unsustainable quotas common in areas where monitoring lions is conducted unscientifically, not at all or provides insufficient demographic or population data to determine accurate quotas (Lindsey et al., 2013; Whitman, Starfield, Quadling, & Packer, 2007). Following these recommendations, age-based hunting was implemented as a management tool first in Niassa National Reserve in Mozambique starting in 2006 and later (2007–2013) in Tanzania and Zimbabwe. To date, Niassa National Reserve (hereafter, "Niassa") supports the most well-established, transparent and longest term system of age-based lion sport hunting, representing an opportune site for evaluating the outcomes of age restrictions on lion hunting.

Niassa is a vast protected area of 42,200 km<sup>2</sup> in northern Mozambique and one of only eight populations with more than 1,000 lions (Riggio et al., 2012). The protected area is divided into 17 management units allocated for ecotourism and sport hunting. Hunting fees fund 30% of the annual operational costs of the reserve as well as anti-poaching and management activities (Jorge et al., 2013). A total of 27,986 km<sup>2</sup> has been designated for sport hunting; this includes six concessions designated since 2003 (covering 20,424 km<sup>2</sup>) and three concessions added for sport hunting in 2010–2011 (covering an additional 7,562 km<sup>2</sup>). Different concessions are active or inactive each year (depending on lion hunt quota allocations, operators choosing not to hunt during certain years or pauses during changes in concession ownership). Sociedade de Gestão e Desenvolvimento da Reserva do Niassa (SRN) managed the reserve prior to 2012 and since then Niassa has been co-managed by Mozambique's National Administration for Conservation Areas (ANAC) and the Wildlife Conservation Society (WCS).

Since 2004, in agreement with the Niassa managing authority, lion trophy monitoring and ageing has been conducted by the Niassa Carnivore Project (NCP), a field-based non-profit organisation that



**FIGURE 1** Percentage of lion trophies in each age category from 2004 to 2015 in Niassa National Reserve, Mozambique. Numbers above bars indicate the number of lions harvested each year [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

partners with reserve authorities to conserve large carnivores. After initial monitoring in 2004, NCP discovered that the majority of harvested lions were immature (78% of trophies were <6 years; Figure 1) and below the science-based age threshold recommended for sustainable hunting (Whitman et al., 2004). At this time there was no information on the lion population density in Niassa and the SRN established lion quotas based on conservative “guesstimates” derived from potential lion density given estimates of prey abundance from aerial census results. Between 2004 and 2006, NCP identified the legal offtake of underage adults through sport hunting as one of the top four potential threats to the lion population in Niassa, in addition to retaliatory killing, bushmeat snaring and potential disease outbreaks.

In an effort to reduce the threat of unsustainable sport hunting of lions and implement sustainable harvest practices in Niassa in the absence of reliable lion population data, NCP worked closely with sport hunting operators, professional hunters and the SRN to develop the Niassa Lion Points System, a system for allocating annual quotas based on the age of lions hunted as trophies rather than population size. The goal of the system is threefold: (1) to adjust annual quotas for each hunting area based on the number of suitably aged lions hunted as trophies (as a proxy of population size), (2) to discourage the harvest of underage lions and encourage the harvest of old lions

and (3) to improve monitoring of trophy harvests. In accordance with science-based age recommendations (Whitman et al., 2004) and practical visual ageing cues of male lions in Niassa (Miller et al., 2016; see “Materials and Methods” for details), the minimum age threshold for hunting was set at 6 years. Under the points system, operators are “penalised” with quota reductions in the following season if underage lions are hunted or “rewarded” with quota increases if all the lions hunted are >6 years (Table 1). A “neutral” middle age range between 4 and 6 years was established to account for individual variation in lions (Miller et al., 2016) and genuine ageing mistakes made by operators under field conditions. If an operator harvests one 4- to 6-year-old lion in a season, this “mistake” will not result in a decreased quota the following year; however, if all lions harvested fall in this age category then the quota decreases. This format incentivises hunters to seek out old lions that are visually obvious rather than focus on lions of the minimum age, which are more difficult to accurately identify. Additionally, new hunting concession areas and/or new operators are given a starting quota of only two lions to ensure that new areas are not overhunted in the first year and that new operators have time to learn how to age lions. This quota can only be increased if both lions taken are >6 years old.

In 2006, Niassa sport hunting operators and the reserve management authority unanimously accepted the Niassa Lion Points System in a public meeting. To assist sport hunters in learning to age lions using visual criteria, NCP developed educational materials (e.g. pocket guide) and provided annual training presentations. The SRN began enforcing trophy age restrictions in 2006, followed by use of the points system to set quotas for the 2007 hunting season onwards based on the previous year’s trophy age. At this time, NCP set a conservation goal for more than 80% of the lion trophies harvested to be older than 6 years.

We examined long-term lion hunting data in Niassa to assess whether lion hunting age restrictions and the points system were effectively implemented and whether these measures reduced the potential risk of unsustainable sport hunting by raising trophy age and reducing offtake. Here we provide the first field-based evidence from the implementation of hunting age restrictions for a large felid species and discuss lessons learned to aid the design and implementation of sustainable, age-based hunting programmes in other countries.

**TABLE 1** Niassa Lion Points System for allocating lion trophy quotas by hunting concession area in Niassa National Reserve, Mozambique. Trophy quotas for each concession for the following year are calculated based on the current year’s trophies as follows: (1) Each lion trophy harvested receives points according to the system shown in the table. (2) Points are summed for that year, divided by 3 and rounded to the nearest whole number. The maximum quota possible is five lion trophies and the final number is the trophy quota for that concession the following year

Number of trophies in each age category	Number of points earned for each lion trophy in a concession			No trophy harvested	Incomplete hunting return form
	<4 years	4–6 years	>6 years		
3–5 trophies	–3	2	4	3	0
2 trophies	0	2	4	3	0
1 trophy	0	0	6	3	0

## 2 | MATERIALS AND METHODS

Hunting data were obtained from hunt return forms submitted for each lion trophy from 2003 to 2015 (Begg, Miller, & Begg, 2017). At the start of the hunting season, NCP provides hunting operators with a hunt return form for each allocated lion trophy, which must be returned by the end of the season (or no points will be assigned for that trophy). Operators are required to report information about the hunting process and trophy, including whether the hunt was successful (lion was harvested), and must submit photographs of the trophy along with each form. We measured hunt effort as the percentage of hunts where lions were successfully harvested. Data on the number of lion licenses purchased (one license required per harvested lion) were collected directly from the SRN prior to 2012, after which operators purchased licenses from the government directly and we assumed the number of purchased lion licenses equalled the number of lion hunts since Niassa operators only purchase licenses for confirmed hunts.

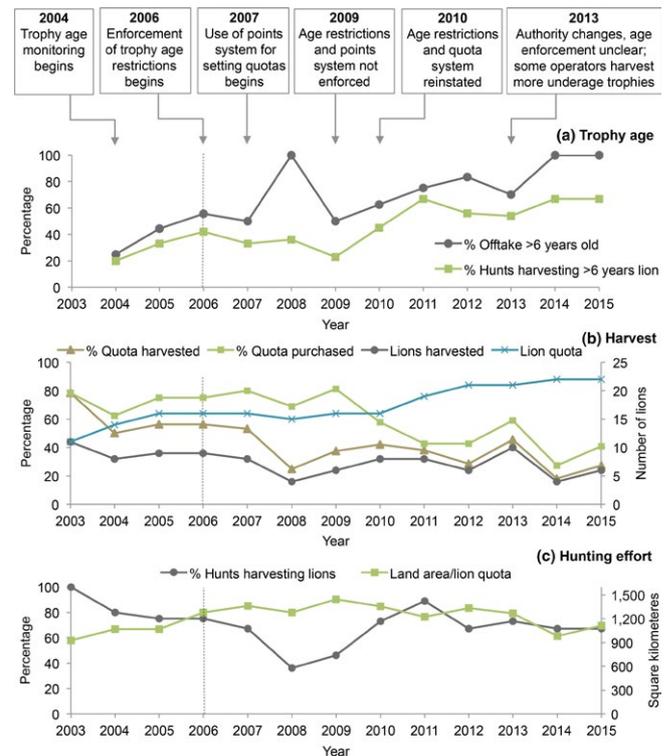
Starting in 2004, all trophies were aged by experienced researchers from NCP before being removed from Niassa. Age estimations were (and continue to be) based on patterns of teeth wear, which vary predictably with age (Smuts, Anderson, & Austin, 1978), as well as standard visual ageing criteria used for African lions generally and tailored by NCP specifically for lions in Niassa. Evidence from known-age individuals sampled from across Africa shows that lion age can be determined *pre-mortem* based on a suite of physical traits (mane development, nose colour, facial scarring, teeth colour and wear and jowl slackness; see Miller et al., 2016; Whitman et al., 2004 for details on age determination). Clear and straightforward guidelines on age determination with these traits provide an objective method for accurately ageing lions with  $\pm 1.0$  year of precision (Whitman & Packer, 2007; [www.agingtheafricanlion.org](http://www.agingtheafricanlion.org)). A small sample of known-age and individually identifiable radiocollared lions (three males and six females) in Niassa were studied over time (range of 4–10 years) to validate regional rates of change in these visual ageing cues. All traits were found to match standard rates of development except for mane growth, which shows slower rates of development in Niassa lions (Begg & Begg, 2007; Miller et al., 2016). This difference can create ageing ambiguity in the 4–6 year age category; however, Niassa lions of 6 years of age and older are clearly identifiable based on mane and the other visual characteristics. Therefore, to provide a buffer for error in the 4–6 year age category, the ages of Niassa lions were estimated according to three age categories: <4 years, 4–6 years or >6 years. We used data on lion trophy age to calculate the percentage of the annual offtake that was >6 years of age (the Niassa age category that is fully compliant with the recommended age for sustainable harvest; Whitman et al., 2004).

## 3 | RESULTS

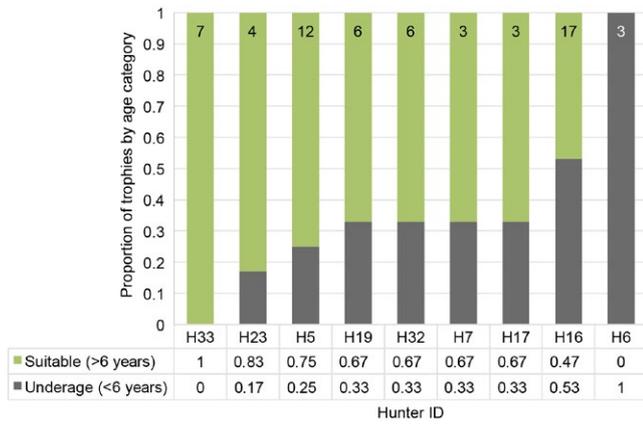
Over the 13-year period in Niassa, hunting operators conducted 138 lion hunts and harvested 87 lion trophies. All lion trophies from 2004

onwards were aged except for one individual in 2011, which was removed from the Niassa Reserve before it could be aged (the operator provided a hunt return but did not receive points for the lion). Hunters increasingly harvested a greater proportion of older lions over the study period and restricted harvests to lions >4 years old after 2009 and >6 years old after 2013 (Figure 1). The percentage of lion trophies >6 years old and the percentage of hunts harvesting trophies >6 years both increased over time (Figure 2a). Over the same time period, the number of lions harvested and percentage of quota harvested decreased, as did the percentage of quota purchased by clients for safari hunts (Figure 2b). Individual hunter records indicated that some hunters were successful in harvesting a large quantity of lion trophies consisting of 100% or near-100% suitably aged lions, whereas others were not (Figure 3).

The total hunting quota for Niassa increased from 14 male lions per year in 2003 to 22 in 2015 due to more active hunting concessions and associated land area available for hunting (Table 2; Figure 2b). These proportional adjustments in lion quota and area hunted resulted in a relatively consistent land area hunted per lion allocated (quota) over the study period (maximum change of  $\pm 278$  km<sup>2</sup>/lion allocated per year, total range of 924–1,362 km<sup>2</sup>/lion allocated; Figure 2c) and offtake per 1,000 km<sup>2</sup> (Table 3). There is no evidence to suggest that new concessions were serving as a primary source of >6-year-old lions since harvest rates of this age class were comparable between new



**FIGURE 2** Enforcement of age restrictions and quotas in Niassa National Reserve, Mozambique between 2003 and 2015 and responses in (a) trophy age, (b) harvests and quotas, and (c) hunting effort. Dotted vertical line represents the year when age restrictions were first enforced (2006) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 3** Proportion of lion trophies harvested by individual hunters in different age categories organised relative to sustainable offtake. “Suitable (>6 years)” indicates that the lion’s age met the recommendations for sustainable hunting; “Underage (<6 years)” indicates that the lion’s age fell into the age categories that did not meet recommendations for sustainable hunting in Niassa (<4 years or 4–6 years; see text for details). The sample is limited to professional hunters (listed anonymously by hunter ID, e.g. “H33”) who harvested more than two lion trophies between 2003 and 2015. Numbers at the top of each bar represent the total trophies harvested over the study period [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

and old concessions. For example, the offtake of >6-year-old lions in the three new concessions (opened in 2010–2011) over the first 3 years of operation (2010–2012) was 0.92 lions/1,000 km<sup>2</sup>. In comparison, over the same period in three concessions that had been constantly hunted since 2004, the overall offtake of >6-year-old lions was 0.83 lions/1,000 km<sup>2</sup>.

Prior to the points system, harvests in several blocks exceeded the science-based recommended level of 0.5 lions/1,000 km<sup>2</sup> (Packer et al., 2011), reaching as high as 1.1 and 0.9 lions/1,000 km<sup>2</sup> in 2004 and 2005, respectively, but more recently since the enforcement of the points system, block-wise harvests rarely exceed 0.5 lions/1,000 km<sup>2</sup> (Table 3). Lions were not harvested from all blocks every year largely due to client availability: for example, lions were not harvested from blocks 6 and 8 in 2014 but were obtained in 2015, and vice versa for block 7.

The percentage of hunts in which lions were successfully harvested decreased dramatically in 2008–2009 but stabilised by 2012 at

around 70%. Note that the percentage of successful hunts remained low in 2009 (46%) despite the lack of enforcement of age restrictions and the points system, indicating that success can be affected by factors external to management.

## 4 | DISCUSSION

Our results show evidence of successful implementation of an age-based hunting system that effectively incentivised hunters to select older trophies, thereby reducing offtakes and the risk of unsustainable harvests. Since NCP began monitoring and ageing lion trophies in 2004, hunters in Niassa gradually harvested fewer young lions (<6 years) and more older lions (>6 years), resulting in fewer trophies annually. After an initial decrease following the enforcement of the ageing system, the percentage of hunts harvesting lions increased and stabilised, demonstrating that hunters were successful in accurately locating and ageing older lions to meet minimum age requirements.

The rapid increase in trophy age following enforcement of the points system empirically demonstrates that hunters can effectively learn to age lions. This finding is notable because age as a selection criteria for hunting lions has long been debated by hunters, managers and scientists, many who questioned whether natural variation in physical characteristics between individual lions is large enough to prevent reliable ageing. The use of three broad age classes in Niassa overcame this concern by accounting for individual variation specific to the region through the use of key indicator traits, which have been subsequently validated by recent research on lion ageing in populations across Africa (Miller et al., 2016). Some hunters harvested all or nearly all their trophies at suitable ages (>6 years), whereas others, who either did not know how or take the adequate care to age, repeatedly hunted underage individuals (<6 years). Within the first 2 years of enforcement of the points system, the percentage of trophies >6 years of age increased from 50% to 100% and since 2014, 100% of trophies have been of suitable age for sustainable hunting. Hunter compliance with age restrictions has been so consistent that they surpassed NCP’s original conservation goal for more than 80% of lion trophies to be older than 6 years.

The willingness and ability of hunters to harvest suitably aged lions was in part due to concerted efforts by NCP to engage with sport hunting operators and professional hunters from the start to address concerns, build trust and educate hunters on ageing lions. For the

**TABLE 2** Hunting quotas, concessions and harvest outcomes from 2003 to 2015 in Niassa National Reserve, Mozambique

Metric	Year													
	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	
Lion quota	14	16	16	16	15	16	16	19	21	21	22	22	22	
Number of active hunting concessions	4	5	5	6	6	6	7	8	8	9	9	7	8	
Area of active hunting concessions (km <sup>2</sup> )	12,936	17,119	17,119	20,424	20,424	20,424	23,064	25,735	25,735	27,986	27,936	21,621	24,531	
Number of lion hunts	11	10	12	12	12	11	13	11	9	9	13	6	9	
Number of lions harvested (offtake)	11	9	9	9	8	4	6	8	8	6	10	4	6	

**TABLE 3** Lion trophy offtake per concession area before (2004–2005) and after (2014–2015) implementation of the points system and age restrictions in Niassa National Reserve, Mozambique

Concession ID	Land area (km <sup>2</sup> )	Before points system				After points system			
		2004		2005		2014		2015	
		Offtake (lions)	Offtake (lions/1,000 km <sup>2</sup> )	Offtake (lions)	Offtake (lions/1,000 km <sup>2</sup> )	Offtake (lions)	Offtake (lions/1,000 km <sup>2</sup> )	Offtake (lions)	Offtake (lions/1,000 km <sup>2</sup> )
1	4,180	0	0	2	0.5	0	0.0	0	0.0
2	4,446	5	1.1	4	0.9	1	0.2	1	0.2
3	2,125	2	0.9	0	0.0	1	0.5	2	0.9
4	2,910	1	0.3	2	0.7	0	0.0	0	0.0
5	3,458	1	0.3	1	0.3	Not operational		Not operational	
6	3,308	Not operational		Not operational		0	0.0	1	0.3
7	2,640	Not operational		Not operational		1	0.4	0	0.0
8	2,251	Not operational		Not operational		0	0.0	1	0.4
9	2,671	Not operational		Not operational		1	0.4	1	0.4
All blocks	27,989	9	0.3	9	0.3	4	0.1	6	0.2

first 9 years after the implementation of age-based regulations, NCP shared all hunting outcomes, along with training and information on how to visually age lions, with sport hunting operators and professional hunters at an annual meeting. Additionally, trophies were aged in the presence of the sport hunting operators and professional hunters to answer questions and facilitate in-person training. These steps helped create a “culture” of trophy monitoring jointly supported by the management authority, hunting operators and NCP. Perhaps due to the initial inclusion of hunters in the decision-making process, hunters did not resist the age-based system initially nor have there been any disputes over the past 10 years of implementation.

The trend in hunting effort further demonstrates that hunters were able to harvest animals at rates comparable to those before age restrictions were enforced. After an initial decrease in 2008, the percentage of hunts harvesting lions increased and stabilised around 70%. The drop in 2008 followed the first reduction of lion quotas in 2007, which caused some hunters to age trophies more judiciously, resulting in a complementary spike in the percentage of offtakes >6 years that same year. The rise in the percentage of successful hunts in years following 2008 could be due to an increasing availability of lions >6 years of age or, more likely, professional hunters becoming better trained and more confident in their abilities to accurately age lions. These changes are unlikely to be due simply to new areas being opened for hunting since they were observed similarly across all blocks, including the three areas that were hunted consistently from 2004 to 2015.

Two biological indicators serve as evidence that the reduced hunting offtake following the enforcement of age restrictions was not caused by a declining lion population. First, results from lion call up surveys conducted in Niassa over the study period show that the number of lion prides responding increased from 4 in 2005 to 16 in 2015, and that the lion population increased from 2005 to 2012 and stabilised thereafter (Appendix S1 and Table S1 in Supporting Information). Second, aerial censuses in the dry season between 2004 and 2014

showed a similar trend for many lion prey species, with an increase between 2004 and 2009 and thereafter a decline. In late 2009, elephant carcasses provided a source of food not recorded previously and the biomass of this food source substantially increased during the study period with the rise in poaching (Table S2 in Supporting Information; Craig, 2006, 2009, 2012; Grossmann et al., 2014), and prey abundance is strongly correlated to lion density (Hayward, O’Brien, Hofmeyr, & Kerley, 2007; Van Orsdol, Hanby, & Bygott, 1985). The trend of the lion population supports our finding that reduced lion offtake resulted from hunters increasing the selectivity of their harvest to comply with age restrictions rather than a decrease in the lion population. There was, however, no measurable change in the lion numbers over the past decade that could be attributed to implementation of this policy alone.

Empirical evidence indicates that age restrictions directly reduced trophy offtake; however, several other factors related to consumer demand may have also contributed to the lower harvest. For example, the world-wide Financial Crisis of 2008 prompted a dramatic decline in client demand for sport hunting, a high-cost tourism activity. All sectors of Mozambique’s economy suffered heavy losses between 2009 and 2010, including the agricultural sector which includes hunting (The World Bank, 2016). This economic decline was reflected in Niassa’s hunting industry by a decrease in the number of lion hunts sold and therefore a decrease in the percentage of quota purchased by hunting clients in 2009–2010, after which the industry began to recover from 2012 to 2013 alongside the country’s economy.

Age restrictions may reduce negative impacts from hunting on lion populations by ensuring that 1–7 young (<6 years) lions per year were retained in the population (based on harvest levels of 11 lions/year from 2003 before age restrictions were enforced). As age-specific variation in appearance decreases with age (Miller et al., 2016) and the points system penalises operators for repeatedly harvesting lions that 4–6 years of age, hunters are incentivised to harvest old lions that are visually obvious in order to minimise their mistakes. This ensures

that lions taken are older than the recommended minimum age for sustainable hunting and more likely to reach the 8 year minimum age recommended more recently by Creel et al. (2016).

Despite an increase in the trophy quota and land area available for hunting over the past 12 years, the number of lions harvested slightly decreased, resulting in a decrease in the number of lions harvested per km<sup>2</sup>. The number of lions harvested in any given year in Niassa is low given the large area managed as sport hunting concessions, representing 1 trophy lion per 5,405 km<sup>2</sup> in 2014 (0.1 lions/1,000 km<sup>2</sup>) and 4,089 km<sup>2</sup> in 2015 (0.2 lions/1,000 km<sup>2</sup>) across all hunting concession land, which is well below the recommended harvest rate for sustainable lion hunting (0.5–1.0 lions/1,000 km<sup>2</sup>; Creel et al., 2016; Packer et al., 2011). At a block level, offtakes ranged from 0 to 0.5 lions/1,000 km<sup>2</sup> in 2014 and 0–0.9 lions/1,000 km<sup>2</sup> in 2015, which also fall within the recommended harvest rate.

Our results demonstrate that the use of trophy age restrictions as a management tool can incentivise an improvement in harvest quality and rate as long as the management authority consistently enforces regulations. However, compliance is directly dependent on enforcement and hunting operators can revert back to harvesting underage animals as soon as they sense weakened commitment from the authority. For example, compliance with age restrictions decreased in 2009 after the management authority temporarily revoked age restrictions, which motivated hunters to harvest younger lions and more trophies. This disruption was mitigated once the ageing system was reinstated in 2010, after which trophy age increased and harvest rates stabilised. In 2012 when the management authority changed, some hunting operators questioned whether age restrictions would continue and chose to harvest underage lions (<6 years), thus increasing offtake for the year. Strict, continuous enforcement is imperative for the efficacy of age-based hunting regulations.

Several critical elements contributed to the success of the ageing system in Niassa and offer lessons for managers of other sites implementing similar age-based hunting systems. First, the management authority was committed to implementing and enforcing the system. Second, the system was developed in conjunction with the reserve management team, professional hunters, hunting operators and researchers and was supported by all stakeholders. Third, trophy ageing and quota setting were consistently audited by an independent third party (NCP), which did not receive funding from Niassa sport hunting operators or the management authority and had no conflict of interest in the process. Fourth, ageing was conducted by the same assessors over the entire period and was based on validated criteria determined from long-term monitoring of known lions in the same area. Ageing categories were simple and included only three categories that could easily be recognised through visual criteria. Finally, the points system was pragmatic: it provided room for mistakes and human error and took into account the actual conditions under which lions are hunted, and provided both penalties and incentives. In summary, the success of the age-based hunting system stemmed from the transparency, trust and pragmatism established among the participants involved, and we encourage other sites implementing hunting age restrictions to strive for these elements.

Our study serves as the first empirical evidence that it is possible to use an age-based system to manage and regulate sport hunting, increase the age of animals harvested and reduce harvests. The points system has been so successful for managing hunting in Niassa that agencies in several other countries that permit lion hunting have adopted similar systems (e.g. Zimbabwe). With recent increases in the regulation of lion trophy imports by top market countries like the United States (U.S. Fish and Wildlife Service, 2015), we expect that hunting systems which prioritise close monitoring and population sustainability, like Niassa's age-based points system, will be more widely adopted across Africa and perhaps even legally mandated to ensure transparency and accountability. However, our paper does not present results to argue whether sport hunting does or does not act as a conservation tool. To test such an effect would require evidence that the activity of sport hunting reduces other sources of lion mortality (illegal poisoning, snaring and retaliatory killing) in the areas under hunting management to offset the non-natural mortality of lions from sport hunting. Additional research is also needed to explicitly measure in the field (rather than simulation modelling) whether age-based hunting results in sustainable offtake relative to these other sources of lion mortality. If management authorities continue to permit sport hunting as a recreational activity, they must do so without negatively impacting species' populations, particularly those considered threatened or endangered.

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## AUTHORS' CONTRIBUTIONS

C.B. and K.B. conceived the ideas and designed methodology; C.B. and K.B. collected the data; C.B., K.B. and J.M. analysed the data; J.M. and C.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Hunting records: Dryad data package <https://doi.org/10.5061/dryad.17fk2> (Begg et al., 2017).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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## Supporting Information

### Effective implementation of age restrictions increases selectivity of sport hunting of the African lion

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#### **Appendix S1.** Lion call up survey methods.

As part of a larger carnivore monitoring program to assess the trend and distribution of lions across Niassa Reserve and their threats, we carried out repeated lion call up surveys. Surveys were conducted in 2005, 2008, 2012 and 2015 using standard and consistent techniques and equipment to obtain comparable results between years (Kiffner *et al.* 2009; Ferreira & Funston 2010; Brink, Smith & Skinner 2012). In all years, surveys were conducted in the dry season from July-September along the available road network in Niassa. As more roads became available in Niassa with time, additional call stations were added to the original stations to increase sampling coverage. New call stations fell within the same spatial extent as the original call stations, thereby increasing sampling effort, and thereby the accuracy of the final estimate, over the same study area.

Call surveys were conducted by broadcasting calls known to attract lions (e.g. bleating wildebeest calf, squealing pig; Kiffner *et al.* 2008) through loudspeakers from a vehicle positioned on high ground in open habitat at predetermined 10 km straight-line intervals. We additionally attracted lions by hanging a goat meat bait at each call station prior to initiating calls. Each call station was surveyed for one hour, which consisted of 10 minutes of calls followed by 10 minutes of silence in a repetitive manner until 60 minutes passed. We scanned for carnivores using a spotlight with a red filter so as not to deter carnivores from approaching. At each call station, we recorded the number of incoming lions and sexed and aged each individual where possible.

Data were analysed to estimate lion population size in a repeatable way using the statistically robust model and parameters developed by Ferreira and Funston (2010b), which account for differential response probabilities based on sex and age as well as the number of calling stations surveyed each year. This model incorporates sampling effort and area, and so accounted for the increased number of call stations over time.

**Table S1.** Lion call up survey results over the study period in Niassa National Reserve, Mozambique.

Parameter	Year			
	2005	2008	2012	2015
Number of call stations	97	104	128	153
Sound area sampled (km <sup>2</sup> )	32.17	32.17	32.17	32.18
Effective land area sampled (km <sup>2</sup> ) <sup>1</sup>	3120.49	3345.68	4117.76	4923.54
Number of lions responding	27	36	40	57
Number of prides responding	4	7	10	16
Population estimate	693	871	1071	973
(95% confidence limits) <sup>2</sup>	(577-810)	(730-1013)	(951-1191)	(842-1104)

<sup>1</sup> Calculated as the number of call sites multiplied by the sound area sampled.

<sup>2</sup> Calculated using the Ferreira and Funston (2010b) model.

**Table S2.** Aerial census results for lion prey from the dry season (September-October) over the study period in Niassa National Reserve, Mozambique. Prey abundance in the dry season is correlated to lion population density (Van Orsdol, Hanby & Bygott 1985; Hayward *et al.* 2007). Data sourced from Craig 2006, 2009, 2012; Grossmann *et al.* 2014.

Lion prey species	Year				
	2004	2006	2009	2011	2014
Buffalo ( <i>Synerus caffer</i> )	6968	2271	6833	6214	7105
Elephant (carcass only) ( <i>Loxodonta africana</i> )	461	588	896	2627	3183
Kudu ( <i>Tragelaphus strepsiceros</i> )	1439	3845	2928	1397	743
Sable ( <i>Hippotragus niger</i> )	13233	13881	14823	9662	7069
Warthog ( <i>Phacochoerus africanus</i> )	5614	8660	10132	4629	3372
Waterbuck ( <i>Kobus ellipsiprymnus</i> )	1219	2308	2973	1662	1492

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