

## Faculty of Agronomy and Forestry Engineering Master in Management and Conservation of Biodiversity

# The Effects of Sport Hunting on Impala (*Aepyceros melampus melampus*) Population Demography and Behaviour in the Niassa Special Reserve

Dissertation by: Sofia Nhalungo

Maputo, August 2024



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Maputo, August 2024

#### DECLARATION OF DOCUMENT ORIGINALITY

I, Sofia André Nhalungo, do hereby declare that this dissertation has never been submitted to obtain any degree or in any other context and is the result of my own work. This dissertation is presented in partial fulfillment of the requirements for the degree of Master in Management and Conservation of Biodiversity, from the Eduardo Mondlane University.

Maputo, August 2024

Sofia André Malungo

(Sofia André Nhalungo)

#### **DEDICATION**

- ✓ To my beloved mother Esmeralda Nhantumbo, who has always given her all for my education and has always been present at every moment of my life.
- ✓ To my father in the Lord, Apostle Lourenço Fole, for the continuous teachings and instructions that shape my being and lead me to victories in Christ Jesus.

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#### ABSTRACT

Sport hunting is an important source of funding for biodiversity conservation. However, it is an activity that can alter the behaviour and population structure of wildlife, which is critical for conservation efforts, as these factors can have an impact on foraging efficiency and population growth rates. In Niassa Special Reserve (NSR) in Mozambique sport hunting has been formally practiced for years, but studies on its impacts on wildlife are still scarce. Therefore, this study evaluated the effects of sport hunting on the behaviour and population demography on a model species, the impala (Aepyceros melampus melampus). For data collection, in November 2022, a vehicle was driven along existing and accessible roads in selected sport hunting and ecotourism areas (serving as a control area) to find groups of impala and record data on their group size, sex, age class, and initial behaviour in response to an approach vehicle. Overall, the group size, proportion of individuals in each age class and sex ratio of impala's population differed between the hunting and ecotourism areas. Impala group size was larger in the ecotourism area than hunting area. The age-sex structure in both hunting and ecotourism area was mainly composed of adult's females, with a sex ratio more skewed towards females in the ecotourism area, although none of the pairwise differences for individual classes between the two areas were significant. The frequency distribution of behaviors exhibited by impalas in response to approaching vehicles differed between the hunting and the ecotourism area, although there were no significant differences in their flight initiation distance between the areas. The results suggest that there is little interference from sport hunting on the response variables measured. However, future evaluations and monitoring in NSR using the results of this study as a baseline to assess the long-term impacts of sport hunting on ungulate populations are recommended.

**Key words:** *Aepycerus melampus,* sport hunting effect, age structure, sex ratio, flight initiation distance.

#### **RESUMO**

A caça desportiva é uma importante fonte de financiamento para a conservação da biodiversidade. No entanto, é uma actividade susceptível de alterar o comportamento e a estrutura das populações de animais selvagens, o que é crítico para os esforços de conservação, uma vez que estes factores podem ter impacto na eficiência da procura de alimentos e nas taxas de crescimento da população. Na Reserva Especial de Niassa (REN), a caça desportiva é praticada formalmente há décadas, mas os estudos sobre os seus impactos na vida selvagem são ainda escassos. Neste contexto, este estudo avaliou os efeitos da caça desportiva no comportamento e demografia da população de uma espécie modelo, a impala (Aepyceros melampus melampus). Para a recolha de dados, no mês de Novembro de 2022 um veículo foi conduzido ao longo de estradas existentes e acessíveis em áreas selecionadas de caça desportiva e ecoturismo (servindo como controle) para encontrar grupos de impalas e registar dados sobre o tamanho do grupo, sexo, classe etária e comportamento inicial em resposta a aproximação de um veículo. Em geral, o tamanho do grupo de impalas, a proporção de indivíduos em cada classe etária e o rácio sexual diferiu entre as áreas de caça e de ecoturismo. O tamanho do grupo de impalas foi maior na área de ecoturismo. A estrutura etária-sexual em ambas as áreas de caça e ecoturismo foi composta principalmente por fêmeas adultas, com um rácio sexual mais inclinado para as fêmeas na área de ecoturismo, embora nenhuma das diferenças entre pares da mesma classe entre as duas áreas tenha sido significativa. A distribuição de frequência dos comportamentos exibidos pelas impalas em resposta à aproximação do veículo diferiu entre a área de caça e de ecoturismo, entretanto, não houve diferenças significativas na distância de início de fuga de impalas entre as áreas. Os resultados sugerem que há pouca interferência da caça desportiva sobre as variáveis analisadas. Contudo, recomenda-se o uso dos resultados deste estudo como referência para futuras avaliações e monitoria de impactos a longo prazo da caça desportiva nas populações de ungulados na REN.

**Palavras-chave:** *Aepycerus melampus,* efeito da caça desportiva, estrutura etária, rácio sexual, distância de início de fuga.

#### ABBREVIATIONS AND ACRONYMS

ANAC	Administração Nacional das Áreas de Conservação (National	
	Administration of Conservation Areas)	
FID	Flight Initiation Distance	
IUCN	The International Union for Conservation of Nature	
MZN	Mozambican Metical	
NSR	Niassa Special Reserve	
NCP	Niassa Carnivore Project	
PA	Protected Area	
SRN	Sociedade Para a Gestão e Desenvolvimento da Reserva do Niassa (Society	
	for the Management and Development of the Niassa Reserve)	
SSC	Species Survival Commission	
USD	United States Dollars	

#### **1. INTRODUCTION**

Protected areas (PAs) worldwide face the challenge of securing sufficient funds to support their management activities, prompting an increasing shift towards self-sustainability (Bhammar et al., 2021; Rylance et al., 2017). One of the most important sources of PA funding is wildlife tourism, which additionally benefits local communities (Buckleu et al., 2003; Higginbottom, 2004).

Wildlife tourism encompasses both consumptive and non-consumptive activities. Nonconsumptive tourism includes ecotourism-related activities (e.g., viewing and photography), while consumptive tourism involves activities where wild animals are intentionally killed, captured, or have any of their body parts used, even if the animals are not actually used for food, for example, sport hunting (Bauer & Herr, 2004; Leisanyane et al., 2013; Rizzolo, 2021; van der Merwe et al., 2021).

Ecotourism has proven successful in providing financial and social benefits for biodiversity conservation (Kruger et al., 2017; Lanier, 2014; Stone & Nyaupane, 2016). However, it is feasible in only very few African PAs, due to the necessity for strong infrastructure (e.g., hotels, food and water supply, waste management facilities), proximity to good transport links, high density wildlife populations for viewing, and local skills and capacity (IUCN, 2016). In contrast, sport hunting is feasible in a wider range of scenarios than ecotourism, including remote areas with a lack of infrastructure, attractive landscapes or high densities of visible wildlife, and areas with political instability, providing a viable alternative or complementary approach to ecotourism in generating revenue, particularly to justify wildlife as a land use outside of protected areas (Damm, 2008; Di Minin et al., 2016; Lindsey, Roulet, et al., 2007).

Some studies have found sport hunting to have a lower environmental impact compared to ecotourism (Deere, 2011; Lindsey, Frank, et al., 2007; Pervaze & Lucas, 2019), as it requires less infrastructures and involves fewer tourists using an area at a given time, reducing habitat degradation (Deere, 2011). Additionally, sport hunting can help manage wild animal populations in the absence of top-down control from wild predators (Hariohay et al., 2018).

In Africa, sport hunting is one of the most significant revenue generators in the biodiversity conservation sector (Di Minin et al., 2016; Lindsey, Frank, et al., 2007; Pervaze & Lucas,

2019), accounting for greater than USD 201 million/annually (Damm, 2008; Deere, 2011). Sport hunting also yields higher income per tourist than ecotourism (Damm, 2008), as hunters are willing to pay substantial sums to hunt rare species or animals with exceptional physical attributes (Coltman et al., 2003; Di Minin et al., 2016; Gomez et al., 2022). In 2019, for example, lions (*Panthera leo*) sold for an average of USD 33,747, elephants (*Loxodonta africana*) for USD 45,013, leopards (*Panthera pardus*) for USD 23,062 and buffalo (*Syncerus caffer*) for USD 12,136 (Bichel & Hart, 2023).

Areas designated for sport hunting in Africa cover around 1.4 million km<sup>2</sup>, an area 22% larger than the combined area of national parks and other PAs where hunting is prohibited (Damm, 2008), across 23 countries. In Mozambique, 65% of the land area legally designated for biodiversity conservation is allocated to sport hunting (ANAC, 2018b; Child & Magane, 2020), which generates 70% of the biodiversity conservation sector's total revenue, approximately USD 10 million annually (Child & Magane, 2020).

Inside the Niassa Special Reserve (NSR), in northern Mozambique, both sport hunting and ecotourism are permitted, each in specifically designated areas (Begg et al., 2018; NCP - Niassa Carnivore Project, 2020; SRN, 2005). Sport hunting is the primary tourism activity, generating around USD 572,046 per year in revenue compared to USD 124,000 per year from ecotourism (Child & Magane, 2020). The majority of spot hunters come for high priced lion, leopard and buffalo packages in an unspoilt and pristine wilderness. Antelope's species (e.g., impala, *Aepyceros melampus melampus*) are also typically included in these big game packages. The offtake rates in NSR, the rate at which the animals can be killed without reducing the population, are low for all game species, with an average of 0.5%, compared to sustainable offtake rates of 2% for buffalo and large plains game, and 3-5% for smaller animals (Child & Magane, 2020).

Despite its importance as a conservation tool in Africa, sport hunting remains a topic of intense debate due to ethical concerns and potential impacts on wildlife populations (Clark et al., 2023; IUCN, 2016; Schindler et al., 2017; Thomsen et al., 2022). The controversy mainly revolves around the highly selective nature of sport hunting: as these hunters desire animals with attractive phenotypic characteristics, old animals and males with impressive body and trophy sizes, such as antlers, tusks, or horns are strongly targeted (Di Minin et al., 2021; Lindsey, Frank, et al., 2007; Loveridge et al., 2007). This can disrupt wildlife

population structures, often skewing the sex ratio towards females and reducing the average age of males (Allendorf & Hard, 2009; Festa-Bianchet, 2003).

In addition to the direct mortality impact of sport hunting, wild animals may learn to perceive humans as predators. This may lead them to exhibit costly anti-predator behaviors (Frid & Heithaus, 2019; Muposhi et al., 2016). Studies have found that hunted animals exhibit increased vigilance and higher flight initiation distances (FID) in response to perceived predation risks (Di Minin et al., 2021; Hariohay et al., 2018; Setsaas et al., 2018). Vigilance and flight are costly behaviors that can result in missed opportunities for feeding, mating, parental care, or other fitness activities, and may have direct energetic costs as well (Creel et al., 2014; Frid & Heithaus, 2019; Kandel et al., 2022). In contrast, ecotourism cause less disruption to the demography and behaviour of wildlife populations and is therefore often used as a baseline for assessing the impacts of sport hunting on wildlife (Hariohay et al., 2018; Muposhi et al., 2016; Ndiweni et al., 2015).

#### 1.1. Problem and justification

The effects induced by sport hunting on the behaviour and population structure of wild animals can have critical conservation impacts, as these can impact the animals' foraging efficiency and population growth rates (Caro, 1999; Frid & Heithaus, 2019; Kandel et al., 2022; Loveridge et al., 2007).

Sport hunting within NSR span 28,827 km<sup>2</sup>, encompassing 78% of the entire reserve (NCP, 2022). These areas are an important source of revenue, supporting 30% of the reserve's annual operating costs, including support for anti-poaching and management activities (Equilibrium Research, 2019; Jorge et al., 2013).

Sport hunting has officially taken place in the NSR for over two decades (SRN, 2005), yet studies on its impacts on wildlife populations remain scarce. While existing studies of game species have mainly focused on large carnivores such as lions and leopards (Begg et al., 2018; NCP, 2020), there is a notable lack of knowledge about impact of sport hunting on ungulate species.

This study aims to fill this gap by providing an initial understanding of the effects of sport hunting on the behaviour and population demography on ungulates in the NSR, using impala as a model species. Impala was selected for this study because it is one of the most commonly targeted antelope species in hunting safaris in Africa (Bauer & Herr, 2004; Pervaze & Lucas, 2019; Southwick Associates, 2015) and is often used as a model species to understand the effects of sport hunting and other anthropogenic disturbances on ungulates (Flolo et al., 2021; Hariohay et al., 2018; Louis, 2020; Lunde et al., 2016; Setsaas et al., 2018; Tarakini et al., 2014). The findings of this study will provide baseline for future ecological monitoring and to inform the state of the ungulate species in the NSR hunting areas to devise management strategies that maintain economically viable wildlife populations.

#### 2. OBJECTIVES

#### 2.1. General objective:

✓ To assess the effects of sport hunting on impala (*Aepyceros melampus melampus*) population demography and behaviour through comparison with non-hunted populations in ecotourism areas within the Niassa Special Reserve.

#### 2.2. Specific objectives:

- ✓ To determine the group size, age classes, and sex ratio of impala population in sport hunting versus ecotourism areas.
- ✓ To compare the behaviour of impalas in response to approaching humans in sport hunting versus ecotourism areas.

#### **3. HYPOTHESES**

**Population demography:** In Mozambique, older male ungulates are the most frequently killed. This is due in part to legal regulations (subadult animals and females of dimorphic species are excluded from hunting quotas; Decree 82/2017) but also because hunters primarily seek large trophies (Magane et al., 2009). Selective hunting of adult males can alter the age and sex structure of the population, leading to a skewed distribution with a higher proportion of females and younger individuals than in non-hunted populations (Festabianchet, 2003).

*Behaviour:* Animals may exhibit anti-predatory behaviors and their consequences in response to the disturbances caused by sport hunting (Jarman & Jarman, 1974; Wirsing et al., 2008). Models of escape behaviour suggest that prey animals increase their flight distances (distances at which they flee from an approaching stimulus) in response to the perceived risk of predation, trading off the increased probability of escape with the energetic and opportunity costs of flight (Cooper & Frederick, 2007; Engelhardt & Weladji, 2011; Ydenberg & Dill, 1986). In addition, many ungulates also employ increased vigilance in locations where they are likely to encounter predators as a means to reducing predation risk (Chitwood et al., 2022; Creel et al., 2014; Zanette & Clinchy, 2019).

The predation avoidance hypothesis predicts that animals group together to enhance their ability to detect potential predators and thus facilitate escape, or to dilute individual risk (Grobis et al., 2013). Consequently, animals with previous predation experience and those that perceive a higher risk of predation will aggregate more than animals without experience or risk of predation (Grobis et al., 2013).

Given the ecological importance of both anti-predatory behaviour and demographics, and the potential for sport hunting to increase the costs and consequences of the behavioral and demographic responses (Jarman & Jarman, 1974; Wirsing et al., 2008), the following hypotheses are proposed:

#### ✓ Null hypothesis:

• There are no differences in impala group size, age classes, sex ratio and behaviour of impala between sport hunting vs. ecotourism areas.

#### ✓ Alternative hypotheses:

- Impalas in the sport hunting area occur in larger group sizes, have a sex ratio more skewed to females, and an age structure of males more skewed to younger classes compared to the ecotourism area.
- Impalas exhibit greater vigilance in response to human approach and increase their flight initiation distance from humans in the sport hunting area as compared to ecotourism area, due to perceived predation risk.

#### 4. LITERATURE REVIEW

#### 4.1. Tourism and protected areas

The viability of protected areas (PAs) depends on demonstrating their long-term economic value in conserving biodiversity, as compared to converting this land into resource use areas (Font et al., 2004; Leung et al., 2018). One strategy PAs can adopt is to showcase their economic value as tourism areas (Font et al., 2004). Tourism offers the potential to generate revenue for maintenance of the natural resources of PAs, while also to contributing to economic and social development. This includes funding infrastructure and services, promoting sustainable practices, providing educational opportunities, creating jobs, and offering additional income sources for local communities through biodiversity-related activities (Secretariat of the Convention on Biological Diversity, 2004).

Within the tourism industry, the term "wildlife tourism" is commonly used to describe tourism activities occurring within PAs. Wildlife tourism encompasses encounters with non-domesticated (wild) animals, both in their natural environment and in captivity (Buckley & Chauvenet, 2022; Chidakel & Child, 2022; Higginbottom, 2004). This type of tourism can be broadly categorized either "non-consumptive" and "consumptive". Non-consumptive wildlife tourism involves recreational activities that do not harm or permanently remove wildlife, while consumptive tourism involves deliberately killing/ removing wild animals or using any part of their bodies, such as sport hunting or recreational fishing (Higginbottom, 2004; Leisanyane et al., 2013; Rizzolo, 2021; van der Merwe et al., 2021). Wildlife tourism experiences can vary from encounters at fixed locations to organized excursions and tourist accommodation offerings independent encounters by unguided travelers (Higginbottom, 2004).

According to the World Travel and Tourism Council (2019), in 2018 non-consumptive wildlife tourism directly contributed USD 120 billion to economies worldwide and directly or indirectly supported 21.8 million jobs. Despite this substantial economic impact, it still falls short of meeting the financial needs of all PAs (Lindsey et al., 2006). Thus, consumptive tourism, particularly sport hunting, represents an additional and important means of generating revenue to conserve biodiversity (Coulson et al., 2018; Damm, 2008; Lindsey, Roulet, et al., 2007).

#### 4.1.1. Sport hunting as a conservation tool

Sport hunting, also known as trophy hunting or safari hunting, involves recreational hunting of wild animals in which the hunter retains the taxidermized part of it (e.g., head, horns, skulls, skins, tusks, teeth) as a representation of the successful hunt (Hellinx & Wouters, 2020; Pervaze & Lucas, 2019).

Africa hosts some of the most desired species for sport hunting, such as the "Big Five": buffalo, lion, leopard, black and white rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) and elephant. Although these are coveted trophies, many international hunters in Africa also target more abundant and less expensive plains game (Pervaze & Lucas, 2019), such as impala, greater kudu (*Tragelaphus strepsiceros*), common warthog (*Phacochoerus africanus*) and plains zebra (*Equus quagga*; Bichel & Hart, 2023).

Sport hunting has characteristics that make this industry significant for biodiversity conservation, including:

#### a. Financial incentives for biodiversity conservation

Sport hunting is the primary revenue-generating activity in the Africa biodiversity conservation sector, bringing in at least USD 201 million annually from 18,500 international hunting tourists (Damm, 2008; Deere, 2011). The Southwick Associates (2015) estimated that the revenue from sport hunting in eight nations of Africa (Botswana, Ethiopia, Mozambique, Namibia, South Africa, Tanzania, Zambia, and Zimbabwe) from 2012 to 2014, including professional hunters' package and fees, transportation, food, souvenirs, was approximately USD 326.50 million per year.

Hunters' willingness to pay large sums for hunting safaris motivates efforts to conserve pristine environments for wild animals (Pervaze & Lucas, 2019). This revenue support law enforcement activities, PA management, and habitat conservation and reduces political and economic pressures to repurpose these areas for domestic livestock production or other uses (Loveridge et al., 2007).

#### b. Reduced environmental impact and an alternative to ecotourism

Due to attracting fewer tourists, sport hunting has fewer environmental impacts (e.g., from garbage and fossil fuel use; Damm, 2008) and requires less infrastructure and amenities than ecotourism. This makes sport hunting a viable conservation incentive, particularly remote areas and degraded areas with low wildlife density and few other land use options (Davies, 2000; Lindsey, Frank, et al., 2007; Lindsey, Roulet, et al., 2007).

#### c. Improvement of local communities' livelihoods

Sport hunting can generate substantial benefits for local communities, including revenue sharing, employment opportunities in hunting camps, and the distribution of meat to community members (Angula et al., 2017).

The need to stimulate rural development on community lands, particularly lands experiencing a variety of environmental pressures and with a continued presence of wildlife, has led to the development of community-based natural resource management (CBNRM) initiatives in southern Africa. CBNRM efforts empower communities with the responsibility for sustainably managing and utilizing natural resources (Bond et al., 2006; Suich, 2013). Sport hunting, through partnerships with private operators, is an important method of generating livelihood returns (Angula et al., 2017), such that it has been associated with in improved attitudes towards wildlife among local communities (Lindsey, Roulet, et al., 2007).

#### d. Control of animal populations

Sport hunting can help manage wildlife populations, particularly herbivores in areas lacking natural predators, to prevent overpopulation and consequent overgrazing (Hearne & Mickenzie, 2000; Simard et al., 2013). It has also been used to control 'problem animals' that are involved in conflict with humans, generating revenue from animals that would have been killed anyway, while reducing retaliatory killings of wild animals by local communities (Lindsey, Frank, et al., 2007; Lindsey, Roulet, et al., 2007; Treves & Karanth, 2003). According to Lindsey et al. (2006), tourists show an interest in hunting problem animals, even if they are not desirable trophies.

#### e. Sustainability

With properly managed and accurate quotas, sport hunting can be sustainable (Lindsey, Roulet, et al., 2007). A "quota" represents the maximum number of animals that can be annually removed from a population in a particular area, without resulting in decline in the animals' population over time (Booth & Chardonmet, 2015). However, maintaining trophy quality and the marketability of the hunting area in the future necessitates a low offtake of animals, such that in many African countries, offtakes have remained below the available quotas (Lindsey, Roulet, et al., 2007). Furthermore, sport hunting is a highly regulated activity, governed by national and international agreements (Pervaze & Lucas, 2019). These regulations help establish hunting quotas, and often restrict the sex, size or age of the animals, and the season during which hunting can be conducted (Hellinx & Wouters, 2020).

Despite the numerous benefits of sport hunting, there are still ethical, social, and biological problems that hinder its role as a conservation tool (Table 1; Damm, 2008; Lindsey, Frank, et al., 2007).

Category	oblem	
Ethical	Practices such as shooting animals from vehicles, hunting young or rare anim	nals,
	using bait and hunting dogs can undermine the public perception of a	sport
	hunting, attracting negative press and fomenting support for a sport hunting	ban.
Social	Failure of governments and hunting operators to return adequate benefi	ts to
	local communities, reducing incentives for rural people to conserve wildlif	e.
	Failure of governments to return ownership of wildlife to communities,	or to
	develop skills among communities that would enable greater participation i	n the
	hunting industry.	
	Inadequate legislation to enforce community benefits.	
	Corruption, from multiple actors, including government scouts who ig	nore
	quota overruns and government ministers who favor certain operators w	when
	granting concessions.	
Biological	Quota setting is often based on guesswork, due to the lack of resources avai	lable
	to conduct an accurate wildlife count in most state wildlife departments.	
	Private hunting land, such as game farms, is usually required by law to	have
	fencing, which can result in disturbed wildlife migrations and ecological	gical
	degradation due to overstocking.	

 Table 1. Issues currently limiting the conservation role of sport hunting (sources: Damm, 2008; Lindsey, Frank, et al., 2007).

#### 4.1.2. Background to sport hunting in Mozambique

Sport hunting takes places in approximately 17% of Mozambique's land area (ANAC, 2018b; Buján & Macandza, 2017), including state-owned concessions (*coutadas*), game farms, hunting blocks, and community areas (ANAC, 2018b; Rylance, 2014).

Sport hunting is regulated through Law 5/2017, and Decrees 89/2017, 82/2017, and 83/2017 (ANAC, 2018b). Hunting is restricted to the quota set by Ministerial Decree and limited to a specific season (01 April to 30 November). Quotas are established through a participatory approach involving the National Administration of Conservation Area (ANAC), provincial authorities, and hunting operators, based on information in Annual Activity Reports submitted by hunting operators and data from wildlife censuses (ANAC, 2018b).

Decree No. 83/2017 sets the offtake fees for various game species, including crocodile, *Varanus* lizard, 30 species of mammal, and 10 groups of birds. Table 2 provides a list of the mammal game species and their respective offtake fees.

English name	Scientific name	Offtake fees
Elephant	Loxodonta africana	10,000
Lion	Panthera leo	3,888.89
Leopard	Panthera pardus	2,222.22
Buffalo	Syncerus caffer	1,111.11
Hippopotamus	Hippopotamus amphibius	1,111.11
Sable	Hippotragus níger	1,111.11
Eland	Taurotragus oryx	1,111.11
Nyala	Tragelaphus angasi	1,111.11
Kudu	Tragelaphus strepsiceros	1,000
Zebra	Equus quagga	1,000
Wildebeest	Connochaetes taurinus	888.89
Hartebeest	Alcelaphus lichtensteinii	666.67
Waterbuck	Kobus ellipsiprymnus	666.67
Bushbuck	Tragelaphus sylvaticus	333.33
Reedbuck	Redunca arundinum	333.33
Suni	Neotragus moschatus	333.33
Blue duiker	Cephalophus monticola	333.33
Spotted hyena	Crocuta crocuta	333.33
Sharpe's Grysbok	Raphicerus sharpie	305.56
Steenbok	Raphicerus campestris	277.78
Impala	Aepyceros melampus melampus	277.78
Oribi	Ourebia ourebi	277.78

Table 2. Mozambique mammals game species and their offtake fee, listed in the Decree nr. 83/2017 of December29.

Red duiker	Cephalophus natalensis	277.78
Warthog	Phacochoerus africanus	250.00
Bushpig	Potamochoerus larvatus	194.44
Common duiker	Sylvicapra grimmia	194.44
Porcupine	Hystrix africaeaustralis	138.89
Baboon	Papio cynocephalus	83.33
Hares	All species	16.67
Springhare	Pedetes capensis	16.67

\*Fee in Mozambican currency (MZN) converted to Dollar: 1 USD = 63 MZN

Sport hunting in Mozambique has significantly contributed to improving the well-being of local communities residing in and around hunting areas, specifically by creating jobs (ANAC, 2018b) and providing meat for dietary and cultural needs (Magane et al., 2011). Local communities in the hunting areas receive quotas exempt from the payment of government fees. In addition, operator must distribute meat from the hunted animals to communities, after supplying the camp and its workers (Magane et al., 2011). By law, 20% of the payment of licensing fees in all hunting areas is channeled by the government to local communities (ANAC, 2018; Rylance, 2014).

#### 4.1.2.1. The case of Niassa Special Reserve

The Niassa Special Reserve (NSR), in northern Mozambique, was officially established as a Game Reserve in 1954. The hunting activity in the reserve began in 2000, when a company conducted three trial hunting safaris in the area. Negotiations with several companies for hunting concessions began in 2001, leading to the signing of a Memorandums of Understanding with three companies (SRN, 2005). In June 2020, the reserve's designation changed from *Niassa National Reserve* to *Niassa Special Reserve* through Decree No. 42/2020

The reserve is divided into 17 blocks/ management units (Allan et al., 2017) with 11 designated for sport hunting and six for biodiversity conservation and/or ecotourism (NCP, 2022). Nine hunting blocks have been granted to hunting operators, covering about 60% of the protected area (NCP, 2020, 2022). Sport hunting concession fees finance 30% of the reserve's annual operating costs, including anti-poaching and management activities (Equilibrium Research, 2019; Jorge et al., 2013).

According to the Ministerial Decree on hunting quotas from 2018-2022 (Diploma Ministerial n.° 29/2018; n.° 23/2019; n.° 61/2020; n.° 26/2021; n.° 14/2022), NSR had a total quota ranging from 1,711 to 2,152 animals, representing between 24 to 27 species, during this period (Table 3). However, the offtakes for all species until 2019 were lower, reaching only around 50% of the allocated quota (Child & Magane, 2020).

English name	Scientific name	Allocated quota				
		2022	2021	2020	2019	2018
Baboon	Papio cynocephalus	120	120	120	108	108
Buffalo	Syncerus caffer	120	120	120	100	100
Bushbuck	Tragelaphus sylvaticus	84	84	84	78	78
Bushpig	Potamochoerus larvatus	66	66	66	60	60
Eland	Taurotragus oryx	75	75	75	63	63
Common duiker	Sylvicapra grimmia	92	92	92	105	72
Sharpe's Grysbok	Raphicerus sharpie	0	45	45	30	45
Hartebeest	Alcelaphus lichtensteinii	74	74	74	62	62
Hippopotamus	Hippopotamus amphibius	10	7	7	8	8
Impala	Aepyceros melampus	70	58	58	50	50
Kudo	Tragelaphus strepsiceros	84	84	84	72	72
Leopard	Panthera pardus	42	28	40	35	35
Lion	Panthera leo	22	15	22	20	20
Porcupine	Hystrix africaeaustralis	7	2	6	15	0
Red duiker	Cephalophus natalensis	90	90	90	45	0
Reedbuck	Redunca arundinum	64	64	64	52	52
Sable	Hippotragus níger	111	111	111	95	95
Spotted hyena	Crocuta Crocuta	40	25	36	25	25
Suni	Neotragus moschatus	36	36	0	0	18
Warthog	Phacochoerus africanus	136	136	136	104	104
Waterbuck	Kobus ellipsiprymnus	106	106	106	94	94
Wildbeest	Connochaetes taurinus	28	28	28	22	22
Zebra	Equus quagga	64	64	64	57	57
Crocodile	Crocodylus niloticus	25	25	25	21	21
Francoline	All species	220	220	220	180	180
Guineafowl	All species	360	360	360	270	270
Bustard	All species, except Ardeotis	6	0	0	0	0
	kori and Neotis denhami					
Total		2,152	2,135	2,133	1,771	1,711

Table 3. Quotas allocated to the Niassa Special Reserve from 2018 to 2022 (source: Diploma Ministerial n.º 29/2018; n.º 23/2019; n.º 61/2020; n.º 26/2021; n.º 14/2022).

#### 4.2. Responses of wild animals to wildlife tourism

The growing interest in tourist travel to developing countries has led to a significant rise in the construction of resorts and hotels, particularly in tropical forests. This expansion in tourism infrastructure can cause significant disturbance to animals and their natural habitats (Korir et al., 2013; Kurleto, 2014). Furthermore, pressures from tourists seeking to photograph or hunt wildlife can negatively disrupt the feeding and reproductive success of some species (Milner et al., 2007), potentially leading to long-term consequences for animal behaviour, demography and ecological relationships (Kiffner et al., 2014; Milner et al., 2007). Activities that occur during sensitive periods of an animal's life cycle (e.g., mating, rutting, or nesting season) and those that involve close observation of wildlife pose a higher risk of disturbance (Korir et al., 2013; Kurleto, 2014). However, the degree of the impact on wildlife from tourism depends on the scale of development and the ability of wildlife to tolerate human presence (Korir et al., 2013; Kurleto, 2014).

Since non-consumptive tourism is hypothesized to cause less disturbance to wildlife than sport hunting (Hariohay et al., 2018; Williamson, 2006), and as many of the reported impacts of wildlife tourism in the literature focus on sport hunting, the following review explores the impacts of sport hunting on wildlife behaviour and population demography.

#### 4.2.1. Effect of hunting on animal behaviour

Sport hunting can significantly impact animal behaviour, influencing movement patterns, occupancy, and habitat selection (Green & Giese, 2004; Lone et al., 2015; Ndaimani et al., 2014). When tourists are active in certain areas, animals may avoid these spaces (Green & Giese, 2004). For example, sable antelope (*Hippotragus niger niger*) in northwestern Zimbabwe prefer safety closed woodland when under hunting pressure to avoid detection by human, while non-hunted sables prefer more open habitats (Ndaimani et al. 2014). Similarly, red deer (*Cervus elaphus*) males in central Norway move to habitats with more cover at the beginning of the hunting season (Lone et al., 2015).

Therefore, by impacting animal behaviour and habitat selection, sport hunting shapes an animals' landscape of fear (LOF) in humans-affected ecosystems (Di Minin et al., 2021; Muposhi et al., 2017; Palmer et al., 2022) The LOF refers to the spatial variation in prey

perception of predation risk, with direct and indirect impacts on animal distribution and behaviour (Bleicher, 2017; Gaynor et al., 2019).

Depending on an animal's degree of behavioral plasticity and their ability to alter patterns of habitat use to avoid people, sport hunting can create ecological traps, forcing animals to utilize poorer-quality habitats than they would otherwise (Muposhi et al., 2017). Consequentially, effective foraging may be compromised, resulting in reduced food consumption and quality (Green & Giese, 2004; Muposhi et al., 2017). For example, during the hunting season, brown bears (*Ursus arctos*) spend less time foraging and are forced into areas without humans, where there is less food to forage, leading to poorer body condition and lower reproductive success (Hertel et al., 2016). Additionally, collared peccaries (*Pecari tajacu*) shift their activity from day to night during the hunting season (Espinosa & Salvador, 2017), suggesting that sport hunting influences both habitat selection and activity patterns (Palmer et al., 2022).

Animals also often exhibit anti-predator behaviors in response to sport hunting, as humans become predators by hunting and removing animals from a population (Frid & Heithaus, 2019; Jarman & Jarman, 1974; Ndiweni et al., 2015). As a result, animal responses to sport hunting may have similar costs to predator avoidance, such as the energetic costs of flight or lost opportunities for feeding, mating, parental care, and other fitness-enhancing behaviors during vigilance or other avoidance activities (Frid & Heithaus, 2019; Palmer et al., 2022). In addition, the flight behaviour of wild animals resulting from hunting can reduce people's ability to approach and see (or hunt) these animals. This highlights the importance of considering animal behaviour when assessing different approaches to tourism and wildlife conservation (Caro & Berger, 2019; Kandel et al., 2022).

However, it is important to highlight that animal's antipredator behaviour can be influenced by the availability of its resources, its current body condition, and other factors that affect its reproductive value (Frid & Heithaus, 2019). Animals that lack alternative "safe" sites with adequate resources or that struggle to maintain an adequate body condition may be unable to leave their current resource patch and flee from disturbance stimuli. Despite the lack of behavioral change, these animals experience decreased foraging efficiency due to increased vigilance, disturbed resting, and digestion cycles (especially important for ruminants), and physiological stress (Frid & Heithaus, 2019). Thus, different environmental conditions and physiological or reproductive states can lead animals to assess risk differently, resulting in a variety of behavioural responses (Neumann et al., 2009). Therefore, the absence of a behavioural response does not necessarily mean that the animal does not perceive risk or experience fitness costs (Frid & Heithaus, 2019).

#### 4.2.2. Population-level responses of animals to sport hunting

The costly anti-predator behaviors triggered by wildlife tourism can lead to nutritional or physiological stress and fitness costs in terms of increased susceptible to disease or other forms of predation (Green & Giese, 2004). When these stresses coincide with periods of food scarcity or high energy demand (e.g., breeding season), there can be long-term negative effects of tourism on survival and reproduction, potentially leading to animal population declines (Green & Giese, 2004; Muposhi et al., 2017).

Sport hunting typically targets specific individuals, often focusing on males with large horns, tusks and antlers, or exceptionally large animals of either sex (Allendorf & Hard, 2009; Di Minin et al., 2021; Lindsey, Frank, et al., 2007; Loveridge et al., 2007). This selective hunting can disrupt the age, sex, and social structure of the species, affecting population growth rates (Milner et al., 2007).

In hunted populations, the adult sex ratio is generally skewed in favor of females (Festabianchet, 2003; Milner et al., 2007). This does not necessarily reduce fertility rates, due to the polygynous mating systems in which one male mates with multiple females (Mysterud, 2011). Recruitment rates may therefore be resistant to a reduction in males, possibly even increasing with a higher proportion of females (Mysterud et al., 2002); however, there may be a threshold sex ratio below which fertility collapses (Milner et al., 2007). This has been observed in the critically endangered saiga antelope (*Saiga tatarica tatarica*), where fertility declined when the sex ratio of adult males dropped to between one adult male for every 36 females (Milner-Gulland et al., 2003). Furthermore, excessive male removal can disrupt mating dynamics: fewer males to mate or less struggle to establish dominance and breeding rights among males could allow less vigorous males to reproduce, increasing the chances of inbreeding and thereby lowering reproductive rates (Pervaze & Lucas, 2019).

As males with larger trophies or body size are usually the oldest, sport hunting can also skew the age distribution of hunted populations towards younger animals (Festa-bianchet, 2003;

Milner et al., 2007). This may reduce fecundity, for instance, if younger males do not have the same ability to mate with a larger number of females than older males (Mysterud et al., 2002).

In some mammal species, older individuals play an important role in leading social groups (Milner et al., 2007). As such, their removal through harvesting can potentially disrupt social systems. For example, in African elephants, older individuals possess enhanced social discriminatory abilities that influence the social knowledge and reproductive success of the entire group (Leclerc et al., 2017; Milner et al., 2007). In some carnivore species (e.g., lion), territorial males increase their reproductive success by killing the offspring of rival males (Palombit, 2015). When these territorial males are removed by sport hunters, younger males may take over the territory and kill the offspring, leading to a decrease in population growth rates (Loveridge et al., 2007). This phenomenon also occurs with Scandinavian brown bears (Leclerc et al., 2017) and leopards (Balme & Hunter, 2013).

Selective sport hunting can also lead to the loss of phenotypic traits that affect sexual selection, further compromising reproductive success (Chiyo et al., 2015; Hall, 2018) and genetic diversity (Muposhi et al., 2017; Pervaze & Lucas, 2019). There is evidence of a reduction in horn size in hunted animals, such as sable and impala (Crosmary, 2012), over time across various hunting areas (Crosmary et al., 2015; Festa-Bianchet, 2017). This reduction in horns size may also reduce the attractiveness of certain hunting destinations (Muposhi et al., 2017), and is therefore of financial concern because tourists are often motivated by sport hunting organization competitions which award hunting prizes in categories such as largest animal (Humane Society of the United States, 2016).

The focus on hunting for extreme trophies may compromise the conservation potential of sport hunting areas, especially in Africa, resulting in a loss of revenue, inadequate conservation funding, and a consequent decline in species numbers due to habitat loss and poaching (Muposhi et al., 2017). Therefore, it is crucial to integrate these impacts into wildlife research and management interventions for the conservation of wildlife species and their habitats (Festa-Bianchet, 2017; Muposhi et al., 2017).

Below (Figure 1.) a summary flowchart of some of the indirect processes and pathways through which selective hunting can affect wildlife populations.



Figure 1. Schematic model of some of the indirect processes and pathways through which selective harvesting can affect population growth rate. Solid lines are mechanisms and effects that are well documented, and dashed lines indicate effects that are less well documented. Dotted lines indicate the pathway through which selective harvesting can increase population growth rate (source: Milner et al., 2007).

#### 4.3. Study species (Aepyceros melampus melampus)

#### 4.3.1. Taxonomy

According to the IUCN SSC Antelope Specialist Group (2016, 2017), the study species is classified as follows:

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Artiodactyla
Family:	Bovidae
Genus:	Aepyceros

# Species:Aepyceros melampusSubspecies:Aepyceros melampus ssp. melampus (Lichtenstein, 1812)

The study species is the common impala (*A. m. melampus*) and is one of the two known subspecies of impala. The other being the black-faced impala (*A. m. petersi*; IUCN SSC Antelope Specialist Group, 2016, 2017; Lorenzen et al., 2006; Nerting & Arctander, 2001).

#### 4.3.2. Physical description

The impala is a medium-sized, slender-bodied antelope with long, thin legs (Figure 2). Its coat is smooth and shiny, with two shades: uniform reddish brown on the back and around the neck, transitioning to a light fawn on the flanks and outer legs. The belly and inside of the legs are white. The color darkens on the forehead and back-saddle of mature territorial males. The impala has large ears, with small black tips and distinctive white patches above the eyes, on the tip of the muzzle and black patch in the middle of the top of the head. The top of the muzzle is darker brown. Another distinctive feature of this species is the black stripe down at the top of the tail and two black stripes down the buttocks, separating the brown and white areas, as well as the oval tufts of blackish hair, resembling "socks", on the hind feet directly above the hooves. These tufts cover glandular areas that secrete an oily, cheese-scented substance (Apps, 2012; Estes, 1990; Furstenburg, 2009; Stuart & Stuart, 2015).



Figure 2. Impala of the Niassa Special Reserve. To the left males in a bachelor group and to the right the females in a breeding group (source: Photography taken during the field work, 2022).

Impala exhibit distinct sexual dimorphism. Only males possess horns, which are deeply furrowed along most of their length but smooth at the tips. The shape of the horns changes with the animal's age. In juveniles, the horns are straight, upright, and short (<150 mm), becoming curved like upright brackets (<250 mm long) when the individuals become subadults (12 to 18 months old). By adulthood, the horns curve backwards into a lyre shape, with an average length of 500 mm (Fritz & Bourgarel, 2013). Adult males are larger than females, with a mean shoulder height of 0.9 m, compared to 0.84m for females (Furstenburg, 2005). Males are 1.6 m long, while females are 1.55 m (Apps, 2012).

#### 4.3.3. Distribution

Endemic to the African continent, impalas are widespread in the Eastern and Southern areas, from Kenya to South Africa (Fritz & Bourgarel, 2013; Furstenburg, 2009). In Mozambique, they historically occurred in most of the country, except in most of the provinces of Nampula and Zambézia (Smithers & Tello, 1976). The civil war (1976 – 1992) caused a decline in their populations (Fritz & Bourgarel, 2013) and impala survived mainly in protected areas of the country, but with few records in the south of Inhambane province and in Zambezia and Nampula provinces (ANAC, 2018a).

#### 4.3.4. Habitat

Impala are an edge species, naturally associated with lightly wooded grassland and open woodlands, well-draining soil with a firm base and no more than a moderate slope (Estes, 1990; Fritz & Bourgarel, 2013; Furstenburg, 2005). They are dependent on water and is never far from it (Apps, 2012). Impalas drink approximately 2.5 to 4 liters daily (Furstenburg, 2005).

#### 4.3.5. Diet

Impalas are mixed feeders (browser-grazer intermediate). They consume both grass and woody plants, including flowers, fruits, pods, bark and fallen leaves (Furstenburg, 2005). The usual ratio of graze: browse is 45:55, however, this can varies with season and locality (Furstenburg, 2005). Impala are very selective about the species and plant parts they eat, with a preference for high nutrient quality, palatable food (Apps, 2012; Fritz & Bourgarel, 2013; Furstenburg, 2005).

#### 4.3.6. Behaviour (activity, social, sexual, and anti-predator)

Impala are primarily diurnal, with some nocturnal activity. They spend 38% of their time feeding, typically in the cooler hours of the morning, the late afternoon, and at night (Furstenburg, 2005, 2016). Impala are non-migratory and have relatively small home ranges (200 to 700 ha). On average, they move about 2.5 to 3 km during a 24 hour day but are often repeatedly found in the same vicinity (Furstenburg, 2005, 2016).

Impalas are gregarious animals, and throughout most of the year, they form either bachelor groups, consisting of males of all ages, or breeding/family groups, consisting of females of all ages, young males, and one or two adult males (Apps, 2014). The size of these groups can vary, ranging from 6 to 30 individuals in the hot and humid summer months and up to 300 in the dry winter period (Furstenburg, 2005, 2016). During the breeding season, groups are composed of either only females or only males (Apps, 2014).

As the rut, which begins in late January, approaches, the strongest adult males establish temporary territories of 4 to 10 ha, which they aggressively defend against other males

(Furstenburg, 2009). In March, the territorial male begins herding females (Apps, 2014). When a breeding group passes through the male's territory, the male chases all the young males out of the group and tries to keep the females in the area for as long as possible (typically, 8-12 days; Furstenburg, 2005, 2016). After this time, the territorial male weakens and allows the females to move on (Furstenburg, 2005, 2016). As a result, the same breeding group may be retained in the territories of up to four different males in the same breeding season (Furstenburg, 2005, 2016).

During mating, the male courts the female and, if she is receptive, mounts her repeatedly for ~10 seconds at a time (Apps, 2012, 2014). The most successful males mate with up to 15 females during a breeding season (Apps, 2012, 2014). After giving birth, females hide their lambs for a day or two before. Unsuccessful males form new bachelor groups and the young males rejoin the breeding group at the end of the breeding season (Apps, 2012, 2014).

Impalas are highly alert and cautious, except for males in heat (Apps, 2012, 2014). Within the group, there is usually at least one individual that refrains from other activities and watches for predators or other threats (Apps, 2012, 2014). If an impala detects something suspicious, it emits a loud snort to alert others and may approach for a closer look (Apps, 2012, 2014). If they see a potential danger, they slowly move away, but if they are directly threatened, they swiftly flee, often jumping between trees and bushes (Apps, 2012, 2014). These jumps can be up to 2.5 m high and cover a distance of 9 m, while the impala's flight speed can reach 60 km/hr (Apps, 2012, 2014). In response to repeated alarm calls or a sudden attack, individuals scatter in all directions, making it difficult for predators to focus on a specific target (Apps, 2012, 2014). After fleeing to 150-400 m, individuals regroup (Furstenburg, 2005).

#### 4.3.7. Reproduction and population structure

Male impala reach sexual maturity between the ages of 16 to 18 months, while females reach maturity between 13 to 16 months (Apps, 2012). However, males do not start reproducing until they are 3 to 5 years old, after they establish territories, while females can start breeding at 18 months (Apps, 2012).

The breeding and birth seasons are relatively short, lasting only three to five weeks, and varying in timing across different regions (Apps, 2012; Furstenburg, 2005). In southern Africa, births take place at the beginning of the rainy season (November to January), when there is higher quality and quantity of food (Fritz & Bourgarel, 2013). Rainfall determines the nutritional quality of forage for ungulates at the time of birth and during lactation, when the nutritional requirements of mothers are highest (Ogutu et al., 2014). In contrast, there is less marked reproductive seasonality in eastern Africa because there is little seasonal variation in rainfall and, consequently, in resources, such that impala births are widely distributed along the year (Fritz & Bourgarel, 2013; Ogutu et al., 2014). Each female gives birth to a single lamb (twins are rare), weighing an average of 5 kg, after a gestation period of 185 to 205 days (Furstenburg, 2005). Impalas typically have a birth interval of 12 to 16 months. Mothers conceal the lamb in tall grass, under bushes, or in scrub for three to five days after birth (Furstenburg, 2005).

The impala's annual population growth rate is influenced by environmental conditions and predation (Furstenburg, 2005). It ranges from 23% to 35% and can be up to 45% in the absence of large predators (Furstenburg, 2005). The natural life expectancy is 12-14 years for females and 10 years for males (Fritz & Bourgarel, 2013).

The sex ratio is relatively even at birth and during the first year, but as they reach adulthood, the ratio tends to favor females (Fritz & Bourgarel, 2013). Overall, the sex ratio of socially mature females to socially mature males is 3:1 (Furstenburg, 2005). Mortality is highest during the first month of life and reaches 0.95 - 0.97 at three years of age (Fritz & Bourgarel, 2013). Survival is strongly affected by environmental factors, sex, and age. For female impala, the survival probability remains constant until 8-9 years of age, after which is starts to decline; for males, survival probability begins to decrease after 6 years of age (Fritz & Bourgarel, 2013), due to male behaviour, such as male-male competition for females and because males are generally less vigilant (Apps, 2012, 2014), leading to a greater risk of predation (Jarman & Jarman, 1973).

#### 4.3.8. Conservation status

The common impala is categorized as "Least Concern" in the IUCN Red List (IUCN SSC Antelope Specialist Group, 2017). While this species has been locally extirpated from some

parts of its range (e.g., Burundi; (Selier et al., 2016), it remains widespread and abundant across Africa (IUCN SSC Antelope Specialist Group, 2017). In many PAs throughout its range, impala populations are either stable or increasing (IUCN SSC Antelope Specialist Group, 2017). While they continue to receive adequate protection and management in both PAs and private conservation units, their population viability is expected to remain secure (IUCN SSC Antelope Specialist Group, 2017; Selier et al., 2016).
## **5. MATERIAL AND METHODS**

### 5.1. Study area

### 5.1.1. Geographical location of the Niassa Special Reserve

The Niassa Special Reserve (NSR) is the largest conservation area in Mozambique, covering 42,500 km<sup>2</sup> in the northern part of the country, adjacent to Tanzania (Figure 3). The reserve lies between 12°38'48"S and 11°27'05.83"S and 36°25'21.16"E and 38°30'23.74"E (NCP, 2020; Ribeiro et al., 2017; Ribeiro, Saatchi, et al., 2008). It extends over the Provinces of Niassa and Cabo Delgado, covering eight districts, namely: the entire District of Mecula, most of the District of Mavago, and portions of the Districts of Muembe, Majune, Marrupa, Sanga, Mueda and Montepuez (Allan et al., 2017; NCP, 2020; SRN, 2005).



Figure 3. Map of the study area with main water courses, distribution of human settlements and showing the management units division, elevation, and different types of vegetation.

### 5.1.2. Climate, relief, and hydrography

Niassa Special Reserve is tropical sub-humid in climate. During the dry season (May – October) the average temperature is 25 °C and there is little or no precipitation. In the rainy season (November – April) the average temperature is 30 °C, with an average rainfall of 900 mm (in the range of 800 mm in the east to 1200 mm in the west). The landscape is composed of a gently undulating plateau and two main peaks, to the west the Jao Mountain and to the east the Mecula Moutain (Ribeiro et al., 2017; Ribeiro, Saatchi, et al., 2008).

The highlands to the west form the watershed of two main rivers: the Rovuma and Lugenda. Both are large, perennial sandy rivers with strong flows, critical to supporting biodiversity and people within the NSR (Allan et al., 2017). The Luatise, Luambala, Luchimua and Lureco rivers are tributaries of the Lugenda River. The tributaries of the Rovuma are the Lucheringo, Messinge and Chiulezi rivers (Mathe, 2013). Mecula Mountain creates orographic rainfall that falls on the nearest surrounding area, feeding the streams that flow along its escarpments (SRN, 2005).

### 5.1.3. Flora and fauna

Encompassing the largest area of miombo woodland in Mozambique, NSR is a key conservation area for this biome in southern Africa. Miombo occupies ~72% of the reserve, dominated by the species *Brachystegia spiciformis*, *Bachystegia boehmii* and *Julbernardia globiflora* (Ribeiro et al., 2017; Ribeiro, Shugart, et al., 2008). In the broad regional context, the following Flora Zambesiaca categories occur in the reserve: (i) Deciduous Dry Miombo Savanna Woodland – Discontinuous Dry Savanna (Lowland); (ii) Deciduous Miombo (North – Easter Lowland and Escarpment) Savanna Woodland; (iii) Tardily Deciduous Miombo (North – Eastern Median Altitude) Savanna Woodland; (iv) Dry Tall Mixed Thicket; (v) Submontane and Montane Grassland; (vi) Moist Evergreen Forest (Desmet, 2004). Another prominent vegetation type in NSR is the dambos wetland, located next to the main drainage areas, within wooded grassland and grassland vegetation, and riverine forest (Ganzin et al., 2010; Rivaes et al., 2019).

The Reserve contains the most diverse array of fauna in Mozambique, including the country's largest populations of elephant (*Loxodonta africana*), lion (*Panthera leo*), leopard

(*Panthera pardus*) and wild dog (*Lycaon pictus*; Government of Mozambique, 2018; NCP, 2015, 2020). It is home to 25 carnivore species (Begg & Begg, 2004) and more than 370 bird species (Nolting, 2017). Other notable large herbivores includes sable (*Hippotragus níger*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), hartebeest (*Alcelaphus lichtensteinii*), kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus sylvaticus*), impala (*Aepyceros melampus melampus*), wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), waterbuck (*Kobus ellipsiprymnus*) and hippopotamus (*Hippopotamus amphibius*) (Craig, 2018; Nolting, 2017).

# 5.1.4. Human population, resource use and economic activities

Niassa Special Reserve contains approximately 45,000 inhabitants spread over 40 villages (Allan et al., 2017). This population lives in poverty, with limited access to infrastructure and social services (Allan et al., 2017). Shifting agriculture is the main source of livelihood, with maize, rice, cassava, and beans as the primary crops (Allan et al., 2017; Jorge et al., 2013). While cattle are absent due to the presence of the tsetse fly, goats, chickens, domestic dogs, and cats can be found in the villages (Allan et al., 2017; Jorge et al., 2013; SRN, 2005). Inhabitants engage in fishing, honey gathering, and trade with Tanzania (Ribeiro et al., 2017; Snook et al., 2015) although illegal activities such as poaching, artisanal mining, and logging do occur (Allan et al., 2017).

This protected area is divided into 17 management units, some of which were granted to private operators for sport hunting and ecotourism (Allan et al., 2017; Begg et al., 2018; NCP, 2020). The NSR management authority annually allocates quotas for sport hunting concessions as well for community use (SRN, 2005). This area is under the co-management of the Government of Mozambique (ANAC - Mozambique National Administration of Conservation Areas) and the WCS- Wildlife Conservation Society (Begg et al., 2018). One management unit was formally designated for community use and two for strict protection of biodiversity (Allan et al., 2017).

#### 5.2. Sampling design

For this study, was utilized the sport hunting area within L8 and L9 management units (total area: 4,999 km<sup>2</sup>) and the ecotourism area within the L5N, L5S and L4 management units (total are: 3,241 km<sup>2</sup>; Figure 4). All sites were situated along the Lugenda River, which served as an impenetrable boundary separating impala populations between the two areas. These specific units were chosen for the following reasons: (i) impala in NSR are more concentrated in habitats surrounding the Lugenda River (Craig, 2018; Grossmann et al., 2017); (ii) both areas are in the same ecological ecosystem, a deciduous dry Miombo savanna woodland (Desmet, 2004); (iii) logistically, the roads in these units were easily accessible and accommodation was readily availability in the vicinity for the data collection team.



Figure 4. Roads driven and impala sightings in sport hunting and ecotourism area.

A research vehicle was driven along existing and accessible roads within selected sport hunting and ecotourism areas to spot impala groups (Hariohay et al., 2018; Setsaas et al., 2007; Tarakini et al., 2014). During the course of this research, were driven a total of 178.19 km of road in Sport Hunting Area and 276.36 km of road in the Ecotourism Area.

### 5.3. Data collection

The vehicle maintained speeds ranging from 10 to 30 km/h, while carrying five people on board at all times, including one driver, one recorder and three observers (Ndiweni et al., 2015). As observers spotted an impala, the vehicle was immediately stopped, the engine was switched off, and the initial behaviour, sex, age class and group size were recorded (Hariohay et al., 2018; Setsaas et al., 2007). After observations were complete, the GPS position of the vehicle was also recorded. All observations were collected within a maximum radius of 500m on each side of the road (Muposhi et al., 2016). The data was recorded on a digital data collection form (Appendix I) using the KobotoolBox App (KoboToolbox, 2022), on a tablet device (Cedar CT8X2).

Observations were conducted during the morning from 5:30 a.m. and 9:00 a.m. and in the afternoon from 4:00 p.m. and 6:00 p.m., as impala activity is high during these cooler daylight hours (Apps, 2012; Furstenburg, 2016). Field work was carried out during the November 2022 hunting season, when the vegetation is dry (the visibility of wildlife is good) and lasted for 15 consecutive days (10th - 24th), firstly exploring all available roads that cross impala habitats in the hunting area and then moving on to the ecotourism area.

To prevent repeated sampling of the same individual impala, previously traveled roads were not revisited. Given that impala has a small home range (200 to 700 ha), the same groups are often repeatedly found in the same vicinity (Furstenburg, 2005, 2016). Prior to commencing new observations, the impala(s) had to be out of visual contact of those previously observed (Setsaas et al., 2007).

### 5.3.1. Group size, age, and sex sctruture

All the individuals in the group were counted and their sexes and age classes recorded. A 'group' was defined as a cluster of individuals where the maximum distance between any two individuals did not exceed 50 m (Flolo et al., 2021). Groups were further classified either a breeding group (composed of females of all age groups, calves, and some adult males) or bachelor group (only males, juveniles, sub-adults, and adults; Apps, 2012; Fritz & Bourgarel, 2013; Furstenburg, 2016). Solitary individuals were also observed and recorded.

Adult males and females were distinguished on the sexual dimorphic characteristic, specifically, the presence of horns in males, which are absent in females (Apps, 2012; Fritz & Bourgarel, 2013; Stuart & Stuart, 2015). Sex was recorded as 'unknown' in situations where it was not possible to identify an animal's sex, such as for calves whose horns had not yet emerged (Furstenburg, 2005, 2009). The sex ratio was defined as the ratio of adult and sub-adult males to adult and sub-adult females (Flolo et al., 2021; Setsaas et al., 2007).

The following age and sex classes was considered: (i) calf, (ii) juvenile female, (iii) juvenile male, (iv) subadult female, (v) subadult male, (vi) adult female and (vii) adult male (Fritz & Bourgarel, 2013; Hariohay et al., 2018). Male age classes were based on horn size, with juveniles displaying straight, vertical, and short (<15 cm) horns, subadults with curved horns resembling upright brackets, adults with horns curved backwards in a lyrate shape (~50 cm; Flolo et al., 2021; Fritz & Bourgarel, 2013). Female age classes were determined based on relative body size, as follows: (i) calves 10 – 40% of adult size; (ii) juvenile: 50 – 60% of adult size; (iii) subadult: 70-80% of adult size and; (iv) adult: 90 – 100% of adult size (Hariohay et al., 2018).

### 5.3.2. Initial behaviour

In each sighting the impala nearest the vehicle was chosen as the focal animal for behavioral observations (Muposhi et al., 2016). The following initial behaviour data were recorded, using binoculars if necessary: (i) feeding (feeding on vegetation or ruminating); (ii) resting (laying down or standing without ruminating); (iii) moving (slowly moving from one place to another); (iv) fleeing; (v) vigilance (time the animal examines the environment, abstaining from any other activity, standing still and craning the neck with the head held high); vi) others (any observed behavior not falling into the previous categories; Hariohay et al., 2018; Setsaas et al., 2018).

#### 5.3.3. Flight initiation distance

Flight initiation distances (FID) is defined as the distance at which animal begins to move or run away from an approaching threat (e.g., a predator or, often, human experimenter; Morelli et al., 2022). FID serves as a simple and standardized measure for assessing tolerance towards different levels of perceived threat (Kandel et al., 2022; Setsaas et al., 2018; Tarakini et al., 2014).

Observers waited two minutes after spotting the impala to allow them to acclimate to the presence of the vehicle and return to a state of no or low vigilance (Setsaas et al., 2018). After this period, a laser rangefinder (LR0600P) was used to measure the starting distance (SD) from the focal animal to the vehicle. Then, one person (referred to as the *test person*, consistent across all observations) carefully opened the vehicle door and walked at a normal constant pace in a straight line towards the animal. The test person stopped walking the moment the focal animal began to flee and an observer in the vehicle recorded the distance to the test person. The FID corresponds to the difference between the SD and the distance to the test person (Muposhi et al., 2016; Setsaas et al., 2007). For cases where animals fled while the test person opened the vehicle door, the SD was taken as FID (Tarakini et al., 2014).

# 5.4. Statistical analyses

Statistical analyses were performed in R version 4.2.2 (Posit team, 2022), at a significance level of alpha = 0.05, as follows:

# 5.4.1. Age structure, sex ratio and group size

Differences in sex ratio, frequencies of age classes and group type (bachelor group, breeding group, and single impala) between the sport hunting and ecotourism area were tested using the Fisher's Exact Test, followed by a post-hoc test for differences in each age class or group type in the hunting and ecotourism areas, using Holm-Bonferroni p-value correction. This analysis used the *fisher\_test* and *row\_wise\_fisher\_test* functions from the *rstatix* package (Kassambara, 2023).

A Student's t-test test was used to test for differences in impalas group size between the sport hunting and ecotourism area, using a *t.test* function from the *stats* package (R-core, 2023). The t-test was applied based on the central limit theorem, which states that in larger samples (>30), the distribution of the sample mean will be normally distributed, even if the data does

not come from a normally distributed population, thereby fulfilling the normality assumption of the parametric test (Whitlock & Schluter, 2015).

## 5.4.2. Initial behaviour

Fisher's Exact Test, followed by a post-hoc test using Holm-Bonferroni p-value correction (*fisher\_test* and *row\_wise\_fisher\_test* functions, *rstatix* package; Kassambara, 2023), was also used to test for differences in the frequency of initial behaviour of impala between sport hunting and ecotourism areas.

# 5.4.3. Flight initiation distance (FID)

A Student's t-test (*t.test* function, *stats* package; R-core, 2023) was used to assess whether there was a difference in flight initiation distance (FID) between the hunting area and the ecotourism area, also based on the central limit theorem, of the normally distribution of the sample mean in large samples (>30; Whitlock & Schluter, 2015).

# 6. STUDY LIMITATIONS

Due to poor conditions of access roads, it was not feasible to cover all the planned impala occurrence areas outlined for the study. Furthermore, restrictions to driving only along the established access routes (without the possibility of off-road driving) may have limited the possibility of additional impala concentrations areas.

# 7. RESULTS

Impala were observed in 76 sightings sites in the hunting area and 79 in the ecotourism area (Figure 4). A total of 757 individuals were recorded, of which 67% (n=510) were from the ecotourism area and 33% (n=247) were from the sport hunting area.

## 7.1. Group size, age, and sex structure

# 7.1.1. Group size

Most of the impala (61% of individuals in hunting area, and 62% in ecotourism area) were found in breeding groups, with the rest in bachelor group or alone (Figure 5). Lone impala 20% of individuals in the hunting area and 14% in the ecotourism area. There was no difference in the observed frequency of these different group types between the two areas (Fisher's exact test, p = 0.58).

Overall impala group size differed significantly between areas (t = 3.20, df = 153, p = 0.001), with a higher mean number of individuals ( $6.46\pm8.50$ ) observed in the ecotourism area compared to the hunting area ( $3.26\pm2.00$ ). Breeding groups were larger in the ecotourism than in hunting area t = -2.88, df = 93, p = 0.005), but there was no difference in bachelor groups size between areas (t = -1.42, df = 32, p = 0.164; Table 4).

	Table 4. Mean (± Standard De	eviation) group size o	of impala in sport h	unting and ecotourism area.
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Group	Area	
	Hunting	Ecotourism
Bachelor group	3.07±1.03	4.16±2.29
Breeding group	4.07±1.99	8.57±10.09
Overall*	3.26±2.00	6.46±8.50

\*Combined for individuals alone, breeding group and bachelor group.

Bolded columns indicate significant differences between areas at 0.05 level according Wilcoxon rank-sum test.



Figure 5. Relative frequency in percentage of the breeding group, bachelor group and impalas observed alone in the sport hunting and ecotourism area.

#### 7.1.2. Age and sex structure

Overall, there was a significant difference in the frequency distribution of age classes between ecotourism and hunting areas (Fisher's exact test, p = 0.0104). However, when each age and sex class was analyzed individually, no statistically significant differences were found between the two study areas (Table 5).

The adult females (46.96% and 42.55% of observations in the hunting and ecotourism area, respectively) followed by adult males (22.08 % and 16.27% of observations in the hunting and ecotourism area, respectively) were the most frequently observed age and sex class. The least recorded in both areas were sub-adult males with 7.29% of observations in the hunting area and 6.86% in the ecotourism area. No juvenile was observed in either of the two areas.

	Number of animal sightings (%)		Statistical tests
Age class	Hunting Area	Ecotourism Area	p.adj
Adult males	22.08	16.27	0.222
Adult females	46.96	42.55	0.0605
Subadult males	7.29	6.86	0.879
Subadult females	7.69	13.92	0.548
Calves	14.98	20.39	0.112

Table 5. Impala age-sex class composition in sport hunting and ecotourism area

There were no significant differences in percentage of sightings in each age class, according to the Fisher's exact test.

In terms of the ratio of males to females, there was a greater skew towards females (including adults and sub-adults) in the ecotourism area (1: 2.44) in relation to hunting area (1: 1.84; Fisher's exact test, p = 0.04). However, when comparing the sex ratio for each age-sex class separately between the areas, no differences was found for either adults (Fisher's exact test, p = 0.25) or sub-adults (Fisher's exact test, p = 0.11; Table 6).

Table 6. Sex ratio (male: female) of impala in different ages classes, in the sport hunting and ecotourism area.

	Area		
Age classes	Hunting	Ecotourism	
Subadults and Adult	1: 1.84	1: 2.44	
Subadults	1: 1.06	1: 2.03	
Adults	1: 2.04	1: 2.61	

Bolded rows indicate significant differences between areas at 0.05 level according to Fisher test

### 7.2. Impala behaviour

### 7.2.1. Initial behaviour

Five different initial behaviors for impala were observed, including vigilance, moving, feeding, fleeing, and fighting (Figure 6). Vigilance was the most common initial behaviour, observed in more than 50% of the sightings in both areas. In the hunting area, 13% of the impalas fled immediately after being sighted, compared to only 1% in the ecotourism area. The frequency distribution of these behaviors differed significantly between the hunting and ecotourism area due largely to this striking difference in flight behaviour (Fisher's exact test, p = 0.007).



Figure 6. Relative frequency in percentage of different initial behaviors of impala in the sport hunting (N = 76) and ecotourism (N = 74) area. Different lowercase letters indicate significant differences between areas within the same behaviour at 0.05 level according to Fisher test.

### 7.2.2. Flight initiation distance (FID)

In the hunting and ecotourism area, 45% and 29% of focal impalas, respectively, were fled out before FID could be measured, a difference which was significant (Fisher's exact test, p = 0.05). For the remaining impala for which an FID was measured, there was no difference in FID between the hunting area (mean:  $46.9 \pm 22.02$  m) compared to the ecotourism area (mean:  $40.2 \pm 21.8$  m; t = -1.33, df = 96, p =0.23; Figure 7).



Figure 7. Flight initiation distance (m) in impalas in sport hunting (n = 42) and ecotourism area (n = 56). The box plots represent the median (horizontal line), mean (cross), first and third quartiles (box), range (whiskers) and possible outliers (dots).

# 8. DISCUSSION

# 8.1. Group size, age, and sex structure

Overall impalas group sizes were larger in the ecotourism area than in hunting area, contrary to the study hypothesis that impala would form larger group sizes in hunting area as an antipredator behavioral mechanism to evade potential hunter or facilitate escape (Grobis et al., 2013). Aggregate into larger groups as a proactive strategy for reducing predation risk by animals and humans has been observed by Creel et al. (2014) and Mremi et al. (2023), respectively, in impala and other ungulates species.

However, the findings of this study corroborate with a similar study in Tanzania, which found that impalas form smaller groups in hunting areas than in non-hunting areas (Hariohay et al. 2018) as result of: (i) direct effects of hunting, which removes individuals from groups and/or (ii) behavioral responses leading impala to select safer habitats further away from roads, which are often used by hunters (Hariohay et al. 2018). The second option aligns with

what was observed in this study (i.e., as a result of impalas fleeing immediately when the research vehicle approached).

Others similar studies did not find differences between group size patterns of impalas in hunting vs. non-hunting areas (Setsaas et al., 2007, 2018) and instead attribute impala group size to food resource availability. Impalas tend to form larger groups when resources are abundant and split into smaller groups when resources become scarce to avoid competition (Furstenburg, 2005, 2016; Mramba, 2022). In this study, efforts were made to minimize the influence of food resource availability by sampling areas with similar ecological conditions (Figures 3, 4; Anderson et al., 2007; Lee et al., 2021).

While there was an overall difference in the age and sex structure of the impala populations in the hunting and ecotourism areas, the findings were contrary to what was hypothesized. It was anticipated an age structure of males more skewed towards the younger classes and a sex ratio more skewed towards females in the hunting area compared to the ecotourism area, which could have been driven by either or both of the following mechanisms: (i) selective removal of older males (Festa-bianchet, 2003; Schindler et al., 2017) or (ii) displacement of young males into areas more explored by humans due to curiosity or lack of experience in interacting with people (Teichman et al. 2016). However, it was found that there were actually slightly higher frequencies of adult's males (relative to subadults and calves) in the hunting area and higher frequencies of females (relative to males) in the ecotourism area (although none of the pairwise differences for individual age-sex classes between the two areas were statistically significant). Similar findings were reported by Hariohay et al. (2018) in Tanzania, where no differences in impala sex ratio were observed between sport hunting and non-hunting area. The ways sport hunting can affect the wildlife population age structures, has not yet been widely studied, so few examples and explanations can be found in published studies.

Studies on the effect of human hunting of impala populations in the Serengeti ecosystem found that the sex ratio of this animal is more skewed towards females in areas with high human activity (including legal and illegal hunting) than in areas with low hunting activity, suggesting that the influence of sport hunting on the sex ratio may depend on the intensity of hunting (Flolo et al., 2021; Setsaas et al., 2007). In the study area, it was possible to see the age and sex structure being maintained in the sport hunting due to the fact that sport hunting consumption in the NSR is very low, with an average rate of 0.5%, compared to

sustainable consumption rates of 2% for big game, and 3-5% for smaller animals, including impalas (Child & Magane, 2020) so the direct removal of individuals in populations by sport hunting may not be significantly affecting the age and sex structure of impalas.

It is worth noting that the sex ratio results obtained in this study did not exceed the natural characteristic of impala populations (one mature male to three mature females), which is biased towards females (Fritz & Bourgarel, 2013), as males suffer higher mortality from behaviors such as male-male competition for females (Apps, 2012, 2014) and reduced vigilance, putting them at greater risk of predation (Jarman & Jarman, 1973). Studies on the age structure of unhunted impala populations also find that adult individuals typically comprise most of the population (Fritz & Bourgarel, 2013; Américo, 2020), in alignment with the observations in both the hunting and ecotourism areas of NSR.

No impala juveniles were observed (according to the criteria considered in this study), likely due to synchronized birthing patterns resulting in the absence of younger age classes during certain months of the year. Juveniles are easily distinguished in males by the shape of the horns, which are straight, vertical and short, becoming curved like vertical brackets in subadults when the individuals are 8-18 months old (Fritz & Bourgarel, 2013; Furstenburg, 2016). The study coincided with the onset of the impala birthing season, which takes place between November and January (Fritz & Bourgarel, 2013). This timing, coupled with the observations of calves, suggests that calves from the previous birth season were already in the sub-adult stage (i.e. older than 8 months) at the time of this study's fieldwork.

# 8.2. Impala behaviour

Vigilance emerged as the main initial behaviour exhibited by impala in both areas and did not differ depending on whether hunting was permissible or not. This result contradicts this study initial hypothesis as well as findings from other areas, which suggest that the ungulates animals, including impala, are more vigilant in the hunting area while in the ecotourism area they are generally more relaxed and engaged in other activities such as feeding (Hariohay et al., 2018; Kandel et al., 2022).

The vigilance behaviour observed across the entire study area may represent an adaptive behaviour that enables impalas coexist with humans (Kiffner et al., 2014). Additionally,

vigilance may also be affected not only by sport hunting but by other risks such as poaching and predation from carnivores, which may homogenize vigilance throughout the study area (Kandel et al., 2022).

While vigilance did not differ between the sport hunting and ecotourism areas, fleeing behaviour differed markedly, and this was notably more pronounced in the hunting area, likely due to the perceived higher risk of predation in this area, as animals may perceive humans as potential predators (Frid & Heithaus, 2019; Muposhi et al., 2016). This behaviour may also result from the frequent loud firearms used to hunt (Muposhi et al., 2016). These noises may induce fear in animals, leading them to decide to flee from threats to avoid the costs of continuous vigilance and reduce the risk of lethal encounters with humans (Blumstein, 2003; Dumont et al., 2012). An increase in anti-predator behaviour like fleeing and vigilance has also been observed in other species and in others hunting areas (Setsaas et al., 2007; Stankowich & Blumstein, 2005).

Although fleeing was a more common response in the hunting area, there was no support for the hypothesis that impalas would increase their FID from humans in the sport hunting area as compared to ecotourism area. No differences in FID between the areas were found, contrary to findings of numerous studies elsewhere for impalas and others ungulates, which documented a clear influence of sport hunting on increased animals' flight initiation distances (Hariohay et al., 2018; Kandel et al., 2022; Matson et al., 2005; Setsaas et al., 2018; Tarakini et al., 2014).

Notably, there is great variability in the FID data in this study (Figure 7), with observed values range from 1-106 m and 9-103 m in the ecotourism and hunting areas, respectively, in contrast to what has been reported as a "typical" impala FID range of 20 - 60 m (Furstenburg, 2009). This variability could be caused by various factors influencing the animal's ultimate decision to flee, such as starting distance and the individual's alertness. Animals tend to flee earlier from threats detected at greater distances to avoid the costs of continuously monitoring the threat, and alert individuals are also able to flee earlier than unaware individuals (Blumstein, 2003; Dumont et al., 2012; Flolo et al., 2021).

Other factors that have been reported to influence FID in impalas and other ungulates include the animal's sex, age, group type, group size, habitat, and the presence of calves in the group (Setsaas et al., 2007; Stankowich, 2008; Stankowich & Blumstein, 2005). These factors may

overshadow the effects of sport hunting on animal behaviour and FID as a potential indicator of human disturbance. Future research in NSR should therefore extend its analysis to factors that may influence FID, to elucidate the effects of sport hunting on animals' anti-predator responses.

To recap, all the findings of this study were contrary to the initial hypotheses about the effect of sport hunting on the behaviour and demography of impala populations in NSR, thus suggesting little influence of sport hunting on the variables analyzed, although the results relating to group size and fleeing behaviour suggest that there is an influence of the status of the area (whether hunting is allowed or not). However, more studies are needed to better clarify these issues, especially given the study's limitations of lack of access to some areas where impala occur. The results of this study establish a baseline for long-term monitoring of the variables analyzed to inform managers about the ecological sustainability of sport hunting in NSR.

# 9. CONCLUSIONS

Based on the findings obtained in this study, the following conclusions can be drawn:

- ✓ Impala were found in smaller groups in the hunting area than in the ecotourism area, suggesting that the status of the area (being hunting or not) influences impala grouping patterns. However, there was no evidence that sport hunting affects age structure and sex ratio, as the impala population was mainly composed by adults (for both females and males) in the hunting area than in the ecotourism area, and the overall sex ratio was more skewed towards females in the ecotourism.
- ✓ The frequency distribution of behaviors exhibited by impalas in response to approaching vehicles differed between the hunting and the ecotourism area, largely due to the marked difference in fleeing behaviour. In hunting areas, impalas were more likely to immediately flee in response to an approach vehicle, although there were no significant differences in their flight initiation distance between the areas.

# **10. RECOMMENDATIONS**

Based on the findings obtained and the limitations of this study, and given the implications for biodiversity conservation in sport hunting areas, the following recommendations have emerged:

- ✓ The results of this study provide a baseline of impala behaviour and population structure in the Niassa Special Reserve, in a scenario where the effects of sport hunting are not significant. Therefore, future assessments and monitoring using the same variables of behaviour and demography as indicators are recommended to NSR managers to assess the long-term impacts of sport hunting on ungulate populations and to inform the necessity of reviewing the ungulates game species offtakes rates as the expected effects of sport hunting become apparent.
- ✓ It is also recommended that similar studies be carried out in other blocks within the Niassa Special Reserve, including other ungulates species and considering in the analysis other variables that may overshadow the effect of sport hunting. This will likely help find clearer results on the effects of sport hunting on animals' behaviour and population demography.
- ✓ Since no juveniles were observed in this study, most likely due to the time of the study, it is important to carry out future studies on the seasonal variation of age classes in order to better clarify the age structure of the population.

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## APPENDIX I. DATA COLLECTION FORM

Data Collection Form_KoboCoilect						
Focal animal behaviour						
The focal animal refers to the individual who is closest to the vehicle						
Feeding Moving Vigilant Resting Urinate Drinking Mating Fleeing						
Fighting						
Another focal animal						
behaviour						
The focal animal is seen in a herd?						
Herd Behaviour						
Feeding Moving Vigilant Resting Urinate Drinking Mating Fleeing						
Fighting						
Another herd benaviour						
Nr. Juvenile males   Nr. Juvenile females   Nr. Subadult males   Nr. Subadult females   Nr. Adult males   Nr. Adult females   Nr. Adult females   Distance from the vehicle to the focal animal     Test person distance   Distance from the vehicle to the test person						
Vigilance level						
I. Kun and stop < 10 metres away						
2. Run and stops 10 - 50 metres away						
$\square$ A Dung and descript stop until it is out of sight (>100 m)						
4. Kuns and doesn't stop until it is out of sight (>100 m)						
Notes						
yyyy-mm-dd hh:mm						
Habitat						

Open Closed		
Block		
Coordinates latitude (x.y °)		
longitude (x.y °)		
accuracy (m)		

# Form Preview on KoboCollect App

Data	a Collection Form 🖬 🦜 🗄	Data Collection Form 🖬	¥. :	Data Collection Form 🖻 🍾 :
* Fo The f	cal animal behaviour ocal animal refers to the individual who is	Stard initiation distance Distance from the vehicle to the focal ani	mal	Coordinates
close	st to the vehicle			Change Location
	Feeding			Latitude: S 12°10'14"
	Moving			Longitude: E 37°32'54"
$\checkmark$	Vigilant			Accuracy: 4.45m
	Resting			
	Urinate			
	Drinking			
	Mating			
	Fleeing			
	Fighting			
	NEXT >	< BACK	NEXT >	< BACK NEXT >

## APPENDIX II. OUTPUT OF DATA ANALYSIS PERFORMED IN R

#### 2.1. Age structure, sex ratio and group type and size

```
> #AGE SCTRUTURE
> age
                ecotourism hunting
calf
                        104
                                  37
                                  19
subadultfemale
                         71
subadultmale
                         35
                                  18
adultfemale
                        217
                                 116
adultmale
                         83
                                  57
>
>
 #the test
  fisher_test(age)
>
#
 A tibble: 1 \times 3
         p p.signif
<dbl> <chr>
      n
*
  <db1>
    757 0.0104 *
1
  row_wise_fisher_test(age,
>
                         p.adjust.method = "bonferroni")
#
 A tibble: 5 \times 5
                                  p.adj p.adj.signif
  group
                          p
<db1>
                      n
*
                   <db1>
  <chr>
                                  <db1>
                                        <chr>
                    757 0.0741 0.37
1 calf
                                        ns
 subadultfemale
                    757 0.012<u>1</u> 0.060<u>5</u> ns
2
3 subadultmale
                    757 0.879
                                1
                                        ns
                     757 0.274
4
 adultfemale
                                 1
                                        ns
                    757 0.0279 0.14
5
 adultmale
                                        ns
  >
#
  A tibble: 10 \times 6
   group1
                                                    p.adj p.adj.signif
                   group2
                                        n
                                                 р
 *
   <chr>>
                   <chr>>
                                    <db1>
                                             <db1>
                                                    <db1> <chr>
                                      231 0.433
                   subadultfemale
 1 calf
                                                   1
                                                           ns
 2 calf
                   subadultmale
                                      194 0.29
                                                   1
                                                           ns
 3 calf
                   adultfemale
                                      474 0.0689
                                                   0.689
                                                           ns
                                      281 \ 0.011\overline{5}
 4 calf
                   adultmale
                                                   0.115
                                                           ns
 5 subadultfemale subadultmale
                                      143 0.114
                                                   1
                                                           ns
 6 subadultfemale adultfemale
                                      423 0.0152
                                                   0.152
                                                           ns
   subadultfemale adultmale
                                      230 0.00246 0.0246
                                                           *
                   adultfemale
 8 subadultmale
                                      386 1
                                                           ns
                                                   1
 9 subadultmale
                   adultmale
                                      193 0.413
                                                   1
                                                           ns
10 adultfemale
                   adultmale
                                      473 0.25
                                                   1
                                                           ns
> #GROUP TYPE
 herd
>
         Ecotourism Hunting
Bachelor
                  19
                           15
                           46
                  49
Breeding
Alone
                  11
                           15
  rstatix::fisher_test(herd)
>
#
  A tibble: 1 \times 3
  n pp.signif
<db1> <db1> <chr>
*
1
    155 0.584 ns
> #SEX RATIO
>
 #Adults and subadults
>
>
  sex
  Ecotourism Hunting
```

```
М
           118
                       75
                      125
F
           288
  rstatix::fisher_test(sex)
>
#
  A tibble: 1 \times 3
  n pp.signif
<dbl> <dbl> <chr> 606 0.041<u>3</u> *
*
1
>
  #Adults
>
>
  asex
  Ecotourism Hunting
83 57
М
            83
           217
F
                      116
  rstatix::fisher_test(asex)
>
#
  A tibble: 1 \times 3
  n pp.signif
<db1> <db1> <chr>
473 0.25 ns
*
1
>
  #Subadults
>
>
  ssex
  Ecotourism Hunting
Μ
            35
                       18
            71
F
                       19
  rstatix::fisher_test(ssex)
>
#
  A tibble: 1 \times 3
       n
               p p.signif
  <db1> <db1> <db1> <chr>
*
     143 0.114 ns
1
 #GROUP SIZE
>
>
> #1. t-test - Group size
  group_ttest <- t.test(individuals ~ area, data = group, var.equa
1 = TRUE
> group_ttest
          Two Sample t-test
         individuals by area
 data:
t = 3.2032, df = 153, p-value = 0.001654
alternative hypothesis: true difference in means between group Eco
tourism and group Hunting is not equal to 0
95 percent confidence interval:
1.228554 5.182839
 sample estimates:
mean in group Ecotourism
                                     mean in group Hunting
                     6.455696
                                                      3.250000
>
 >
 > #1.1.Compare de bachelor group
  group_ttest <- t.test(individuals ~ area, data = Bherd, var.equa
 >
 1 = TRUE
 > group_ttest
          Two Sample t-test
data: individuals by area
t = -1.4238, df = 32, p-value = 0.1642
alternative hypothesis: true difference in means between group Eco
 tourism and group Hunting is not equal to O
95 percent confidence interval:
-0.14248047 0.02524341
 sample estimates:
 mean in group Ecotourism
                                     mean in group Hunting
                    0.4043336
                                                     0.4629521
```

```
> 
> #1.2.Compare de breeding group
> group_ttest <- t.test(individuals ~ area, data = Fherd, var.equa
l = TRUE)
> group_ttest
Two Sample t-test
```

data: individuals by area t = -2.8804, df = 93, p-value = 0.00493 alternative hypothesis: true difference in means between group Eco tourism and group Hunting is not equal to 0 95 percent confidence interval: -0.14598235 -0.02683659 sample estimates: mean in group Ecotourism mean in group Hunting 0.4820007 0.5684102

#### 2.2. Initial behaviour

```
> #INITIAL BEHAVIOUR
> behav
         Ecotourism Hunting
Feeding
                  16
Fighting
                   0
                            1
                           10
Fleeing
                   1
Moving
                  17
                           12
Vigilant
                  45
                           46
> library(rstatix)
  rstatix::fisher_test(behav)
>
 A tibble: 1 \times 3
#
    n pp.signif
dbl> <dbl> <chr>
155 0.006<u>95</u> **
*
  <db1>
1
>
  #Post hoc
>
 >
 A tibble: 10 \times 6
#
   group1
             group2
                                   p p.adj p.adj.signif
                           n
 * <chr>
                              <db1> <db1> <chr>
                       <db1>
             <chr>
 1 Feeding
            Fighting
                          24 0.333 1
                                           ns
                          34 0.002<u>4</u> 0.024
 2
  Feeding
             Fleeing
                                           *
 3 Feeding
                          52 0.563
            Moving
                                     1
                                           ns
 4 Feeding
             Vigilant
                         114 0.104
                                     1
                                           ns
 5 Fighting Fleeing
                          12 1
                                     1
                                           ns
                          30 0.433
 6
  Fighting Moving
                                     1
                                           ns
                          92 ľ
 7 Fighting Vigilant
                                     1
                                           ns
 8 Fleeing
             Moving
                          40 0.0106 0.106 ns
 9 Fleeing
             Vigilant
                         102 0.011<u>4</u> 0.114 ns
10 Moving
             Vigilant
                         120 0.404
                                    1
                                           ns
 row_wise_fisher_test(behav,
>
                         p.adjust.method = "bonferroni")
# A tibble: 5 \times 5
  group
                n
                         р
                          p.adj p.adj.signif
                    <db1>
*
            <db1>
                            <db1> <chr>
  <chr>
              155 0.070<u>4</u>
                           0.352
1 Feeding
                                 ns
              155 0.49
2
 Fighting
                           1
                                  ns
              155 0.00417 0.0208
3 Fleeing
                                  *
4 Moving
              155 0.413
                           1
                                   ns
                           1
5 Vigilant
              155 0.745
                                   ns
```

## 2.3. Flight initiation distance

```
> #Compare animals that fled before FID mensure
> Flight
              Ecotourism Hunting
Fled
                                        34
                            23
didntFled
                            56
                                        42
>
> library(rstatix)
  rstatix::fisher_test(Flight)
>
# A tibble: 1 \times 3
   n pp.signif
<db7> <db7> <chr>
155 0.047<u>6</u> *
*
1
>
> # t-test - Fid
> fid_ttest <- t.test(FID ~ area, data = fid, var.equal = TRUE)</pre>
> fid_ttest
            Two Sample t-test
data: FID by area
t = -1.1987, df = 96, p-value = 0.2336
alternative hypothesis: true difference in means between group Ecotouris
m and group Hunting is not equal to 0
95 percent confidence interval:
    -14.244235 3.518044
cample estimates
sample estimates:
mean in group Ecotourism
                                           mean in group Hunting
                          40.8750
                                                                 46.2381
```