Assessment of the abundance and selected population characteristics of Hartmann's mountain zebra *Equus zebra hartmannae* in Iona National Park, Angola

Milcíades Rafael Chicomo

Thesis submitted in partial fulfillment of the requirements for the degree of Master of Natural Resources Management at the Namibia University of Science and Technology

NAMIBIA UNIVERSITY
OF SCIENCE AND TECHNOLOGY

Supervisor: Prof. Morgan Hauptfleisch
(NUST Biodiversity Research Centre)
Co-Supervisor: Pedro Monterroso, PhD
(CIBIO-InBIO UP, Portugal)

MARCH 2021

Declaration

I, *(Milcíades Rafael Chicomo)*, hereby declare that the work contained in the thesis entitled: *(Assessment of the abundance and selected population characteristics of Hartmann's mountain zebra Equus zebra hartmannae in Iona National Park, Angola)* is my own original work and that I have not previously in its entirety or in part submitted it at any university or higher education institution for the award of a degree.

Signature:…………………………………………………… Date: 03/06/2021……………………………….

Retention and Use of Thesis

I, *(Milcíades Rafael Chicomo)*, being a candidate for the degree of *(Master of Natural Resources Management)* accept the requirements of the Namibia University of Science and Technology relating to the retention and use of theses deposited in the Library and Information Services.

In terms of these conditions, I agree that the original of my thesis deposited in the Library and Information Services will be accessible for purposes of study and research, in accordance with the normal conditions established by the Librarian for the care, loan or reproduction of theses.

Signature:………………………………………………… Date: 03/06/2021……………………………

Table of Contents

List of Figures

List of Tables

List of Acronyms

SCIONA	Skeleton Coast Iona
TFCA	Trans-frontier Conservation Area
HMZ	Hartmann's Mountain Zebra
EU	European Union
VU	Vulnerable
IUCN	International Union for the Conservation of Nature
CMZ	Cape Mountain Zebra
UNDP	United Nations Development Program
CT	Camera Trap
EDF	Encounter Data File
TDF	Trap Deployment File
IBEIS	Image Based Ecological Information System
SCR	Spatial Capture-Recapture
AIC	Akaike Information Criterion
BIC	Bayesian Information Criterion
CDF	Cumulative Distribution Function
HR	Home Range

Acknowledgements

I am deeply grateful to my supervisor Professor Morgan Hauptfleisch for his mentorship and commitment to help and guide me on this project with his experience. I'm thankful for his inputs into this project, as well as the endless advice and motivation to overcome difficult moments.

I would like to express my sincere gratitude to my co-supervisor Pedro Monterroso, PhD, who promised to help me build a great project. He indeed helped me achieve this, even from far away. I'm thankful for his endless inputs to make this project better. Words are not enough to express my gratitude for his advice, guidance and motivation to keep my head up and keep going.

Thank you to the SCIONA project, which co-designs conservation technologies for the Iona-Skeleton Coast Transfrontier Conservation Area (TFCA) of Angola and Namibia and is funded by the European Union [EuropeAid/156423/DD/ACT/Multi], for this great opportunity and for providing the financial support for this study.

I would like to offer my special thanks to the SCIONA project's PI Dr Fernanda Lages, who introduced me to the project and trusted me to be part of this great initiative. I appreciate her organizing the conditions for the development of this study and always ensuring a great atmosphere.

To Dr Vera de Cauwer, I'm thankful for all your help and guidance, thanks for your commitment and persistence. At the beginning of the study, I couldn't design a map, and I thought it was complicated. Thanks to you, I can now do it by myself.

To the SCIONA coordinator Amber Nott, thanks for helping, advising and guiding me in very difficult situations, without your experience it would have been immensely more complicated. From the first moment, you always ensured that I had everything I needed to conduct the study.

I would like to extend my sincere thanks to the Iona National Park management, particularly the manager Mr. Sango de Sá for allowing me to conduct the study in the park. I would also like to extend my gratitude to the park rangers Mr. Maximino Cassuete, Mr. Leonardo Aguiar, and Mr. Wanderley Nascimento (*in memory*), who tirelessly helped with setting up and reviewing the cameras.

Thank you to Bruce Bennett, who with his invaluable ground knowledge of the park and the wildlife communities guided and helped us to set a camera trapping system that successfully sampled the target species.

A sincere thank you to the owner of Omahua Lodge, Mr. Álvaro Baptista, for allowing us to pass through his property and access some zebra spots where we set up some cameras, and for providing help for our expeditions. I would like to extend my thanks to Mr. Valdemar de Jesus Pontes Viveiro (Mr. Marinho), a special Omaua Lodge worker, for his guidance and help to track the spots normally used by zebras. With his knowledge of the area, I successfully found important places for the camera stations.

To my colleagues Telmo António and Jackson Hamutenya, who faced the extreme conditions of Iona National Park to help me set up the cameras, and especially for their friendship and moral support, I want to say a special thank you. And I would like to extend my acknowledgements to the great team of colleagues who were there all the time, giving support in all the activities, and for providing a great environment for adaptation and study.

A sincere thank you to Jon Crall, PhD, who patiently helped me with the identification process. Since the beginning he advised and guided me to successfully set up the software, and then proceed with the management. Without your input it would be more complicated to process one of the most important analyses of this study.

To my family, for always being there and extraordinarily supporting me and keeping me focussed to accomplish this important objective in my life, thank you.

I am deeply grateful to my girlfriend Martina Mayer for the support she has been giving to me, even from afar she was always there supporting me.

To Gerda Schuler, thank you for providing the best accommodation, a place where I could rest well and recharge. Without your help during the two years, it would have been very difficult, especially in 2020, when you were there to give all the support.

To Mr. Walter Buehler, thank you for donating a laptop to me in a very crucial moment, so that I could keep going with my research. I will always be grateful for your support.

To the Population Ecology Team EcoPop, from University of Porto, Portugal, I am thankful for your priceless advice and guidance to improve my thesis.

Dedication

I dedicate this thesis to my parents, *Moisés Chicomo* and *Graciana Nkhuluavo*, for their love and unconditional support on my academic journey!

Abstract

Monitoring wildlife populations across time and space is key to their conservation and management. This was the basis for my study about Hartmann's mountain zebra (*Equus zebra hartmannae*). Since peace was achieved in Angola, a rapidly increasing level of collaboration between Angolan and visiting scientists and institutions has seen biodiversity research prospering. As a result of these collaborative initiatives, monitoring of wildlife is gaining a new dynamic. To contribute to this dynamic, ensure continuous wildlife monitoring in Angola, and promote the development of management and conservation strategies, we carried out the present study. Its goal was to assess the abundance and population characteristics of Hartmann's mountain zebra, a near-endemic species restricted to the extreme south-west of the country, in Iona National Park (INP). This study was carried out under the scope of the SCIONA project, funded by the European Union, which aims to strengthen cross-border ecosystem management and wildlife protection in the Namibian-Angolan Iona-Skeleton Coast Transfrontier Conservation Area (TFCA). It was implemented a camera trapping approach centered on waterholes, as means of non-invasively sampling the Hartmann's mountain zebra (HMZ) population, and used spatial capture-recapture (SCR) to provide estimates of demographic parameters such as abundance and density. Results showed a population size of HMZ of 428 adult individuals, 33 juveniles, and 17 foals. The population of HMZ is dominated by females at all age classes, indicated by the sex ratio of 1:3.46 (male:female), which is typical of some equid member species. This HMZ population presented an age structure dominated by adult individuals, representing 89.6% of the total population, and this proportion suggests an aged population which raises concern due to anthropogenic and environmental threats that the population is subject to. Of particular concern, the study unveiled an emerging population of hybrids of *Equus zebra* and *Equus asinus,* so-called zonkey, with a population of 19 adult individuals. HMZ, donkey and zonkey are active at waterholes all day, as shown by their activity levels, but the three species present distinct periods in which one of the species is more active. HMZ, donkey and zonkey are active at waterholes during all day, but their activity peaks at different periods, at night for HMZ, and during middle afternoon for donkey and zonkey. This shift of HMZ to nocturnal activity can be associated with a learned or acquired fear behaviour from human disturbance at waterholes during daylight, mostly by stock farmers with goats and cattle. This population estimate, based on rigorous camera trapping census methodologies, constitutes an accurate baseline population for a continuous monitoring programme in the park, and highlights conservation concerns for HMZ growth and success in Iona.

Keywords: *Angola*, *abundance, activity level, camera trapping, Hartmann's mountain zebra, Iona National Park, monitoring, population structure, spatial capture-recapture, SCR.*

Chapter 1: Introduction

1.1 Background

South-western Angola's wildlife conservation

The south-west of Angola is known as a hotspot for rare species with limited distribution because of its desert ecosystems, which cover a small portion in the extreme south-western corner of the country (Huntley and Ferrand 2019). Although historically present in the region, many species of large mammals such as black rhinoceros (*Diceros bicornis*), African lion (*Panthera leo*), Angolan giraffe (*Giraffa camelopardalis angolensis*) and African elephant (*Loxodonta africana*) have been extirpated from Angola's southwest because of human activities (Huntley 2017). However, local populations of some iconic species such as the cheetah (*Acinonyx jubatus*), brown hyena (*Hyaena brunnea*), gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*) and Hartmann's mountain zebra (HMZ) (*Equus zebra hartmannae*) were reduced to critically low numbers due tointense poaching as well as the civil war, and the increasing of human presence led to the destruction and reduction of their habitats (Huntley and Ferrand 2019). Given the fragility of their current populations in Angola's south-west, these species need to be targeted for accurate population assessments and continuous monitoring, in order to better understand their status, and guide sound strategies for their management and conservation.

Importance of monitoring wildlife populations

Monitoring animal populations can be defined as 'the estimation of some state variables (e.g. abundance or occupancy) or vital rate (e.g. survival or reproductive rate) relevant to populations for the purpose of drawing inferences about variation over space and/or time' (Nichols *et al.* 2017). Monitoring populations across time and space is a key element of wildlife conservation and management (Palmer *et al.* 2018) and since peace in Angola was achieved, a rapidly increasing level of collaboration between Angolan and visiting scientists and institutions has seen a prosperous era of biodiversity research (Huntley and Ferrand 2019). As a result of these collaborative initiatives, monitoring of wildlife is gaining a new dynamic. Several wildlife species' distribution and relative abundance has been assessed in Angola, mostly in the protected areas in the north, centre and east of Angola (Funston *et al.* 2017, Overton *et al.* 2017, Baptista *et al.* 2019, Pinto 2019, Monterroso *et al.* 2020), but a gap remains regarding the status of wildlife species occurring in the south-west of the country.

HMZ in Angola

In response to the need, and with the intention of continuing with initiatives of monitoring Angola's biodiversity, I directed my attention to one of the most emblematic species in the country, the HMZ, which has a restricted distribution range in INP, and is classified as 'vulnerable' (VU) by the International Union for Conservation of Nature (IUCN) (Gosling *et al.* 2018). The HMZ is one of the species that is still found in the south-west of Angola, despite hard conditions and anthropogenic activities. In spite of the suspected vulnerability of HMZ, the population status was never assessed regionally to ensure its conservation and management. I provide the first robust assessment of HMZ population in INP, and further characterize its structure at the sex and social group level. I further assess the population of phenotypically-identified HMZ x donkey (*Equus africanus asinus*) hybrids, commonly known as *zonkeys*, as hybridization has been proposed as a potentially important threat to the HMZ population in INP (Brown and Jenkins 1987, Hrabar *et al.* 2016).

Understanding the HMZ population in Angola

Camera trapping is one of the most common techniques for non-invasively estimating the abundance of wide-ranging and secretive wildlife species that exhibit distinctive external patterns (Royle *et al.* 2013), such as HMZ and *zonkey*. However, despite its potential feasibility for the focal species, this approach has never been employed to investigate the population abundance of HMZ, as most studies have been carried out either through direct observation or through remote tracking of collared animals in Namibia (Muntifering *et al.* 2019). Therefore, this study provides the first proof-of-concept about the reliability of camera trap-based spatial capture-recapture (SCR) protocols for the assessment of HMZ and *zonkey* in a desert environment.

SCIONA

This study was carried out under the SCIONA Project, which aimed at strengthening cross-border ecosystem management and wildlife protection in the Iona – Skeleton Coast Tran-frontier Conservation Area (TFCA), through co-designing and implementing conservation monitoring technology in collaboration with the park authorities and surrounding communities. One of the project's goals was to contribute to the increase of the wildlife populations in general, and specifically of endemic or endangered species. Without any current formal wildlife monitoring being performed in INP, it is important to provide baseline estimates of the numbers and distribution of its animals, as well as to test possible methods for continued monitoring.

1.2 Literature review

1.2.1 Hartmann's mountain zebra

Zebras belong to the order Perissodactyla, which comprises three living families – Equidae, Rhinocerotidae and Tapiridae, and the order is characterized by the presence of either one or merged toes (Hutchins *et al.* 2004, Groves and Grubb 2011). They are further classified as members of the odd-toed ungulates, because their hooves end in functional toes (Hutchins *et al.* 2004, Groves and Grubb 2011), and as part of the Equidae family, which comprises the horse-like species characterized by a terminal single-toed hoof (Estes 1999, Hutchins *et al.* 2004). All currently living wild species of equids belong to the genus *Equus*, which includes horses, zebras and asses, and the species are mostly distributed throughout Africa (Kingdon 2015).

Three species of zebra are currently recognized, and they all occur in Africa: i) the Grevy's zebra (*E. grevyi*), with a distribution range restricted to the Horn of Africa, especially Ethiopia and Kenya (Rubenstein, Low Mackey, *et al.* 2016); ii) the plains zebra (*E. quagga*), occurring from the north-east of South Africa northwards to south-eastern Sudan, southern Ethiopia and southern Somalia (King and Moehlman 2017); and iii) the mountain zebra (*E. zebra*), occurring from the arid mountains and escarpment running from south-western Angola, to the mountains of the Cape and the Karoo in South Africa (Kingdon 2015, Hrabar *et al.* 2016, Gosling *et al.* 2018) (Fig.1).

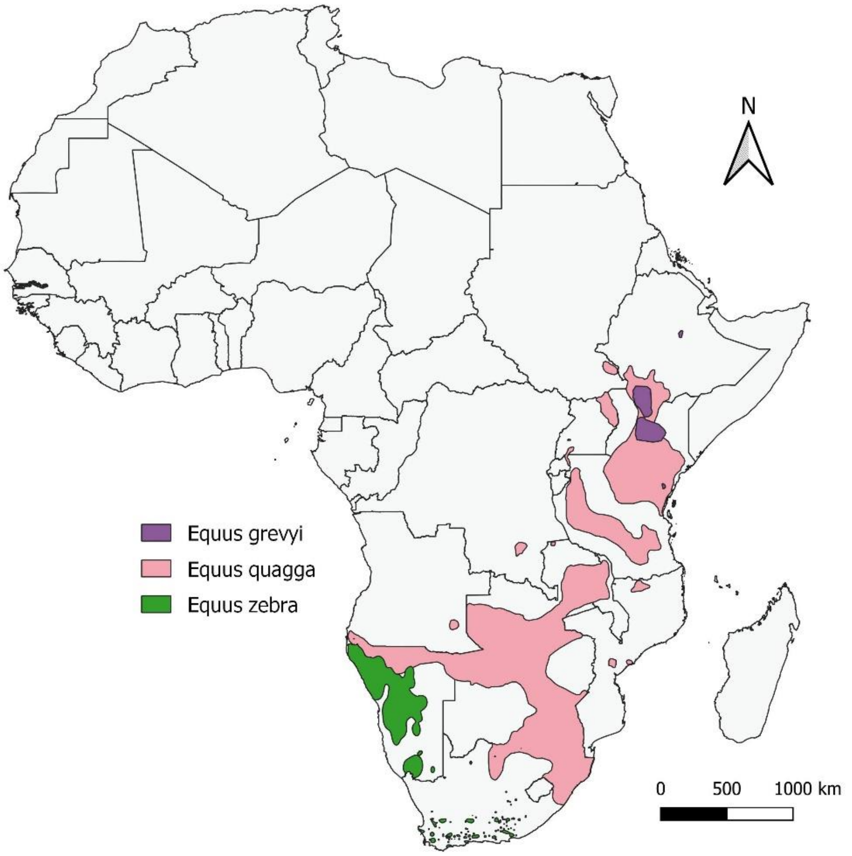


Figure 1. Distribution of zebras in Africa: Equus zebra (Source: Rubenstein et al. *2016); Equus quagga (Source: King and Moehlman 2017); and Equus zebra (Source: Hrabar* et al. *2016, Gosling* et al. *2018).*

All the species present a striped body pattern and the main phenotypic differences between them regard the number of stripes and the rump pattern, with a specific arrangement characterizing each group (Bard 1977). The set of stripes on the body of the animals is formed by a single mechanism, which operates during the gestation period at different stages in each group: during the third week in plains zebra, the fourth week in mountain zebra and the fifth week in Grevy's zebra (Bard 1977). Additionally, each individual in all species exhibits a different side-specific pattern of stripes, which, similar to fingerprints, allows for individual identification (Penzhorn 1979, Skinner and Chimimba 2005).

The mountain zebra comprises two subspecies: i) The Hartmann's mountain zebra (*Equus zebra Hartmannae*), occurring from the montane escarpment in extreme south-western Angola, throughout Namibia, southwards to South Africa (Penzhorn 1988, Skinner and Chimimba 2005, Gosling *et al.* 2018); and ii) the Cape mountain zebra (CMZ) (*Equus zebra zebra*), for which occurrence is restricted to a small set of conservation areas on the escarpment of the Cape province (Stuart and Stuart 2015, Hrabar *et al.* 2016). The current distribution of both HMZ and CMZ is shown in Figure 2, and the distribution of HMZ is hardly noticeable in Angola.

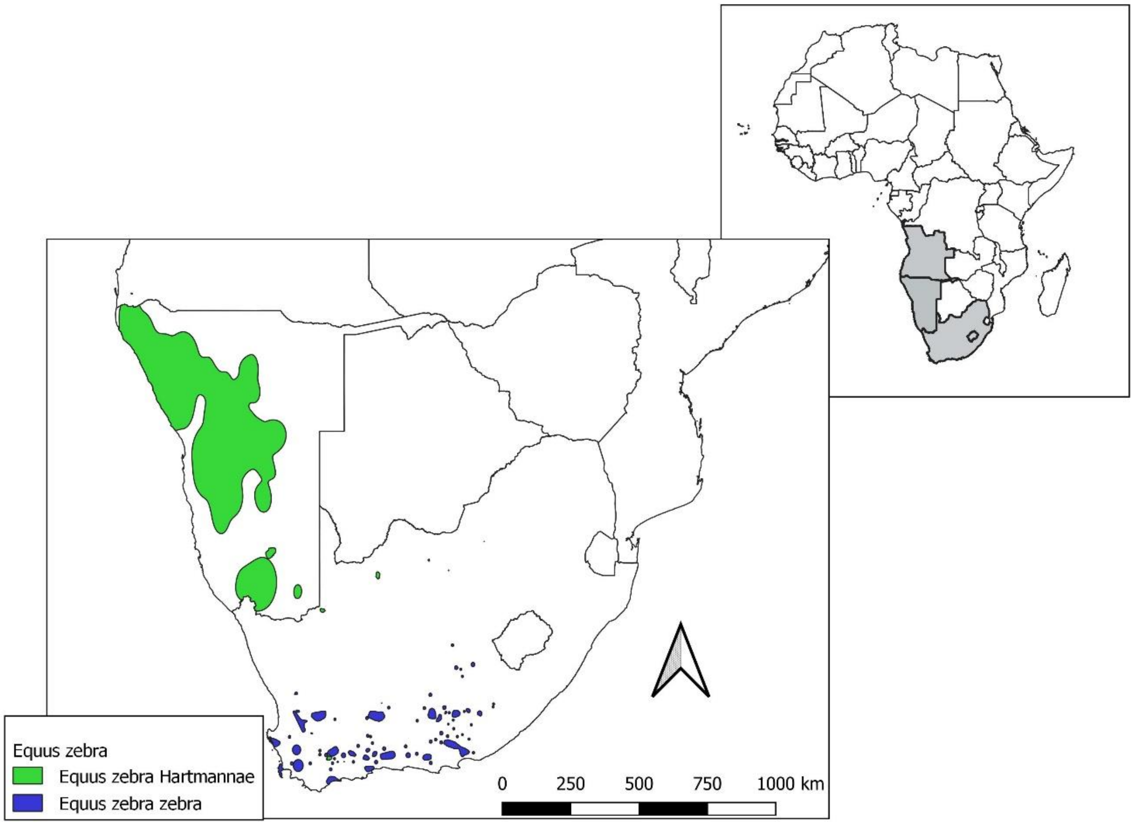


Figure 2. Current distribution of mountain zebra: Equus zebra hartmannae (Source: Gosling et al. 2018) and Equus zebra zebra (Source: Hrabar et al. 2016).

Even with populations known to be healthy, The HMZ is a protected species and classified as 'vulnerable' due to the various threats it faces (Gosling *et al.* 2018).

The two subspecies of mountain zebra differ in several regards: The HMZ has a slightly larger body size than the CMZ, the black stripes of HMZ are not as wide as those of the CMZ, and the mane of the HMZ extends further forward between its ears than that of the CMZ (Novellie *et al.* 2002). In fact, Groves & Bell (2004) suggested that there is enough evidence to consider the two as different species, based on the following morphological differences: i) the CMZ female is generally larger than the male, which isn't the case in HMZ; ii) the HMZ is generally larger than the CMZ; and iii) they are allopatric species. Regardless, HMZ and CMZ are still officially considered conspecifics (Moodley and Harley 2006, Kingdon 2015), therefore I followed that taxonomic reference in this study.

Phenotypic distinctiveness

Mountain zebras are evenly striped equids, which differ from other zebras by the presence of a dewlap on the throat, and a grid pattern on the rump, so called ‘gridiron’ (Stuart and Stuart 2015) (Figure 3).

Figure 3. Dewlap (left) and gridiron (right), the main phenotypic features that distinguish HMZ from other zebra species.

In north-western Namibia, the HMZ distribution range overlaps with that of the plains zebra (Hrabar *et al.* 2016, Gosling *et al.* 2018) (Figure 4 and 5), but the two species are easily distinguished by their external features (Figure 6). The plains zebra presents: i) a shallow stripe between the black stripes, ii) its vertical black stripes normally connect together under the belly, iii) the absence of a dewlap, and iv) the absence of the gridiron, which is characteristic of mountain zebras (Bard 1977, Stuart and Stuart 2015).

Figure 4. Hartmann's mountain zebra in front and plains zebra in the background - the two species overlap in Etosha National Park, Namibia. Photo: Prof. Morgan

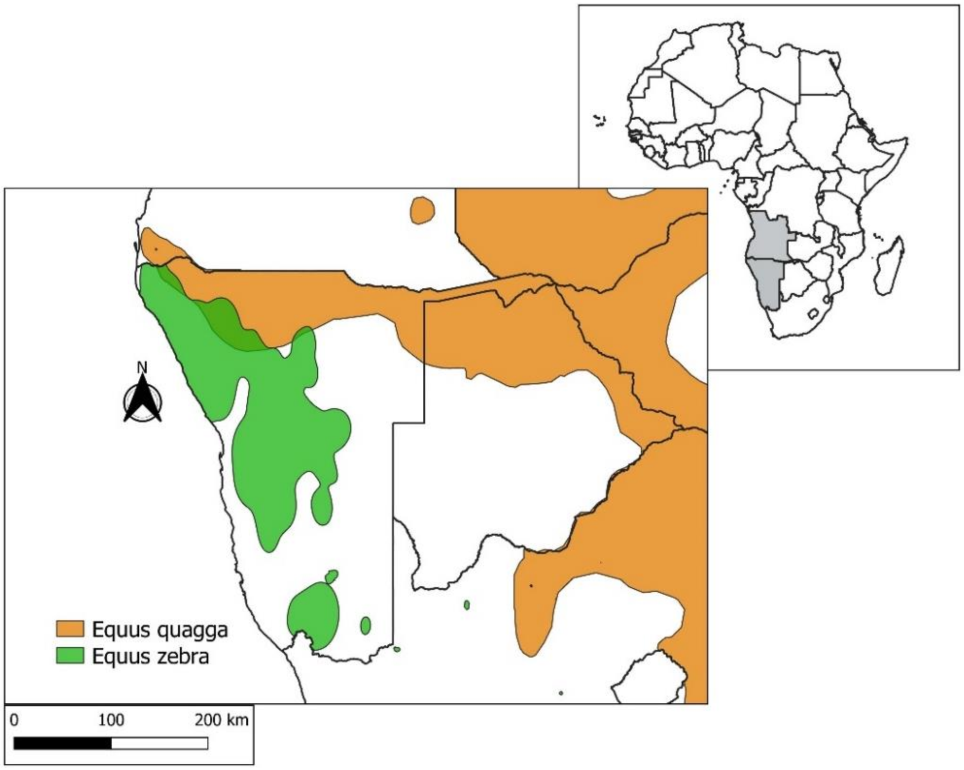


Figure 5. Mountain zebra and plains zebra overlap (Source: Gosling et al. 2018, King and Moehlman 2017).

Figure 6. HMZ (left) and plains zebra (right) phenotypes. (plains zebra image copyright: Yathin S. Krisnappa).

Social organization, behaviour and vital rates

HMZ is a gregarious and non-territorial species, and its social organization is based on breeding herds and bachelor groups (Joubert 1972a, Klingel 1974, Penzhorn 1979, Estes 1999). Breeding herds typically consist of a single adult stallion with his mares and foals (Joubert 1972a, Klingel 1974, Estes 1999). The size of breeding herds vary according to the number of foals born to the herd, and to the number of foals that leave their maternal herds after maturing (Penzhorn 1979). Regardless, breeding herds tend to be composed of a mean of 4.7 individuals, with a range from 2 to 8 individuals (Joubert 1972a, Penzhorn 1979). Breeding herds are usually stable and permanent units (Klingel 1974). Mares remain in the same group until death, whereas old and sick stallions are displaced from herds by stronger individuals (Klingel 1974). The stallions show an aggressive behaviour towards each other to defend exclusive access to their mares, and fights have been shown to be the natural way for stallions to develop and protect their own breeding herds (Joubert 1972a, Klingel 1974).

The bachelor groups are made up of young stallions, as well as stallions that have either been displaced from breeding herds or that have not yet established their own breeding herds (Joubert 1972a, Klingel 1974). In bachelor herds, the leader is always an adult stallion, but there is no order of dominance among the sub adult stallions, which make up the majority of these groups (Joubert 1972a, Penzhorn 1979).

HMZ are water dependent. Where they are protected or not disturbed, HMZ visit sources of surface water to drink throughout the day, whereas they tend to visit water sources during the night or early morning in areas where they are hunted (Muntifering *et al.* 2019).

As seen in other wildlife, HMZ populations are shaped by fecundity, survival, emigration and immigration, collectively coined ‘vital rates’ (Mills 2012), each of which is subject to a suite of biological and ecological inputs across space and time (Ransom and Kaczensky 2016a). How these inputs influence population dynamics varies between populations (Ransom and Kaczensky 2016a). Vital rates contribute to population dynamics, and are influenced by many factors, with resource availability being one of the most important natural factors. Limited availability of resources (e.g. forage or water) impacts the body condition and fitness of individuals, making them more susceptible to disease and parasites, thereby reducing fecundity and survival, which ultimately limits population growth (Ransom and Kaczensky 2016a).

Female HMZ can give birth from 2.5 years old, after achieving sexual maturity at 1.5 years old (Joubert 1974), and they have been documented to give birth at ages as high as 21 years old (Joubert 1974). They typically give birth to one offspring annually, with a mean birth rate of 0.20 ± 0.002 (± SE) (95% CI = 0.16 - 0.45) (Joubert 1974). The birth rates in wild populations reflect offspring born and observed, rather than the pregnancy rate, which is presumably higher in most cases (Ransom and Kaczensky 2016a).

Mountain zebras live in environments without significant predation pressure and exhibit relatively high survival rates across all age classes (Ransom and Kaczensky 2016a). On average, the annual survival rates are 0.98 ± 0.001 (± SE)(95% CI = 0.87 - 0.98) for foals and 0.92 ± 0.001 (± SE) (95% CI = 0.91 - 0.93) for adults (Joubert 1974). Much of the variation in annual survival rates of both foals and adults by population may be attributed to localized predation, but in places with low risk of predation like in INP, the survival rates are normally associated with drought.

Hartmann’s mountain zebra in Angola

Little is known about the HMZ population occurring in the INP, apart from the raw estimates of their numbers through aerial surveys conducted by the Namibian Ministry of Environment and Tourism in 2003 (N = 263) and 2017 (N = 304), which aimed to assess the status of wildlife and livestock in the park (Kolberg and Kilian 2003, van der Westhuizen *et al.* 2017). In addition to the aerial surveys, multiple occasional observations (Bruce Bennet *unpublished data*; João Ferrand *unpublished data*) confirmed that there is indeed a population of HMZ in INP, even though HMZ were thought to be regionally extinct (Novellie *et al.* 2002). However, the aerial surveys represented an experimental approach, more of a reconnaissance activity which cannot be considered a monitoring survey, because it does not provide robust estimations of accuracy or precision. This study provides the first systematic, robust and repeatable approach to assess the population ecology and opportunity for population growth of HMZ in the INP. Despite a number of studies on HMZ social organization and behaviour in Namibia and South Africa (Joubert 1972a, Penzhorn 1988, Moodley 2002, Sasidharan 2005), none have been carried out on the Angolan population, where the HMZ is at the extreme of its distribution range (van der Westhuizen *et al.* 2017).

At the moment, the Angolan range of the HMZ is thought to be restricted to the INP and isolated from the other populations (Gosling *et al.* 2018). Therefore, its population needs an urgent assessment not only to define proper conservation actions aimed at its recovery locally, but also for the assessment of HMZ’s conservation status in the country.

HMZ in INP still face many of the threats reported by Huntley (1974) in the 1970’s, particularly those regarding habitat loss and grazing competition with livestock. The latter has become even more intense with the recent demographic increase and expansion of the human population into the park, and with the “concurrent extension of livestock occupancy towards wildlife’s preferred grazing areas” (Silva 2019). Here, zebras can only access water sources near recently established human settlements during night-time, when disturbance is minimal (Joubert 1972a). These anthropogenic pressures have been pushing zebras and other wildlife away from their most favorable habitats towards the water- and vegetation-deprived plains, where they can access the few available springs at any time of the day to satisfy their hydric needs (Bruce Bennet, *personal* *communication*). However, HMZ's water dependency and particular sensitivity to human disturbance (Joubert 1972a) pose particular challenges to their survival in this arid environment. The HMZ in Iona are confined to a small geographic area: In the west, this is bounded by the Atlantic ocean and by sandy dunes, which are not suitable for zebra survival because of the scarcity of feeding resources and water, and because of the unsuitability of zebra foot morphology for wandering through sandy soils (Joubert 1972a). In the east, human communities form a barrier, limiting the access to otherwise suitable habitat for HMZ. Given these pressures acting on this isolated HMZ population, a plan to mitigate or revert their effects on HMZ population in INP is urgently needed, so as to ensure population growth and healthy recovery.

Hybridization with donkeys

The hybridization between members of equid family is a topic that has been attracting the interest of ecologists, especially when it occurs in natural environments. The mechanism was reported involving plains and Grevy's zebras in the wild at the northern edge of plains zebra range (Cordingley *et al.* 2009), and between the mountain zebra and plains zebra at the southern edge of plains zebra range (Altrichter *et al.* 2011). In Namibia the same mechanism was reported involving HMZ and donkey with the hybrids being observed dwelling with breeding herds of zebras (Joubert 1972a, Brown and Jenkins 1987). In a crescent scale, the mechanism has been reported in Angola's INP (Bruce Bennet *personal communication*), probably due to a permanent contact and interaction between the two relatives. However, as for the HMZ, the status and population size of hybrids (hereafter zonkeys) in Iona are not well understood because they were never studied. There are only anecdotal reports of its existence as being a strange kind of striped donkey.

Although hybridization between closely related species is a natural phenomenon that can operate as an important evolutionary force, it has also contributed to the extinction of numerous species (Hill 2009).

1.2.2 Camera trapping

Camera trapping is a monitoring technique developed in the late 1890s, and it has gained prominence among ecologists as a means to monitor wildlife populations (Rovero *et al.* 2010). It has become a very popular approach in wildlife studies due to it being a non-invasive technique and due to its practical implementation (Rovero *et al.* 2010). Apart from being non-invasive, the use of camera trapping is advantageous because it provides an objective record, or evidence, of an animal's presence and identity through photographs, which also increases its suitability to study rare, elusive, and nocturnal animals that avoid humans (Rovero *et al.* 2010). Camera trapping is also beneficial because it allows traps to be left in the field for weeks, without having to be checked (Hoffmann *et al.* 2010, Rovero *et al.* 2010). The most common camera trapping system relies on remotely trigged cameras equipped with a passive infrared motion detector, to let us obtain wildlife detection records (Rovero *et al.* 2010, Sollmann 2018).

Due to the success of the implementation of camera trapping in wildlife studies, not much attention has been given to the disadvantages that might arise with the use of this technique (Swann et al. 2004). Failure in appropriate camera operation leads to loss of data, and because in some cases cameras are placed in remote areas, this problem can remain unnoticed for months. Loss of data can also occur due to theft or vandalism, particularly when cameras are placed near human settlements (Swann et al. 2011). One major issue with camera trapping is that they have a limited detection zone, which does not allow for perfect detection (Rovero *et al.* 2013, Burton *et al.* 2015).

Camera trapping has developed into one of the most commonly used techniques used by ecologists to assess different parameters of mammal populations, such as abundance (O'Connell and Nichols 2011), distribution (Funston *et al.* 2017), density (Rowcliffe *et al.* 2008), activity patterns of species (Bridges and Noss 2011), species' interactions (Linkie and Ridout 2011) or behaviour (Bridges and Noss 2011). The exponential development of camera trapping technology and concurrent analytical methods provides the means to understand previously challenging patterns of terrestrial mammals' ecology. The biggest challenge to wildlife biologists in this context is to use these data to the greatest extent possible, and to make unbiased inferences about the state parameters of the target populations under investigation (O'Connell and Nichols 2011).

Camera trapping is a particularly suitable technique to investigate species with a distinctive external pattern, which allows for individual identification (Nipko *et al.* 2020). It has been implemented on a wide range of species, such as tigers (*Panthera tigris*) (Karanth 1995), snow leopards (*Panthera uncia*) (Buzzard *et al.* 2017) or ocelots (*Felis pardalis*) (Trolle and Kéry 2003), plains zebra (De Vos 2017), and mountain zebra (Cape mountain zebra) (Olivier *et al.* 2019). Although zebras are one of the easiest groups of animals to be individually identified by their coats, due to the pattern formed by black stripes and white interspace (Bard 1977, Sasidharan 2005), the implementation of camera trapping to studies of zebras is still far from its levels of implementation in other species.

During the last few years, camera trapping has been used to assess the ecology and behaviour of HMZ populations in different areas of Namibia where the subspecies occur (Gosling 2018). Given the promising results obtained via camera trapping in zebra studies elsewhere, this technique constitutes the backbone of the field methods used in this project. This is particularly because of the difficulty in frequenting some of the areas where the species occur in INP, which make it challenging to use methods such as aerial surveys or distance sampling through direct counts. In this study I estimated different population parameters of the HMZ from the camera trapping data, which provided the possibility to understand its ecology through photographic records.

1.3 Problem statement

The investigation of wildlife distribution patterns, demographic parameters, threats, and interactions with humans and with the environment has been severely neglected in south-western Angola. The absence of wildlife population monitoring, which represents one of the most important aspects for conservation planning and management of animal populations, has further contributed to this knowledge gap. Consequently, much remains unknown about these wildlife populations and about their ecological, physiological and behavioural adaptations to the arid conditions of the south-western extreme of the country. Among several species occurring in south-western Angola, I focused on the near-endemic species of mountain zebra.

Very little is known about the HMZ population that occurs in Angola's Iona National Park. This profound knowledge gap relates to most aspects of HMZ ecology, and is further emphasized by the shrinking distribution area of HMZ regionally and by the many threats posed to HMZ conservation, especially with the exponential increase of human populations and concurrent competition for grazing grounds with livestock (PNUD 2016, Silva 2019).

Therefore, it is necessary to investigate HMZ numbers, population structure and basic ecological requirements, in order to inform an empirically based plan to ensure HMZ conservation and management. Moreover, given the fragility of this arid ecosystem and vulnerability of its wildlife community, it is deemed necessary to design and implement a long-term monitoring system to assess HMZ's trends over time.

Two initiatives have recently been carried out with the objective of informing us about the status of HMZ's population in Iona National Park: i) unstructured game counts performed under the scope of the project *Conservation of Iona National Park*, which encompassed the period of 2013-2017 (Bruce Bennet Unpublished Data; Rocha et al. Submitted); and ii) an aerial survey between 2016 and 2017 (van der Westhuizen *et al.* 2017). These initiatives suggested that the HMZ are more associated with the desert plains than with the mountainous scrublands, its preferred habitat (Joubert 1973, Skinner and Chimimba 2005, Stuart and Stuart 2015). This discrepancy between the expected and potentially realized distribution of HMZ in this national park suggests that the HMZ currently exploits sub-optimal habitats, potentially due to an avoidance behaviour towards livestock and human presence (Joubert 1973).

Informed by the above-mentioned issues, I addressed the following questions regarding Hartmann's mountain zebra in Iona National Park:

What is the population size of HMZ in INP?

How is the HMZ population structured?

Does the number of hybrids represent a threat to the HMZ population?

The answer to these questions represents an import contribution to building the basic ecological knowledge of this subspecies of mountain zebra occurring in Angola, and also intends to draw attention to the importance of protection and conservation of this iconic subspecies. This study makes recommendations regarding long-term monitoring and conservation of the population of HMZ.

1.4 Research objectives

The aim of this research was to assess the abundance and population characteristics of Hartmann's mountain zebra *Equus zebra hartmannae* in Iona National Park, Angola.
The objectives are:

- To estimate the abundance and density of HMZ and zonkey in INP based on camera trapping and spatial capture-recapture models;
- To characterize the HMZ population structure (sex ratio and age classes);
- To compare the group size estimates based on camera trapping and from unstructured game counts;
- To assess the threat of hybridization with donkeys;
- To assess the activity pattern of HMZ, donkey and zonkey at waterholes; and
- To establish a baseline population estimate for continuous monitoring;

The population parameters were estimated under the following hypotheses:

- The age structure of HMZ population in INP is female skewed;
- The limited field of view in camera traps under-estimate the true HMZ group size.
- The presence of donkeys and zonkeys at waterholes do not affect their use by zebras.

Chapter 2: Methodology

2.1 Study area

2.1.1 Iona National Park

The Iona National Park (INP) was the first Angolan national park created. It was founded in 1937 as a hunting reserve (Huntley 1974). It was only later, in 1957, that it was upgraded to a national park with the objective of protecting and conserving the wildlife species of the arid biomes of south-western Angola (Kuedikuenda and Xavier 2009). INP represents the first practical manifestation of conservation plans in Angola, which were first implemented in 1936 (Huntley 1974). With an area of 15,150 km^2, INP is located in the Namibe province at the extreme south-west of Angola. It is bordered by the Curoca river in the north and by the Cunene river (known as the Kunene river in Namibia) in the south, which demarcates the border with Namibia's Skeleton Coast (Huntley 1974, Mendelsohn and Mendelsohn 2019). The Atlantic ocean defines INP's western border, whereas the Otchifengo valley defines the border to the east (PNUD 2016, van der Westhuizen *et al.* 2017, Silva 2019).

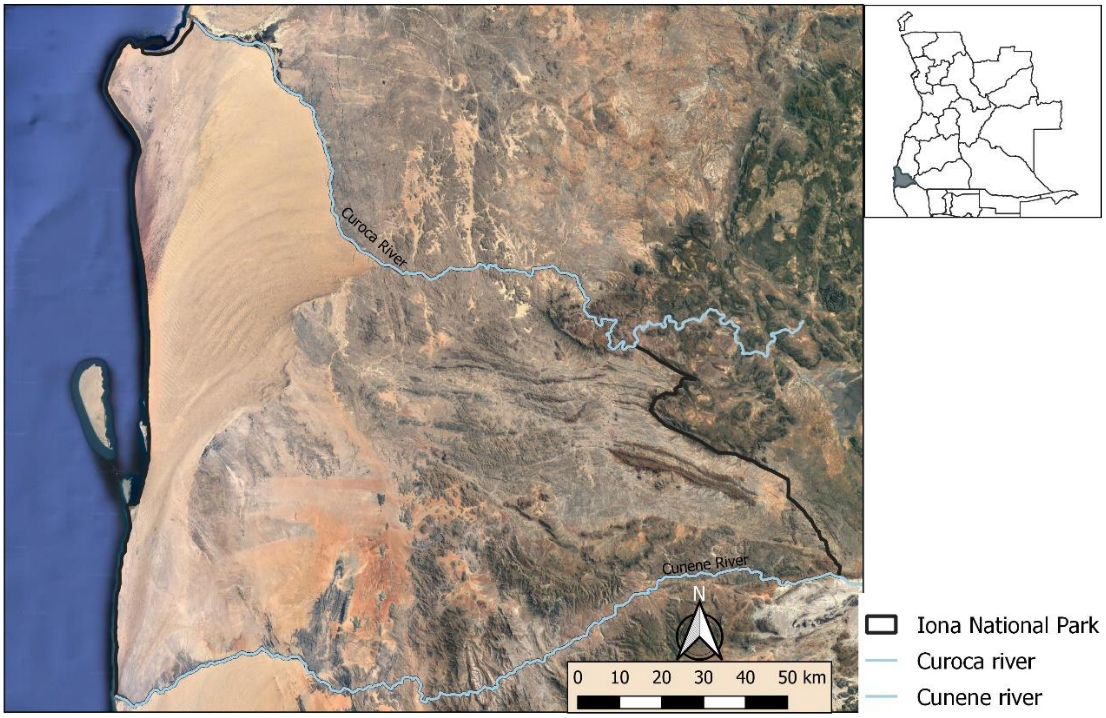


Figure 7. Geographic location of Iona National Park. From the west to the east, we can see the Atlantic ocean, the landscape formed by the coastal dunes, the central plains, as well as the escarpment which separates the plains and highlands further east. The Curoca and Cunene rivers in the north and south, respectively, demark the borders of INP at the two extremes.

INP is situated in the south-western of Angola, which includes two morphological zones, the western coastal lowlands and the eastern highlands, which are separated by a long escarpment running from north to south. These zones are characterized by three landscape units: the coastal dunes, the coastal plains and the chela plateau (Mendelsohn and Mendelsohn 2019).

The vast plains, wild and mobile dunes as well as mountains are the main characteristics of Iona National Park's ecosystems (Huntley 1974, van der Westhuizen *et al.* 2017, Mendelsohn and Mendelsohn 2019). INP is also characterized by moderate temperature due to the cool air that comes from the cold currents of the Atlantic ocean in the west, with mean temperature of 24.5° (Mendelsohn and Mendelsohn 2019). This cool air is also a factor that limits the rainfall in INP, which has a low gradient ranging from < 20 mm at the coast to 300 mm in the eastern parts (Mendelsohn and Mendelsohn 2019). However, a small amount of more regular water from fog sustains many plants and animals (Mendelsohn and Mendelsohn 2019). Due to its characteristics, INP is home to a typical fauna of the south-west arid biome, such as the gemsbok (*Oryx gazella*), Hartmann's mountain zebra, springbok (*Antidorcas marsupialis*), impala (*Aepyceros melampus*), steenbok (*Raphicerus campestris*), meerkat (*Suricata suricata*), bat-eared fox (*Otocyon megalotis*), Cape fox (*Vulpes chama*), black-backed jackal (*Canis mesomelas*), aardwolf (*Proteles cristata*), and brown hyena (*Hyaena brunnea*) (Huntley 1974, van der Westhuizen *et al.* 2017, Beja *et al.* 2019).

Similarly to all other national parks in Angola, INP suffered from severe defaunation during the last decades, which was particularly intense during the colonial and civil wars (Huntley 2017, Morais *et al.* 2018). The presence of pastoral groups with livestock place a great strain on the water and forage supplies in the region (Huntley 1974, Silva 2019). From about 300 habitants in 1974, the human population increased to more than 3000 individuals (PNUD 2016).

Since 2007, the Angolan government has started implementing plans to recover the national parks in partnership with international organizations (Kuedikuenda and Xavier 2009), and INP is one of the parks that benefitted from a management plan that allowed its reconstruction, in addition to the creation of a management team led by an administrator (PNUD 2016, Silva 2019). The steps taken forward from these initiatives call for the involvement of wildlife ecologists and other wildlife professionals to assess the biodiversity status of the different ecosystems that characterize INP, and to inform the best strategies for its conservation.

2.2 Data collection

2.2.1 Camera trapping

Camera-trap (CT) placement within INP followed a stratified design, aimed at maximizing detection probability and ensuring inter-camera distancing that allowed for the same individual to be recorded at multiple sites (hereafter, spatial captures). Final CT locations were selected based on HMZ’s habitat preferences and water dependence, as well as logistic feasibility. Some potentially suitable sites were discarded due to high human disturbance and frequent livestock presence. These factors not only constrain site use by HMZ (van der Westhuizen *et al.* 2017), but also cause sites to have a high likelihood of vandalism and equipment theft by local people as previously reported in INP (Bruce Bennett, *unpublished data*), which entails significant loss of valuable data and equipment. Taking all these factors into account, I adopted a deliberately-biased approach for the camera trap placement, using the waterholes within and around the area that Hartmann's mountain zebra is mostly seen to maximize the detections (Meek *et al.* 2014, 2019) and provide a reasonable sampling of the population.

A total of 12 sampling stations were established at: i) waterholes (n=7), ii) paths to waterholes (n=3), and iii) independently of waterholes (n=2) (Figure 8).

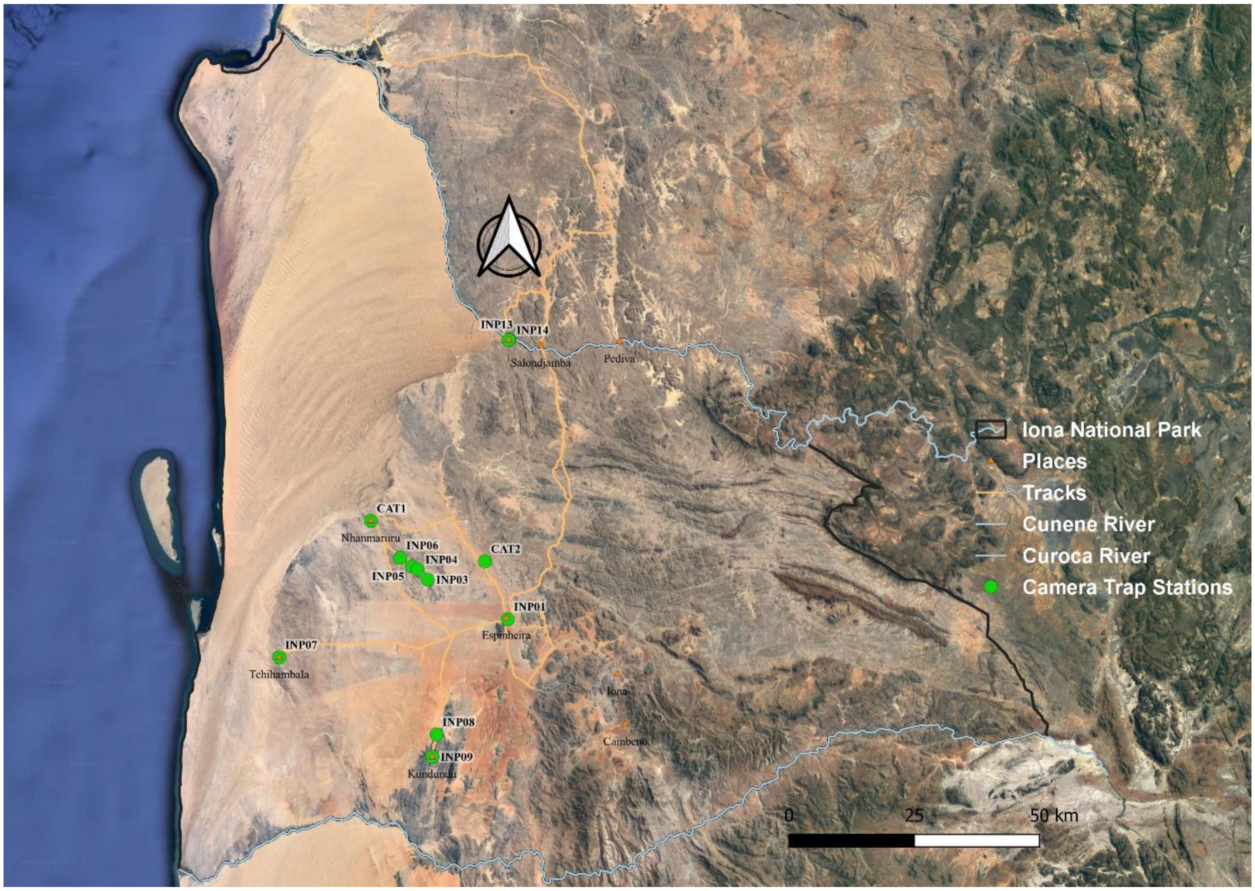


Figure 8. Camera trapping stations' locations.

The rationale underlying this sampling design was to ensure a representative sampling of the area known to be used by HMZ, while accounting for potential sources of variability in detection probabilities. Given the aridity of the study area, this waterhole-centred design ensured a greater spatial coverage of the sampling area and maximized the trapping success (Rovero *et al.* 2010, Sollmann 2018). Twenty-five MINOX (DTC 550, Germany) remotely triggered cameras were deployed at sampling stations at a mean number of 2.08 ± 0.29 cameras/station. While cameras were paired at most waterholes, three cameras were deployed at one waterhole because of its diameter, which deemed it impossible to sample adequately with just two cameras. At each station, cameras were deployed facing each other to allow for capturing of both sides of each individual (Niedballa *et al.* 2016) (Figure 8), thereby enhancing the probability of identifying individual zebras and zonkeys using coat pattern recognition (Karanth 1995, Dey *et al.* 2017). In other studies, camera traps are usually mounted onto trees or other natural structures (Rovero *et al.* 2010, Meek *et al.* 2012). However, such structures were rarely available at the sampling stations. Therefore, CTs were fixed either to metal poles, specially designed to fit the needs, or fixed to natural rocks, as far as this was practically possible (e.g. Figure 9).

Figure 9. Camera traps set up facing each other

CT's were fixed in suitable positions at a mean height of 76.75 ±26.82 cm (mean ±SD), which allowed to take the full body picture which was necessary for individual identification as one of the requirements for this study. A unique code was assigned to each CT (Table 1), which allowed the association of the detections to a specific camera within each station location, generating the spatiotemporal information required for the spatial capture-recapture approach.

Table 1. Camera trap stations and cameras codes, setup dates and times, retrieval dates and times, and models.

Station code	Camera code	Setup date	Setup time	Retrieval date	Retrieval time	Camera model
CAT1	CAT1N	15/10/2019	10:58	19/01/2020	10:03	MINOX DTC 550
CAT1	CAT1E	15/10/2019	10:58	19/01/2020	10:03	MINOX DTC 550
CAT2	CAT2N	22/10/2019	17:05	20/01/2020	17:05	MINOX DTC 550
CAT2	CAT2S	22/10/2019	17:05	20/01/2020	17:05	MINOX DTC 550
INP01	INP01N	17/09/2019	16:20	19/01/2020	18:20	MINOX DTC 550
INP01	INP01S	17/09/2019	16:20	19/01/2020	18:20	MINOX DTC 550
INP03	INP03E	17/09/2019	12:41	20/01/2020	12:30	MINOX DTC 550
INP03	INP03W	17/09/2019	12:41	20/01/2020	12:30	MINOX DTC 550
INP04	INP04N	17/09/2019	13:29	20/01/2020	12:00	MINOX DTC 550
INP04	INP04S	17/09/2019	13:29	20/01/2020	12:00	MINOX DTC 550
INP05	INP05E	17/09/2019	11:47	20/01/2020	11:32	MINOX DTC 550
INP05	INP05W	17/09/2019	11:47	20/01/2020	11:32	MINOX DTC 550
INP06	INP06N	17/09/2019	11:04	20/01/2020	10:49	MINOX DTC 550
INP06	INP06S	17/09/2019	11:04	20/01/2020	10:49	MINOX DTC 550
INP07	INP07N	19/09/2019	10:58	20/01/2020	15:53	MINOX DTC 550
INP07	INP07E	19/09/2019	10:58	20/01/2020	15:53	MINOX DTC 550
INP07	INP07W	19/09/2019	10:58	20/01/2020	15:53	MINOX DTC 550
INP08	INP08E	16/10/2019	15:07	21/01/2020	12:36	MINOX DTC 550
INP08	INP08W	16/10/2019	15:07	21/01/2020	12:36	MINOX DTC 550
INP09	INP09N	16/10/2019	12:29	21/01/2020	10:25	MINOX DTC 550
INP09	INP09S	16/10/2019	12:29	21/01/2020	10:25	MINOX DTC 550
INP13	INP13N	11/10/2019	13:15	19/01/2020	9:21	MINOX DTC 550
INP13	INP13S	11/10/2019	13:15	19/01/2020	9:21	MINOX DTC 550
INP14	INP14E	11/10/2019	14:01	19/01/2020	9:45	MINOX DTC 550
INP14	INP14W	11/10/2019	14:01	19/01/2020	9:45	MINOX DTC 550

The following information was recorded upon camera deployment and revision: camera ID, date and time, location (coordinates), altitude, and possible camera malfunctions. The database accommodating CT spatial deployment and functioning data was created using Excel 2016, and imported into R to be managed using the packages camtrapR (Niedballa *et al.* 2016) and oSCR (Sutherland *et al.* 2019), resulting in the camera operation matrix, termed '*trap deployment file*' (TDF) (Royle *et al.* 2013, Niedballa *et al.* 2016). The TDF was built to describe the trapping effort per station of daily sampling occasions (Royle *et al.* 2013). Cameras were set to capture a sequence of nine pictures per triggering event, with a time delay of five seconds between events. To ensure sufficient quality on the pictures in order to perform individual identification, I set the CTs to a resolution of 12MP, the maximum resolution possible on this camera model.

Field sampling was carried out over four months (from 17th September 2019 to 20th January 2020), which was considered short enough to fit population demographic closure and was therefore accounted for as a single session. Following the recommendations of Rovero *et al.* (2010), cameras were checked twice for troubleshooting, and for replacement of batteries and SD memory cards.

2.3 Data processing and analysis

There are multiple ways to organize camera trapping data, which have been significantly simplified with recent technological advances, namely in the field of data management, artificial intelligence and image pattern recognition (Sanderson and Harris 2013, Tabak *et al.* 2019). Camera trapping data in my study was organized and classified using three complementary software packages: i) the camtrapR 2.0.2 package (Niedballa *et al.* 2016) on R 3.6.3 (R Core Team 2019) for record and file organization; ii) Digikam 6.3.0 (KDE, Germany) for image classification and tagging of species, age class and group size; and iii) the standalone version of the Image Based Ecological Information System (IBEIS) software (Crall 2017), for individual identification of HMZ and zonkey records by the external stripe pattern.

The remainder of the data analysis (specified in 2.3.4 to 2.3.6 below) was performed in R using multiple packages, especially the tidyverse 1.2.1 system (Wickham *et al.* 2019) for database organization and data manipulation. All SCR models and related statistical inferences were implemented with the oSCR package (Sutherland *et al.* 2019).

2.3.1 Image classification with Digikam

Image classification consists of tagging pictures according to different categories that fit the needs and goals of a particular study (Sanderson and Harris 2013). The most commonly used classifications regard to species, sex and age, although behavioural aspects are also frequently used (Sanderson and Harris 2013, Niedballa *et al.* 2016). I classified camera trapping records according to species, age, sex, and group size to obtain the required information to investigate population structure. Image tagging was performed with Digikam, which provides functions to easily organize and manage photographs (Kulzer *et al.* 2010), namely those generated through camera trapping, with a structure compatible with the requirements of the camtrapR package (Niedballa *et al.* 2016). Specific tags for species, age classes, group size and sex were created in Digikam (Kulzer *et al.* 2010), and assigned to the metadata of each respective picture, in order to build a structured database of records (Niedballa *et al.* 2016). The adequate extraction of metadata tags with camtrapR requires them to be structured into a maximum of two hierarchical levels (Niedballa *et al.* 2016). I organized the tagging structure such that the first hierarchical level comprised the different categories (i.e. species, age, sex and group size), and the second level comprised the species' scientific name (for the species' category) or the numbers that defined how many individuals belonged to each age class (adults vs. juveniles vs. foals), which the total comprised the group size, and sex (males vs. females), (Niedballa *et al.* 2016). The species were identified according to their morphology and other external features, with the aid of specific field guides (Kingdon 2015, Stuart and Stuart 2015). The list of potential mammal species occurring in Iona National Park was built based on Huntley (1974), as well as on the likelihood of occurrence based on each species' biological requirements and known distribution range (Stuart and Stuart 2015).

I determined the sex and age based on the external sexual morphology and body size, respectively. Group size was determined as the maximum number of different individuals of a given species observed in a picture or sequence of pictures with less than one minute separating individual pictures.

The tags were arranged to accommodate situations where more than one species was observed in the same picture, as in Niedballa *et al*. (2016). I established a list of species in alphabetical order, where the first species to be classified on the picture is the one that comes first in the sequence. According to the list order we assigned Sp1, Sp2 and Sp3 as references to the species' sequence for classification. To those characters we associated categories such as age, sex and group size as shown in the table below:

Table 2. Tags structure on Digikam.

Tags	**Description**
Sp1_A.NI	species one (Sp1), adult (A), not identified (NI)
Sp1_AF	species one (Sp1), adult female (AF)
Sp1_AM	species one (Sp1), adult male (AM
Sp1_J	species one (Sp1), juvenile (J)
Sp1_GS	species one (Sp1), group size (GS)

The metadata tags generated and assigned to the pictures with Digikam were extracted into R using the camtrapR package, which allowed me to construct a single database containing all records and respective stations' IDs, species, dates, times, age classes, sexes and group sizes of all wildlife detections.

2.3.2 Individual Identification with IBEIS

I performed identification of HMZ individuals with the Image Based Ecological Information System (IBEIS) software (Crall 2017).

IBEIS is a program that stores and manages images, and derives data for use in computer vision algorithms, which allows us to gain ecological insights (Crall 2017). This software was built based on three algorithms that together address the problem of individual identification:

- Rank-Based Identification Algorithm;
- Pairwise Verification Algorithm; and
- Semi-automatic Graph Identification Algorithm.

Each of the algorithms implements a certain level of specificity to the system, and in most cases the use of the tasks associated with the rank-based identification algorithm are enough to process the individual identifications. However, this implies that the final decision to match the annotations that contains the same individual needs to be done manually. The IBEIS program can be used for a wide range of species such as zebra, giraffe, lionfish, cheetah and others with distinctive phenotipic patterns, and is still being improved to increase the range of species that it could be applied to (Crall 2017). I found IBEIS to be the most suitable software to identify individuals of zebras, because besides its high levels of accuracy it also presents a user-friendly interface that makes the identification process easy to manage and less time-consuming. I based the individual identification on the Rank-based Identification Algorithm, where a given annotation containing a description of an unknown animal is compared to a database of annotations to produce a ranking with the most likely individual in the database that matches with the unknown animal (Crall 2017).

Although this process suggests the most likely individual identifications for each individual record, it still depends on a final human review to either accept or decline the software's suggestion, and to determine which of the top-ranked individual assignments is the correct one. Two concepts are important to consider in this process:

'*Annotation*' is a rectangular region of interest around a specific animal within an image.

'*Name*' refers to a group of annotations known to be of the same individual.

I conducted the individual identification in the two steps proposed by Crall (2017). First, I selected detection records addressing factors that could influence identification such as occlusion, indistinctive viewpoints (e.g. when animals are looking straight, or with the back straight to the cameras with no possibility to see the flanks), and image quality. Because pictures were taken under uncontrolled conditions, some of the factors that influence identification couldn't be avoid. All the images that accounted for these limitations, as exemplified in table 3 below, were discarded from the identification procedure.

Table 3. Factors affecting individual identification: occlusion, viewpoint, and poor image quality.

Factors affecting image identification	**Image representing the factors**
OCCLUSION	
VIEWPOINT	
VIEWPOINT	
POOR QUALITY	

Whenever individuals stood in front of the camera for long periods of time, I selected the most easy-to-identify pictures, taking into consideration the time and any variation in viewpoint. Selected images used for individual identification were those showing the left or right flank, with a visible overview of the focal body part on the shoulder, alongside the body and on the back leg (Figure 10 and appendix 2). After processing, all images were moved into a database previously created on IBEIS, and individual identification was performed as described below.

The identification process was performed following Crall (2017), and it is described as follows.

The images were cropped to create an 'annotation' by drawing a rectangular feature around the animal represented in the picture. This process allows removing the background and all sources of disturbance to the identification process. Therefore, the annotation information is extracted and then indexed into the database of annotations to create a match score for each of them. Afterward, the features on the picture are weighted and assigned to where they belong either the background or foreground according to a certain probability. To successfully perform the identification of a name (e.g. '*hmz*') referring to the species was assigned to each annotation. Note that, the name assigned to the annotation is not the same as the one given to each individual in the annotation after being identified, but a reference to the species being identified. For instance, if the annotations do not have a species name assigned, the software refuses to match the annotations.

After processing, the annotations were matched against the database of individuals. A query was performed to match and see if the annotation matches with a known individual from the database of names. Then the matched annotations are ranked based on the score starting from the highest to the lowest. The decision to accept or not if the annotation matched was mine, assigning 'true' when correct and 'false' when not. When the individuals match I gave them the same name, for example, '*inphmz001*' for zebras, and '*zk001r*' for zonkey.

Once the individual identification process was completed, Hartmann's mountain zebra and zonkey databases were created, compiling a record of which individual(s) were assigned to each detection, for the SCR analysis.

Being animals that move in groups, it was often difficult to match the left and the right flanks, so I performed individual identification independently for each flank, as identifying different individuals. The individuals identified from the left or right flanks constitute two different samples of the population, and I separated them as independent sessions.

To each unique individual animal, I assigned sex information and age class, to assess the population structure in these categories. It was a process similar to the one used for image classification, which is more a general view, especially for age determination. For sex determination I used the same procedure as described above. For age determination I applied the same technique implemented by Klingel (1969) in plains zebra and adapted by Penzhorn (1982) in Cape mountain zebra, where the age was determined by comparing individuals according to size (Figure 11). With this process I tried to be more precise, determining whether an individual was an adult, juvenile, or a foal. For this purpose, I established foals to be individuals < 1 year old, juveniles to be individuals older than 1 but younger than 2 years old, and adults to be individuals over 2 years old. Juveniles were considered to be up to two years old because it was considered the limit up to which precise age class could be estimated, thus avoiding the risk of confusing them with adults. Zebras reach maturity at age of 3-4 for females and 4-5 for males (Joubert 1972a). The resulting database includes information about individual ID, station where the individual was detected, date and time, sex, and age class.

Figure 10. Images with suitable viewpoints showing the hotspots on the shoulder and back legs, good quality and without occlusion.

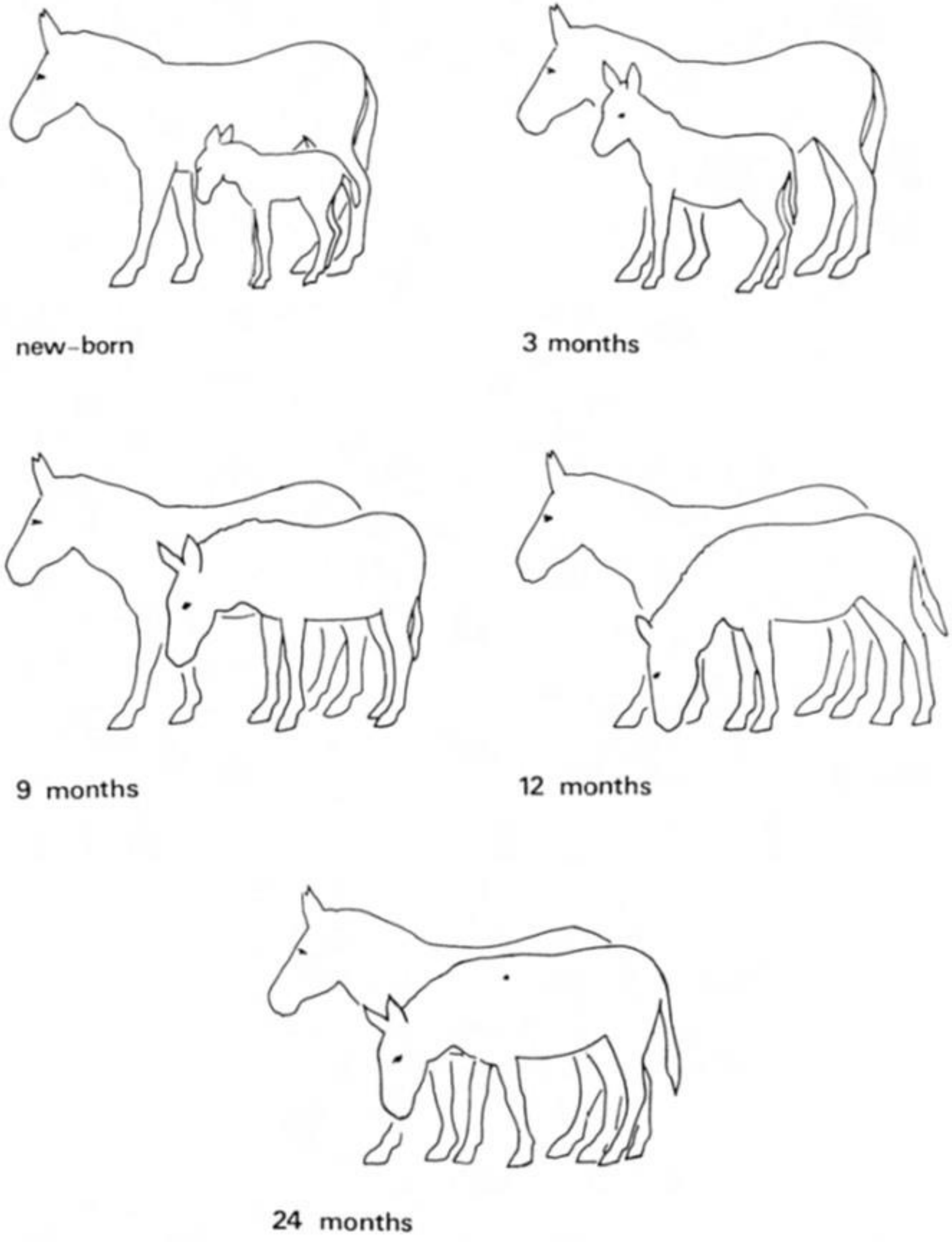


Figure 11. Age determination diagram (Source: Penzhorn, 1982).

2.3.3 Preparation of encounter histories and trap deployment

For spatial capture-recapture analysis, data are organized in two spreadsheets, the *encounter data file* EDF and the *trap deployment file* TDF (Sutherland *et al.* 2019). These files contain information about trap coordinates, survey effort, covariates and individual encounter histories (Royle *et al.* 2013).

The TDF contains the coordinates of each detector (camera trap), along with information indicating which sample occasions each detector was operating (Royle *et al.* 2013). Additional information such as specific covariates characterizing each station was also assigned (Sutherland *et al.* 2019). In the file the trap covariates were separated from the remaining trap attributes by a column with a backslash character "\". The TDF was created in R, resulting in a data frame where each row represents a detector, and the columns showing detector information.

The EDF contains records about the traps and sampling occasion (i.e. day) where each individual encounter occurred (Royle *et al.* 2013). The EDF data object was built with information about the numeric session being similar for all the records, which for this study was only one session represented by the number 1, the unique individual identifier, individual's age and sex, the code for the detector where the individual was detected, and the occasion when the individual was encountered (Sutherland *et al.* 2019). The sex and age class information allowed us to perform a SCR class-structured approach (Royle et al., 2015).

2.3.4 Spatial capture-recapture (SCR)

The SCR modelling approach integrates a set of submodels that jointly allow the estimation of demographic parameters such as population size, density and trends (Pollock 2000, Royle *et al.* 2013). The fundamental input of any capture-recapture (CR) model is the individual encounter history, i.e. the number of times an individual was encountered ('captured') during sampling over time, and contains information about encounter probability, abundance, individuals movement and distribution (Royle *et al.* 2013).

Spatial capture-recapture models emerged to accommodate the spatial component of how individuals in a population are distributed, and how their distribution and movement may affect the observation process, hence formalizing the link between individuals and space (Royle *et al.*

2013). After their development (Efford 2004, Royle and Young 2008), SCR models underwent quick development, especially boosted by the widespread use of non-invasive techniques such as camera trapping and hair snares for DNA sampling (Efford *et al.* 2009, Royle *et al.* 2018, Sutherland *et al.* 2019). They provide a coherent and flexible framework for making ecological processes explicit in models of individual encounter history data, and for studying animal populations processes such as individual movement, resource selection, space usage, population dynamics, and density (Royle *et al.* 2013). They differ from the classical capture-recapture because they rely on a spatial point process model applied to individuals' locations, therefore allowing capture probability to be dependent on spatial location (Royle and Young 2008).

Conceptually, the SCR model is any 'individual encounter model' where auxiliary spatial information is also obtained (Royle *et al.* 2013). It involves a class of models for collecting random variables such as activity centre $\boldsymbol{s}$, individuals' location $\mathbf{u}$ at time of sampling, and the observation of the individual $\mathbf{y}$.

SCR are easily analyzed due to the availability of several analytical tools (standalone software of R packages), each offering unique capabilities (Royle *et al.* 2018). I implemented SCR models on camera trapping data for HMZ and zonkey using the open source spatial capture-recapture package (oSCR) (Sutherland *et al.* 2019), because of its sex-structured and flexible nature, and because it is particularly suitable for individually-identified camera trapping data.

Model formulation

In general, SCR are types of hierarchical models (Royle and Young 2008), i.e. a set of sub-models developed independently but resulting in a unified structure, which allows for inferences about a certain population.

I implemented a 'single-session sex-structured model' with a single sampling period, and the sex information of most of the individuals was available (Royle *et al.* 2015), allowing for a sex-based variability in estimate of population parameters.

Despite the differences on the structure of the SCR models they all relay on the principle that a certain population $\boldsymbol{N}$ is sampled with an array of $\boldsymbol{J}$ traps during $\boldsymbol{K}$ occasions, producing a sample of $\boldsymbol{n}$ individual (Efford 2004, Royle and Young 2008, Royle *et al.* 2013). Therefore, the individuals of that population are distributed randomly around the study are, and each of them has its activity centre $\boldsymbol{s}$, 'a spatial location $\boldsymbol{s_i} = (\boldsymbol{s_{ix}}, \boldsymbol{s_{iy}})$ from where their movement is distributed according to some probability' (Royle *et al.* 2013). The observation of individuals activity centres follows a 'statistical spatial point process' (Illian *et al.* 2008), 'describing the spatial structure of the sampled population' (Sutherland *et al.* 2019), 'associating the spatial coordinates to each individual in the population' (Royle *et al.* 2018) The individuals activity centres were assumed to be uniformly distributed, not being considered any source of variability on the density of activity centres across the sampling area as denoted below.

$$s_i \sim Uniform\ (S)$$

Where $\boldsymbol{S}$ is the state-space of the point process, the effective area covered by the trapping array, which represents the population being sampled (Royle *et al.* 2018). .

During the sampling period individuals are encountered at a trap with a certain frequency $\boldsymbol{y_{i,j,k}}$. Therefore, the frequencies at which individuals are encountered were assumed to be Bernoulli outcomes as denoted below, resulting on the individuals encounter histories.

$$y_{i,j,k} \sim Bernoulli(p_{i,j,k})$$

where $p_{i,j,k}$ is the probability of encountering individual $\boldsymbol{i}$ at a trap $\boldsymbol{j}$, at occasion $\boldsymbol{k}$ (Royle *et al.* 2013, Fuller *et al.* 2016).

The probability to encounter an Individuals in the population was assumed to be a function of the linear distance from the individual activity centre $\boldsymbol{s}$ and the trap location $\boldsymbol{x}$, known as the Euclidean distance (Royle *et al.* 2013), and it is represented by the half-normal distribution, denoted by

$$p_{i,j,k} = p_{0,j,k} \times e^{-(1/2\sigma^2)d(x_j,s_i)^2}$$

where p_0 is the baseline encounter probability model, which may vary by individual, trap and occasion, and the parameter σ, is the rate of decrease in the detection probability as a function of the distance, Euclidean distance $d(x_j, s_i)$ $\boldsymbol{j}$ $\boldsymbol{s}$ (Royle *et al.* 2018, Sutherland *et al.* 2019). Furthermore, the Individuals are encountered independently throughout the sampling area (Sutherland *et al.* 2019). The parameter σ, also known as the movement parameter, represents the space use of an animal about its activity centre, and by assuming a 'bivariate normal model for detection, the estimated σ can be converted into a 95% home range radius' (Reppucci *et al.* 2011, Maronde *et al.* 2020).

From the encounter probability, a likelihood is derived to find the most probable observed data. In SCR models, the likelihood has the form of a marginal likelihood (Royle *et al.* 2013, Sutherland *et al.* 2019). More details on the derivation of the marginal likelihood are given in Royle et al. (2013) and Sutherland et al. (2019), here I only present the resulting joint likelihood for simple data representing $\boldsymbol{n}$ observed individuals, and $\boldsymbol{n_0} = \boldsymbol{N} - \boldsymbol{n}$ non-observed individuals with marginal probability $\boldsymbol{\pi_0}$. The joint likelihood is denoted by

$$\mathcal{L}(\theta, n_0|y) = \frac{N!}{n!\, n_{0!}} \left\{ \prod_{i=1}^{n} [y_i|\theta] \right\} \pi_0^{n_0}$$

(Royle *et al.* 2013, Sutherland *et al.* 2019).

As stated somewhere in this work, the population is sex-structured requiring to implement a form of likelihood that accommodate the sex data (Royle *et al.* 2015), and parameter estimates are portioned into sex classes. The likelihood presented here is the same implemented by default in oSCR (Sutherland *et al.* 2019) for a sex-structured approach.

Following Royle et al. (2015) and Sutherland et al. (2019), for the encounter histories where the sex information is available for at least some individuals, the likelihood has the form:

$$\mathcal{L}(p, \psi, n_0 \mid y) = \frac{N!}{n!\, n_0} \left\{ \prod_{i=1}^{n_1} [y_i|c_i = 1, \theta] \psi^{c_i} (1-\psi)^{1-c_i} \right\} \left\{ \prod_{i=1}^{n_2} [y_i|\theta] \right\} \pi_0^{n_0}$$

Where $\boldsymbol{n_1}$ denotes the encountered individuals with sex data, and $\boldsymbol{n_2}$ the encountered individuals with missing sex data, and $\boldsymbol{n_0} = \boldsymbol{N} - \boldsymbol{n_1} - \boldsymbol{n_2}$ denotes undetected individuals. The sex data is denoted by c_i having possible values $\boldsymbol{c} \in (\mathbf{0}, \mathbf{1})$ with probabilities $(\mathbf{1} - \boldsymbol{\psi}, \boldsymbol{\psi})$ (Sutherland *et al.* 2019).

The resulting sex-structured spatial capture-recapture model allowed to perform estimates of the parametersp_0, σ as well as population size **N** or density **D** (Sutherland *et al.* 2019, Royle *et al.* 2018) of HMZ and Zonkey**.**

The SCR analysis was performed by implementing the oSCR package in R. The oSCR package implements multi-session sex-structured spatial capture-recapture (MSSS-SCR) models (Royle *et al.* 2015, Fuller *et al.* 2016), which accommodates sex information in the form of a categorical individual variable (Royle *et al.* 2015), based on the probability that an individual belongs to the baseline group (e.g. 'female'), while also allowing to accommodate discrete groups or sessions (Sutherland *et al.* 2019). With the age information available three different models were developed, one for foals, one for juveniles, and one for adults. This approach allowed me to estimate the age structure of the population, by estimating the number of individuals of each age class.

Spatial capture-recapture implementation in oSCR

The SCR analysis on oSCR was performed according to Sutherland *et al*. (2019), and is described as follows.

The scrFrame: The scrFrame is the main data object for spatial capture recapture analysis in oSCR and it was created by linking the TDF and EDF objects. The resulting scrFrame includes a set of objects: caphist (the individual encounter history), traps (location of the camera trap stations), trapCovs (list of trap covariates, here it was addressed only one and denoted whether a particular station was in or off the waterhole), trapOperation (a binary matrix denoting whether the trap was operational (=1) or not (=0)), indCovs (a binary covariate which in this case denotes the individuals' sex (0 = female and 1 = male), and the sigCovs (a data frame with the covariates that affect the spatial scale parameter, the sigma σ).

State-space definition: The state-space represents the key element of spatial capture-recapture models, 'the effective sampling area' covered by the cameras during the sampling period (Royle and Young 2008). The state-space 'is an explicit definition of where the individuals can live, and the population of interest about which inferences will be made' (Royle *et al.* 2013). In general, the state-space represents the activity centre of all detectable individuals (Sutherland *et al.* 2019). The state-space object was built in oSCR using the trap coordinates stored in the $\mathrm{scrFrame}$ object, the indexed 1.5x of the mean maximum distance moved (mmdm) generated by the SCR model, which defines the buffer size around the trapping array and it is represented by the parameter $\boldsymbol{\sigma}$, a resolution of 25000000m^2 (25 km^2), which represents the size of each pixel that forms the state-space, and a defined resolution that determines the spacing of the state-space centroids. The resulting object is the ssDF, which includes all centroids that encompass the individuals in the population.

To obtain the total area covered by the state-space, the total number of centroids was multiplied by the pixel area. And because the focal populations were structured by age, it allowed for developing an age-specific state-space. Considering that juveniles move as much as the adults in the breeding herds, it was assumed the state-space to be the same for juveniles and adults. Under the assumption of an age-structured population and similarity in movement among adults and juveniles, two state-space objects were derived, one representing adults and juveniles, and the other representing foals. For zonkey it was obtained only a state-space for adults, which was similar to that for adult and juvenile HMZ.

Model fitting and selection: The SCR models were fit using the $\mathrm{scrFrame}$ and the ssDF developed for each age class, along with a list specifying the model structure with the prescribed covariates that may introduce variation in the state and observation parameters. The density parameter D was assumed to be constant, the baseline detection p_0 assumed to be constant or varying by sex, and the spatial scale of detection σ to be constant. The spatial scale parameter was assumed to be constant taking into account the social organization of the HMZ described in section 1.2.1, which strongly suggests that females and males, especially adults, move the same distance because they are always together in herds where each group of mares is always accompanied by a stallion and by male and female juveniles (Klingel 1968, Joubert 1972a). Then, all the covariates were combined to create the set of SCR models containing all combinations of the above-described parameterizations. oSCR ranks models under an information-theoretic approach and uses the Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) to rank models in a model set. Therefore, the AIC value was calculated for each model, and the absolute difference to the lowest AIC model value (ΔAIC) was used to rank candidate models. Models with the lowest AIC are considered models with the highest support, and models within a ΔAIC of 2 considered equally-supported best-models (Burnham and Anderson 2002). Top-ranked models are considered as having the highest predictive performance in the model set (Fuller *et al.* 2016).

Predictions: From the best model, it was predicted the baseline detection probability, spatial scale of detection, and population size and density for both HMZ and zonkey populations.

2.3.5 Population structure: group size, sex ratio and age structure

Group sizes were estimated by using camera trapping and direct observation from game counts. From camera trapping, group size was estimated as described in section 2.3.1. Camera trapping records were filtered into independent detections, defined as the number of individuals of a particular species recorded at a station within an interval of 30 minutes (Jenks *et al.* 2011, Funston *et al.* 2017). Therefore, the maximum group size recorded at that particular interval was defined as the best estimate of the true group size. Conversely, group size from game counts was defined as the total number of aggregated individuals per observation. For both camera trappings and game counts, parameter estimates were obtained by testing the best-fitting distribution to the observed data. Hence, a set of potentially suitable distributions was compared, following Delignette-Muller and Dutang's (2015) recommendations to check which distribution would fit better to the data which I was drawing inferences about. Based on the nature of the variable (discrete) characterizing the empirical data (counts), two of the most common theoretical distributions, the Poisson and the negative binomial distributions revealed to be the best candidates in this case. Two goodness-of-fit plots were generated comparing how the theoretical distributions (Poisson and negative binomial) would fit to the empirical data in terms of density and the cumulative density function (CDF) (Delignette-Muller and Dutang 2015). The relative goodness-of-fit was obtained from both chi-squared statistics and from information criteria such as the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC). According to these criteria, the best-fitting theoretical distribution is the one with the smallest chi-square statistic as well as the lower AIC or BIC (Delignette-Muller and Dutang 2015). Once the candidate distribution was selected, descriptive parameters of group size such as mean, median, and 95% confidence interval were extracted. This process was performed in R using the package fitdistrplus 1.1-3 (Delignette-Muller and Dutang 2015).

The sex ratio is a demographic measure of the relative number of males per female (Mills 2012), and was derived from the SCR model estimates. Age structure was defined as the relative contribution (proportion) of each considered age class to population (Ransom and Kaczensky 2016a), and was also derived from the class-specific SCR model estimates.

2.3.6 Activity at waterholes

The daily activity pattern of equids comprises a set of behaviours, of which we focus on grazing, movement and drinking as some of the most consistent and more time consuming (Joubert 1972b, Klingel 1974, King *et al.* 2016). Here we address the drinking behaviour of three species: HMZ, donkey, and zonkey, as phenotypically identified, in terms of their activity levels at waterholes as recorded with camera trapping. For the purpose of this study, we defined activity level as the proportion of time in a day that a given species spends at waterholes (Rowcliffe *et al.* 2014).

To assess the activity levels, camera trapping records were filtered to independent detections, defined as detection records of individuals taken at the same station with >30 minutes interval, unless individuals were individually identified (Linkie and Ridout 2011, Funston *et al.* 2017). These data were regarded as a random sample from an underlying distribution that describes the probability of a photograph being taken within any particular interval of the day (Linkie and Ridout 2011).

To estimate the activity levels, we implemented the method proposed by Rowcliffe *et al.* (2014), which involves fitting a flexible circular distribution to time-of-detection data to describe the underlying activity pattern, and then calculating the overall proportion of time active from this distribution. The time of observation was converted to a radians which ranges from 0 to 2π, to fit a probability density function (Rowcliffe *et al.* 2014). The activity patterns were estimated nonparametrically using a kernel density function (Ridout and Linkie 2009), where the area under the circular probability function is considered proportional to the total activity level (Rowcliffe *et al.* 2014).

The pairwise comparison between HMZ, donkey and zonkey activity patterns was performed by estimating the coefficient of overlap, denoted by Δ, defined as the area under the curve that is formed by taking the minimum of the two density functions at each time point (Linkie and Ridout 2011). The coefficient of overlap ranges from 0 to 1, where $\Delta = 1$ when there is a complete overlap and $\Delta = 0$ when there is no overlap (Ridout and Linkie 2009). Considering the high number of detections from the focal species', it was used the estimator $\hat{\Delta}_4$ for large samples size (Ridout and Linkie 2009, Linkie and Ridout 2011).

The significance of pairwise comparisons, either between relative activity levels at different times of the day, or between overall activity levels, was estimated using a Watson-Wheeler test, and the confidence intervals were estimated by 500 bootstrap samples (Linkie and Ridout 2011).

The data was analyzed with the implementation of the package activity (Rowcliffe *et al.* 2014) in R 3.6.3 (R Core Team 2019).

Chapter 3: Results

3.1 General results

3.1.1 Trapping effort

Sampling effort totalled 1,135 trapping days from 12 stations, with a mean of 94.58 ± 30.38 (± SD) trapping days per station (Table 4).

Table 4. Trapping effort per station.

Stations	Active days
CAT1	97
CAT2	91
INP01	32
INP03	38
INP04	126
INP05	126
INP06	103
INP07	124
INP08	98
INP09	98
INP13	101
INP14	101

A total of 2,735 independent detections were obtained from seven orders of mammals, birds and livestock, of which 1,684 were ungulates (orders CETARCTIODACTYLA and PERISSODACTYLA), 355 were carnivores, 24 were primates, 5 were lagomorphs, 3 were rodents, 2 were hyracoidea, and 685 were birds. Livestock accounted for 153 independent records. In total, 27 wildlife species were recorded, of which 18 were mammals (Tables 5, 6 and 7) and 9 were birds (Table 8). Each station detected a mean of 11.91 ± 3.55 species.

HMZ was detected at 9 of 12 stations with a total of 643 independent detections (Table 6). Zonkeys were detected at 7 stations with a total of 103 independent detections.

Table 5.Number of independent detections of CARNIVORA species.

Order	Family	Species name	Common name	Independent detections
CARNIVORES	CANIDAE	*Canis lupus familiaris*	Domestic dog	21
		Canis mesomelas	Black-backed jackal	126
		Vulpes chama	Cape fox	10
	FELIDAE	*Acinonyx jubatus*	Cheetah	6
		Caracal caracal	Caracal	2
		Felis silvestris	African wild cat	2
	HYAENIDAE	*Hyaena brunnea*	Brown hyena	181
		Proteles cristata	Aardwolf	1
	VIVERRIDAE	*Galerella sanguinea*	Slender mongoose	3
		Genetta tigrina	Spotted genet	3

Table 6. Number of independent detections of CETARTIODACTYLA *and* PERISSODACTYLA *species.*

Order	Family	Species name	Common names	Independent detections
CETARTIODACTYLA	BOVIDAE	*Antidorcas marsupialis*	Springbok	269
		Bos taurus	Cattle	8
		Capra aegagrus	Goat	17
		Oreotragus oreotragus	Klipspringer	5
		Oryx gazelle	Gemsbok	387
		Ovis aries	Sheep	17
		Raphicerus campestris	Steenbok	1
PERISSODACTYLA	EQUIDAE	*Equus zebra*	Mountain zebra	634
		Equus asinus	Domestic donkey	90
		Equus asinus x Equus zebra	Zonkey	103

Table 7. Number of independent detections of RODENTIA, HYRACOIDEA, LAGOMORPHA and PRIMATA species.

Order	Family	Species name	Common names	Independent detections
RODENTIA	Hystricidae	*Hystrix africaeaustralis*	Porcupine	3
HYRACOIDEA	Procaviidae	*Procavia capensis*	Rock dassie	2
LAGOMORPHA	Leporidae	*Pronolagus randensis*	Red rock rabbit	5
PRIMATA	Cercopithecidae	*Papio ursinus*	Chacma baboon	24

Table 8. Number of independent detections of BIRD species distributed into the different order orders and families.

Order	Family	Species name	Common name	Independent detections
ACCIPITRIFORMES	ACCIPITRICIDAE	*Melierax canorus*	Pale chanting goshawk	9
		Necrosyrtes monachus	Hooded vulture	9
COLUMBIFORMES	COLUMBIDAE	*Spilopelia senegalensis*	Laughing dove	81
		Streptopelia capicola	Ring-necked dove	11
OTIDIFORMES	OTIDIDAE	*Neotis ludwingii*	Ludwig's bustard	7
PASSERIFORMES	CORVIDAE	*Corvus albus*	Pied crow	236
	STURNIDAE	*Onychognathus nabouroup*	Pale-winged starling	9
PTEROCLIFORMES	PTEROCLIDAE	*Pterocles namaqua*	Namaqua sandgrouse	270
STRUTHIONIFORMES	STRUTHIONIDAE	*Struthio camelus*	Common ostrich	53

3.2 Abundance estimation

3.2.1 Individual identification

From the HMZ camera trapping records (n = 3,826), I identified a total of 205 individuals from the left flank and 211 from the right flank. In addition, I identified 11 zonkeys from both the left and right flanks, from a total of 1,396 pictures. The resulting number of individuals uniquely identified represented our sample of the target populations. With the additional sex and age class information, the observed population is characterized as shown in the table below.

Table 9. Number of identified individuals according for each sex and age class. L – left flank, R – right flank.

Species	**Age Class**	**Female**		**Male**		**Unknown**	
		L	**R**	**L**	**R**	**L**	**R**
Zebra	Adult	88	98	37	36	52	53
	Juvenile	8	11	4	5	3	2
	Foal	8	2	1	1	4	3
Zonkey	Adult	3	3	5	5	2	1
	Juvenile	1	2	0	0	0	0

3.2.2 State-space

For HMZ it was obtained a state-space for adults and juveniles consisting of 308 pixels, corresponding to an effective sampling area of 7,700 km^2 (Figure 12). For HMZ foals it was obtained a smaller state-space, consisting of 13 pixels, which translates to an effective sampling area of 325 km^2. The state-space calculated for zonkey was similar to that of adult and juvenile HMZ.

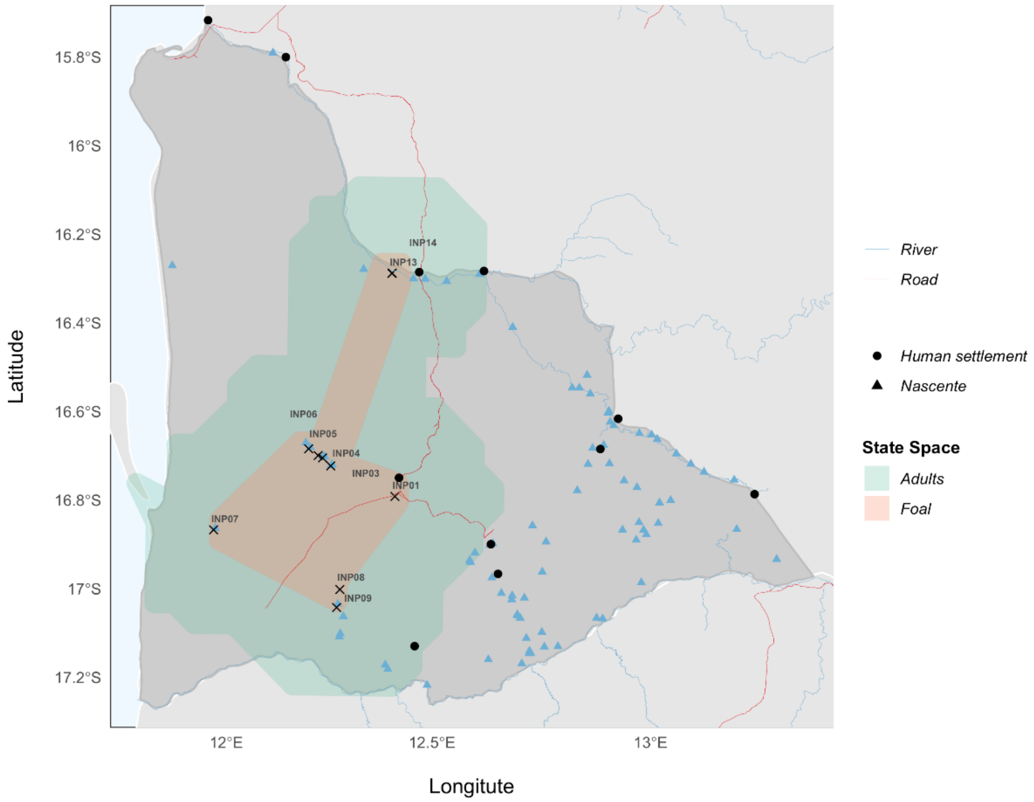


Figure 12. State-space polygon extension in the park, for adults in green and foals in brown. The black crosses are camera trap stations' locations, black dots are the human settlements, blue triangles are the water sources, grey lines are rivers and the brown line are the roads.

3.2.3 SCR models: Model selection, baseline detection probability and spatial scale parameter

The best-supported model for HMZ included constant density (D~1), sex-varying baseline detection probability (p_0~sex) and a constant spatial scale parameter (sig~1) for all age classes (Table 10). The difference between the best-supported and the less-supported models was given by the ΔAIC. For HMZ, the estimated difference for adults was $\Delta AIC_{ad} = 5.78$, and juveniles was $\Delta AIC_{juv} = 0.10$, and foals was $\Delta AIC_{foal} = 4.53$. The top-supported model for zonkey included all constant parameters and the difference from the less supported model is ΔAIC = 1.99.

Table 10. Model set for HMZ and zonkey according to age class. logL – Log-likelihood, K – number of parameters, AIC – Aikaike Information Criterion value, ΔAIC – Difference in AIC value to the top-ranked model; weight – relative support within the model set.

Species	Age Class	Model	logL	K	AIC	ΔAIC	weight
HMZ	Adult	D(~1) p(~sex) sig(~1)	3126.95	5	6263.90	0.00	0.94
		D(~1) p(~1) sig(~1)	3130.84	4	6269.69	5.78	0.05
	Juvenile	D(~1) p(~sex) sig(~1)	547.36	5	1104.72	0	0.51
		D(~1) p(~1) sig(~1)	548.41	4	1104.83	0.10	0.48
	Foal	D(~1) p(~sex) sig(~1)	206.31	5	422.62	0	0.90
		D(~1) p(~1) sig(~1)	209.58	4	427.16	4.53	0.09
Zonkey	Adult	D(~1) p(~1) sig(~1)	384.79	4	777.59	0	0.73
		D(~1) p(~sex) sig(~1)	384.79	5	779.59	1.99	0.26

The top-ranked model for HMZ supports sex-specific detection probability, whereby there is a higher probability to detect males compared to females across all age classes (Table 11 and Figure 13). Furthermore, the difference in detection probability between sexes decreases with age class from foals, for which males are eight-fold likely to be detected as females, to adults, for which males are twice as detectable as females. Daily detection probabilities were below 10% and reach percentages as low as 1%. The baseline detection probability of adult zonkeys was similar for both sexes and is equivalent to that found for male HMZ, with p_0 = 0.02± 0.00. (Table 13).

Table 11. Observation model parameter estimates (mean ± standard error [95% confidence interval]) for HMZ and zonkey according to each age-specific top-ranked model. $\hat{p}_0$– estimated baseline detection probability, $\hat{\sigma}$ - spatial scale parameter (km).

Species	Age Class	Sex	$\widehat{p_0}$	$\hat{\sigma}$
HMZ	Adult	Female	0.01 ± 0.00 [0.01-0.01]	8.53 ± 0.38 [7.81-9.32]
		Male	0.02 ± 0.00 [0.01-0.03]	8.53 ± 0.38 [7.81-9.32]
	Juvenile	Female	0.02 ± 0.01 [0.01-0.05]	7.46 ± 0.70 [6.21-8.97]
		Male	0.06 ± 0.02 [0.03-0.12]	7.46 ± 0.70 [6.21-8.97]
	Foal	Female	0.01 ± 0.00 [0.00-0.04]	1.75 ± 0.38 [1.15-2.68]
		Male	0.08 ± 0.05 [0.02-0.26]	1.75 ± 0.38 [1.15-2.68]
Zonkey	Adult	Female	0.02 ± 0.00 [0.01-0.04]	7.72 ± 1.03 [5.95-10.02]
		Male	0.02 ± 0.00 [0.00-0.04]	7.72 ± 1.03 [5.95-10.02]

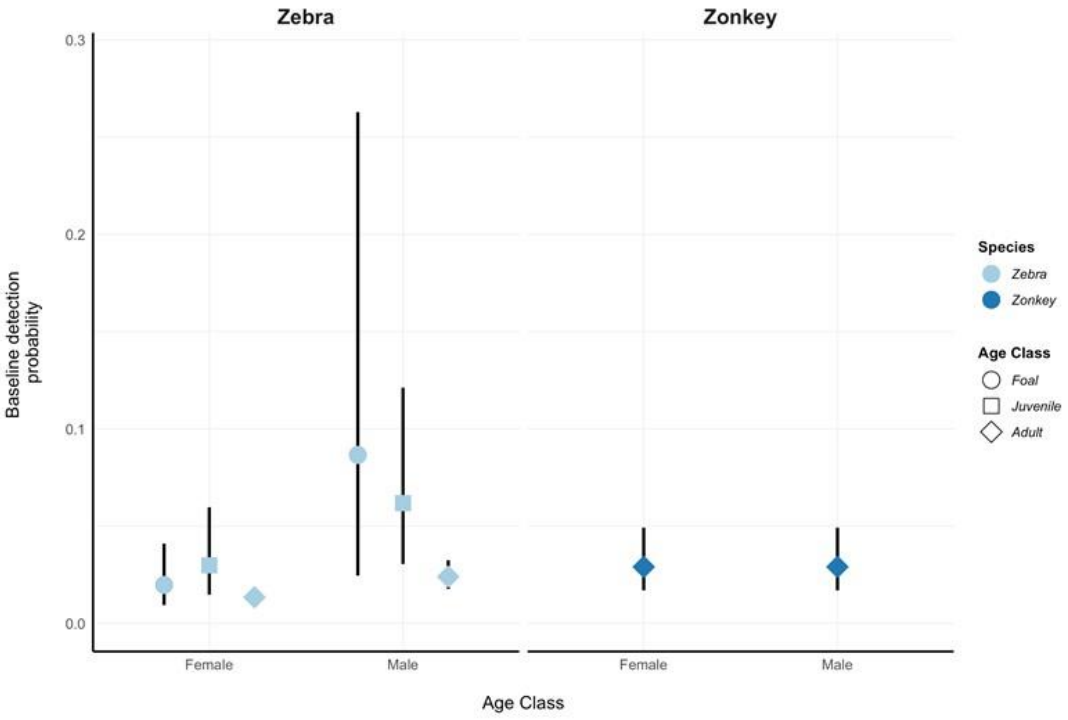


Figure 13. Baseline detection probability of females and males of HMZ and zonkey for adults, juveniles and foals.

Age-specific estimates of the spatial scale parameter indicate that HMZ movement patterns increase until adulthood. However, there were only slight differences in the estimate of σ for adults and juveniles, with estimates for these two age classes largely overlapping: 95% CI σ_{ad} = 7.81 – 9.32 km; 95% CI σ_{juv} = 6.21 – 8.97 km. However, the spatial scale parameter for foals was significantly lower: σ_{foal} = 1.75 ± 0.38 (± SE) km (Table 11). The spatial scale parameter,σ, once converted into a home range radius, provided an age-specific estimate of home range size (HR): HR_{ad} = 178.10 km^2, HR_{juv} = 136.22 km^2, and HR_{foal} = 7.49 km^2.

For zonkey the estimate of the spatial scale parameter is very similar to the wild conspecific, with σ_{ad} = 7.72 ± 1.03 km (Table 11, Figure 14), which converted to a home range size of HR_{ad} = 145.88 km^2.

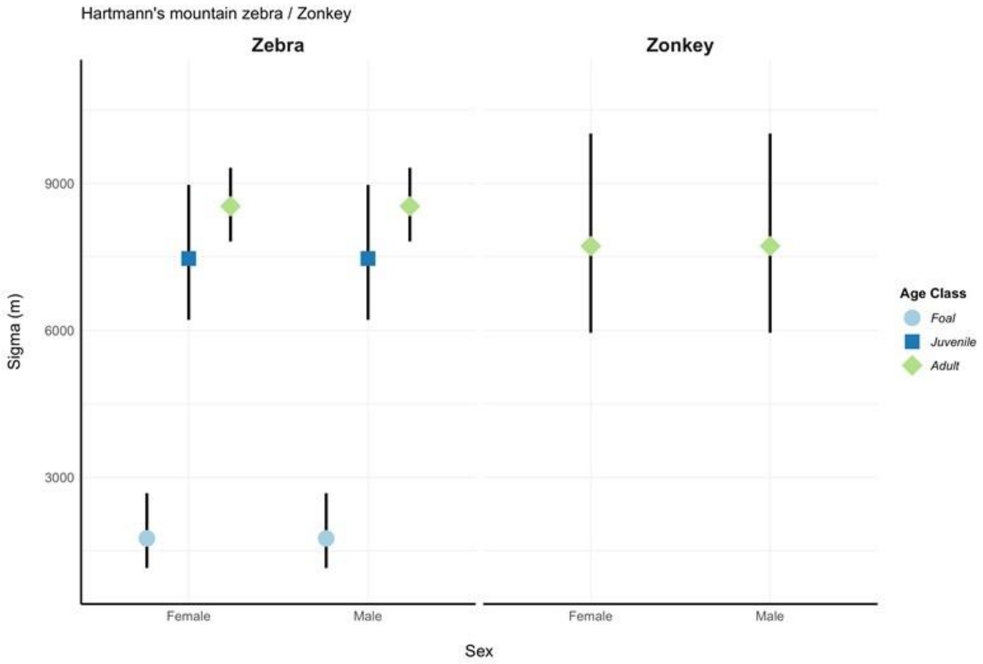


Figure 14. Spatial scale parameter the rate of movement over the state-space.

The half-normal slope denoting the Euclidean distance shows that the increasing distance from the individuals' activity centers decreases the spatial detection probability at all age classes. For HMZ, the declining curve in detection probability was slightly different, where males with high detection probability indicated a faster decline than females, although the decline in detection probability approached zero earlier for females, at a distance of 17 km for adults and juveniles and 5 km for foals. In contrast, for zonkey with a similar sex-specific baseline detection probability, the declining curve in the spatial detection probability was also similar for both males and females. The spatial detection probability approached zero at a distance of 16 km from the individual's activity centre (Figure 15).

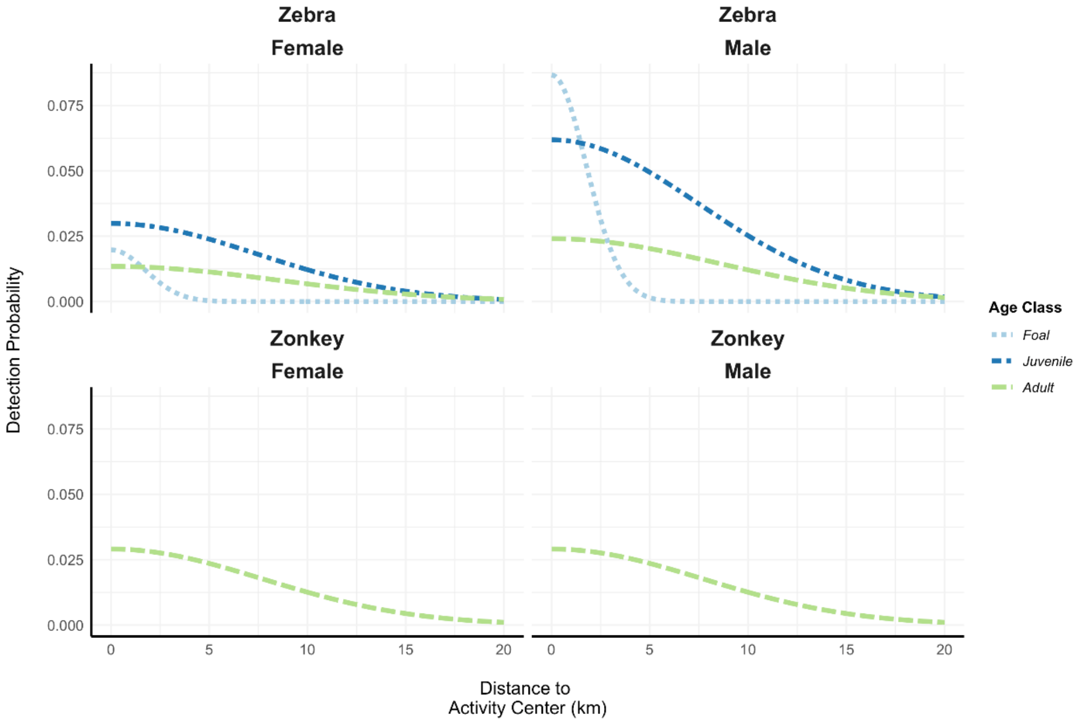


Figure 15. Estimated detection probability of females and males of zebra (HMZ) and zonkey for adults, juveniles and foals, as a function of the distance to their individual activity centre, as denoted by the half-normal function.

3.2.4 Estimated abundance and density

The population of HMZ in INP was estimated at 478 animals, divided into the three age classes, with adults being the most abundant class with 428 individuals, and with a significant difference in numbers especially between juveniles and adults, which suggests an aged population as shown by the demographic pyramid (Table 12 and Figure 16). For zonkey, the estimated population comprises 19 individuals (Table 12 and Figure 16).

As supported by the model with the highest support, the density was constant under the prescribed state-space, but has sex-specific variations for each of the age classes. Because of the explicit consideration of a prescribed state-space in the spatial models, I was able to estimate an absolute density (Table 12). The apparent high density of foals refers to a smaller state-space, i.e. the effective sampling area was smaller.

Table 12. Estimated abundance and density (mean ±standard error [95% confidence interval]) for both of HMZ and zonkey according to each age-specific top-ranked model. $\widehat{N}$ – estimated abundance, $\widehat{D}$- estimated density/100km^2.

Species	**Age Class**	**Sex**	$\widehat{N}$	$\widehat{D}$
HMZ	Adult	Female	332 ± 34 [273-405]	4.32 ± 0.44 [3.54-5.26]
		Male	96 ± 13 [73-126]	1.24 ± 0.17 [0.95-1.63]
	Juvenile	Female	23 ± 6 [14-39]	0.30 ± 0.08 [0.18-0.50]
		Male	10 ± 3 [5-19]	0.13 ± 0.04 [0.07-0.24]
	Foal	Female	16 ± 5 [8-30]	4.79 ± 1.57 [2.52-9.11]
		Male	1 ± 1 [0-5]	0.42 ± 0.30 [0.10-1.69]
Zonkey	Adult	Female	7 ± 3 [3-17]	0.10 ± 0.04 [0.04-0.23]
		Male	12 ± 4 [6-25]	0.16 ± 0.06 [0.08-0.32]

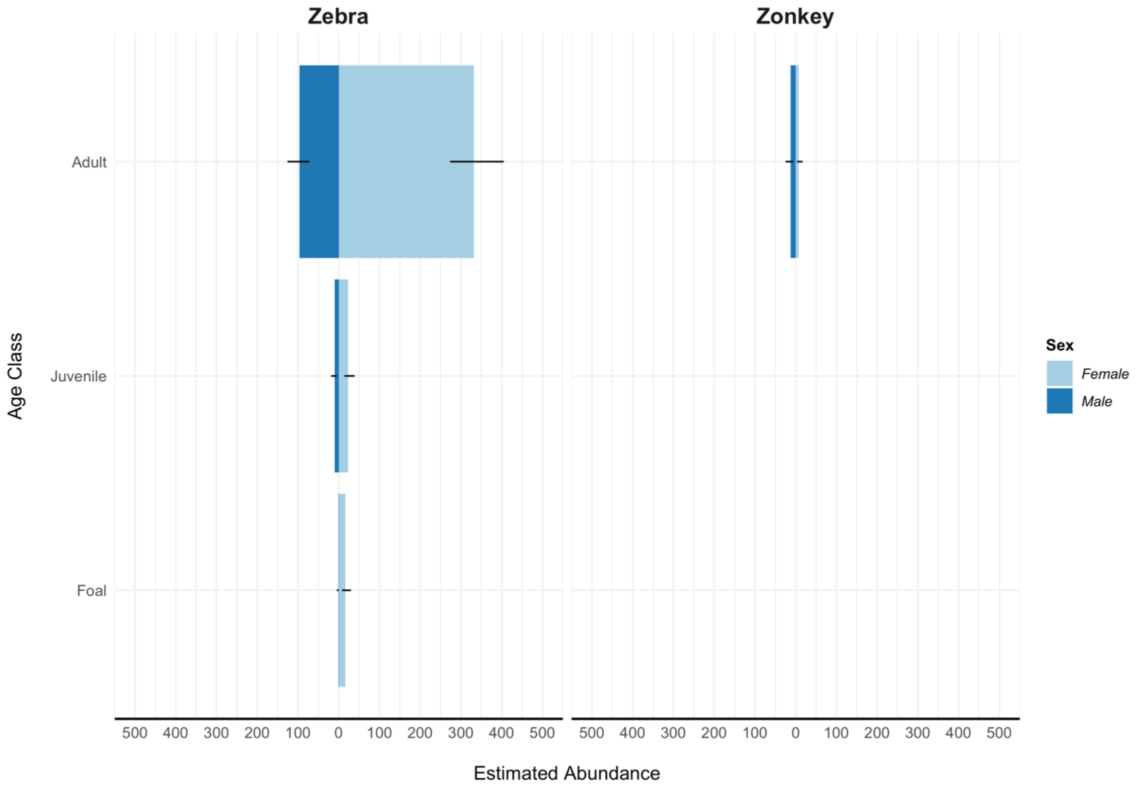


Figure 16. Estimated demographic pyramid of Hartmann's mountain zebra and adult population of zonkey in the Iona National Park.

3.3 Population structure

3.3.1 Group size, sex ratios and age structure

From the camera trapping data we estimate a mean group size of 3.75 (95% CI = 0 - 10), ranging from 1 – 15 individuals, and a mode of 1. From game counts, in contrast, a mean of 8.46 (95% CI = 0 - 27) individuals per group was estimated, and a mode of 4 (Figure 17).

The observations from both methods follow a negative binomial distribution, but with different parameters: μ_{GC} = 8.47 [7.69-9.33] vs. μ_{CT} = 3.73 [3.55-3.93]; $size_{GC}$ = 1.71 [1.42-2.09] vs. $size_{CT}$ = 5.82 [4.44-8.09].

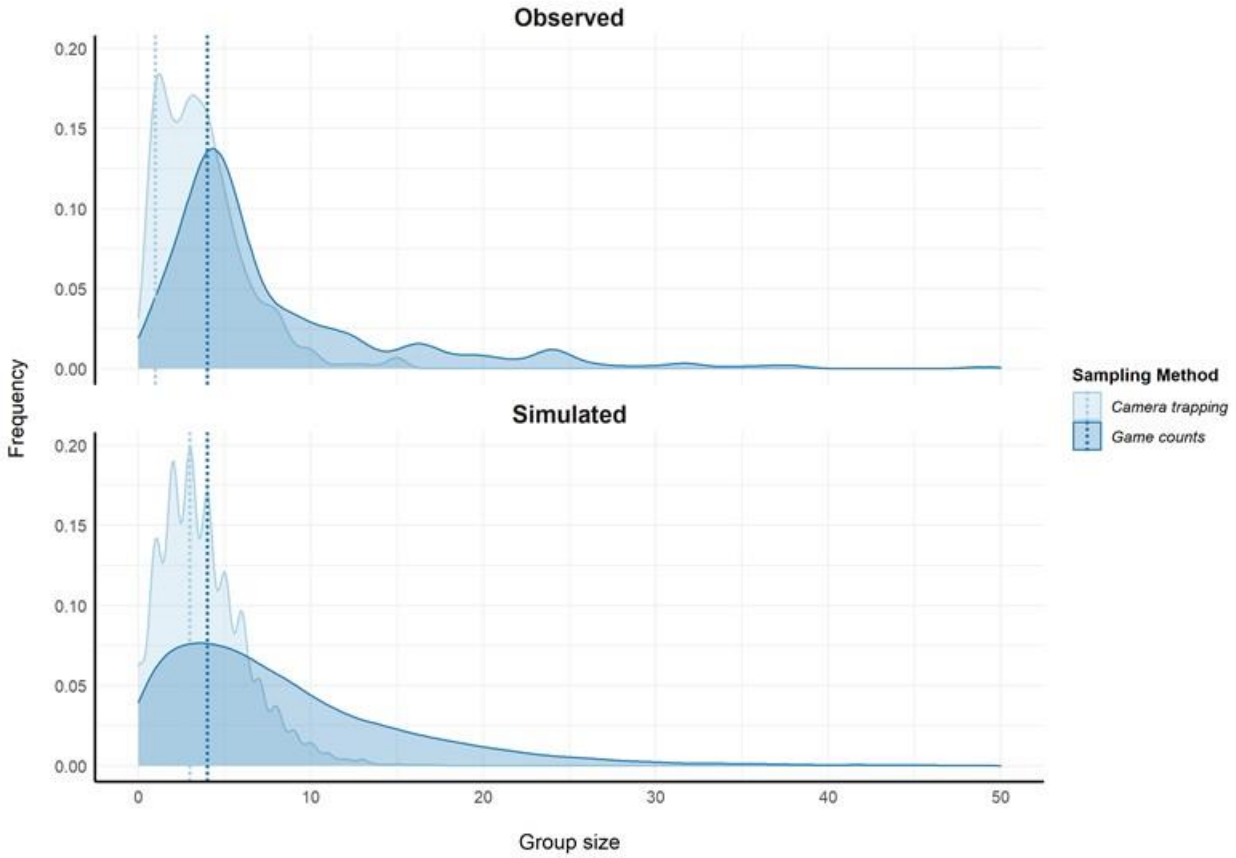


Figure 17. HMZ group size distributions from camera trapping and game count, as obtained from the raw data (observations) and from the fitted negative binomial distributions. Vertical dotted lines represent the most frequent group size (mode).

The HMZ population has a higher number of females than males in all age classes, with an estimated sex ratio of 1:3.46 (95% CI = 0.16 - 6.6.07) (male: female, n = 478). The estimated sex ratio for the different age classes were 1:3.45 (95% CI = 2.16 – 6.16; n = 428) for adults, 1:2.3 (95% CI = 0.73 – 7.8; n= 33) for juveniles, and 1:16 (95% CI= 1.6-30, n = 17) for foals. In contrast, the estimated sex ratio for zonkey was 1:0.58 (95% CI = 0.12 – 8.33; n = 19), with males appearing in higher numbers.

The age structure of the HMZ population in general suggests a skewed structure biased toward, which are estimated to account for 89.53% (69.45% female and 20.08% male) of the population. Juveniles and foals are estimated to constitute 6.90% (4.85% female and 2.09% male), and 3.55% (3.34% female and 0.20% male) of the HMZ population in the INP, respectively. For zonkey, due to the reduced number of camera captures of juveniles, which prevented the estimation of its population size, I only present the adult population, of which 69.69% are males and 30.30% are females.

3.4 Activity at waterholes

Hartmann's mountain zebra, zonkey and donkey were recorded at waterholes at all hours of the day. The activity density function revealed a unimodal activity pattern, with each species showing different activity peaks. For HMZ, the activity peak occurred during late night until the early hours of the morning before dawn, from 23:00 to 5:00, while zonkeys were mainly active during late afternoon, from 15:00 to 17:00, and donkeys showed an activity peak during the afternoon, from 13:00 to 17:00. (Figure 18).

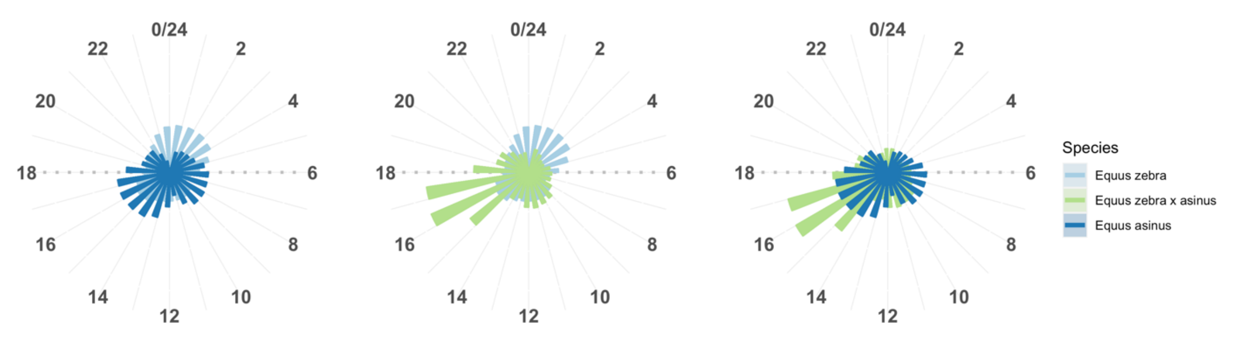


Figure 18. Diel activity patterns and overlap of HMZ, donkey and zonkey at waterholes in Iona National Park.

The results suggest that the three species spend different amounts of time around waterholes. HMZ individuals were estimated to spend 15.6 ± 0.6h [CI95%: 14.1-16.6] at waterholes per day, whereas donkeys spend 14.2 ± 1.5h [CI95%: 10.5-16.4] around these features per day. Zonkeys, however, were found to only spend 7.1 ± 1.2h [CI95%: 5.3-9.8] active at waterholes per day. Waterholes were used for significantly less time by zonkeys than by HMZ (W = 39.62, p-value < 0.001) or by donkeys (W = 13.09, p-value < 0.001), but the difference in usage time was not significant between HMZ and zonkeys (W = 0.72, p-value < 0.4) (Table 13).

Table 13. Mean diel time spent by HMZ, zonkey and donkey at waterholes (upper-right diagonal), and respective coefficients of overlap (lower-left diagonal) at Iona National Park, as estimated by camera trapping.

		HMZ	Zonkey	Donkey	
HMZ	Activity Overlap ($\hat{\Delta}$)	-	8.4 ± 1.4***	1.4 ± 1.7	Activity Level Difference
Zonkey		0.72***	-	-7 ± 1.9***	
Donkey		0.75***	0.78***	-	

*** - p < 0.001

The coefficient of overlap revealed that HMZ, zonkey and donkey have a high overlap at waterholes, with overlap estimates of $\hat{\Delta}_4 > 0.7$ (Table 13). However, despite the high overlap, their activity at waterholes still revealed significant differences (p-value < 0.01, Table 13 and Figure 18).

Chapter 4: Discussion

4.1 General Discussion

Historically, Angola had thriving populations of wildlife (Huntley 2017). This changed after European colonization started in 1575 and declines accelerated during the protracted civil war between 1975 and 2002 (Huntley 2017). HMZ were one of the few species which maintained viable populations in the arid south-west (Huntley 2017). Wildlife conservation and tourism are now, during time of peace, a national priority (Kuedikuenda and Xavier 2009, Silva 2019). As a near endemic and charismatic species, HMZ is an animal which is important to protect and its population is important to manage (Gosling *et al.* 2018). In order to do this, however, an accurate baseline population estimate was needed.

This study presents the first contemporary insight into the HMZ population in Iona National Park, with an estimation of abundance and density, with respective demographic structure, through robust spatial capture-recapture analysis of camera trapping data. The SCR estimates resulted in a population of 478 individuals of HMZ, with females being the most abundant gender at all age classes, and consequently I observed a female-biased sex ratio of 1:3.46 (male:female). The structure of the population follows the patterns observed in other equid members in terms of proportional representation of each age class to the population, with adults being the most abundant class (Ransom and Kaczensky 2016a). However, the extremely adult-biased demographic structure of the HMZ population in INP raises concern regarding the management and conservation of the species in the area. This approach presents a baseline class-structured population estimate for HMZ in INP, which can be used to guide continued monitoring programs and allows assessing the effectiveness of conservation and management actions through a continuous monitoring system, which allows to address population dynamics (Nichols *et al.* 2011). It also provides important information for the species in the northernmost distribution (Skinner and Chimimba 2005, Kingdon 2015), since Gosling et al. 2018 (IUCN red list) estimated the overall population size and structure of the HMZ population based almost exclusively on the Namibian population.

Furthermore, my study showed that the viability of the HMZ population may be threatened by hybridization with feral donkeys. Although hybridization between closely related species is a natural mechanism that can operate as an important evolutionary force, it has nevertheless contributed to the extinction of numerous species (Hill 2009). Although the number of hybrids may not represent a major concern yet, their continued presence (including juveniles) suggests recurrent interbreeding events. Hence, in the absence of a plan to control HMZ-donkey interactions in the park, hybridization has the potential to escalate, as the two species continue to share the same space and resources, potentially elevating the threat to the viability of the isolated population of HMZ in the INP.

4.2 Suitability and effectiveness of the employed methods

Camera trapping is a powerful tool not only to record the presence of wildlife populations, but also to provide relevant information about their ecology (Rovero *et al.* 2010, O'Connell and Nichols 2011). This field sampling method proved suitable to study HMZ in a desert environment, providing important insights into the ecology of HMZ and zonkey populations within INP. Additionally, camera trapping revealed to be an appropriated tool to sample HMZ populations and its characteristics in a remote area such as the INP, and allowed access to study individuals in areas where other methods, such as aerial surveys or direct observation, would be particularly challenging to employ due to the arrangement of the landscape shaped by mountains and valleys (Mendelsohn and Mendelsohn 2019). Also, the preference for nocturnal activity of zebras and other wildlife, particularly in anthropogenically-disturbed areas (Gaynor *et al.* 2018), further compromise methods such as aerial and game count. Therefore, as other recent non-invasive sampling methods such as DNA it is a competitive alternative. The frequent presence of livestock that competes for resources with wildlife in INP forces HMZ to access water sources mostly during nighttime, which emphasizes the usefulness of camera trapping to study rare and elusive animals that are mostly active at night (O'Connell and Nichols 2011, Rovero *et al.* 2013, Burton *et al.* 2015).

When we used abundance as the state variable of interest, camera trapping proved particularly efficient, because HMZ and zonkey individuals could be individually identified through photographs, hence allowing implementation of SCR estimation methods (Nichols *et al.* 2011). For unmarked individuals, the application of camera trapping to estimate abundance may not be as efficient, particularly when using low numbers of camera stations (Rowcliffe *et al.* 2008). This difficulty limited the estimation of the population size of donkeys, whose abundance remains unknown despite is tremendous importance for the management of HMZ population at INP. Abundance estimation is currently widely employed using camera trapping records, and is currently assumed to be one of the most reliable method for abundance estimation (Royle *et al.* 2013). SCR methods strongly rely on the spatial arrangement of detector devices to accurately estimate detection probability (Sun *et al.* 2014), because placement of the cameras across the study area affects the ability to detect the individuals (O'Brien 2011, Dupont *et al.* 2020). Therefore, the cameras should be placed at locations that maximize the chance of detecting the target species (O'Brien 2011). In fact, simulation studies have suggested that trap spacing needs to be considered relative to the target species' home range size, ideally with traps spaced less than twice the spatial scale parameter (Sun *et al.* 2014). However, field and other logistic constrains may limit one's liberty to deploy cameras at the best possible places. For this study, I deliberately chose a sampling design focused on waterholes, which allowed us to optimize capture probability and to obtain a representative sample of the population for accurate abundance and density estimations, even when data was split into different age classes. As demonstrated by the complete absence of HMZ records from the cameras away from waterholes, placing cameras more randomly would have wasted resources which were already limited. Additionally, the risk of losing data due to theft and vandalism of equipment was also a factor that limited more extensive sampling of the area (Meek *et al.* 2019).

Camera-trapping further allowed the collecting of, and addressing of additional aspects of HMZ's ecology, such as demographic structure, activity and group size.

Individual identification was processed on IBEIS (Crall 2017), which was appropriated through its advanced concept that provides more accurate ranking than standard recognition techniques. Together with Hotspotter (Crall *et al.* 2013) and Wild-ID (Bolger *et al.* 2012), IBEIS represents an important tool that improved the efficiency of identifying individual animals from camera trapping (Crall 2017, Nipko *et al.* 2020). With the advances in the recognition technology applied to wildlife ecology, the problem of animal identification is more easily overcome and this has given rise to a wide expansion of research in terms of species studied (Crall 2017).

The distribution of the available waterholes deemed the spacing between cameras to be irregular. Regardless, while the spacing between some stations was too large according to the recommendations for good estimates of population parameters (Sollmann *et al.* 2012, Sun *et al.* 2014), this approach turned out to be advantageous in the sense that it allowed to see that zebras can move long distances to find water and grazing throughout the study area. As observed in some simulation studies, leaving spacing that is too large between cameras causes gaps in the sampling design, limiting the probabilities of obtaining spatial recaptures (Sollmann *et al.* 2012, Sun *et al.* 2014). But in areas like INP, where the trap configuration is dependent on the availability of waterholes, it is difficult to comply with spacing and movement assumptions. However, HMZ are known to have large home ranges as they move long distances in search for water and food (Altrichter *et al.* 2011, Ransom and Kaczensky 2016b). Therefore, and given the limitation of appropriate settings, the geographic locations were revealed to be appropriate to capture long range movements of HMZ and effectively estimate all required parameters.

The spatial scale parameter can be directly related to home range size, as it tends to be proportional to the home range radius (Reppucci *et al.* 2011). The estimates suggest that HMZ home ranges in INP range from 136 to 176 km^2 for juveniles and adults, respectively, and are within the range reported for other equids (Schoenecker *et al.* 2016). To my best knowledge, only two HMZ home range estimates have been produced so far: one was obtained from a population in a relatively small area, with estimates ranging from 6 to 20 km^2 (Joubert 1973), resulting in significantly smaller estimates than those obtained here; the other indicates values closer to those observed in most of the equid members, ranging from 256 to 685 km^2 (Muntifering *et al.* 2019), which is larger than what was obtained through the SCR approach implemented in this study. This estimates by Muntifering (2019), suggest that collars are suitable to assess HMZ home ranges. Equids are reported to present variable home range sizes reaching several thousand square kilometers (Schoenecker *et al.* 2016). Zonkeys were normally observed among groups of

HMZ, which suggests that they dwell together. Moreover, the sigma value of zonkey, which is equivalent to that obtained for HMZ, suggests that these animals may closely coexist, and share similar ecological requirements.

The detection probability sub-model reveals a constantly lower probability of detecting females than males of HMZ, across all age classes. In the case of HMZ, this behaviour may be associated with its ecology: Firstly, the higher exposure of stallions at waterholes may help them to secure access to water to HMZ mares, in addition to preventing abduction of mares by other males (Klingel 1974, King *et al.* 2016). Secondly, the existence of bachelor groups mainly formed by males, which are more active at waterholes, may be trying to abduct females to form their own breeding herds (Joubert 1972a, Klingel 1974). Finally, the group formation characteristics of zebra sometimes pose difficulties to the detection of all individuals when they come together at a waterhole.

Although the behaviour and ecology of zebras and other equids have been widely investigated (Joubert 1972a, Klingel 1974, Penzhorn 1982, Valeix *et al.* 2007, Owen-Smith 2013, King *et al.* 2016, Gosling *et al.* 2018, Muntifering *et al.* 2019), most studies, particularly those concerning HMZ, involved direct observation to investigate how HMZ react to certain conditions (Joubert 1972a, Gosling 2012). Only a few studies were implemented using camera trapping (Valeix *et al.* 2007, 2009, De Vos 2017, Olivier *et al.* 2019), and none of those studies refers to sex-biased differences in detectability, nor to its underlying causes.

4.3 Demographic characteristics of Hartmann's mountain zebra in Iona National Park

Abundance and status

The estimates of abundance obtained by SCR suggest that the number of HMZ individuals in Iona National Park is higher than previously thought (478 individuals), which proves encouraging for the animal's management and conservation. Two past surveys have attempted to assess the status of wildlife in INP through aerial counts, carried out by the Namibian Ministry of Environment and Tourism in 2003 (Kolberg and Kilian 2003) and 2016-2017 (van der Westhuizen *et al.* 2017). These surveys estimated a population of 260 and 304 HMZ individuals, respectively, but did not allow an assessment of the demographic structure of the population. These two approaches were mainly performed for recognition purposes and did not allow for robust population size estimations with measures of accuracy and precision as requirements for wildlife monitoring estimates (Nichols *et al.* 2017). These differences in sampling approaches limit an appropriate comparison of HMZ population size across sampling periods. Also, given the low number of foals in the population, it is very unlikely that the population size has significantly changed (304 in 2017 vs. 478 in 2020) in just three years. Furthermore, my estimates reveal a population represented by 89.5% mature individuals, a higher proportion than the 72.6% reported by IUCN based on the estimates from 2003 aerial counts, with aerial counts in fact being more aligned to the expected proportion of mature individuals of the equids (Ransom and Kaczensky 2016b). These differences could also be due to differences in the detection capacity of both methods, or alternatively, there might have been a change in the demographic structure in Iona's HMZ population in the last 17 years. Robust estimates of abundance rely on appropriately accommodating the detectability of individuals for unbiased inferences (O'Brien 2011, Bischof *et al.* 2014). This is a key concept taken into account by this study, which allowed to produce more robust estimations than the other two approaches used on the same population.

The population of HMZ in INP is the only known population of this species in Angola and, to my best knowledge, it appears to be the smallest across its distribution range. The number of mature HMZ individuals in Namibia is estimated to be 32,416 individuals, and 594 – 724 animals in South Africa (Gosling *et al.* 2018). If correct, the Angolan population therefore comprises only 1% of the global population of HMZ, in comparison to 97% and 2% for the Namibian and South African populations, respectively. The importance of the Angolan population is further exacerbated as it represents the northernmost range of the species.

HMZ tend to occur in remote areas where accessibility constitutes a major challenge. This limitation could constitute one of the major reasons for the shortage of demographic information about this species across its distribution range (Novellie *et al.* 2002, Gosling *et al.* 2018). Despite these challenges, aerial and game counts have been implemented in Namibia, which hosts the majority of the HMZ population, contributing to minimizing this knowledge gap (MET/NACSO 2018). These counts provide an approximated estimate of how many animals exist, but, most importantly, they provide a means to track changes and trends in population numbers over time (MET/NACSO 2018). However, while these methods may prove useful for assessing trends (as they assume constant detection probability across sampling periods), they remain inappropriate for estimating population size, at least under a single-sweep design.

The estimates of density for adults and juveniles were 0.043 and 0.004 per km^2, respectively, and 0.052 per km^2 for foals. The limited availability of abundance estimates for HMZ population across its distribution range implies that density estimates are also not available, because the two parameters are strictly related (Karanth 1995, O'Brien 2011). The only rough density estimates of HMZ populations were performed in Namibia from aerial and game counts in the north-western communal land, and from a nationwide questionnaire to farm holders about where most of the known HMZ populations in the country were expected to be found (MET/NACSO 2018). The average density estimate of HMZ in Namibia is 0.45 animals per km^2, from a population of 44,712 animals (Gosling *et al.* 2018). Nonetheless, many reasons suggest that these data underestimate the real population both in communal lands and in farmlands (Gosling *et al.* 2018).

No similar approach with regards to estimates of abundance and density for the three age classes considered in this study has been used before in INP. This study represents one of the monitoring initiatives to contribute on the management and conservation of HMZ in Angola.

The fact that a HMZ population of over 400 adult individuals exists in INP suggests some degree of resilience of the animal, which allows it to endure threats that could have driven it to local extinction, such as war, poaching, habitat destruction and grazing competition with livestock (PNUD 2016, Huntley 2019). However, these threats have displaced HMZ to suboptimal habitats (Rocha *et al.* Submitted). Regardless, ignorance about historical numbers of HMZ in the past precludes an assessment of how much the population has actually declined. Irrespective of their recent demographic history, our results expose that the strongly adult-biased and low recruitment of contemporary HMZ population at INP entails an intrinsic slow recruitment rate, and consequent low recovery rate in the face of sudden population declines caused by environmental changes or increasing anthropogenic pressure that can lead it to a critical status. This study also shows a population of zebra-donkey hybrids (zonkey), which could be considered a threat to the HMZ population in INP, as reported elsewhere involving hybridization among other equids (Cordingley *et al.* 2009). The estimates suggests that phenotypic hybrids comprise 4.5% of the adult HMZ population in INP. While these numbers may not appear problematic yet, it reveals that hybridization with donkeys is occurring, and could compromise zebra population growth if donkey-HMZ interactions become more frequent and intense (Hill 2009, Altrichter *et al.* 2011). Despite some local knowledge about this ongoing hybridization process, it appears that little attention has been paid to it (Cordingley *et al.* 2009). However, it deserves being carefully investigated to assess the scale and the frequency at which this mechanism is occurring. As hypothesized by Cordingley *et al*. (2009) elsewhere, the most evident reason for hybridization in INP could be the presence of feral donkeys roaming alongside zebras, and the limited mating opportunities for male feral donkeys among its feral conspecifics. In fact, HMZ and donkeys coexist permanently in INP, as observed from camera trapping records and direct observations, frequently co-occurring at waterholes. Moreover, both species use the same type of resources, and drought could drive them to forage at the same places. It is likely that this constant coexistence scenario the mechanism may be limiting the number of strictly zebra mating opportunities, reducing the number of zebra foal births, which may well contribute to the observed demographic structure of reduced number of juveniles and foals in the HMZ population. Furthermore, it in fact highlights the need to reduce zebra-donkey interactions and increase the reproductive success of zebras, thereby promoting demographic restructuring towards a sustainable HMZ population, where there are sufficient offspring for the maintenance of the population. Hybridization among equids is not a topic that has received much attention, especially involving wild populations. There have only been a few reported cases of hybridizations of HMZ and donkeys in the past (Joubert 1974, Brown and Jenkins 1987). Therefore, the reasons driving this mechanism and its impacts on wild equid populations remains largely unknown. While this work does not explicitly aim to investigate the drivers and consequences of the HMZ-zonkey hybridization problem, it definitely exposes and provides a first visual quantification of the problem, and it highlights that more research is needed to understand and revert this process in order to safeguard the long-term survival of HMZ in INP.

Group size and social structure

Estimates of group size were different when based on camera trapping and on game count, highlighting one of the camera trapping limitations. The limited field of view leads to imperfect detection of all individuals present during a capture event (Rovero *et al.* 2010, O'Brien 2011, Burton *et al.* 2015). Therefore, direct observation is the more efficient method if the goal is to assess group size and social structure of HMZ. However, camera traps allow overcoming of HMZ's shyness, especially in remote areas such as INP (De Vos 2017). Both results revealed the social nature of the HMZ, and the resulting group size estimates remain within the range of values expected for the species (Klingel 1968, Joubert 1972a). The mean group size for HMZ was at 4.7 individuals, with a range from 2 to 8 individuals (Klingel 1968, Joubert 1972a, Penzhorn 1979). Studies investigating waterhole use by ungulates, and with a special reference to zebras, revealed that they normally approach in numerous groups as a way to minimize predation (Valeix *et al.* 2009, Crosmary *et al.* 2012). Hence, gregariousness in zebras appears to provide the combined advantages of minimizing predation while also proving an efficient reproductive strategy (Klingel 1969, 1974, Altrichter *et al.* 2011).

I found females to be consistently more abundant than males at all age classes, but the spatial scale parameter to be four to five times smaller for foals than juveniles and adults, respectively. The smaller movement of foals could also constrain the movement of their mothers, forcing mothers to have smaller home ranges than is typically of adults while they have dependent offspring (Schoenecker *et al.* 2016). Moreover, it highlights the importance of waterholes for sustaining zebra reproduction in the desert. The limited availability of water resources could be a factor contributing to the low number of young animals, because they are forced to be close to water due to limited movement capacity (Klingel 1969, Rubenstein 2010).

Sex structure

The female-biased sex ratio found in INP is a reflection of a gregarious social organization, characteristic of zebras (De Vos 2017). Among equids, a male-biased sex ratio at birth is frequent (Ransom and Kaczensky 2016a), and this would be a reason to expect a male-biased sex ratio at least among the youngest age classes. Therefore, among equids, the average sex ratio of foals does not differ from parity 1.1:1 male to female, but extreme cases are also observed. Curiously, one of them was reported in mountain zebra, with a sex ratio of 2.2 males to 1 female (N = 19) (Hrabar and Kerley 2013, Ransom and Kaczensky 2016a). As individuals become adults, sex ratio should balance out through the establishment of the adult social structure into breeding herds and sex-biased survival rates. However, I found the opposite pattern, with a significantly female-skewed sex ratio among HMZ foals in INP. But this is not a singular case among equids, it was also observed in a resource-stressed population of plains zebra and a feral horse population, with a sex ratio of 0.27 males to 1 female (n = 19) and 0.47 males to 1 female (n = 25) respectively (Shultz and Stanley 2012, Hrabar and Kerley 2013, Ransom and Kaczensky 2016a). It is likely that a part of the estimated skewness could be due to the combined effect of the difficulty in determining the sex of a large proportion of foals, as well as to the small sample size of this age class. Therefore, for adults, the observed sex ratio seems representative of HMZ, especially because of their social organization.

Age structure

The age structure found in the HMZ population follows the normal tendency observed among equids, with adults being the most abundant class. My findings further suggest an aged population with juveniles and foals comprising only 10.5% of the population, which warrants some concern. The typical age structure for wild equids comprises 8 – 15% foals, 15 – 28% juveniles and 71 – 78% adults. In a studied population in Namibia, HMZ age structure follows the common pattern observed in other equid populations, with adult individuals representing 72% of the population (Gosling *et al.* 2018). However, the HMZ in INP exhibits an unexpected adult-skewed structure, pointing either to a low foaling rate or high infant mortality, or a combination of both (Ransom and Kaczensky 2016a). Continued monitoring, namely estimating this population's vital rates – i.e. abundance, survival, fecundity, emigration and immigration (Mills 2012) would help us understand the reasons behind this disproportional population structure in INP, as well as its dynamics. However, understanding the drivers shaping the age-specific survival could further elucidate HMZ's demographic dynamics in INP. Most zebra predators are currently absent from the area, so drought is expected to constitute the main threat to survival of the relatively low population of foals, which consequently affects recruitment to the juvenile and adult population (Ransom and Kaczensky 2016a).

4.4 Activity patterns at waterholes

Activity pattern

The activity level estimates show that HMZ, donkey and zonkey are active around waterholes at all hours of the day, but each species presents a specific period when its activity is more intense. An active use of waterholes is expected for equids because of their high water dependency (King *et al.* 2016, Makin *et al.* 2017). I found HMZ to have a peak of activity at waterholes during late night and dawn, between 23:00 and 05:00, and the opposite was observed in donkey and zonkey, whose activity peaks during daylight. This pattern suggests a shift from HMZ's normal drinking activity at INP, possibly due to learned or acquired fear behaviour from human related activities (Joubert 1972b, Kaczensky *et al.* 2010, Crosmary *et al.* 2012). There is not strict avoidance of daytime use of the waterholes. It is just less intense or frequent. It is likely that the waterhole use is nocturnal, but with a component of higher intensity during nighttime, likely from not very strongly-acting constrains (Zhang *et al.* 2015). Shifts in waterhole use timing is common among ungulate species, especially to avoid predation risk (Valeix *et al.* 2009, Périquet *et al.* 2010, Crosmary *et al.* 2012, Makin *et al.* 2017), human-related activities such as hunting, in addition to livestock presence (Attum *et al.* 2009, Kaczensky *et al.* 2010, Zhang *et al.* 2015). Given the high temperatures during daytime at INP, a more diurnal peak in drinking activity by HMZ was expected, as observed in the donkeys and zonkeys (Altrichter *et al.* 2011, Hayward and Hayward 2012, Zhang *et al.* 2015, King *et al.* 2016). A similar shifted pattern was observed in HMZ populations in Namibia, which preferentially used waterholes more frequently at night from

20:00 to 22:00 and during early morning from 04:00 to 06:00, in response to hunting activities (Joubert 1972b). Equivalent behavioral shifts have been reported in Asiatic wild asses (*Equus hemianus*) (Zhang *et al.* 2015), which accessed waterholes more frequently at night due to human-related disturbance and due to the presence of potential competitors. However, the latter factor should not be important for the HMZ in INP, which appear not to exhibit any avoidance behaviour towards potential competitors' (e.g. gemsbok, *Oryx gazella*) presence, as they were frequently recorded together. There are other reported cases of equid populations more intensively drinking during nighttime, arguably due to similar reasons to those occurring in INP: human related activities such as hunting and livestock presence (Altrichter *et al.* 2011, Crosmary *et al.* 2012). It is clear that human activities are a key factor influencing equid drinking activity (Kaczensky *et al.* 2010, Zhang *et al.* 2015). Without a management plan to ensure normal and safe access to water, fulfilling its hydric needs remains a challenge for a water-dependent animal like the HMZ. Increasing drought is driving pastoral groups to expand their livestock grazing areas closer to waterholes, a fact that is more evident in the southern part of the park, which contributes to increasing competition for a fundamental resource of HMZ.

Waterholes can be high-risk areas, especially where predation is a matter of concern. However, this should not be the case in INP, as most equid predators have been extirpated or their numbers have been severely reduced (Altrichter *et al.* 2011). In the absence of species that effectively prey on HMZ in INP, predation does not represent a risk or a factor leading towards a shift in drinking intensity to nighttime.

Activity level

As expected, HMZ still spend a significant part of the diel cycle at waterholes, as do donkeys, which don't face the same pressure. Conversely, zonkeys were found to spend less time at waterholes, but that may be due the low number of individuals and to their restricted occurrence in a set of waterholes in the park. Furthermore, the daily activity pattern of HMZ comprises a range of activities, with emphasis on grazing and movement throughout the home range, looking for water and food resources (Schoenecker *et al.* 2016, Muntifering *et al.* 2019). These activities also influence the frequency at which zebras go to water and the amount of time they spend around water sources. It is expected that zebras spend more time on grazing and drinking than on other activities (Joubert 1972b, Altrichter *et al.* 2011). There is a considerable distance between the available water sources for wildlife in INP and, with scarce resources of grazing areas, HMZ have to move long distances to find these important resources (Muntifering *et al.* 2019). Whereas zebras normally temporarily settle close to water sources (Valeix *et al.* 2009, Rubenstein 2010, Altrichter *et al.* 2011, Muntifering *et al.* 2019), their movement is important for finding other areas with further available resources.

Coefficient of overlap

As close relatives it is not surprising that HMZ, donkey and zonkey activity at waterholes overlaps significantly (Rubenstein, Cao, *et al.* 2016). The scarcity of water sources in INP leads most herbivores to co-occur at waterholes. I found none of the species – HMZ, donkey or zonkey – showing avoidance behaviour toward each other. As suggested in other studies investigating niche overlap, it is expected that equids exhibit overlapping niches, they could apply different strategies allowing them to coexist and prevent competition (Rubenstein, Cao, *et al.* 2016). For example, it was observed that the Grevy’s zebra and plains zebra niches largely overlap (Rubenstein 2010). Therefore, the difference in the need to access water minimizes co-occurrence times at waterholes, even though they have a similar activity patterns around this feature (Rubenstein 2010). However, avoidance behaviour is also found among other equids. Przewalski horses and Asiatic wild asses avoid each other, with Asiatic wild asses showing predominantly nocturnal activity at waterholes in response to the presence of Przewalski’s horse during the day, as it shows a more diurnal activity (Zhang *et al.* 2015). The larger size of the Przewalski’s horse was suggested as the main factor intimidating the Asiatic wild ass.

The overlap of closely related species such as HMZ and donkeys can give rise to undesirable consequences, by providing opportunities for hybridization. This mechanism is happening between the HMZ and donkeys in INP, and it enables to a population of hybrids, threatening the health of the zebra population (Hill 2009), and this hybrid or so-called zonkey also highly overlaps with its ascendants.

4.5 Limitations

Overall, camera trapping allowed for an effective sampling of the HMZ population. However, the analysis of the factors influencing the spatial distribution of abundance (habitat use) is a limitation of the study. It was not assessed due to the low number of sites surveyed and limited variability in the potential covariates, therefore their potential spatial effects could not be discussed, as they would be merely speculative. An additional limitation of this study is that abundance estimates provided here cannot be extrapolated to the whole Angolan potential range of HMZ, as sampling efforts concentrated around the waterholes and avoided human-disturbed areas in INP.

Chapter 5: Conclusion

The abundance estimates show that the HMZ population comprises approximately 478 individuals, which is encouraging for its management and conservation in INP. However, the fact that only 10.5% of the population constitutes juveniles and foals warrants some concern, by showing clear evidence that the population is aging. In observance of environmental and anthropogenic threats that the species is subject to, it stresses the need for an appropriate management approach aimed at preventing scenarios that could put the species in additional danger.

It was obtained a mean group size estimate of 3.73 from camera trapping and 8.46 from game counts. These estimates expose the social nature of the HMZ, although they highlight one of the limitations of camera trapping: its imperfect detection of all individuals in a group due to the limited field of view. Therefore, direct observation is the more efficient method to assess group size and the social structure of HMZ.

The age structure found in HMZ population follows a normal tendency generally observed among equids, with adults being the most abundant class. However, the HMZ in INP exhibits an unexpected adult-skewed structure, pointing to a low foaling rate, high infant mortality, or a combination of both.

The HMZ population in INP presents a female-biased sex ratio at all age classes, reflecting the gregarious social organization characteristic of zebras. A male-biased sex ratio at birth is common among equids, and this would be a reason to expect a male-biased sex ratio at least among the youngest age classes. Therefore, it is likely that part of the estimated skewness could be due to the combined effect of the difficulty in determining the sex of a large proportion of foals, as well as to the small sample size of this age class.

Hartmann's mountain zebra, donkey and zonkey are active all day at waterholes. This pattern highlights the water dependency of these species, which is characteristic of their ecology. However, each species exhibits a different period when its activity is more intense at waterholes, which is between 23:00 and 05:00 for HMZ, 15:00 and 17:00 for zonkeys, and between 13:00 and 17:00 for donkeys. Of the three species, HMZ was found to spend more time at waterholes, followed by donkey and zonkey. HMZ, donkey and zonkey exhibit high overlap at waterholes.

This study also shows the presence of a zebra-donkey hybrids (zonkey) population, which could be considered a threat to the HMZ population in INP. The estimates suggest that the phenotypic hybrids comprise 4.5% of the adult HMZ population. While these numbers may not appear problematic yet, they reveal that hybridization with donkeys is ongoing, and that this hybridization could start compromising zebra population growth if donkey-HMZ interactions become more frequent and intense.

5.1 Recommendations

This study presents a baseline estimate of HMZ population, and it exposes the need for a continued monitoring program to address other ecological questions, as well as a need to monitor the trends of the population over time. These recommendations are important to HMZ population management and conservation.

Camera trapping seems to be one of the most suitable technique to assess HMZ population demography, because of the possibility of identifying the individuals by their unique stripe patterns that can be recognized in photographic records. Therefore, it allows to overcome the HMZ's shyness towards human presence. Additionally, the fact that the species occurs in a remote area with a challenging landscape would make it difficult to assess the population demography by alternative methods, such as aerial and game counts, as these methods would fail to survey critical spots where HMZ spend most of their time, for example mountains and valleys. With the advances observed in genetics, assessing HMZ demographic structure through DNA samples it is one alternative to assess HMZ demographic structure.

The SCR framework used to draw inferences from the HMZ populations provide excellent demographic insights into the HMZ and zonkey populations, and its flexibility allowed for straightforward inferences. This technique allows comparisons over time, which seem to be appropriate for a continuous monitoring plan like the one we have started with this study on HMZ.

I recommend that the threat caused by hybridization have to be minimized, to prevent negative consequences of this phenomenon. This can be done by developing and implementing a plan consisting of a definition of core areas of exclusive use for wildlife, as well as steps for the removal of feral donkeys from these areas.

References

Altrichter, M., Beck, H., Burton, J., Byers, J., d'Huart, J.P., Dinerstein, E., Franklin, W., and Altrichter, M., 2011. *Hoofed mammals*. Barcelona: Lynx.

Attum, O., El Noby, S.K., and Hassan, I.N., 2009. The influence of landscape characteristics and anthropogenic factors on waterhole use by vulnerable Nubian ibex Capra nubiana. *Oryx*, 43 (4), 564–567.

Baptista, N.L., António, T., and Branch, W.R., 2019. The hepertofauna of Bicuar Nacional Park and surroundings, southwestern Angola: a preliminary checklist. *Amphibian & Reptile Conservation*, 13 (2), 96–130.

Bard, B.J., 1977. A unity underlying the different zebra striping patterns. *Journal of Zoology*, 183 (4), 527–539.

Beja, P., Vaz Pinto, P., Veríssimo, L., Bersacola, E., Fabiano, E., Palmeirim, J.M., Monadjem, A., Monterroso, P., Svensson, M.S., and Taylor, P.J., 2019. The Mammals of Angola. *In*: B.J. Huntley, V. Russo, F. Lages, and N. Ferrand, eds. *Biodiversity of Angola*. Cham: Springer International Publishing, 357–443.

Bischof, R., Hameed, S., Ali, H., Kabir, M., Younas, M., Shah, K.A., Din, J.U., and Nawaz, M.A., 2014. Using time-to-event analysis to complement hierarchical methods when assessing determinants of photographic detectability during camera trapping. *Methods in Ecology and Evolution*, 5 (1), 44–53.

Bolger, D.T., Morrison, T.A., Vance, B., Lee, D., and Farid, H., 2012. A computer-assisted system for photographic mark-recapture analysis: *Software for photographic mark-recapture*. *Methods in Ecology and Evolution*, 3 (5), 813–822.

Bridges, A.S. and Noss, A.J., 2011. Behavior and activity patterns. *In*: *Camera traps in animal ecology*. Springer, 57–69.

Brown, C.J. and Jenkins, R., 1987. SHORT NW: Hybridization between a Hartmann's Mountain Zebra and Donkey. *Madoqua*, 15, 2, 193–194.

Burnham, K.P. and Anderson, D.R., 2002. A practical information-theoretic approach. *Model selection and multimodel inference, 2nd ed. Springer, New York*, 2.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., and Boutin, S., 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52 (3), 675–685.

Buzzard, P.J., Li, X., and Bleisch, W.V., 2017. The status of snow leopards Panthera uncia, and high altitude use by common leopards P. pardus, in north-west Yunnan, China. *Oryx*, 51 (4), 587–589.

Cordingley, J.E., Sundaresan, S.R., Larison, B.J., Shapiro, B., and Rubenstein, D.I., 2009. Grevy's zebra conservation: overcoming threats of isolation, genetic hybridization and demographic instability. *Animal Conservation*, 12 (6), 520–521.

Crall, J.P., 2017. *Identifying Individual Animals Using Ranking, Verification, and Connectivity*. Rensselaer Polytechnic Institute.

Crall, J.P., Stewart, C.V., Berger-Wolf, T.Y., Rubenstein, D.I., and Sundaresan, S.R., 2013. Hotspotter—patterned species instance recognition. *In*: *2013 IEEE workshop on applications of computer vision (WACV)*. IEEE, 230–237.

Crosmary, W.-G., Valeix, M., Fritz, H., Madzikanda, H., and Côté, S.D., 2012. African ungulates and their drinking problems: hunting and predation risks constrain access to water. *Animal Behaviour*, 83 (1), 145–153.

De Vos, C., 2017. Ecology of plains zebra (Equus quagga) in Majete Wildlife Reserve, Malawi. Stellenbosch: Stellenbosch University.

Delignette-Muller, M.L. and Dutang, C., 2015. fitdistrplus: An R package for fitting distributions. *Journal of statistical software*, 64 (4), 1–34.

Dey, S., Delampady, M., Karanth, K.U., and Gopalaswamy, A.M., 2017. A spatially explicit capture recapture model for partially identified individuals when trap detection rate is less than one. *arXiv preprint arXiv:1712.10035*.

Dupont, G., Royle, J.A., Nawaz, M.A., and Sutherland, C., 2020. Optimal sampling design for spatial capture-recapture. *Ecology*.

Efford, M., 2004. Density estimation in live-trapping studies. *Oikos*, 106 (3), 598–610.

Efford, M.G., Borchers, D.L., and Byrom, A.E., 2009. Density Estimation by Spatially Explicit Capture–Recapture: Likelihood-Based Methods. *In*: D.L. Thomson, E.G. Cooch, and M.J. Conroy, eds. *Modeling Demographic Processes In Marked Populations*. Boston, MA: Springer US, 255–269.

Estes, R.D., 1999. *The safari companion: a guide to watching African mammals including hoofed mammals, carnivores, and primates*. Chelsea Green Publishing.

Fuller, A.K., Sutherland, C.S., Royle, J.A., and Hare, M.P., 2016. Estimating population density and connectivity of American mink using spatial capture–recapture. *Ecological Applications*, 26 (4), 1125–1135.

Funston, P., Henschel, P., Petracca, L., Maclennan, S., Whitesell, C., Fabiano, E., and Castro, I., 2017. The distribution and status of lions and other large carnivores in Luengue-Luiana and Mavinga National Parks, Angola. *KAZA TFCA Secretariat, Kasane, Botswana*.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., and Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science*, 360 (6394), 1232–1235.

Gosling, L.M., 2012. *Mark-recapture estimate of mountain zebras in Etosha National Park*. Windhoek, Namibia: Namibia Nature Foundation.

Gosling, L.M., 2018. *Mountain Zebra Project – 8 th progress report Population ecology of Hartmann's mountain zebra*. Newcastle upon Tyne, UK, Progress report.

Gosling, L.M., Muntifering, J.R., Kolberg, H., Uiseb, K., and King, S.R.B., 2018. *Equus zebra ssp. hartmannae*. The IUCN Red List of Threatened Species.

Groves, C. and Grubb, P., 2011. *Ungulate taxonomy*. JHU Press.

Hayward, M.W. and Hayward, M.D., 2012. Waterhole use by African fauna. *African Journal of Wildlife Research*, 42 (2), 117–127.

Hill, R.A., 2009. Is isolation the major genetic concern for endangered equids? *Animal conservation.*, 12 (6), 518–519.

Hoffmann, A., Decher, J., Rovero, F., Schaer, J., Voigt, C., and Wibbelt, G., 2010. Field methods and techniques for monitoring mammals. *Manual on field recording techniques and protocols for all taxa biodiversity inventories*, 8, 482–529.

Hrabar, H., Birss, C., Peinke, D., King, S., Kerley, G., and Child, M.F., 2016. *A conservation assessment of Equus zebra zebra*. The Red List of Mammals of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute and Endangered WIldlife Trust.

Hrabar, H. and Kerley, G., 2013. Selective breeding in the Quagga Breeding Program–the effect of translocations and inbreeding on Plains zebra reproduction. *Report C127. Nelson Mandela Metropolitan University, Port Elizabeth, South Africa*.

Huntley, B.J., 1974. Outlines of wildlife conservation in Angola. *South African Journal of Wildlife Research-24-month delayed open access*, 4 (3), 157–166.

Huntley, B.J., 2017. *Wildlife at war in Angola: the rise and fall of an African Eden*. Protea Book House.

Huntley, B.J., 2019. Angola in Outline: Physiography, Climate and Patterns of Biodiversity. *In*: B.J. Huntley, V. Russo, F. Lages, and N. Ferrand, eds. *Biodiversity of Angola*. Cham: Springer International Publishing, 15–42.

Huntley, B.J. and Ferrand, N., 2019. Angolan Biodiversity: Towards a Modern Synthesis. *In*: *Biodiversity of Angola*. Springer, Cham, 3–14.

Hutchins, M., Cleiman, D.G., Geist, V., and McDade, M.C., 2004. Grzimek's Animal Life Encyclopedia, vol. 15, Mammals IV. *Gale Group, Detroit*.

Illian, J., Penttinen, A., Stoyan, H., and Stoyan, D., 2008. *Statistical analysis and modelling of spatial point patterns*. John Wiley & Sons.

Jenks, K.E., Chanteap, P., Kanda, D., Peter, C., Cutter, P., Redford, T., Antony, J.L., Howard, J., and Leimgruber, P., 2011. Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses–an example from Khao Yai National Park, Thailand. *Tropical Conservation Science*, 4 (2), 113–131.

Joubert, E., 1972a. The social organization and associated behaviour in the Hartmann zebra Equus zebra hartmannae part 1. *Madoqua*, 1972 (Series 1 Issue 6), 17–56.

Joubert, E., 1972b. Activity patterns shown by Hartmann zebra Equus zebra hartmannae in South West Africa with reference to climatic factors. *Madoqua*, 1972 (Series 1 Issue 5), 33–52.

Joubert, E., 1973. Habitat preference, distribution and status of the Hartmann Zebra Equus zebra hartmannae in South West Africa. *Madoqua*, 1973 (Series 1 Issue 7), 5–15.

Joubert, E., 1974. Notes on the reproduction in Hartmann zebra Equus zebra hartmannae in South West Africa. *Madoqua*, 1974 (Series 1 Issue 8), 31–35.

Kaczensky, P., Dresley, V., Vetter, D., Otgonbayar, H., and Walzer, C., 2010. Water use of Asiatic wild asses in the Mongolian Gobi.

Karanth, K.U., 1995. Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. *Biological conservation*, 71 (3), 333–338.

King, S.R., Asa, C., Pluhacek, J., Houpt, K., and Ransom, J.I., 2016. Behavior of horses, zebras, and asses. *Wild equids: Ecology, management, and conservation*, 23, 40.

King, S.R.B. and Moehlman, P.D., 2017. *Equus quagga. The IUCN Red List of Threatened Species 2016; e. T41013A45172424*.

Kingdon, J., 2015. *Field guide to African mammals*. Second edition. London: Bloomsbury.

Klingel, H., 1968. Soziale Organisation und Verhaltensweisen von Hartmann-und Bergzebras (Equus zebra hartmannae und E. z. zebra). *Zeitschrift für Tierpsychologie*, 25 (1), 76–88.

Klingel, H., 1969. The social organisation and population ecology of the plains zebra (Equus quagga). *African Zoology*, 4 (2).

Klingel, H., 1974. A comparison of the social behaviour of the Equidae. *The behaviour of ungulates and its relation to management*, 1, 124–132.

Kolberg, H. and Kilian, W., 2003. Report on an aerial survey of Iona National Park, Angola, 6 to 14 June 2003. *Directorate of Scientific Services, Ministry of Environment and Tourism, Windhoek*.

Kuedikuenda, S. and Xavier, M., N.G., 2009. *FRAMEOWRK REPORT ON ANGOLA'S BIODIVERSITY*. Luanda, Angola: Ministry of Environment.

Kulzer, G., Caulier, G., Stone, E., Doerr, O., Hoelzer, R., and Ahrens, J., 2010. The digiKam Handbook.

Linkie, M. and Ridout, M.S., 2011. Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology*, 284 (3), 224–229.

Makin, D.F., Chamaillé-Jammes, S., and Shrader, A.M., 2017. Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. *Animal Behaviour*, 127, 225–231.

Maronde, L., McClintock, B.T., Breitenmoser, U., and Zimmermann, F., 2020. Spatial capture–recapture with multiple noninvasive marks: An application to camera-trapping data of the European wildcat (Felis silvestris) using R package multimark. *Ecology and evolution*.

Meek, P., Ballard, G.-A., and Fleming, P., 2012. A permanent security post for camera trapping. *Australian Mammalogy*, 35.

Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D.E., Tobler, M., and Townsend, S., 2014. Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation*, 23 (9), 2321–2343.

Meek, P.D., Ballard, G.A., Sparkes, J., Robinson, M., Nesbitt, B., and Fleming, P.J.S., 2019. Camera trap theft and vandalism: occurrence, cost, prevention and implications for wildlife research and management. *Remote Sensing in Ecology and Conservation*, 5 (2), 160–168.

Mendelsohn, S. and Mendelsohn, J., 2019. *Sudoeste de Angola | South West Angola. A protrait of land and life*. Porto: Arte e Ciência.

MET/NACSO, 2018. *The state of community conservation in Namibia - a review of communal conservancies, community forests and other CBNRM activities*. Windhoek, Namibia: Ministry of Environment and Tourism (MET) and Namibian Association of CBNRM Support Organizations (NACSO).

Mills, L.S., 2012. *Conservation of wildlife populations: demography, genetics, and management*. John Wiley & Sons.

Monterroso, P., Rocha, F., van Wyk, S., António, T., Chicomo, M., Kosmas, S., Lages, F., Fabiano, E., and Godinho, R., 2020. Updated ranges of the Vulnerable cheetah and Endangered African wild dog in Angola. *Oryx*, 1–3.

Moodley, Y., 2002. Population structuring in Southern Africa zebras. University of Cape Town.

Moodley, Y. and Harley, E.H., 2006. Population structuring in mountain zebras (Equus zebra): The molecular consequences of divergent demographic histories. *Conservation Genetics*, 6 (6), 953–968.

Morais, J., Castanho, R.A., Pinto-Gomes, C., and Santos, P., 2018. Characteristics of Iona National Park's visitors: Planning for ecotourism and sustainable development in Angola. *Cogent Social Sciences*, 4 (1).

Muntifering, J., Ditmer, M., Stapleton, S., Naidoo, R., and Harris, T., 2019. Hartmann's mountain zebra resource selection and movement behavior within a large unprotected landscape in northwest Namibia. *Endangered Species Research*, 38, 159–170.

Nichols, J.D., Karanth, K.U., Gopalaswamy, A.M., and Delampady, M., 2017. Animal Population Monitoring: A Unified Conceptual Framework. *In*: *Methods For Monitoring Tiger And Prey Populations*. Springer, 35–46.

Nichols, J.D., Karanth, K.U., and O'Connell, A.F., 2011. Science, conservation, and camera traps. *In*: *Camera traps in animal ecology*. Springer, 45–56.

Niedballa, J., Sollmann, R., Courtiol, A., and Wilting, A., 2016. camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7 (12), 1457–1462.

Nipko, R.B., Holcombe, B.E., and Kelly, M.J., 2020. Identifying Individual Jaguars and Ocelots via Pattern-Recognition Software: Comparing HotSpotter and Wild-ID. *Wildlife Society Bulletin*, 44 (2), 424–433.

Novellie, P., Lindeque, M., Lindeque, P., Lloyd, P., and Koen, J., 2002. Status and Action Plan for the Mountain Zebra. *Equids: Zebras, Asses, and Horses: Status Survey and Conservation Action Plan*, 28.

O'Brien, T.G., 2011. Abundance, density and relative abundance: a conceptual framework. *In*: *Camera traps in animal ecology*. Springer, 71–96.

O'Connell, A.F. and Nichols, J.D., eds., 2011. *Camera traps in animal ecology: methods and analyses*. Presented at the International Mammal Congress, Tokyo: Springer.

Olivier, J., Leslie, A.J., and Ransom, J.I., 2019. Demographics and habitat preference of Cape mountain zebra (Equus zebra zebra) in Bakkrans Nature Reserve, South Africa. *Ecology and habitat suitability of Cape mountain zebra (Equus zebra zebra) in the Western Cape, South Africa*, 4 (53), 26.

Overton, J., Fernandes, S., Elizalde, D., Groom, R., and Funston, P., 2017. A large mammal Survey of Bicuar and Mupa National Parks, Angola. *Unpublished report. Instituto Nacional da Biodiversidade e Áreas de Conservação, Luanda*.

Owen-Smith, N., 2013. Daily movement responses by African savanna ungulates as an indicator of seasonal and annual food stress. *Wildlife Research*, 40 (3), 232–240.

Palmer, M.S., Swanson, A., Kosmala, M., Arnold, T., and Packer, C., 2018. Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *African journal of ecology*, 56 (4), 791–803.

Penzhorn, B.L., 1979. MOUNTAIN ZEBRA EQUUS Z. ZEBRA IN THE. *Koedoe*, 22, 115–156.

Penzhorn, B.L., 1982. Home range sizes of Cape mountain zebras Equus zebra zebra in the Mountain Zebra National Park. *Koedoe*, 25 (1), 103–108.

Penzhorn, B.L., 1988. Equus zebra. *Mammalian Species*, (314), 1–7.

Périquet, S., Valeix, M., Loveridge, A.J., Madzikanda, H., Macdonald, D.W., and Fritz, H., 2010. Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Animal Behaviour*, 79 (3), 665–671.

Pinto, P.V., 2019. The Giant Sable Antelope: Angola's National Icon. *In*: *Biodiversity of Angola*. Springer, 471–491.

PNUD, 2016. *Plano Integrado de Gestão do Parque Nacional do Iona*. Luanda: Ministério do Ambiente.

Pollock, K.H., 2000. Capture-recapture models. *Journal of the American Statistical Association*, 95 (449), 293–296.

R Core Team, 2019. *R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing*. Viena, Austria.

Ransom, J.I. and Kaczensky, P., 2016a. Wild and Feral Equid Population Dynamics. *In*: *Wild Equids: Ecology, Management, and Conservation*. Baltimore: Johns Hopkins University Press, 248.

Ransom, J.I. and Kaczensky, P., eds., 2016b. *Wild equids: ecology, management, and conservation*. Baltimore: Johns Hopkins University Press.

Reppucci, J., Gardner, B., and Lucherini, M., 2011. Estimating detection and density of the Andean cat in the high Andes. *Journal of Mammalogy*, 92 (1), 140–147.

Ridout, M.S. and Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14 (3), 322–337.

Rovero, F., Tobler, M., and Sanderson, J., 2010. Camera trapping for inventorying terrestrial vertebrates. *Manual on field recording techniques and protocols for All Taxa Biodiversity Inventories and Monitoring. The Belgian National Focal Point to the Global Taxonomy Initiative*, 100–128.

Rovero, F., Zimmermann, F., Berzi, D., and Meek, P., 2013. ' Which camera trap type and how many do I need?' A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, 24 (2).

Rowcliffe, J.M., Field, J., Turvey, S.T., and Carbone, C., 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 1228–1236.

Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C., and Jansen, P.A., 2014. Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5 (11), 1170–1179.

Royle, J.A., Chandler, R.B., Sollmann, R., and Gardner, B., 2013. *Spatial capture-recapture*. Academic Press.

Royle, J.A., Fuller, A.K., and Sutherland, C., 2018. Unifying population and landscape ecology with spatial capture–recapture. *Ecography*, 41 (3), 444–456.

Royle, J.A., Sutherland, C., Fuller, A.K., and Sun, C.C., 2015. Likelihood analysis of spatial capture-recapture models for stratified or class structured populations. *Ecosphere*, 6 (2), 1–11.

Royle, J.A. and Young, K.V., 2008. A hierarchical model for spatial capture–recapture data. *Ecology*, 89 (8), 2281–2289.

Rubenstein, D., Low Mackey, B., Davidson, Z., Kebede, F., and King, S.R.B., 2016. Equus grevyi; e.T7950A89624491.

Rubenstein, D.I., 2010. Ecology, social behavior, and conservation in zebras. *In*: *Advances in the Study of Behavior*. Elsevier, 231–258.

Rubenstein, D.I., Cao, Q.S., and Chiu, J., 2016. Equids and ecological niches: behavioral and life history variations on a common theme. *Wild equids: ecology, management and conservation*, 58–68.

Sanderson, J. and Harris, G., 2013. Automatic data organization, storage, and analysis of camera trap pictures. *Journal of Indonesian Natural History*, 1 (1), 11–19.

Sasidharan, S.P., 2005. Comparative genetics of selected southern African Mountain zebra populations. MSc thesis, Faculty of Veterinary Science, University of Pretoria.

Schoenecker, K.A., King, S.R., Nordquist, M.K., Nandintsetseg, D., and Cao, Q., 2016. Habitat and diet of equids. *Wild equids: Ecology, management, and conservation*, 41–57.

Shultz, S. and Stanley, C.R., 2012. Mummy's boys: sex differential maternal-offspring bonds in semi-feral horses. *Behaviour*, 149 (3–4), 251–274.

Silva, F., 2019. Turismo em Angola: desenvolvimento sustentado do Parque Nacional do Iona. *Império e Turismo. Antologia de ensaios*, 57–71.

Skinner, J.D. and Chimimba, C.T., 2005. *The mammals of the southern African sub-region*. Cambridge University Press.

Sollmann, R., 2018. A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, 56 (4), 740–749.

Sollmann, R., Gardner, B., and Belant, J.L., 2012. How does spatial study design influence density estimates from spatial capture-recapture models? *PloS one*, 7 (4), e34575.

Stuart, C. and Stuart, M., 2015. *Stuarts' field guide to mammals of southern africa: including Angola, Zambia & Malawi*. Penguin Random House South Africa.

Sun, C.C., Fuller, A.K., and Royle, J.A., 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. *PloS one*, 9 (2), e88025.

Sutherland, C., Royle, J.A., and Linden, D.W., 2019. oSCR: a spatial capture–recapture R package for inference about spatial ecological processes. *Ecography*, 42 (9), 1459–1469.

Tabak, M.A., Norouzzadeh, M.S., Wolfson, D.W., Sweeney, S.J., VerCauteren, K.C., Snow, N.P., Halseth, J.M., Di Salvo, P.A., Lewis, J.S., and White, M.D., 2019. Machine learning to classify animal species in camera trap images: Applications in ecology. *Methods in Ecology and Evolution*, 10 (4), 585–590.

Trolle, M. and Kéry, M., 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of mammalogy*, 84 (2), 607–614.

Valeix, M., Chamaillé-Jammes, S., and Fritz, H., 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia*, 153 (3), 739–748.

Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J.E., Murindagomo, F., and Macdonald, D.W., 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, 63 (10), 1483–1494.

van der Westhuizen, J., Thomas, J., and Haraes, L., 2017. An aerial photographic wildlife survey of the Iona National Park, Angola, November 2016 to February 2017. *Unpublished report. Ministry of Environment of Angola, Luanda*.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., and Hester, J., 2019. Welcome to the Tidyverse. *Journal of Open Source Software*, 4 (43), 1686.

Zhang, Y., Cao, Q.S., Rubenstein, D.I., Zang, S., Songer, M., Leimgruber, P., Chu, H., Cao, J., Li, K., and Hu, D., 2015. Water use patterns of sympatric Przewalski's horse and khulan: interspecific comparison reveals niche differences. *PloS one*, 10 (7), e0132094.

Appendices

Appendix 1 Field sheet for camera trapping deployment

Wildlife Monitoring

Camera trap deployment form

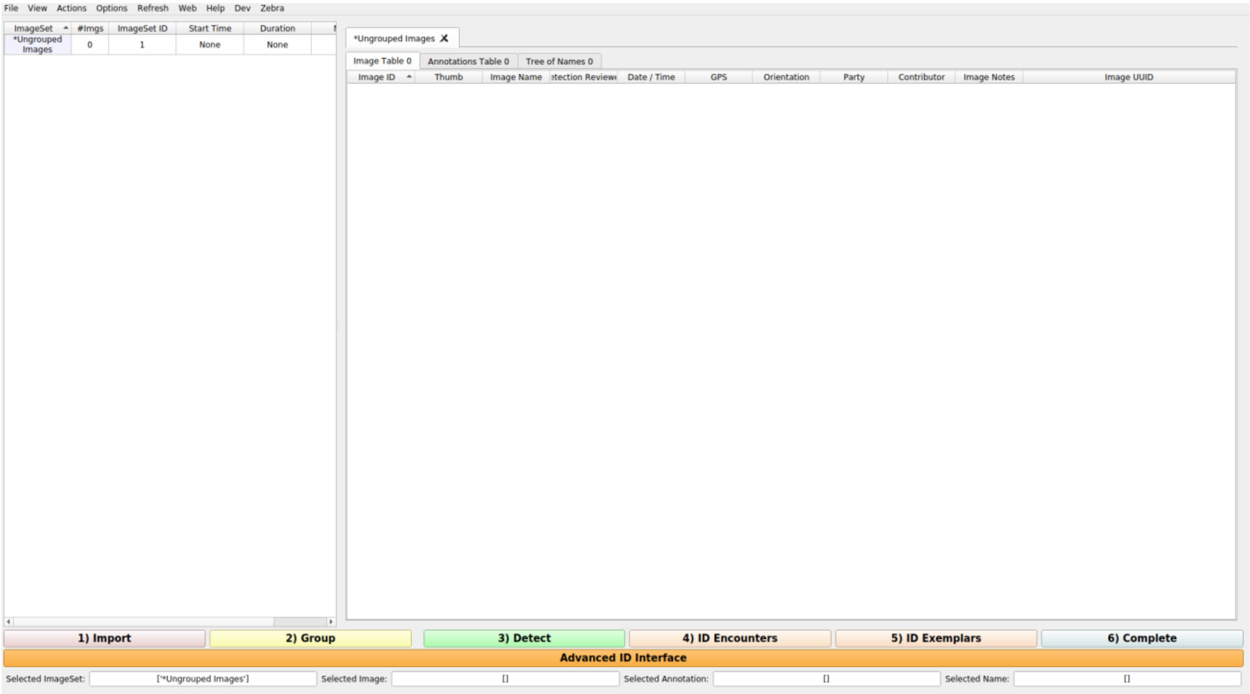
Project: SCIONA

Study area: Iona National Park

Field recorder(s)…………………………………………

Camera ID	Date	Time	Latitude	Longitude	Altitude	Camera Height	Notes

Appendix 2 Individual Identification process on IBEIS: New database; Image normalization: cropping, resizing an rotate the annotation into the database; Matching annotations against the database: making decisions (True or False) according the Rank;



ImageSet	#Imgs	ImageSet ID	Start Time	Duration
*Ungrouped Images	0	1	None	None

Image ID	Thumb	Image Name	etection Reviewe	Date / Time	GPS	Orientation	Party	Contributor	Image Notes	Image UUID

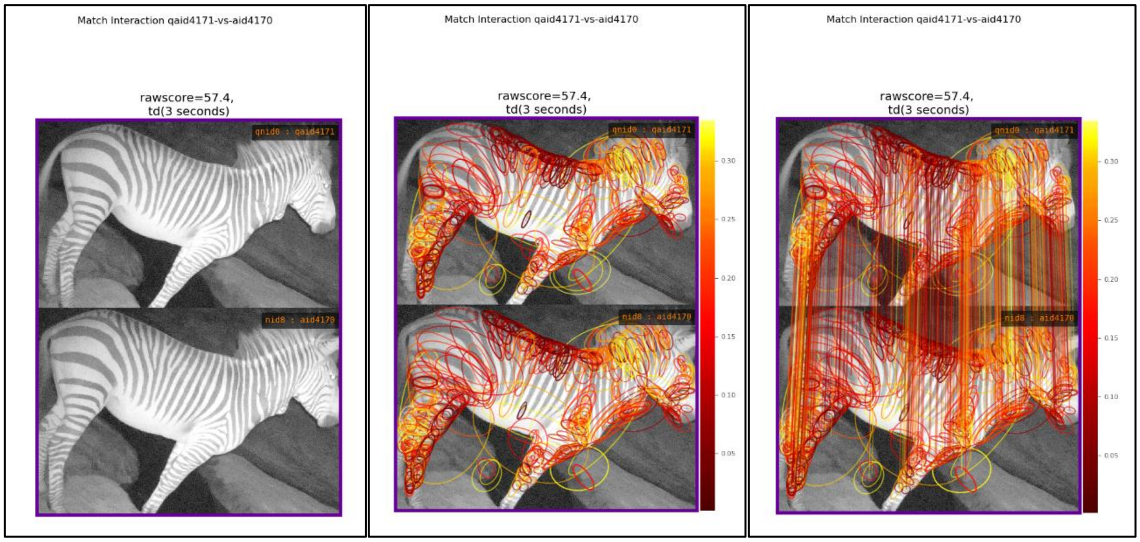
Selected ImageSet: ['*Ungrouped Images']
Selected Image: []
Selected Annotation: []
Selected Name: []

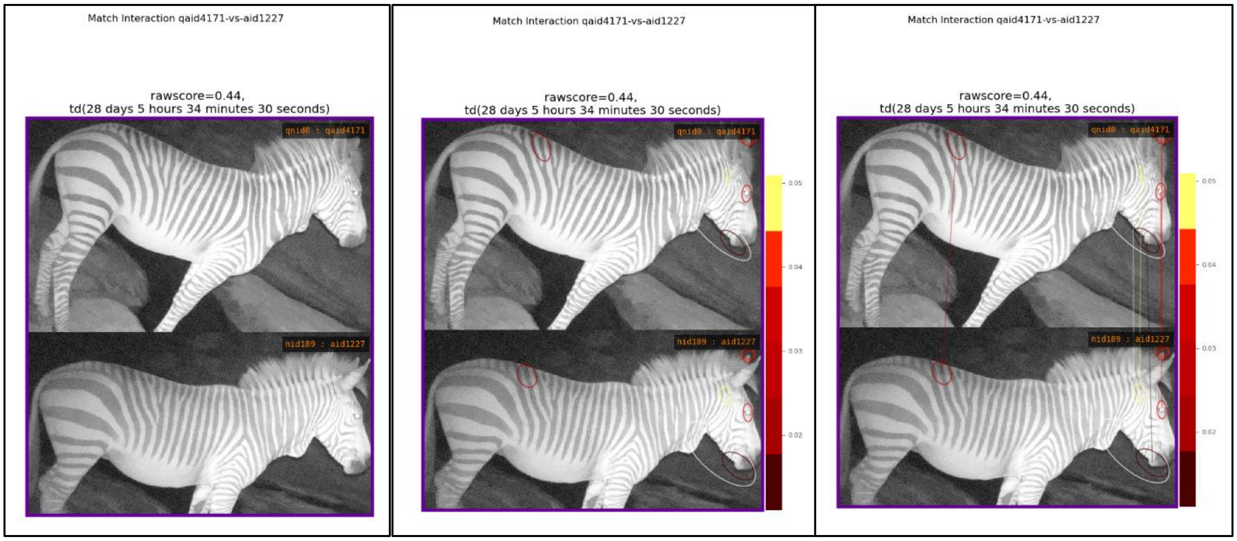

Click and drag to select/move/resize/orient an ANNOTATION
Press tab to cycle through annotation species


Click and drag to select/move/resize/orient an ANNOTATION
Press tab to cycle through annotation species

Query Results: Selected-vs-None all_species nRows=0

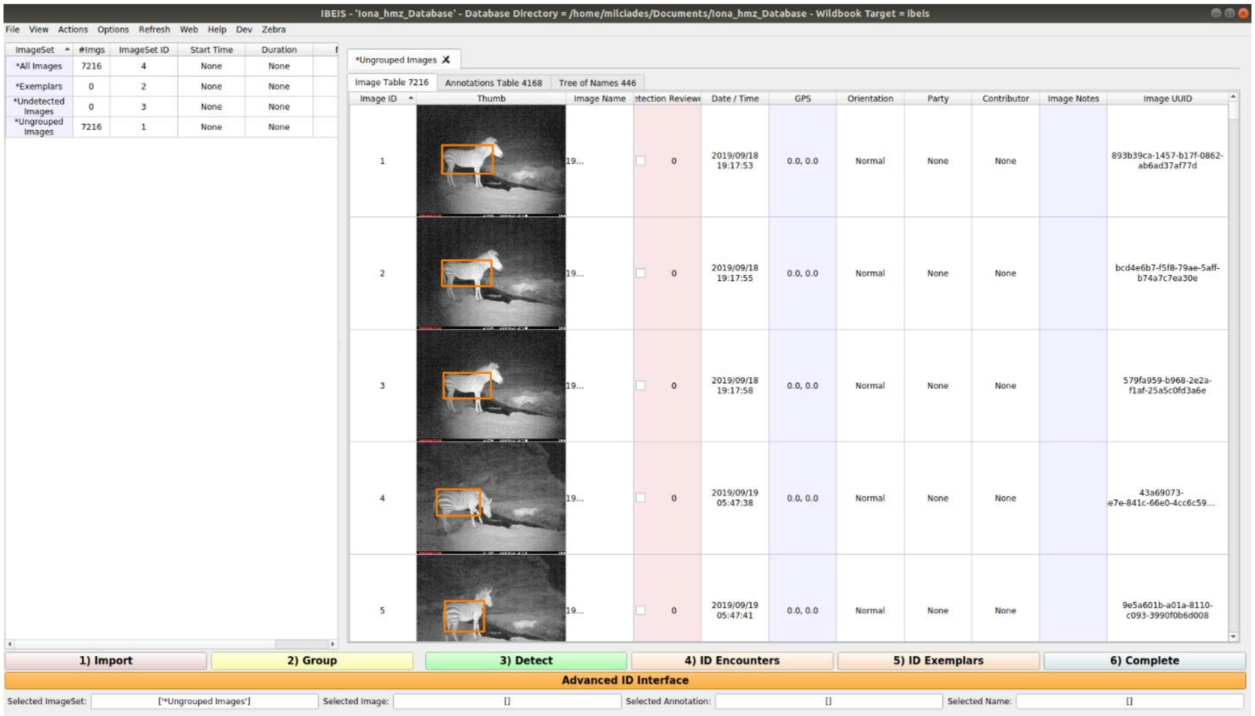
ult_inc	score	Reviewed	Matched	querythumb	ResThumb	MatchThumb	qaid	aid	rank	timedelta	dnGt	qnGt	tags	qname	name
0	57.35	Unrevie...	Unknown				4171	4170	0	00:00:03	132	0		___	inphmz003r
1	0.4401	Unrevie...	Unknown				4171	1227	1	4 weeks 05:34:30	33	0		___	inphmz039r





ult_inc	score	Reviewed	**Matched**	querythumb	ResThumb	MatchThumb	qaid	aid	rank	timedelta	dnGt	qnGt	tags	qname	name
0	57.35	User-reviewed	Positive				4171	4170	0	00:00:03	133	133		inphmz003r	inphmz003r
1	0.4401	User-reviewed	Negative				4171	1227	1	4 weeks 05:34:30	33	133		inphmz003r	inphmz039r

Appendix 3 Database visualization: image table, annotations table, and tree of names.


IBEIS - 'Iona_hmz_Database' - Database Directory = /home/milciades/Documents/Iona_hmz_Database - Wildbook Target = ibeis

File View Actions Options Refresh Web Help Dev Zebra

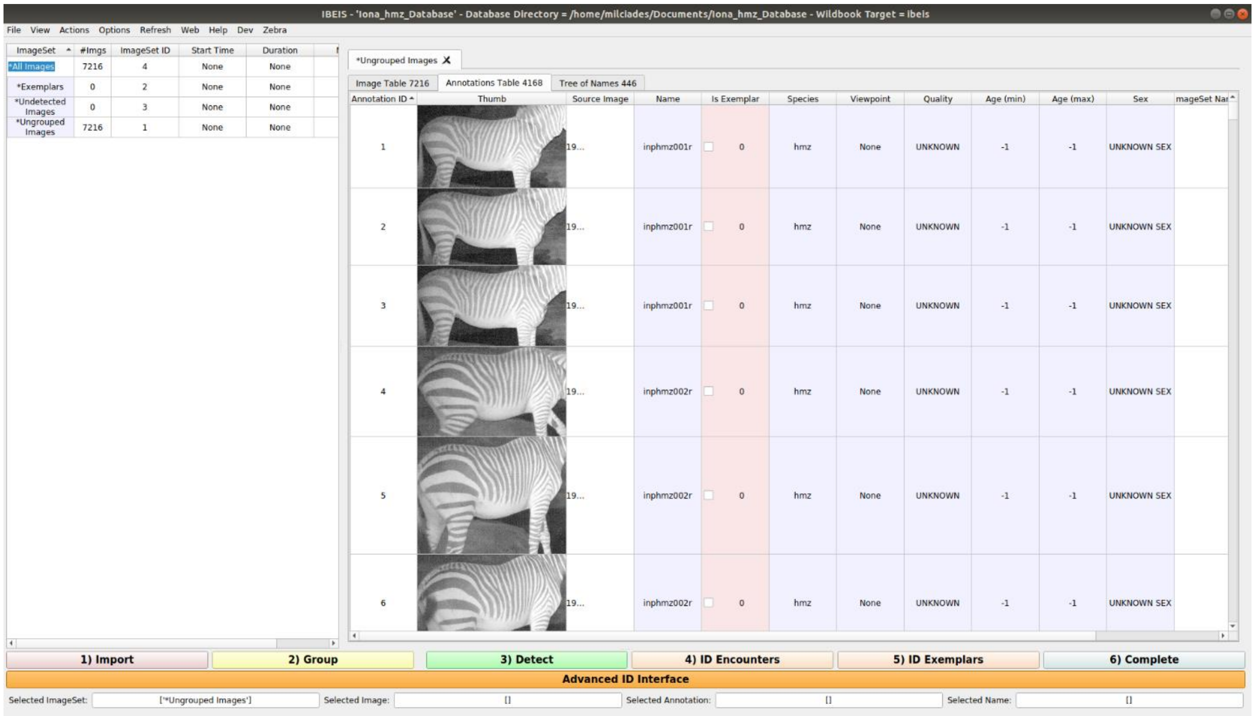
ImageSet	#Imgs	ImageSet ID	Start Time	Duration
*All Images	7216	4	None	None
*Exemplars	0	2	None	None
*Undetected Images	0	3	None	None
*Ungrouped Images	7216	1	None	None

*Ungrouped Images

Image Table 7216 | Annotations Table 4168 | Tree of Names 446

Image ID	Thumb	Image Name	›tection Reviewe	Date / Time	GPS	Orientation	Party	Contributor	Image Notes	Image UUID
1		19...	☐ 0	2019/09/18 19:17:53	0.0, 0.0	Normal	None	None		893b39ca-1457-b17f-0862-ab6ad37af77d
2		19...	☐ 0	2019/09/18 19:17:55	0.0, 0.0	Normal	None	None		bcd4e6b7-f5f8-79ae-5aff-b74a7c7ea30e
3		19...	☐ 0	2019/09/18 19:17:58	0.0, 0.0	Normal	None	None		579fa959-b968-2e2a-f1af-25a5c0fd3a6e
4		19...	☐ 0	2019/09/19 05:47:38	0.0, 0.0	Normal	None	None		43a69073-e7e-841c-66e0-4cc6c59...
5		19...	☐ 0	2019/09/19 05:47:41	0.0, 0.0	Normal	None	None		9e5a601b-a01a-8110-c093-3990f0b6d008

Selected ImageSet: ['*Ungrouped Images'] Selected Image: [] Selected Annotation: [] Selected Name: []


IBEIS - 'Iona_hmz_Database' - Database Directory = /home/milciades/Documents/Iona_hmz_Database - Wildbook Target = ibeis

File View Actions Options Refresh Web Help Dev Zebra

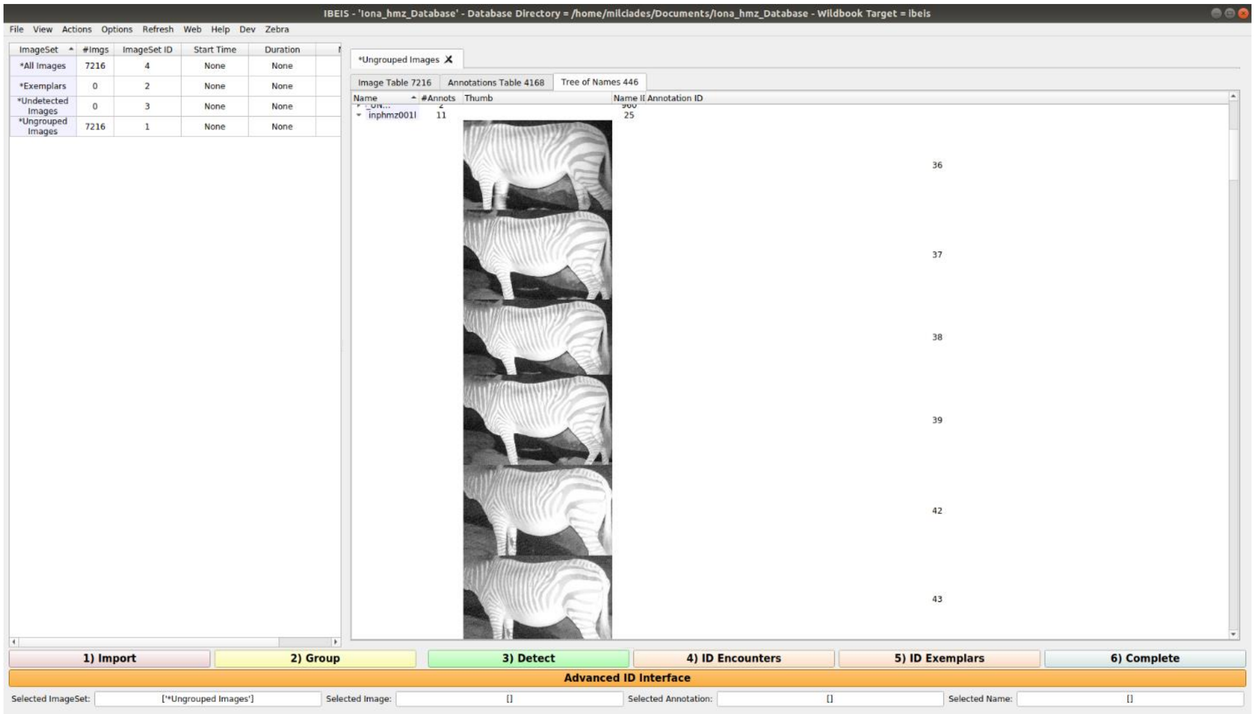
ImageSet	#Imgs	ImageSet ID	Start Time	Duration
*All Images	7216	4	None	None
*Exemplars	0	2	None	None
*Undetected Images	0	3	None	None
*Ungrouped Images	7216	1	None	None

*Ungrouped Images

Image Table 7216 | Annotations Table 4168 | Tree of Names 446

Annotation ID	Thumb	Source Image	Name	Is Exemplar	Species	Viewpoint	Quality	Age (min)	Age (max)	Sex	mageSet Na
1		19...	inphmz001r	☐ 0	hmz	None	UNKNOWN	-1	-1	UNKNOWN SEX	
2		19...	inphmz001r	☐ 0	hmz	None	UNKNOWN	-1	-1	UNKNOWN SEX	
3		19...	inphmz001r	☐ 0	hmz	None	UNKNOWN	-1	-1	UNKNOWN SEX	
4		19...	inphmz002r	☐ 0	hmz	None	UNKNOWN	-1	-1	UNKNOWN SEX	
5		19...	inphmz002r	☐ 0	hmz	None	UNKNOWN	-1	-1	UNKNOWN SEX	
6		19...	inphmz002r	☐ 0	hmz	None	UNKNOWN	-1	-1	UNKNOWN SEX	

Selected ImageSet: ['*Ungrouped Images'] Selected Image: [] Selected Annotation: [] Selected Name: []



ImageSet	#Imgs	ImageSet ID	Start Time	Duration
*All Images	7216	4	None	None
*Exemplars	0	2	None	None
*Undetected Images	0	3	None	None
*Ungrouped Images	7216	1	None	None

Name	#Annots	Thumb	Name II	Annotation ID
_UN...	2		900	
inphmz001l	11		25	
				36
				37
				38
				39
				42
				43

Selected ImageSet: ['*Ungrouped Images']
Selected Image: []
Selected Annotation: []
Selected Name: []