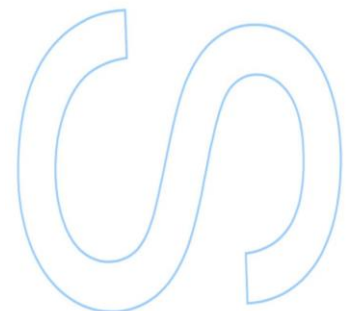
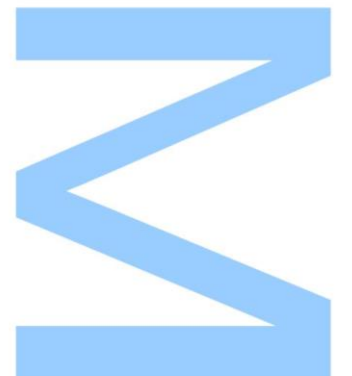




Assessing colonization trends of translocated ungulates using camera trapping data



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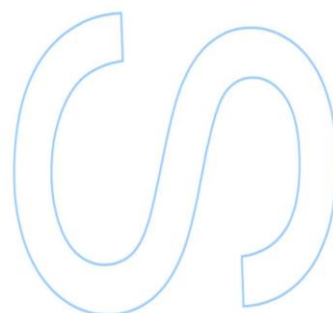
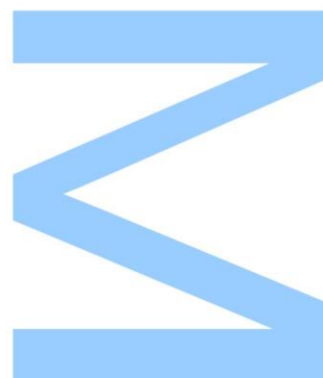
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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

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Abstract

Biodiversity loss is currently a major concern, with habitat destruction and fragmentation, growing climate change, over-hunting, and species translocations being its major drivers. Defaunation – the depletion of a population or species from a region – plays a major role in the current rate of biodiversity loss. In Angola, local biodiversity was greatly impacted during the Angolan civil war, but following peace, many conservation initiatives started to be implemented in the country, not only through recovery actions and improvements in Protected Areas (PA) and National Parks (NP) but also the performance of conservation translocations.

As part of a conservation initiative in Angola, Angolan giraffes (*Giraffa camelopardalis angolensis*), plains zebras (*Equus quagga*), black-faced impalas (*Ayepicerus melampus petersi*), common elands (*Taurotragus oryx*), and greater kudus (*Tragelaphus strepsiceros*) were translocated into the Cuatir Conservation area (CCA), located in the province of Cuando-Cubango, Southeastern Angola. The main goal of this study is to estimate the released species' site-specific colonization-extinction rates applying dynamic occupancy models as well as the main factors underlying these processes, and the variation of the occupancy of the new habitat over time. Raw data for this work was gathered by camera traps settled in CCA from November 2020 to May 2021.

The obtained results for the species colonization dynamics evidence that plains zebra had the highest colonization probabilities inside the fenced area and no temporal trend was observed for this colonization. This species explored the new habitat with no evidence of neophobic or anti-predator behaviors. Similarly, common eland colonization did not show a temporal trend in the colonization. This species evidenced some negative effects of the distance to the release site, suggesting a level of fidelity to that region. Differently, black-faced impala increased its colonization probabilities over time, while greater kudu showed a positive, although variable, effect of time. Results for these two species might be related to more time needed to colonize the space owing to more caution and neophobic behaviors, and the seeking for shelter.

The proportion of occupied area by the target species has been growing since the release, with zebra and kudu occupying 24% and 16% of the available area, respectively, by the end of the sampling period. Black-faced impala covered 21% of the total area, including an area outside the fence by May 2021. Common eland showed a constant growth in the percentage of occupied area and was the species with the lowest level of occupation (12%).

This study revealed that the released species have been able to expand their ranges in the new environment at different rates, which is mainly related to their ecological, biological, and behavioral features. These results constitute a positive start for the performed translocations since the capacity of translocated species to occupy the new host habitat is a key point for the success of these procedures.

Moreover, the obtained results provide useful knowledge about these species, and conservation translocations, that can be applied in similar future initiatives. Future studies on these translocations rely on maintaining the monitoring of their colonization trends, as well as on the occupation of the host habitat, and eventually performing additional analyses regarding habitat preference/use and behavior.

Keywords: Conservation translocation; Reintroduction; Population reinforcement; Angola; Cuango-Cubango; Cuatir; Angolan giraffe; plains zebra; black-faced impala; common eland; greater kudu; colonization.

Resumo

A perda de biodiversidade é uma grande preocupação atual, sendo a destruição e fragmentação de habitats, as crescentes alterações climáticas, caça excessiva e a translocação de espécies os seus maiores causadores. A defaunação – o desaparecimento de uma população ou espécie de uma determinada região – desempenha um papel preponderante nas atuais taxas de perda de biodiversidade. Em Angola a biodiversidade local foi gravemente impactada durante a Guerra Civil, mas após a instalação da paz, várias iniciativas de conservação começaram a ser postas em prática no país, não só através de ações de recuperação e de melhoria de áreas protegidas e parques nacionais, como de translocações de espécies.

Como parte de uma iniciativa de conservação em Angola, foram libertadas girafas angolanas (*Giraffa camelopardalis angolensis*), zebras de planície (*Equus quagga*), impalas de face negra (*Ayepicerus melampus petersi*), eland comum (*Taurotragus oryx*) e kudus (*Tragelaphus strepsiceros*) na *Area de Conservação do Cuatir (CCA)*, localizada na província de Cuando-Cubango, no Sudeste de Angola. O principal objetivo deste estudo é estimar as taxas de colonização-extinção das espécies libertadas, aplicando modelos dinâmicos de ocupação, bem como os principais fatores por elas responsáveis, e a variação da ocupação do novo habitat ao longo do tempo para cada espécie. Para tal, foram usadas fotografias captadas entre novembro de 2020 e maio de 2021, por câmaras colocadas na CCA.

Os resultados das dinâmicas de colonização de cada espécie revelam que as zebras apresentam maior probabilidade de colonização dentro da zona vedada, e a mesma não aparenta uma tendência temporal. Esta espécie explora o novo habitat sem evidência de comportamentos de neofobia ou anti predação. À semelhança das zebras, os elandes também não apresentam uma tendência temporal de colonização. Porém, esta espécie evidencia uma relação negativa com a distância ao local de libertação, o que pode estar relacionado com um nível de fidelidade a essa região. Por sua vez, a população de impalas de face negra foi a única a ocupar claramente a zona não vedada, aumentando a sua probabilidade de colonização ao longo do tempo, enquanto que os kudus tiveram algum efeito positivo do tempo na colonização, mas variável. Este padrão pode dever-se à necessidade de mais tempo para que estas espécies colonizem o espaço, devido a comportamentos mais cautelosos ou neofóbicos, e também pela procura de abrigo para proteção.

A proporção de área ocupada pelas espécies tem vindo a crescer desde a sua libertação, com as zebras e kudus a ocupar respetivamente 24% e 16% da área no final

do período de amostragem. As impalas aumentaram a porção de área ocupada ao longo do tempo, alcançado 21% de área colonizada, que inclui a região fora da vedação. Os elandes apresentaram um crescimento constante da porção de área ocupada, e é a espécie que evidencia menores valores – 12%.

Este estudo revelou que as espécies libertadas foram capazes de expandir as suas áreas de ocupação no novo habitat, embora a diferentes ritmos, o que está essencialmente relacionado com as suas características ecológicas, biológicas e comportamentais. Estes resultados representam um início positivo para estas translocações, visto que a capacidade de indivíduos libertados ocuparem o novo habitat é uma parte vital do sucesso destes procedimentos.

Sobretudo, os resultados conferem conhecimento útil sobre estas espécies e sobre ações de translocação com fim de conservação que poderá ser aplicado em futuras iniciativas semelhantes. Estudos futuros nestas translocações baseiam-se em manter a monitorização das taxas de colonização e de ocupação de área destas espécies, eventualmente efetuando mais análises incluindo preferência e uso de habitat, e também comportamento.

Palavras-chave: Reintrodução; Reforço populacional; Angola; Cuando-Cubango; Cuatir; Girafa angolana; Zebra de planície; impala de face negra; eland comum; kudu; colonização.

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List of Abbreviations

AIC - Akaike's Information Criteria

LH – Large herbivore(s)

CCA – Cuatir Conservation Area

PA – Protected area(s)

GIS – Geographic information systems

NP – National Park(s)

ENP – Etosha National Park

1. Introduction

1.1. The threat of biodiversity loss

Over the last centuries up until today, biodiversity levels have been facing severe declines, being marked by strong decreases of several wild populations, and the complete disappearance of populations or species (Dirzo et al., 2014). During Earth's history, five mass extinctions have been documented, essentially caused by natural phenomena such as vulcanism, fires, and meteorite impacts (McElwain & Punyasena, 2007). However, it is currently suggested that the accelerated biodiversity declines registered over the last 500 years are strongly influenced by human actions and are almost reaching the intensity of the previous five mass extinctions (Barnosky et al., 2011; Dirzo et al., 2014). The increasing human population and its impact on ecosystems indicate that such a declining trend in biodiversity levels might become more severe in upcoming decades (Díaz et al., 2019; Figure 1). Therefore, protecting the remaining biodiversity by preventing further losses is the biggest challenge for conservation biologists and ecologists of our century (Brennan et al., 2014; Di Marco et al., 2019).

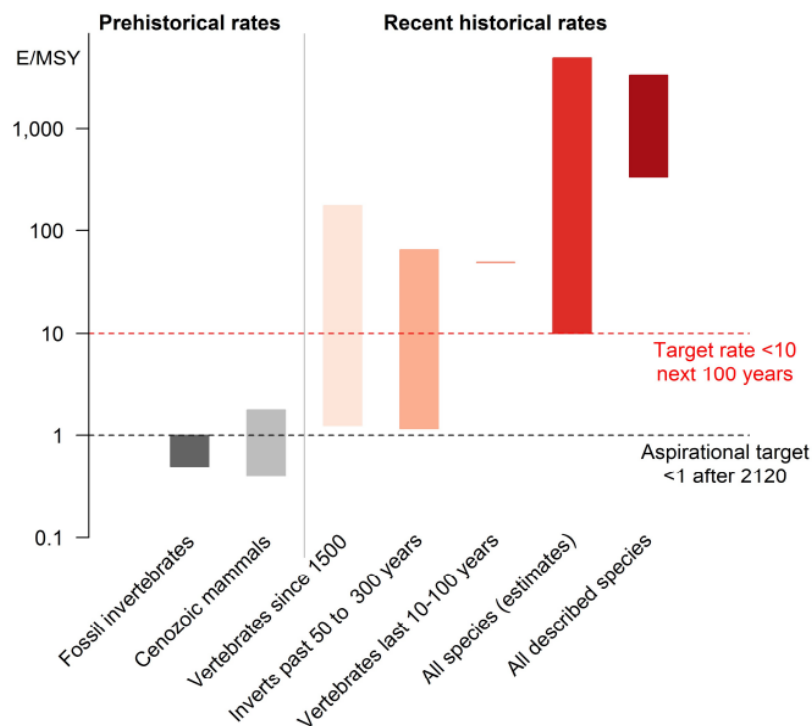


Figure 1. Estimated extinction rates (E/MSY) across a variety of taxonomic groups for different historical time-periods, related to the proposed extinction rate target for the next 100 years and the aspirational target (background extinction rates) from 2120. Plot adapted from Rounsevel (2020).

Habitat loss and degradation are among the main processes causing biodiversity loss (Chase et al., 2020; Haddad et al., 2015). Natural habitats can be destroyed or altered due to natural causes such as floods, wildfires, and earthquakes, or anthropogenic activities (Bodo et al., 2021). Anthropogenic habitat changes have been imposed on natural environments for millennia, either for agriculture, livestock production, or for the construction of infrastructures (Grabenstein & Taylor, 2018; Kaplan et al., 2009; Miller et al., 2005), and became more intense in recent centuries to fulfill the needs and desires of the growing human population (Díaz et al., 2019). Environmental exploitation led to the damage of ecosystems, especially forests, and resulted in the fragmentation (Fahrig, 2003) or destruction of natural habitats, culminating in intense wildlife population declines and local extinctions (Almeida-Rocha et al., 2017; Gibson et al., 2011). The Giant panda (*Ailuropoda melanoleuca*) is a flagship example of a species that suffered intense population declines and isolation due to habitat fragmentation and destruction (Yang et al., 2018).

Overhunting is the second biggest promotor of biodiversity loss (Romero-Muñoz et al., 2019; Dirzo et al., 2014; Woodroffe & Ginsberg, 1998). In general, species are excessively hunted for food (Wilkie et al., 2019), trophies (Lindsey et al., 2007), or to mitigate human-wildlife conflicts (Garshelis et al., 2020). A well-known example of extinction by overhunting is the dodo (*Raphus cucullatus*), a flightless avian species from the Mauritius islands that were driven to extinction due to overharvesting after the arrival of settlers to the island (Sakurai, 2019).

An additional major threat to biodiversity is climate change (Cahill et al., 2013). Climate change-induced threats can be caused by natural phenomena like shifts in solar radiation but are mainly triggered by Human activities (Muluneh, 2021), with current anthropogenic emissions of green-house effect gases towards the atmosphere being the main promotor of global warming (Crowley, 2000; Röck et al., 2020). Climate change can have drastic impacts on organisms, affecting their physiology, body size, and other aspects of their ecology and behavior (Bestion et al., 2015). Over the last decades, climate change impacted species abundance and distribution and has directly or indirectly contributed to wildlife extinctions (Thomas et al., 2004; Parmesan & Yohe 2003; Root et al., 2003; Pounds et al., 1999). Examples of such events are several local extinctions of lizard species (Thomas et al., 2004), or the local changes in the distribution of the desert-dwelling mountain sheep (*Ovis canadensis*) in California (Epps et al., 2004).

Organisms have been translocated by Humans for centuries, either intentionally or unintentionally (Seddon et al., 2007), but their current rate of introduction outside original habitats is higher than ever before due to international commerce, modern technology,

and human mobility (Meyerson & Mooney, 2007). The introduction of alien species can trigger biodiversity loss by several causes, such as niche displacement or competitive exclusion (Pyšek et al., 2017; Mooney & Cleland, 2001). Examples of these events are the habitat-shift of the native red squirrel (*Sciurus vulgaris*), in Britain, following the introduction of the North American gray squirrel (*Sciurus carolinensis*) (Sheehy et al., 2018), or the extinction of many native avian species following the introduction of the Pacific rat (*Rattus exulans*) in New Zealand (Pyšek et al., 2017).

Overall, establishing effective conservation strategies is a priority considering the present rates of biodiversity loss, not only to prevent further losses but also to secure ecosystem processes and human survival (González-García et al., 2022; Rands et al., 2010). Nowadays, several conservation initiatives have been created on a global scale, mainly based on *in situ* conservation strategies like the creation of National Parks and other protected areas, sustainable use, or local community efforts, and many have been achieving promising results (Fetene et al., 2019; Rands et al., 2010). However, these strategies are not always sufficient, and more extreme actions are then required or might be more adequate to prevent or reverse biodiversity declines (Schwartz & Martin, 2013).

1.2. Wildlife translocations a conservation tool

Despite the negative connotation associated with species translocations (Ricciardi & Simberloff, 2009), this management tool has been performed for conservation purposes for almost a century (Seddon et al., 2014; Seddon & Armstrong, 2016) and are currently widely used as an *ex-situ* strategy for biodiversity conservation (Müller & Eriksson, 2013; Thomas, 2011). Conservation translocations, as this process is commonly named, are intentional displacement of individuals from one place to another, with the main purpose of promoting their conservation (IUCN/SSC, 2013) and have contributed effectively to counteract defaunation and restore natural populations (Seddon et al., 2014; Yang et al., 2018). These procedures have shown a tendency to be more frequent in recent years (Figure 2), with the most common forms of conservation translocations being reintroductions and population reinforcements (Berger-Tal et al., 2020). Both these strategies imply the liberation of individuals into their native range and aim to restore or foster the growth of wild populations (IUCN, 2021).

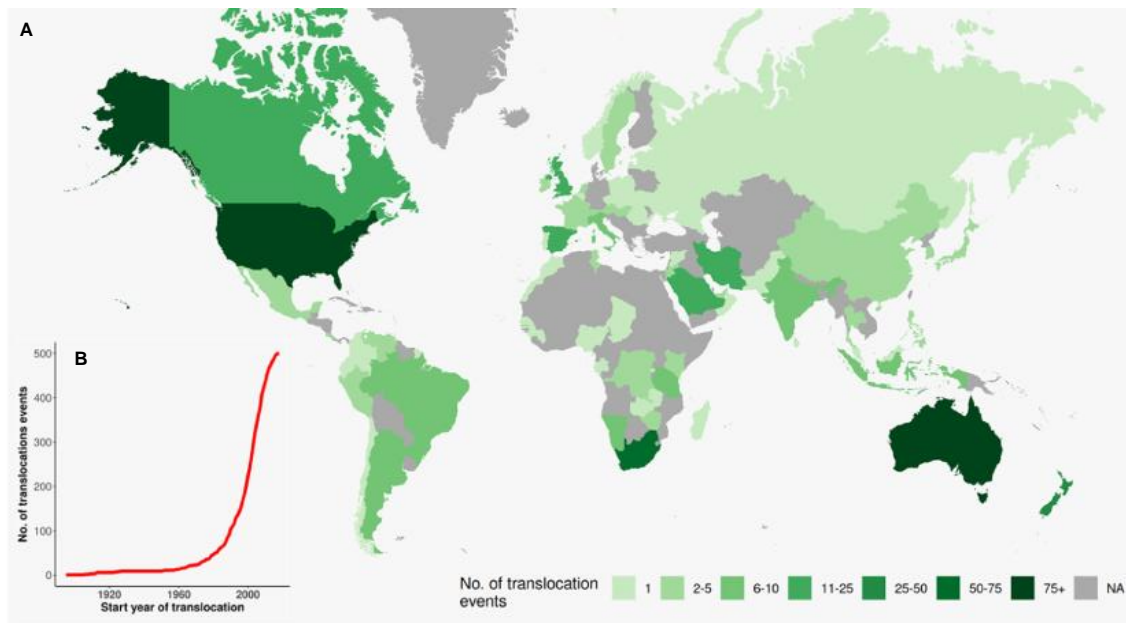


Figure 2. The spatial and temporal spread of conservation translocations of terrestrial vertebrates. **A** - Number of translocations that have taken place in countries worldwide ($n = 514$). **B** - Cumulative increase of translocations through time ($n = 500$, 14 had no definitive start year). The apparent recent slow-down may be caused by the lag (median 9 years, mean 13.67, SD 16.03) between the start of the translocation program and publication. Plot adapted from Morris (2021).

Population reinforcements consist of the liberation of individuals in an area with already residing populations of the same species, to improve survival and stabilize small populations (IUCN/SSC, 2013; Carstairs et al., 2019). Reinforcements contribute strongly to mitigating biodiversity loss and have a vast history of implementations, such as reinforcement of a one-hoarded rhino (*Rhinoceros unicornis*) in Manas National Park, in India, that much contributed to the re-establishment of the species in that area (Barman et al., 2014; Soorae, 2018). For populations with low survival rates in the wild, reinforcements can be a medium-term strategy to decrease extinction risk but not a definitive solution, as suggested for the population of the Egyptian Vulture (*Neophron percnopterus*) in the Balkans (Oppel et al., 2021). Regardless, it is still a useful tool for stabilizing a population while survival in the wild is not improved at its core (Oppel et al., 2021).

Reintroductions consist of the release of wild or captive-bred organisms into areas where they previously existed and from where they were extirpated (IUCN/SSC, 2013). The main purpose of reintroduction is to establish healthy and viable populations, and it is a major strategy to directly revert defaunation (Seddon et al., 2014) - the disappearance or loss of animal species from ecological communities (Giacomini and Galetti, 2013; Dirzo et al., 2014). Several reintroductions have been performed over the

last decades and involved several groups of organisms, including mammals (Hayward et al., 2007), birds (Sanz and Grajal, 1998) plants (Maschinski & Duquesnel, 2007), and insects (Marttila et al., 1997). Reintroductions, as other translocations, have a blended history of success and failures. The reintroduction of both wild-caught and captive-bred rock hyraxes (*Procavia capensis*) into a reserve in the Province of KwaZulu-Natal, South Africa, failed allegedly due to predation on released individuals, which resulted from other factors (Wimberger et al., 2009). In Gorongosa National Park (GNP), Mozambique, several mammal species suffered critical decline or extinction owing to the extensive period of war that dominated the country (Correia et al., 2017). In 2004 was founded the Gorongosa Project (Pringle, 2017) under whose auspices many mammal species were successfully reintroduced in GNP – such as plains zebra (*Equus quagga*), Blue wildebeest (*Connochaetes taurinus*), and eland (*Taurotragus oryx*) – that highly contributed to revert the defaunation in the region (Correia et al., 2017; Stalmans et al., 2019).

The first documented reintroduction concerns the release of 15 American bison (*Bison bison*) in a reserve in Oklahoma (Kleiman, 1989), in 1907 (Seddon et al., 2007). Since that time, several other attempts to reintroduce wildlife have been performed, contributing to the ambiguous story of conservation translocations. The initially documented translocations were done as a management possibility or to fulfill investigation goals (Seddon et al., 2007). Only later, in the decades of 1970 and 1980, reintroductions started being admitted as a useful conservation tool, following the reintroductions of several species such as the Peregrin Falcon (*Falco peregrinus*) (Cade et al., 2003) and the Arabian oryx (*Oryx leucoryx*) (Price, 1989). However, the available information regarding the reintroduction performed during this period suggests that establishing viable populations was a rare outcome (Seddon et al., 2007; Griffith et al., 1989; Wolf et al., 1996). These procedures were made without giving the needed attention to several important aspects about the organisms being introduced such as their ecology and behavior, or the quality of the new habitat where they would be introduced into (Seddon et al., 2007).

As a response to such lack of success, the decade of 1990 was marked by an increasing amount of research and available literature on reintroductions (Armstrong & Seddon, 2008). In 1988, the Reintroduction Specialist Group (RSG) was created (Price & Soorae, 2003) as a part of the International Union for Conservation of Nature and Natural Resources Species Survival Commission (IUCN/SSC) and was dedicated to offering specific guidance on reintroduction projects and lead to the formulation of the first Reintroduction Guidelines (IUCN/SSC, 2013). These principles include performing

a risk assessment, gaining extensive knowledge on the translocated species and the new environment, and strongly advising post-release monitoring (IUCN/SSC, 2013).

Nowadays, translocating organisms is a common practice and is increasingly needed to rescue species and ecosystems (Seddon & Armstrong, 2016; Swan et al., 2016, 2018). A known example of a successful reintroduction is the reestablishment of the grey wolf (*Canis lupus*) population in the Yellowstone National Park in 1995-1996 (Vonholdt et al., 2008) where they were reintroduced after a 70-year alleged absence (Bangs, 1996; Phillips & Smith, 1996). Since then, the ecosystem recovered in several aspects and wolves were able to establish a thriving population (Ripple & Beschta, 2012). Due to the growing threats of global climate change and habitat modification (Novak et al., 2021), environmental conditions are expected to swiftly change over the coming decades, making the environment less suited for the wildlife it currently harbors and leading to extensive local extinction of already fragile wildlife populations. Consequently, reclaiming and restoring natural habitats, coupled with translocations arise as a prime option for future strategies in this context (Seddon et al., 2014).

Despite the different main-purposes and definitions, every translocation implies equivalent procedures and shares the same level of complexity and elevated costs. While planning any conservation translocation, many different challenges appear, consequently, knowledge regarding many different fields is necessary. It is also useful to previously consider the different difficulties that may be encountered to manage them and ensure the maximum success of these processes (Berger-Tal et al., 2020).

1.3. Challenges and potential solutions to conservation translocations

Conservation translocations become more frequent over the last decades (Morris et al., 2021), and efforts have been made to improve knowledge on the factors underlying previous successes and failures, as a response to the debatable history of these procedures, especially of reintroductions (Seddon et al., 2014). Most factors that jeopardize translocation success are essentially biological, environmental, or human-related due to lack of strategy or organization skills. Therefore, it is recommended that reintroductions must be dealt with in a multidisciplinary way, otherwise, they will most likely fail (Berger-Tal et al., 2020). The IUCN/RSG provides The Global Re-introduction Perspectives Series, a compilation of case studies regarding conservation translocations, that not only document several reintroduction processes but also provide a critical assessment of the reasons leading to their success or failure (Figure 3). This

collection exposes the difficulties encountered by wildlife managers, conservationists, and researchers, and proposes possible solutions (Soorae, 2018).

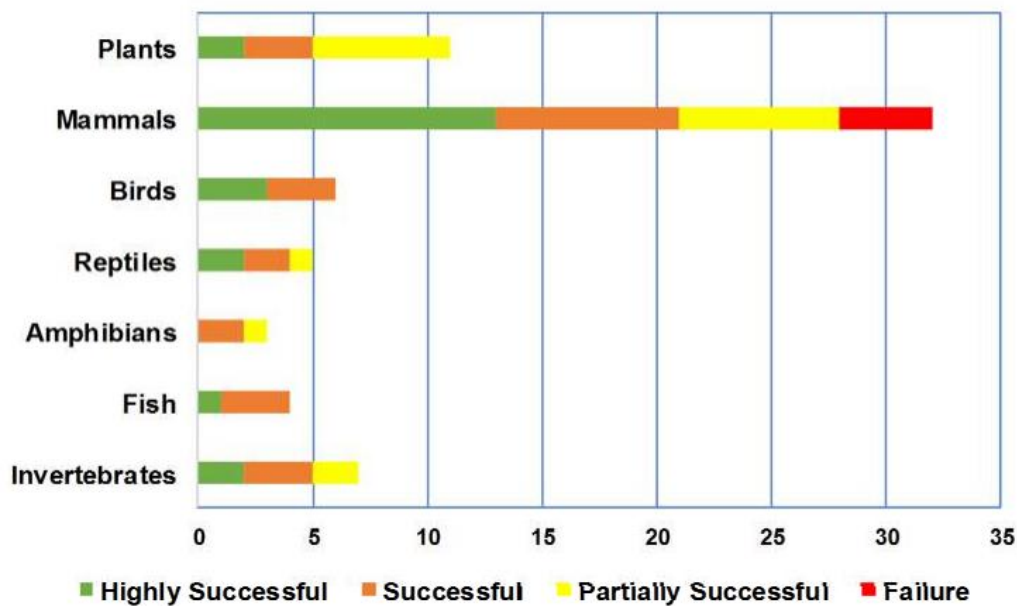


Figure 3. Success/Failure of reintroduction projects according to major taxa. Adapted from Global Reintroduction Perspectives (2018).

Starting with logistic issues, lack of funding is one of the most significant problems faced by wildlife managers and conservation biologists, because reintroductions are costly procedures and conservation projects usually face multiple economic pressures (Swaigood, 2010). Another frequent constraint is the absence of accurate monitoring of the reintroduced populations. Proper supervising allows evaluating the progress of populations for multiple biological, ecological, sanitary, and other parameters, and test previous suppositions about reintroductions. Moreover, monitoring permits quantifying the success or failure of reintroductions and an early identification of problems that can then be addressed through strategies of adaptive management (Allen & Garmestani, 2015; Varley & Boyce, 2006). In addition, lack of appropriate knowledge or trained staff is a serious concern. The complexity and multidisciplinary nature of reintroduction operations, require extensive knowledge about the translocated species ecology, behavior, environmental conditions (including stressors and threats) of the area animals would be reintroduced into, or about the history and causes for the vanishment of historical populations. The lack of such knowledge might lead to operational malpractice that jeopardizes the reintroduced species establishment and persistence (Berger-Tal et al., 2020).

Population-intrinsic difficulties are also frequent, mainly due to the small sizes of the reintroduced populations (Le Gouar et al., 2012) and to the behavior of the translocated individuals (Berger-Tal et al., 2020). Small populations are usually prone to suffer allele effects and have low genetic diversity, which is even more problematic when dealing with rare or endangered species (Armstrong & Seddon, 2008). Additionally, survival in the new environment is strongly dependent on an individual's choices and behaviors (Bell, 2016), where evolutionary history and individual experiences dictate the dispersal from the release site and the adaptation capacity to new environmental conditions (Le Gouar et al., 2012; Stamps & Swaisgood, 2007).

Initial behavioral responses are often not ideal, and animals can move out of the release area, fail to disperse their ranges from the release site, or be over-predated due to the lack of anti-predation behaviors (Blumstein et al., 2019). Failure to adapt to the release area often deems animals not to succeed in establishing viable populations. This matter is especially concerning when reintroductions are carried out with captive-bred individuals because they are usually naive against predators, hunting, or other threats to their survival (Berger-Tal et al., 2020). However, such constraints can be at least partly mitigated with techniques to train individuals before their release (Blumstein et al., 2019). Moreover, animals might be capable of adapting their behavior as they gain more experience in the new habitat, a process that can be called "post-release behavioral modification" (Berger-Tal et al., 2014; Berger-Tal & Saltz, 2014).

Problems related to the habitat and climate conditions can also occur. Firstly, species might not be able to adapt to the environment because of inadequate conditions or insufficient resources, which reinforces the need for extensive knowledge on this subject. The suitability of the hosting environment is particularly worrying under current climate and human-induced changes because of the uncertainty about the maintenance of conditions considered suited over the following decades (Griffith et al., 1989; Wolf et al., 1996, Berger-Tal et al., 2020). These constraints might be mitigated through continuous monitoring or by forecasting the distribution of available suitable habitat using geographic information systems (GIS), as done for the reintroduction of the wild boar (*Sus scrofa*) in Scotland (Seddon et al., 2007).

Lacking community support and media cover on reintroduction procedures can further challenge conservation actions and undermine the success of translocations. Having the support of local communities that live close to conservation areas is a very important part of any conservation effort, especially when these involve large carnivores and top predators, while media cover generally helps with captivating public opinion and

promotes the attention and fundraising for conservation translocations (Seddon et al., 2007).

Currently, there is an increasing effort to improve the success of reintroductions and overcome the above-mentioned and other difficulties. Nevertheless, the concept of “success” in reintroduction biology is hard to reach and can be considered on an individual, population, or even at the species level (Moehrenschrager et al., 2013; Seddon, 1999). Also, the success of any reintroduction must be judged against the main purpose of the procedure (Ewen et al., 2014) and is only applicable for the time when the population was evaluated (Hardy et al., 2018; Seddon, 1999). Initial success does not ensure long-term viability, and many reintroductions only fail after some time (Armstrong & Seddon, 2008). The IUCN Guidelines for Reintroductions are a great help in guiding reintroduction initiatives, and in improving all the involved procedures from the experimental design to the post-release monitoring (Soorae, 2018).

1.4. Study area

1.4.1. The Angolan biodiversity in outline

The African continent accounts for a big part of Earth’s biodiversity, with many of its countries being considered biodiversity hotspots (Cincotta et al., 2000; Huntley et al., 2019). Angola is a large country located in southwest Africa, plated by the Atlantic Ocean to the west and surrounded by the Democratic Republic of Congo, Republic of Congo, Zambia, and Namibia (Figure 4).

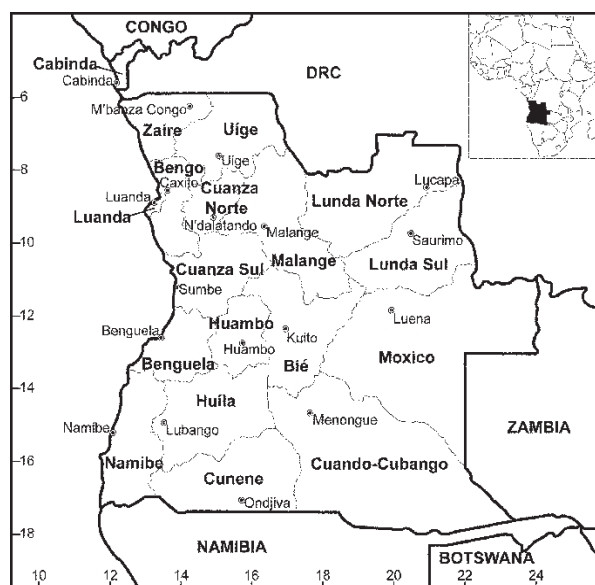


Figure 4. Map of Angola, showing the country’s location in Africa and its division in provinces. Adapted from Kloppe et al (2009).

The country has a variable topographic regimen constituted by lowland along the coast, followed by a mountainous incline – the Angola escarpment – and a high-altitude plateau, a division that has great ecological value (Welwitsch, 1858) and encompasses several ecoregions with characteristic plant species (Huntley et al., 2019; Figure 5).

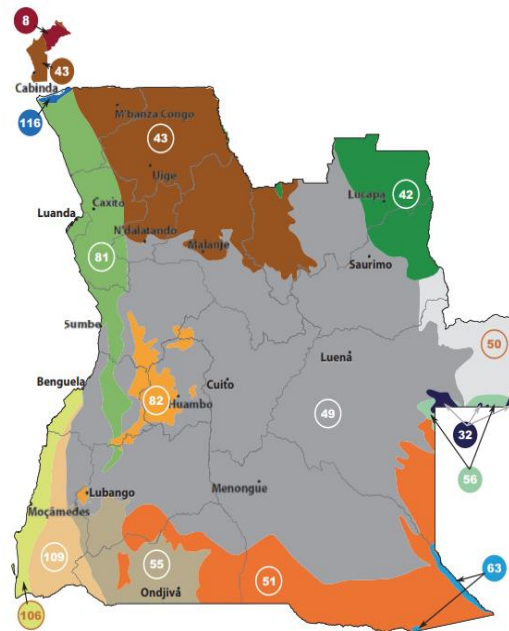


Figure 5. Ecoregions of Angola. 8 Atlantic Equatorial Coastal Forest • 32 Zambeian *Cryptosepalum* Dry Forest • 42 Southern Congolian Forest-Savanna Mosaic • 43 Western Congolian Forest-Savanna Mosaic • 49 Angolan Miombo Woodland • 50 Central Zambeian Miombo Woodland • 51 Zambeian *Baikiaea* Woodland • 55 Angola Mopane Woodland • 56 Western Zambeian Grassland • 63 Zambeian Flooded Grasslands • 81 Angolan Scarp Savanna and Woodland • 82 Angolan Montane ForestGrassland Mosaic • 106 Kaokoveld Desert • 109 Namib Escarpment Woodlands • 116 Central African Mangroves. (After Burgess et al. 2004, map used with permission). Map adapted from Huntley (2019).

Angolan climate is diverse, with well-defined seasons, marked by wet and warm summers from October to May, and moderate to cold dry winters between June and September (Huntley et al., 2019). Precipitation patterns are responsible for the structure of entire habitats, with rainfall season hitting the north of the country from the beginning of summer, and only affecting the southern part later in the season (Huntley et al., 2019). Several studies suggest that humans can be affected by Angola's climate (Carvalho et al., 2017) and that the current rates of climate change can result in increasing droughts with potentially harmful effects to all organisms (Huntley et al., 2019). Angola's richness in biomes includes dry or wet tropical and subtropical forest, mountainous grass and shrublands, grasslands, savanna, and others (Olson et al., 2001).

Angola has a fascinating diversity of ecosystems and species, which were poorly documented until very recently. Between 1975 and 2002, Angola was the center of

several extensive wars and other problems that inhibited progress on biodiversity research (Huntley et al., 2019), and had negative impacts on several species such as the giant sable (*Hippotragus niger*), an Angolan emblematic species that barely escaped extinction during that period (Pinto, 2018). Following peace in 2002, the number of investigation programs and international collaborations increased significantly and provided great information regarding Angolan biodiversity (Huntley et al., 2019).

Many Angolan populations of mammals have been harshly reduced or extirpated by overhunting or habitat loss. Here, carnivores – Cheetah (*Acinonyx jubatus*), African wild-dog (*Lycaon pictus*) – and herbivores – Black-faced impala (*Aepyceros melampus petersi*) and black rhinoceros (*Diceros bicornis*) – are included (Emslie & Brooks, 1999; Overton et al., 2017; Van der Westhuizen et al., 2017). Other species like the common eland (Crawford-Cabral & Veríssimo, 2005; Huntley, 1973) and the greater kudu (*Tragelaphus strepsiceros*) (Overton et al., 2017), still inhabit the country, but their distribution is not widely as it once was. The Angolan giraffe (*Giraffa camelopardalis angolensis*) and plains zebras were also widespread in Angola, but the species were thought extinct in the country by 1990 and 1992, respectively. However, the presence of small populations of a few individuals of these species was recently suggested (Chase, 2017; Overton et al., 2017).

In recent years, Angola has given high focus to biodiversity research and conservation planning, due to the current projects conducted by the Angolan government and the valuable support from international researchers (Huntley et al., 2019). Apart from the vast system of protected areas in the country, conservation translocations became an additional strategy to restore and enhance Angola's biodiversity.

1.4.2. Cuando-Cubango Province

The Angolan Province of Cuando-Cubango is located in Southwestern Angola (Figure 4), overlaps with the Zambebian *Baikiaea* Woodland ecoregion, and its biome richness includes savanna, shrubland, woodland, and grassland biomes (Burgess et al., 2004), with a big part of the province consisting of a mosaic of open woodland separated from thick woodland and forest (Huntley et al., 2019; Figure 5).

The diversity of habitats in the province makes it suitable for several groups of organisms, which contributes to the high species richness of the region. However, the present diversity is only a fraction of the historical one, since the ecosystems and biodiversity of Cuando-Cubango were severely impacted during the Angolan war and are scourged by wildfires every year (Huntley et al., 2019). Presently, several carnivores

inhabit the region, including cheetah, leopard (*Panthera pardus*), or African wild dog (*Lycaon pictus*) (Monterroso et al., 2020). The region was thought to be a stronghold for African lions (*Panthera leo*), but recent surveys have revealed a severely depressed and male-biased remnant population in the southeastern corner of the province (Beja et al., 2019; Funston et al., 2017). The herbivore community is also rich. In the past, the province of Cuando-Cubango was inhabited by many mammal species, that were extirpated from the area or whose population sizes decreased. Angolan giraffe, and plains zebra (Crawford-Cabral & Veríssimo, 2005; Huntley, 1973, 1974; Huntley et al., 2019), both species considered Vulnerable by IUCN (IUCN, 2021), once populated the province. The greater kudu and the common eland – Least Concern (IUCN, 2021) - still exist in low numbers in the southeastern region of Cuando-Cubango (Funston et al., 2017; Veríssimo, 2008).

1.5. Herbivore reintroductions in the Cuatir Conservation Area

In November of 2020, five species of ungulates were translocated into the CCA's core area, for conservation and ecotourism purposes. Angolan giraffes, plains zebras, and black-faced impalas were reintroduced in the reserve, to establish viable populations. Greater kudus and common elands were also released to reinforce the small populations of these species that are known to exist in the area (Figure 6).

All the translocated species are ungulates and play an essential role as ecosystem engineers (Baruzzi & Krofel, 2017). Each species has its ecology and habitat preference but also shares some common characteristics. The Angolan giraffe and greater kudu are browsers and use different vegetation types, being able to inhabit heterogeneous landscapes (Mandinyenya et al., 2019). These species browse similar woody plant species of distinct heights (Makhabu, 2005) but in heterogeneous landscapes, the giraffe tends to prefer open vegetation types, whereas greater kudu prefers dense vegetation (Pellew, 1984; Valeix et al., 2011). Both species preferentially feed on nutrient-rich plant species (Mitchell et al., 2015) and have distinct top heights of feeding to reduce competition (Du Toit, 1990).

Plains zebra use a wide range of habitats, but prefer savannas, grasslands, and woodlands (Doku et al., 2007; Estes, 1997; Stuart & Stuart, 1997). Key habitat requirements of the plains zebra are mainly linked with the abundance of eatable tall grass species and the availability of surface water (Doku et al., 2007). The black-faced impala is generally associated with the semi-arid regions of Namibia and Angola. This species has high ecologic flexibility (Green & Rothstein, 1998) but is water-dependent,

and is highly dependent on shade for thermoregulation and protection (Matson et al., 2005; Jarman, 1973).

Common elands have been suggested as intermediate feeders (Hofmann, 1973; Hofmann & Stewart, 1972) and grazers (Lamprey, 1963). In general, elands prefer herbaceous or woody plant species with low fiber content. Elands have been documented in multiple habitat types, but generally prefer plateau regions during the early wet season and prefer valleys in the late wet season (Watson & Owen-Smith, 2000).

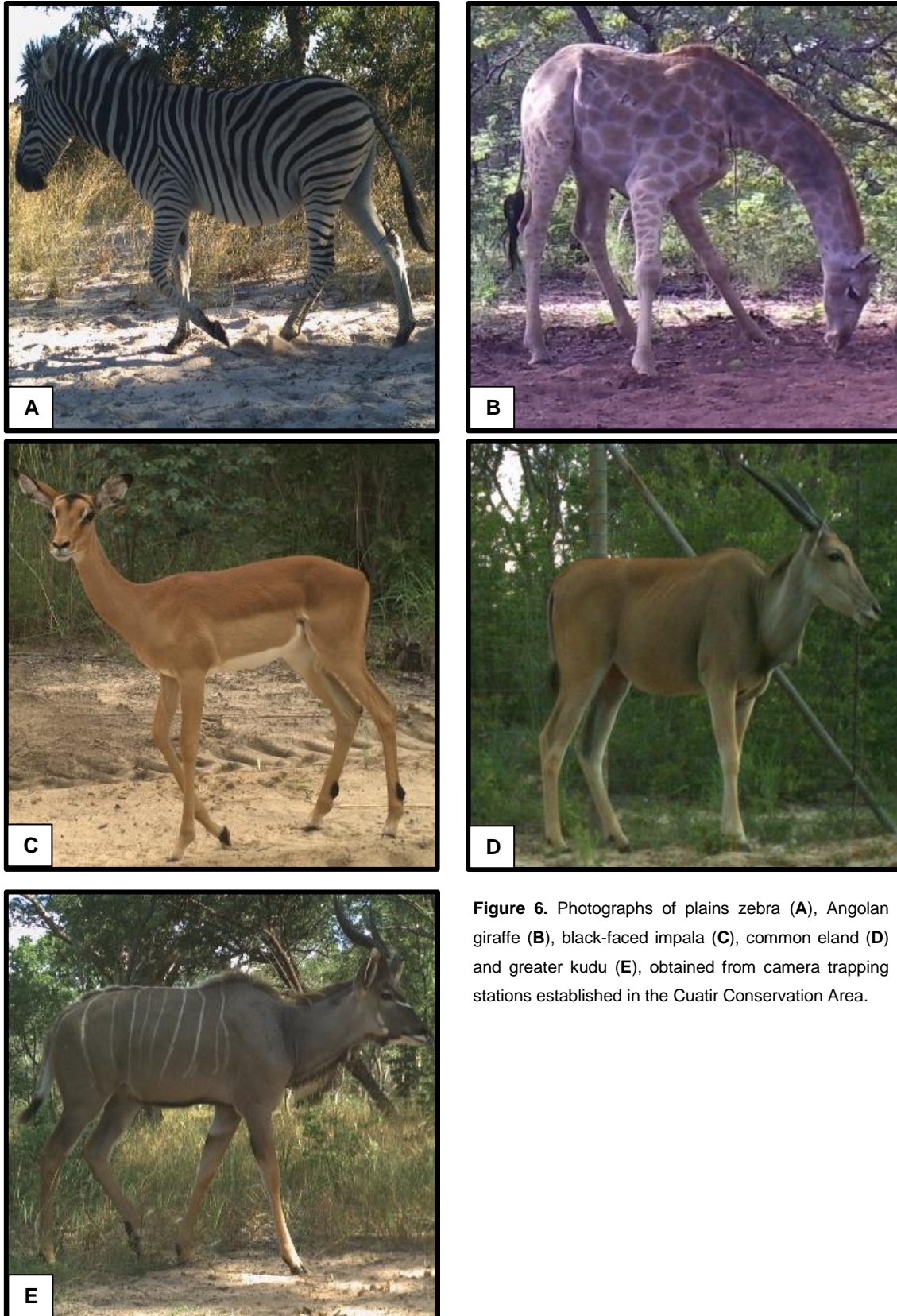


Figure 6. Photographs of plains zebra (A), Angolan giraffe (B), black-faced impala (C), common eland (D) and greater kudu (E), obtained from camera trapping stations established in the Cuatir Conservation Area.

1.5.1. The use of camera trapping in conservation translocations

Gathering data on population abundance, distribution and ecology represent a fundamental step of any conservation initiative, being the main tool to understand population trends and requirements and guide adequate management. Traditionally, these data were acquired through direct observations, during aerial and ground surveys, or by live-trapping methods that might have limited effectiveness regarding the temporal/spatial coverage and the quality of the required information. Furthermore, traditional wildlife monitoring protocols often include invasive or disturbing procedures that can influence the obtained results or may even be dangerous for researchers (Rowcliffe, 2017; Taylor et al., 2021). Such constraints can be largely overcome with camera trapping surveys (Taylor et al., 2021), which have been used for documenting wildlife for more than a century (Wearn & Glover-Kapfer, 2019).

Camera trapping techniques went through an impressive innovation in the last 20 years (Rowcliffe, 2017; Wearn & Glover-Kapfer, 2019) and are currently the gold standard for conservation monitoring purposes (Agha et al., 2018; Royle & Gardner, 2011). These techniques facilitate collecting data about species distribution, abundance, and richness. Moreover, camera trapping allows investigation of wildlife behavior, namely activity patterns, antipredator behaviors, or anthropogenic influences on wildlife (Caravaggi et al., 2017; Frey et al., 2017).

Concerning the monitorization of wildlife reintroductions, camera trapping has the potential to provide information about multiple population parameters, including dispersal, population abundance, and post-release behavior (Royle & Gardner, 2011). In addition, allows continuous monitoring for considerable periods and cover extensive areas, allowing the collection of large amounts of unequivocal data on the dynamics of reintroduced species' extent of occupancy. Moreover, camera traps collect data non-invasively and require minimal human intervention, decreasing disturbance on wildlife (Taylor et al., 2021; Wearn & Glover-Kapfer, 2019). Costs related to camera trap are also lower when compared with traditional methods and are expected to further decrease in the coming decades (Clare et al., 2015).

An example of camera trapping utility on reintroduction studies is the monitoring of the reintroduced western quoll (*Dasyurus geoffroyi*), in Australia. The western quoll is a carnivore marsupial native from Australia, that once occupied around 80% of the country's mainland, but is currently reduced to the region of Western Australia (Abbott, 2013; Moseby et al., 2021). This species was reintroduced in the Ikara-Flinders Ranges National Park between 2014 and 2016, a program that was continuously and intensely

monitored by radiotracking, cage trapping, and camera trapping methods. Data collected from camera traps showed that cats inhabiting the park were preying on western quolls and were responsible for high mortality rates. The understanding of these problems allowed its control and enhance western quoll survival in the release area (Moseby et al., 2021).

As with all methods for studying wildlife, camera trapping has disadvantages that need to be acknowledged and managed. Key logistic disadvantages of camera trapping methods regard the triggering speed and the detection zone, which should be adequate for the size and velocity of the species under study (Meek et al., 2014). Furthermore, occasional poor-quality images and false triggers are additional constraints. Large amounts of empty pictures not only reduce the battery life as increase memory use but also makes species identification and classification procedures extremely time-consuming and exhaustive. Most of these problems are currently being managed due to the growing interest in this technique (Rowcliffe, 2017), namely through artificial intelligence and automatic image classification (Norouzzadeh et al., 2019; Tabak et al., 2019).

1.6. Objectives

Monitoring conservation translocations, in a broad sense, intends to assess over time the status of released individuals in their new environment. Understanding how and at which rate species colonize new habitats by expanding their ranges from the release site, as well as the factors affecting the rates of colonization and extinction over time, help predict the outcomes of future translocations and allow overcoming unforeseen difficulties.

The main goal of this study was to assess the species-specific effectiveness of conservation translocations into a privately-owned conservation area in southern Angola. To achieve this main goal, a set of secondary goals were established:

- i) Estimate site-specific colonization and extinction rates and how these vary with time after release;
- ii) Identify key factors affecting each species' colonization rates in their new environment;
- iii) Assess the effectiveness of camera trapping methods to monitor wildlife reintroductions;

To achieve these goals, camera trapping data collected over six months, from November 2020 through May 2021, were analyzed using dynamic occupation models to account for imperfect detection (MacKenzie et al., 2003), and infer the factors underlying colonization-extinction and occupancy probabilities in all species. I expect that the results of this research could contribute to improving future translocation protocols, aimed at maximizing survival and adaptation of wildlife to the new hosting environments.

2. Material and Methods

2.1. Study area and translocated species

The Cuatir Conservation Area (CCA, S 16.5°, E 18.2°) is a private reserve located in the Eastern Cuando-Cubango province along the margins of the Cuatir river, a subsidiary of the Cubango river, in Southeastern Angola. It is included in the Zambebian *Baikiaea* Woodland ecoregion (Huntley et al., 2019), which includes savanna, shrubland, woodland, and grassland habitats (Burgess et al., 2004) that make the area suitable for several groups of organisms (Huntley et al., 2019). The weather is warm, with a mean maximum temperature of around 30°C and a mean minimum temperature between 9° to 12°C. Rainfall can reach 800 mm during the wet season (Kopij, 2017; Werger and Coetzee, 1978). CCA is dominated by *Baikiaea-Burkea* woodlands that provides several distinct landscapes (Figure 7), with grass species thriving during the rainy season.



Figure 7. Photographs obtained from camera trapping stations established along the Cuatir Conservation Area, illustrating its landscapes.

The reserve also comprises a floodplain along the riverbeds of the Cuatir and Luatuta rivers (Monterroso et al., 2020), and is composed by two distinct regions – an open area, and the core conservation area, delimited by an artificial fence towards the surrounding woodlands, but open to the Cuatir floodplains, along which the two regions are connected (Figure 8). The fenced region as an area of 800 ha, which extends to the peripheral woodlands and floodplains, and occupies about 30% of the total area that is covered by camera trapping stations. The fence is 3m high, and is not buried in the ground, which makes it permeable to many wild species (e.g., carnivores, bushpigs, and warthogs), but limits the movements of large herbivores (LH). Animals with larger sizes (e.g., greater kudu, common eland, etc.) might cross over the region delimited by the river when the water-levels are low, therefore colonizing the open area.



Figure 8. Schematic representation of the Cuatir Conservation area and its' main structures. The fence is represented by the yellow lines in the map, evidencing the region open towards the Cuatir river, represented by the blue lines. The release site is represented by the green mark inside the fenced area, and waterholes are also represented in the map by the blue spots.

Cuatir contains a valuable species richness. The carnivore community includes resident populations of cheetah (Monterroso et al., 2020), leopard, serval (*Leptailurus serval*), and caracal (*Caracal caracal*), and there is evidence that African wild dog and spotted hyena (*Crocuta crocuta*) also occur. Ungulate populations in Cuatir include

reedbuck (*Raphicerus campestris*), steenbok (*Redunca arundinum*), wild bushpig (*Potamochoerus larvatus*), and roan antelope (*Hippotragus equinus*), and is also the home for the iconic sitatunga (*Tragelaphus spekii*) (Figure 9).

The main purpose of CCA is wildlife conservation, but it also comprises activities connected to ecotourism, such as safaris along the reserve. Hunting is not allowed in the area.



Figure 9. Photographs of a leopard (*Panthera pardus*) cub and a male sitatunga (*Tragelaphus spekii*) obtained from camera trapping stations established in the Cuatir Conservation Area.

In November of 2020, five species of ungulates were translocated into the CCA's core area, with conservation and ecotourism purposes. Four Angolan giraffes – one male and three females, 19 plains zebras, and 40 black-faced impalas (IUCN, 2021) were reintroduced in the reserve, to establish new populations. Two female greater kudus and 20 common elands were released to reinforce the small population known to exist in the reserve (Figure 6). All these individuals were transported from a ranch in Namibia, where they lived under wild conditions, and were released inside the fenced area in CCA (Figure 8), in the same location and at the same time. The fence doors were opened one day after release so that the animals could naturally disperse.

2.2. Field data collection

Under the scope of an ongoing wildlife monitoring program carried out by the Research Center in Biodiversity and Genetic Resources of the University of Porto (CIBIO/InBIO-UP), 70 camera trapping stations were deployed at CCA, under a design considered suited to evaluate the area colonized by the translocated species since the release day (Figure 10). The data for this purpose was collected between November 2020 and May 2021, encompassing the entire wet season. The cameras were placed throughout the study area, following a grid-shaped network with 2 km inter-camera distance, ensuring spatial independence (Figure 10).

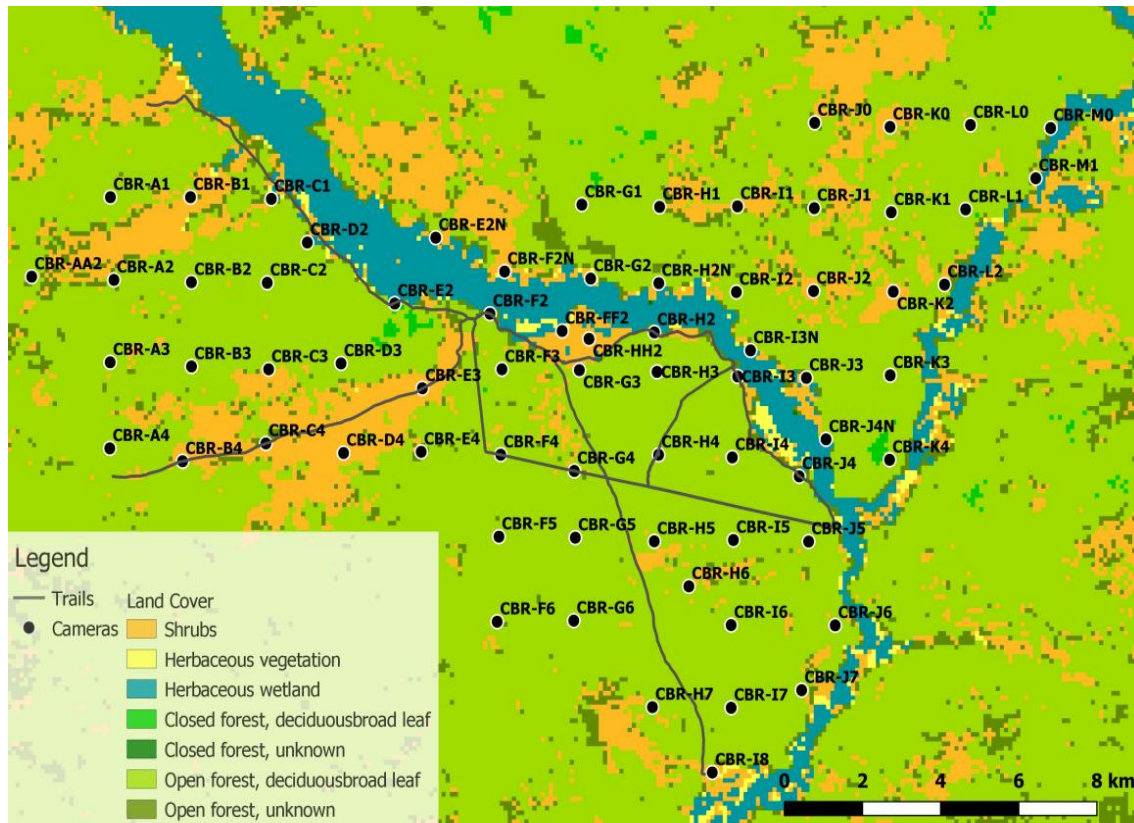


Figure 10. Map of the Cuatir Conservation Area, evidencing the network of camera trapping stations established along the region, different types of landcover and location of human trails.

The camera trapping network includes cameras positioned inside and outside the fenced area, as shown in Figure 10. Cameras CBR – FF2 and CBR – HH2 were considered as located inside the fenced area, since these are placed in an area surrounded by the floodplain of the Cuatir river, the natural fence (Figure 10). Moreover, some of the cameras were positioned on trails (Table 1). From the original 70 cameras located in CCA, only 47 cameras were considered for this study, due to the loss of equipment and data because of theft or equipment malfunctioning.

Table 1. Set of camera trapping stations placed on human trails in Cuatir Conservation Area.

<i>Cameras on trails</i>	<i>CBR-B4</i>	<i>CBR-C4</i>	<i>CBR-E2</i>	<i>CBR-E3</i>	<i>CBR-F4</i>	<i>CBR-G4</i>	<i>CBR-H2</i>	<i>CBR-I3</i>	<i>CBR-J4</i>
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Four models of camera traps were used: Reconyx Hyperfire HC500, Reconyx Hyperfire HC600, Reconyx Hyperfire 2 (Reconyx, Holmen, Wisconsin, US), and Cuddeback C1 Strobe Flash (Cuddeback, Green Bay, Wisconsin, USA). Cameras were placed on tree trunks, at an approximate height of 0.6 m from the ground and were set to shoot a set of 5 (Cuddeback) or 10 (Reconyx) photographs when triggered. The

photographs were taken with no delay time (0 seconds), to maximize the number of photos taken per trigger. Camera trapping stations were verified bimonthly for maintenance, troubleshooting, and battery check, and memory card replacement.

2.3. Data organization, identification, and classification

The collected photographs were initially organized in hierarchical structure with a folder corresponding to each camera inside which subfolder for each species were created. All image files were then renamed using the *camtrapR* 2.0.2 package (Niedballa et al., 2016) on R software (R Core Team, 2021) so that camera code, date, and time of each of each detection record would be assigned to each specific file name. Following these procedures, all photographs were manually classified to the species level, and organized through a drag-and-drop process into each respective species subfolder inside each camera folder. The list of potentially occurring species was built based on Huntley et al (2019).

The metadata tags recorded on the camera trap data were then extracted into R using *camtrapR* package. The information regarding all records from each camera trap stations' dates, times, species, and group sizes were compiled in a record table. In this step, photographs taken at the same time were considered duplicates and therefore discarded. Any camera trap records of the same species within 30 minutes of each other, were considered as a single trapping event (Monterroso et al., 2013).

2.4. Statistical modeling

R software was initially used to create a camera functioning matrix from the survey start to end dates, where each row corresponds to a camera station and each column to a sampling day. Cameras were initially filtered to only include those active during the sampling period, and malfunctioning periods or periods in which cameras could have temporarily not been deployed were assigned as *NA* (missing values). These filtration steps resulted in a final number of 40 cameras to be included in subsequent analysis.

Target-species detection records were extracted from the renamed files using *camtrapR* and filtered to the five target species and sampling period to build a record table. Species-, camera- and date-specific records were used to build encounter histories on daily sampling occasions in the camera functioning matrix such that days with records were assigned '1' and days with no records were assigned '0'.

2.4.1. State and detection covariates

Following Pollock's robust design (Pollock, 1982), the total survey period of 180 sampling days was subdivided into 18 primary periods, each comprised of 10 secondary sampling occasions (i.e., days). Under this design site occupancy is assumed to be static or unchanging within each primary period (i.e., complies with the closure assumption), but allows for state change (i.e., colonization and extinction) across subsequent primary periods (MacKenzie et al., 2017). Therefore, secondary sampling occasions are regarded as replicates of the same state across sampling units (i.e., camera trap locations).

For the specific goals of this research, I considered covariates hypothesized to affect two distinct processes: detection and colonization rates (Table 2).

Table 2. Set of detection and colonization covariates considered on the present study, and respective associated variables, hypothesized effects on detection and colonization processes, and references supporting the presented hypothesis.

<i>Process</i>	<i>Covariate</i>	<i>Variable</i>	<i>Hypothesis Reasoning</i>	<i>References</i>	
Detection	Camera placement	On a trail	The position of a camera relatively to a trail influences species detection probability, that is higher for cameras located on human trails.	Kolowski et al. 2017	
		Out of a trail			
Colonization	Distance to last colonized site		Colonization probabilities are higher for a site/camera located to other already occupied sites/cameras.	Davies et al., 2018	
	Distance to release site		Species with higher dispersal capacity will colonize cameras that are more distant from the release site.	Morgan et al., 2019	
	Camera location regarding fence	Inside the fence	Outside the fence	The fence limits animal movement, and is semi permeable: small animals can cross, but LH do not.	Pirie et al., 2017
	Temporal trend		Colonization probabilities are expected to increase over time, as well as the rates of occupation of the new environment.	Seddon et al., 2007	

Detection probabilities are expected to increase when camera traps are in or at the edge of trails, as these structures can be used as energy-efficient travel routes and marking spots for multiple wildlife species (Bruggeman et al., 2007; Kolowski & Forrester, 2017; Rafiq et al., 2020). Therefore, camera position on or off human trails was included as a binary covariate to account for this effect on detection probability, whereby '1' denotes cameras deployed on trails and '0' denotes cameras deployed off trails.

Four covariates were investigated as to their potential effects on colonization rates: i) distance to release site (boma); ii) distance to closest known occupied site (camera where the species was recorded in the previous primary period; see section 2.4.2. Fitting dynamic occupancy models); iii) location of the cameras with respect to the core conservation area, i.e., inside or outside the fenced area; and iv) temporal trend since release, in days. Distance covariates were calculated as the linear Euclidean distance to each respective location. These covariates and respective variables are expected to influence colonization probabilities in different ways, and their inclusion was based on specific expected hypotheses and responses (Table 2).

For the single detection covariate applied in this study, the location of a camera inside a trail or outside a trail, we hypothesized that the detection probabilities of the target species are higher in cameras that are located inside trails than in cameras that are located outside trails. This covariate was tested because animals may prefer to travel through human trails or paths (Kolowski & Forrester, 2017) rather than across more natural environments (i.e., by the middle of woodland or forest), due to energy saving or other reasons.

Regarding the colonization covariates, the effect of distance to the last colonized site was tested to infer whether more distant locations are less likely to be colonized, as proposed by the metapopulation paradigm (Davies et al., 2018; Hanski, 1999; Prugh et al., 2008), while the effect of the distance to release site (boma) was tested to investigate the effect of distance in a species dispersal capacity (Armstrong & Seddon, 2008; Morgan et al., 2019). The position of the cameras relatively to the fence was also tested to investigate if the colonization outside the fenced area was lower than the colonization inside the fenced area, as expected, because fences are a physical barrier that can be a constraint to animal movement. Finally, it was hypothesized that the colonization probabilities would increase over time, since individuals often need time to overcome neophobia and start exploring the new environment (Seddon et al., 2007).

The effect of spatial heterogeneity covariates in initial occupancy was not tested since all species were released at the same time. Additionally, species were released in

CCA, and their initial occupancy was known. Also, temporal heterogeneity on extinction rates was not verified because this process was not of interest in this study.

2.4.2. Fitting dynamic occupancy models

Dynamic occupancy models allow the estimation of several vital rates of wildlife populations: occupancy, colonization, and extinction probabilities (MacKenzie et al., 2017). The key input of every dynamic occupancy model are the detection histories across the sampled area i.e., whether the species is detected or not detected in each sampling occasion for each site, allowing to estimation of the proportion of sites occupied (MacKenzie et al., 2003).

Occupancy models consider spatial and temporal heterogeneity in the environment as main sources of variation in the occupancy and colonization/extinction processes, respectively. MacKenzie et al (2002) proposed a method to estimate the proportion of occupied sites by a species when the probability of detecting that species is less than 1, where N sites are visited on each of T sampling occasions and for each detection or non-detection of the species is recorded on each visit. The model allows the incorporation of covariates (e.g., habitat type, environmental variables) and assume that each site is closed to changes during the sampling period, which is the primary period established in any analysis.

2.4.2.1. Model Formulation

Dynamic occupancy models are defined as hierarchical multi-season models since they are applied to multiple “seasons” (i.e., primary sampling periods, the suited time of each survey) and allow between-seasons occurrence dynamics. Under these models’ formulation, state parameters of the dynamic occupancy model (initial occupancy - ψ -, colonization probability - γ -; and extinction probability - ϵ) and observation parameters (detection probability - p) are estimated separately, under two sub models: one regarding the ecological process, that describes the occurrence dynamics for all sites; and one regarding the observation process, that describes the probability of detecting the species.

Under the ecological sub model, the initial state is denoted by z_{i1} and represents true (potentially unobserved) occurrence state at site i during season 1, which is described by a Bernoulli trial governed by the occupancy probability in the first season, ψ_{i1} :

$$z_{i1} = \text{Bernoulli}(\psi_{i1})$$

The sample quantity “occurrence” at a site, z , differs from the population quantity “occupancy probability”, ψ because the former is the realization of a Bernoulli random variable with parameter ψ . This distinction becomes important when computing the number of occupied sites among the sample of surveyed sites (Royle & Kéry, 2007; Weir et al., 2009). For all subsequent seasons, occurrence probability is a function of occurrence at site i at time $t-1$ and one of two parameters that describe the colonization-extinction dynamics of the system. These dynamic parameters are the probability of local survival ϕ_{it} , also called probability of persistence (= 1 minus the probability of local extinction), and the probability of colonization γ_{it} .

$$z_{it} \sim \text{Bernoulli}(z_{i,t-1}\phi_{it} + (1 - z_{i,t-1})\gamma_{it})$$

Hence, if site i is unoccupied at $t-1$, $z_{i,t-1} = 0$, and the success probability of the Bernoulli is $0 * \phi_{it} + (1-0)*\gamma_{it}$, so the site is occupied (colonized) in season t with probability γ_{it} . Conversely, if site i is occupied at $t-1$, $z_{i,t-1} = 1$, the success probability of the Bernoulli is given by $1 * \phi_{it} + (1-1)*\gamma_{it}$, so the site is occupied in (=survives to) season t with probability ϕ_{it} . Occupancy probability ψ_{it} and occurrence $z_{i,t}$ at all later times t can be computed from ψ_{i1} , $z_{i,1}$, ϕ_{it} and γ_{it} .

The observation sub model describes the observation process, and accounts for the observation error (specifically, false-negative observations), under a conventional Bernoulli detection process, such that:

$$y_{ijt} \sim \text{Bernoulli}(z_{it}p_{ijt})$$

Here, p_{ijt} is the detection probability at site i during survey j and season t , where detection is conditional on occurrence and multiplying p_{ijt} with z_{it} ensures that occurrence can only be detected where in fact a species occurs (where $z_{it} = 1$). Therefore, the observed data y_{ijt} regards to whether a species is detected at site i during the replicate survey j in season t , such that $y_{ijt} = 1$ if at least one individual is detected and $y_{ijt}=0$ if none is detected.

The above-described model formulation assumes the detection and occupancy as constant across sites. Spatial and temporal heterogeneity in the state and detection

processes can modeled as a function of site- and sampling-specific covariates, x , under the form of linear regressions using a logit-link function as follows:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} \dots \beta_k x_{ik}$$

$$\text{logit}(p_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} \dots \beta_k x_{ik}$$

Occupancy models, as the described above, rely on three key assumptions (MacKenzie et al., 2017):

- The occupancy state across sampling sites during a particular season are independent (or else dependency must be modeled).
- The occurrence state z_{it} (see below) does not change over replicate surveys at site i during season t .
- There are no false-positive errors, i.e., a species can only be overlooked where it occurs, but it cannot be detected where it does not in fact occur.

2.4.3. Model fitting

Prior to model fitting, all continuous covariates were tested for multicollinearity using nonparametric Spearman' correlation, using the psych R package (Revelle, 2017), and any covariates considered correlated ($|\rho| > 0.7$; (Zuur et al., 2010)) were precluded from being included in the same model. All continuous predictors were re-scaled between 0 and 1' to avoid data dispersion bias and facilitate model numeric convergence (MacKenzie et al., 2017). The covariates "distance to nearest colonized site" and "distance to boma" were found to be correlated and, therefore, could not be used in the same models. Dynamic occupancy models were fitted to each species' camera-trapping encounter histories using package *unmarked* v1.1.1 (Fiske & Chandler, 2011) in R software (R Core Team, 2021), with 18 primary periods of 10 sampling occasions (days) each.

After investigating correlation among potential explanatory covariates, I generated a set of models including all covariate combinations, with the constraint that correlated covariates could not be included in the same model, since predictors with strong linear relationships may bias model averaging. These dynamic occupancy models, as defined

by Mackenzie et al (2003), were fitted with the *colext* function in the *unmarked* package, generating a set of multiple species-specific competing models potentially explaining the underlying ecological and observation processes.

Model selection was based on the Akaike's Information Criterion (AIC) and on Akaike model weights (Burnham & Anderson, 2002), using the *MuMIn* package (Barton & Barton, 2015). These selection criteria weigh the likelihood of the model over the total number of parameters, identifying the best fitting and most parsimonious model (i.e., smallest AIC). Smaller AIC values indicate more robust models (Burnham & Anderson, 2002). Models with a $\Delta AIC < 7$ (measure of each model performance relative to the best model; Burnham and Anderson, 2011) were considered as having substantial support (Burnham & Anderson, 2002). Models with a $\Delta AIC < 2$ (measure of each model performance relative to the best model) were considered top-supported models (Burnham & Anderson, 2002). Multimodel inference were based on model averaging, a technique that improves the predictive ability by combining estimates from a model set. Model-averaged parameter estimates were estimated using the "*modavg*" function of *AICcmodavg* package (Mazerolle, 2020), using the obtained models with an $\Delta AIC < 2$. The predicted values for each state and detection parameters were calculated from model-averaged estimates of the untransformed data, with respective standard errors and 95% confidence intervals. Projected occupancy trajectories – the projection of the number of occupied sites over time since the release date (Weir et al., 2009) - were obtained from the *projected.mean* slot of the best fitting occupancy model's output, considering constant occupancy probabilities, and the estimated colonization and detection probabilities in each model.

The results obtained regarding the reintroduced Angolan giraffes will not be presented nor discussed, since the small number of individuals from this species did not allow an accurate estimation of the parameters by model averaging.

3. Results

3.1. General Results

The sampling effort totaled 6,119 trapping days from 40 stations, with a mean of 130.19 ± 68.50 trapping days per station (Table 3).

Table 3. Global trapping effort for the sampling period.

<i>Camera</i>	<i>Total active days</i>	<i>Camera</i>	<i>Total active days</i>
<i>CBR-A4</i>	86	<i>CBR-H4</i>	5
<i>CBR-B4</i>	119	<i>CBR-H5</i>	183
<i>CBR-C4</i>	108	<i>CBR-H6</i>	94
<i>CBR-D4</i>	117	<i>CBR-HH2</i>	183
<i>CBR-E2</i>	183	<i>CBR-I1</i>	181
<i>CBR-E3</i>	125	<i>CBR-I2</i>	181
<i>CBR-E4</i>	156	<i>CBR-I3</i>	133
<i>CBR-F2</i>	183	<i>CBR-I3N</i>	181
<i>CBR-F2N</i>	181	<i>CBR-I4</i>	150
<i>CBR-F3</i>	183	<i>CBR-I5</i>	94
<i>CBR-F4</i>	180	<i>CBR-J0</i>	182
<i>CBR-FF2</i>	183	<i>CBR-J1</i>	182
<i>CBR-G1</i>	181	<i>CBR-J2</i>	182
<i>CBR-G3</i>	183	<i>CBR-J3</i>	182
<i>CBR-G4</i>	53	<i>CBR-J4</i>	182
<i>CBR-G6</i>	105	<i>CBR-J4N</i>	182
<i>CBR-H1</i>	181	<i>CBR-J5</i>	128
<i>CBR-H2</i>	183	<i>CBR-K1</i>	182
<i>CBR-H2N</i>	95	<i>CBR-K2</i>	182
<i>CBR-H3</i>	183	<i>CBR-K4</i>	182

A total of 4358 independent detections of several species were obtained. The target species were detected in 19 (47.5%) of the cameras. The black-faced impala is the species with the highest number of independent detections ($n=127$) and was detected in 10 cameras, followed by plains zebras that produced 86 independent detections in 10 cameras. The Angolan giraffe collected 68 independent detections at three cameras. Common eland was detected 85 times in five cameras, and 62 detections in 15 cameras were obtained from the greater kudu. The total number of independent detections for the target species is shown in Table 4.

Table 4. The number of independent detections obtained for each target species per camera with detections, and total number of detections obtained inside and outside the fenced area in Cuatir.

<i>Location</i>	<i>Camera</i>	<i>Black-faced impala</i>	<i>Plains zebra</i>	<i>Giraffe</i>	<i>Common eland</i>	<i>Greater kudu</i>
<i>Inside fence</i>	CBR-F3	0	11	2	5	1
	CBR-F4	76	10	60	62	38
	CBR-FF2	4	8	0	0	3
	CBR-G3	2	0	0	9	0
	CBR-G4	4	10	6	0	0
	CBR-H2	8	7	0	1	1
	CBR-H3	1	5	0	0	2
	CBR-H4	0	0	0	8	1
	CBR-HH2	5	16	0	0	3
	CBR-I3	0	6	0	0	0
	CBR-I4	2	2	0	0	1
	CBR-J4	2	6	0	0	3
<i>Outside fence</i>	CBR-F2	23	0	0	0	0
	CBR-G6	0	0	0	0	2
	CBR-H1	0	0	0	0	3
	CBR-I2	0	0	0	0	1
	CBR-J0	0	0	0	0	1
	CBR-J3	0	0	0	0	1
	CBR-K4	0	0	0	0	1
<i>Total detections</i>	<i>Inside fence</i>	104	86	68	85	53
	<i>Outside fence</i>	23	0	0	0	9

Several carnivore species were also detected on the cameras (leopard, cheetah, caracal; Table 5). Leopard was the carnivore that accounted for more independent detections, and detected in more cameras, followed by the caracal with 16 independent detections in four cameras, the serval, that was detected 15 times in three cameras and the cheetah, with five detections in four cameras. Spotted hyena was only detected one time in one camera.

Table 5. The number of independent detections obtained for several carnivores per camera with detections, and total number of detections obtained inside and outside the fenced area in Cuatir.

<i>Location</i>	<i>Camera</i>	<i>Cheetah</i>	<i>Caracal</i>	<i>Spotted hyena</i>	<i>Serval</i>	<i>Leopard</i>
<i>Inside fence</i>	CBR-F4	0	9	0	0	3
	CBR-H2	0	4	0	0	3
	CBR-I3	1	1	0	0	3
	CBR-J4	0	0	0	8	2
<i>Outside fence</i>	CBR-B4	0	2	0	0	3
	CBR-C4	0	0	0	0	1
	CBR-E3	0	0	1	0	0
	CBR-F2	0	0	0	6	1
	CBR-I1	1	0	0	0	1
	CBR-I3N	2	0	0	0	1
	CBR-J3	0	0	0	1	0
	CBR-K1	1	0	0	0	1
<i>Total detections</i>	<i>Inside fence</i>	1	14	0	8	11
	<i>Outside fence</i>	5	2	1	7	8

A set of statistical models was obtained for each species, explaining their occupancy dynamics, i.e., colonization and detection probabilities. The reduced number of detections for the Angolan giraffe precluded further analyses, therefore occupancy dynamics for this species was not assessed.

3.2. Target species occupancy dynamics

3.2.1. Plains zebra

a) Model selection

All substantially supported models ($\Delta AIC < 7$) obtained for zebra included the location inside the fenced area as a colonization covariate. The top-supported models ($\Delta AIC < 2$) included temporal trend, distance to boma and distance to last colonized site as covariates, and the position of camera on a human trail as covariate for detection probability. Of the model set within $2 < \Delta AIC < 7$, two models include camera positioned on trails as a detection probability covariate, five models include time trend as colonization covariate, two models include distance to last colonization site and two models include distance to boma (Table 6).

Table 6. Selection of models with substantial support - $\Delta AIC < 7$ - for colonization (γ) and detection (p) of plains zebra, *Equus quagga*. The colonization covariates considered are the location of a camera in the fenced area – fenced, distance to last colonized site – dcol, distance to boma- dboma, and the detection covariate is the position of a camera on a trail– trail. The model information contains number of model parameters -K, log-likelihood – logLik, the value of the information criterion used – AIC; the delta- ΔAIC , the “Akaike weight” – ω_i and the cumulative “Akaike weight” – $Cum\omega_i$.

<i>Model</i>	<i>logLik</i>	<i>K</i>	<i>AIC</i>	ΔAIC	ω_i	<i>Cum</i> ω_i
$\psi (.) \gamma (fenced) \varepsilon (.) p (trail)$	322.65	6	657.31	0.00	0.28	0.28
$\psi (.) \gamma (fenced+trend) \varepsilon (.) p (trail)$	322.21	7	658.43	1.11	0.16	0.44
$\psi (.) \gamma (fenced+dcol) \varepsilon (.) p (trail)$	322.45	7	658.91	1.59	1.28	0.57
$\psi (.) \gamma (fenced+dboma) \varepsilon (.) p (trail)$	322.64	7	659.29	1.97	1.06	0.68
$\psi (.) \gamma (fenced) \varepsilon (.) p (.)$	324.83	5	659.66	2.35	8.79	0.76
$\psi (.) \gamma (fenced+dcol+trend) \varepsilon (.) p (trail)$	321.91	8	659.82	2.50	8.13	0.85
$\psi (.) \gamma (fenced+dboma+trend) \varepsilon (.) p (trail)$	322.20	8	660.40	3.08	6.08	0.91
$\psi (.) \gamma (fenced+trend) \varepsilon (.) p (.)$	324.20	6	661.07	3.75	4.35	0.95
$\psi (.) \gamma (fenced+dcol+trend) \varepsilon (.) p (.)$	323.97	7	661.94	4.62	2.82	0.98
$\psi (.) \gamma (fenced+dboma+trend) \varepsilon (.) p (.)$	324.52	7	663.05	5.73	1.62	0.99

b) Covariate effects

None of the tested colonization covariates showed a significant effect on local colonization probabilities. Except for the covariate “fenced”, all covariates are included in the top-supported models ($\Delta AIC < 2$) only once (Table 6). The obtained model-averaging estimates for distance to last colonized site and time trend are 3.15 (± 4.24) and 1.76 (± 1.97), respectively, showing high values of standard error for both variables. The same was observed for the variable “distance to boma”, with a value of -0.21 (± 1.66). Moreover, all 95% confidence intervals for these variables were wide. None of these variables had a significant effect in explaining the probability of an unoccupied site being colonized. The only covariate with a consistent effect on colonization probabilities is the presence of the fence, which is included in all the substantially supported models ($\Delta AIC < 7$). However, the lack of plains zebra detections outside the fenced area does not allow for precise estimation of the effect of this covariate in colonization. Regarding the detection covariate, the position of camera on trails was included in all the top-supported models with a value of 0.55 (± 0.27) (Table 7), supporting the positive effect of position of cameras on trails for plains zebras.

Table 7. Untransformed estimates of probabilities of initial occupancy, ψ extinction, ε , colonization, γ , and detection, p , estimated for plains zebra, and respective effect of tested colonization and detection covariates. $\hat{\beta}$ – untransformed model-averaged coefficient; SE – standard error; CI95- 95% confidence interval; *dboma*- distance to release site (*boma*); *dcol* – distance to last colonized site; *fenced* – effect of the fence; *trend* – effect of time trend; *trail* – effect of the position of a camera on a trail.

	$\hat{\beta}$ (SE)	CI95
ψ	-2.56 (0.73)	[-4.00; -1.13]
γ	-2.18 (0.83)	[-3.79; -0.56]
ε	-3.02 (0.92)	[-4.83; -1.21]
p	-2.80 (0.21)	[-3.23; -2.37]
<i>dboma</i>	-0.21 (1.66)	[-3.74; 3.03]
<i>dcol</i>	3.15 (4.24)	[-5.16; 11.47]
<i>fenced</i>	-9.93 (21.97)	[-53.00; 33.13]
<i>trend</i>	1.76 (1.97)	[-2.10; 5.62]
<i>trail</i>	0.55 (0.27)	[0.027; 1.08]

c) Colonization-extinction and detection probabilities

The mean plains zebra detection probability was 0.06 (± 0.55) and raised to 0.10 (± 0.62) when cameras were deployed on trails (Table 8). The mean probabilities of initial occupancy for this species are 0.07 (± 0.68), and that an occupied patch becomes unoccupied (i.e., local extinction) was 0.05 (± 0.72). Colonization probability across primary sampling periods was of 0.10 (± 0.69) inside the fenced area, whereas it tended to 0 in unfenced areas (Table 8).

Table 8. Estimated values of plain zebras' probabilities of initial occupancy ψ , colonization γ inside and outside the fenced area, extinction, ε and detection p by cameras located on trails and of trails. $\hat{\beta}$ – untransformed model-averaged coefficient; SE – standard error; CI95- 95% confidence interval.

Process	Parameter	$\hat{\beta}$ (SE)	CI95
Ecological	ψ	0.07 \pm 0.68	[0.02; 0.24]
	γ (inside fence)	0.1 \pm 0.69	[0.02; 0.36]
	γ (outside fence)	0 \pm 1	[0; 1]
Detection	ε	0.05 \pm 0.72	[0.01; 0.23]
	p (off trail)	0.06 \pm 0.55	[0.04; 0.08]
	p (on trail)	0.1 \pm 0.62	[0.04; 0.22]

d) Proportion of occupied area over time

The area occupied by the reintroduced zebra population started increasing right after release. Initial occupancy was of 0.03, and it started stabilizing around day 100, reaching 22% of occupied area, which nearly corresponds to all the fenced area, that occupies 30% of the study area. Hence, plains zebra took around three months to colonize the near totality of the fenced area. Further increases reached 24% of occupied area of, the highest value recorded for the proportion of occupied area by plains zebra (Figure 11).

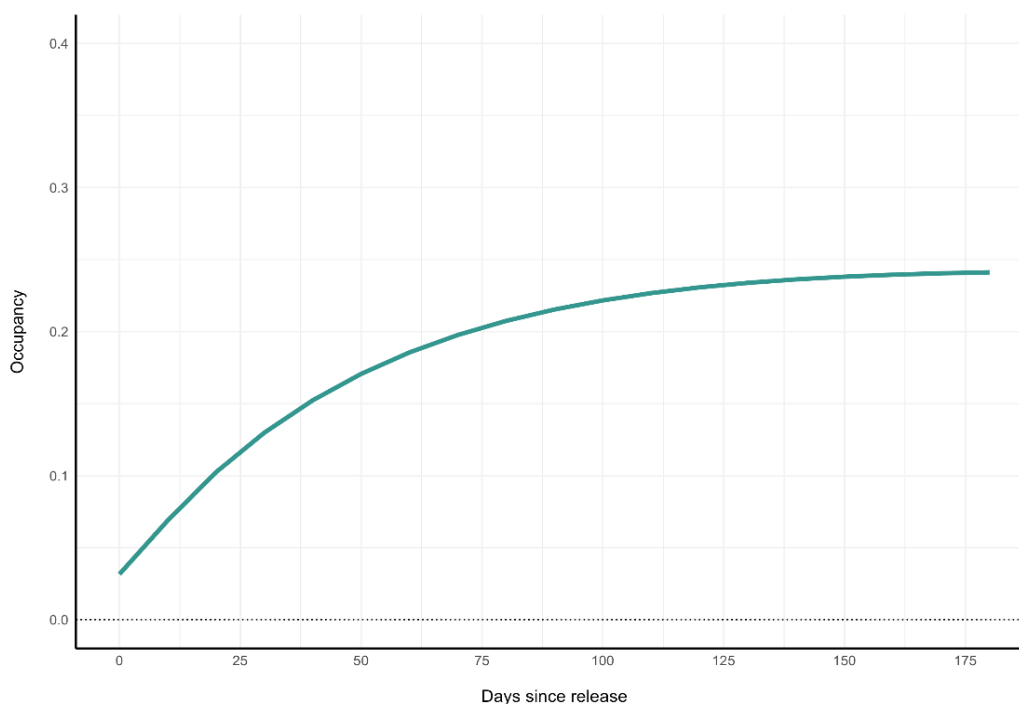


Figure 11. Proportion of occupied area by plains zebra population in Cuatir. The period corresponds to the number of days since the release date, and occupancy values represent the proportion of area occupied at each period.

3.2.2. Black-faced impala

a) Model selection

The three top-supported models suggest a near-informative effect of the temporal trend on colonization probability of black-faced impala, with a cumulative Δ AIC weight of 82% for these models (Table 9). The covariate “fenced” is included in all substantially supported models, while the covariates “distance to boma” and “distance to last colonized site” are included in one of the three top-supported models, and once in the

models with $2 < \Delta AIC < 7$. Regarding detection covariates, the position of camera on trails is included in all the models obtained for black-faced impala (Table 9).

Table 9. Selection of models with substantial support - $\Delta AIC < 7$ - for colonization (γ) and detection (p) of black-faced impala, *Aepyceros melampus petersi*. The colonization covariates considered are the location of a camera in the fenced area – fenced, distance to last colonized site – dcol, distance to boma- dboma, and the detection covariate is the position of a camera on a trail– trail. The model information contains number of model parameters -K, log-likelihood – logLik, the value of the information criterion used – AIC; the delta- ΔAIC , the “Akaike weight” – ω_i and the cumulative “Akaike weight” – $Cum\omega_i$.

<i>Model</i>	<i>logLik</i>	<i>K</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>ω_i</i>	<i>Cumω_i</i>
$\psi (.) \gamma (fenced+trend) \mathcal{E} (.) p (trail)$	276.26	7	566.52	0.00	4.35	0.43
$\psi (.) \gamma (fenced+dcol+trend) \mathcal{E} (.) p (trail)$	275.91	8	567.82	1.29	2.27	0.66
$\psi (.) \gamma (fenced+dboma+trend) \mathcal{E} (.) p (trail)$	276.25	8	568.51	1.99	1.60	0.82
$\psi (.) \gamma (fenced) \mathcal{E} (.) p (trail)$	278.72	6	569.44	2.92	1.00	0.92
$\psi (.) \gamma (fenced+dcol) \mathcal{E} (.) p (trail)$	278.69	7	571.39	4.86	3.81	0.96
$\psi (.) \gamma (fenced+dboma) \mathcal{E} (.) p (trail)$	278.70	7	571.41	4.89	3.76	0.99

b) Covariate effects

The location of the camera relatively to the fence showed a significant negative effect on colonization probabilities, with a value of $-3.63 (\pm 1.09)$, and supported by the 95% confidence intervals (Table 10). The parameter “fence” was estimated with more accuracy for black-faced impala due to the detections of the species outside the fence. Moreover, there was a near-informative positive effect of the temporal trend on colonization probabilities, with a value of $3.24 (\pm 1.74)$. The covariate “distance to last colonized site” had an estimated effect of $2.03 (\pm 3.62)$, while “distance to boma” showed a negative effect of $-0.17 (\pm 1.57)$ on colonization probability, both non-significant. The tested detection covariate demonstrated a significant positive effect of $1.73 (\pm 0.31)$, supporting that black-faced impalas are more likely to be detected by cameras deployed on trails.

Table 10. Untransformed estimates of probabilities of initial occupancy, ψ extinction, ε colonization, γ , and detection, p , estimated for black-faced impala, and respective effect of tested colonization and detection covariates. $\hat{\beta}$ – untransformed model-averaged coefficient; SE – standard error; CI95- 95% confidence interval; dboma- distance to release site (boma); dcol – distance to last colonized site; fenced – effect of the fence; trend – effect of time trend; trail – effect of the position of a camera on a trail.

	$\hat{\beta}$ (SE)	CI95
ψ	-2.46 (0.74)	[-3.92; -1.01]
γ	-3.58 (1.56)	[-6.64; -0.52]
ε	-1.70 (0.65)	[-2.99; -0.42]
p	-2.95 (0.26)	[-3.46; -2.44]
dboma	-0.17 (1.57)	[-3.25; 2.90]
dcol	2.03 (3.62)	[-5.06; 9.14]
fenced	-3.63 (1.09)	[-5.79; -1.48]
trend	3.24 (1.74)	[-0.17; 6.66]
trail	1.73 (0.31)	[1.12; 2.35]

c) Colonization- extinction and detection probabilities

Results for black-faced impala show that the species is more likely to be detected by cameras deployed on trails ($p = 0.23 (\pm 0.64)$) than by cameras outside trails ($p = 0.05 (\pm 0.56)$). Black-faced impalas' probability of initial occupancy was 0.08 (± 0.68), and mean colonization probabilities were 0.03 (± 0.83) inside the fenced area, and 0 outside the fence (Table 11).

Table 11. Estimated values of black-faced impalas' probabilities of initial occupancy ψ , colonization γ inside and outside the fenced area, extinction, ε and detection p by cameras located on trails and of trails. $\hat{\beta}$ – untransformed model-averaged coefficient; SE – standard error; CI95- 95% confidence interval.

Process	Parameter	$\hat{\beta}$ (SE)	CI95
Ecological	ψ	0.08 \pm 0.68	[0.02; 0.27]
	γ (inside fence)	0 \pm 0.93	[0; 0.12]
	γ (outside fence)	0.03 \pm 0.83	[0; 0.37]
Detection	ε	0.15 \pm 0.66	[0.05; 0.4]
	p (off trail)	0.05 \pm 0.56	[0.03; 0.08]
	p (on trail)	0.23 \pm 0.64	[0.09; 0.48]

d) Proportion of occupied area over time

Initial occupancy for black-faced impala was 3% and increased to 7% from the first to the second primary occasions. This species showed a continuous expansion across occupation of the fenced area, but despite the detections outside the fenced area, the

maximum value obtained for occupancy was 20% (Figure 12), which is slightly lower than that obtained for zebra.

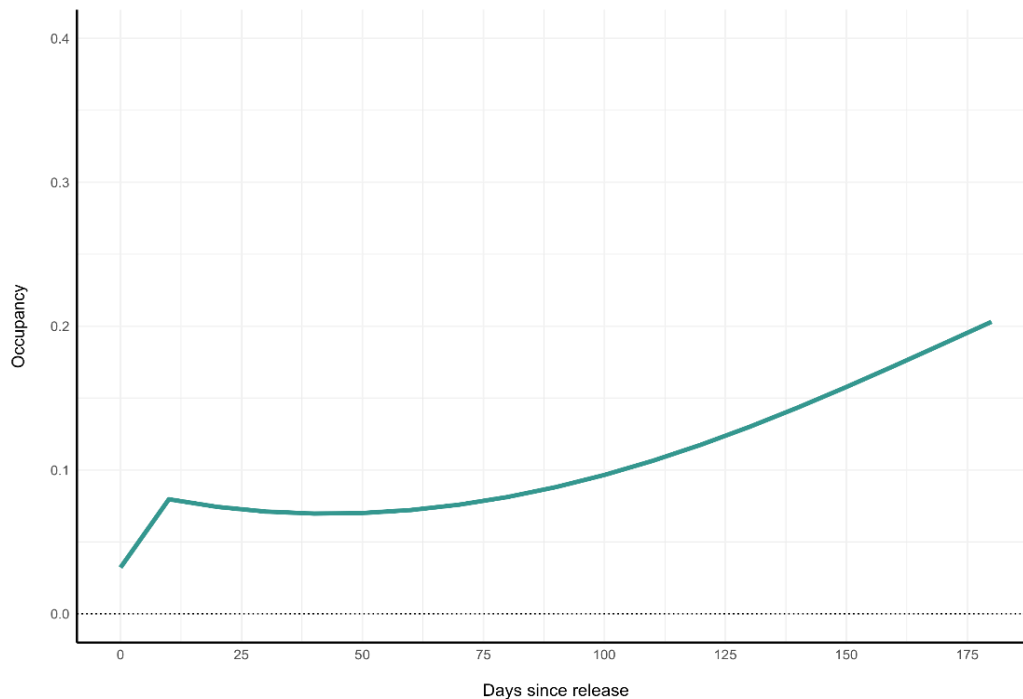


Figure 12. Proportion of occupied area by black-faced impala population in Cuatir private reserve. The period corresponds to the number of days since the release date, and occupancy values represent the proportion of area occupied at each period.

3.2.3. Common eland

a) Model selection

For common eland there were six models with $\Delta AIC < 7$, five of which being top-supported models with $\Delta AIC < 2$. Regarding colonization covariates, the position inside the fenced area was included in all the models, the distance to last colonized site and the distance to boma were both included in two of the six models, while time trend was included in three models (Table 12). All the substantially supported models included the detection covariate, “location of camera on trail”.

Table 12. Selection of models with substantial support - $\Delta AIC < 7$ - for colonization (γ) and detection (p) common eland, *Taurotragus oryx*. The colonization covariates considered are the location of a camera in the fenced area – fenced, distance to last colonized site – dcol, distance to boma- dboma, and the detection covariate is the position of a camera on a trail– trail. The model information contains number of model parameters -K, log-likelihood – logLik, the value of the information criterion used – AIC; the delta- ΔAIC , the “Akaike weight” – ω_i and the cumulative “Akaike weight” – $Cum\omega_i$.

Model	loglik	K	AIC	ΔAIC	ω_i	$Cum\omega_i$
ψ (.) γ (fenced) \mathcal{E} (.) p (trail)	186.36	6	384.73	0.00	2.92	0.29
ψ (.) γ (fenced+dboma) \mathcal{E} (.) p (trail)	185.53	7	385.07	0.33	2.46	0.53
ψ (.) γ (fenced+dcol) \mathcal{E} (.) p (trail)	186.12	7	386.25	1.51	1.36	0.67
ψ (.) γ (fenced+dboma+trend) \mathcal{E} (.) p (trail)	185.12	8	386.25	1.52	1.36	0.81
ψ (.) γ (fenced+trend) \mathcal{E} (.) p (trail)	186.18	7	386.36	1.62	1.29	0.94
ψ (.) γ (fenced+dcol+trend) \mathcal{E} (.) p (trail)	186.04	8	388.09	3.35	5.46	0.99

b) Covariate effects

None of the tested colonization covariates had a significant effect on colonization probabilities (Table 13). Overall, “distance to boma” is the covariate with the highest support (-3.12 (± 2.52)). As occurred for black-faced impala and plains zebra, the detection probability is significantly positively affected by the position of cameras on trails, being more likely to detect elands on cameras positioned on trails (Table 13).

Table 13. Untransformed estimates of probabilities of initial occupancy, ψ extinction, \mathcal{E} colonization, γ , and detection, p , estimated for common eland, and respective effect of tested colonization and detection covariates. $\hat{\beta}$ – untransformed model-averaged coefficient; SE – standard error; CI95- 95% confidence interval; dboma- distance to release site (boma); dcol – distance to last colonized site; fenced – effect of the fence; trend – effect of time trend; trail – effect of the position of a camera on a trail.

	$\hat{\beta}$ (SE)	CI95
ψ	-3.41 (1.02)	[-5.41; -1.41]
γ	-2.65 (1.01)	[-4.64; -0.66]
\mathcal{E}	-2.45 (0.80)	[-4.03; -0.87]
p	-2.91 (0.27)	[-3.45; -2.36]
dboma	-3.12 (2.52)	[-8.08; 1.82]
dcol	-2.75 (4.28)	[-11.15; 5.65]
fenced	-9.70 (31.92)	[-72.26; 52.85]
trend	1.19 (1.79)	[-2.33; 4.72]
trail	1.70 (0.34)	[1.03; 2.37]

c) Colonization-extinction and detection probabilities

The mean detection probabilities of common eland was 0.05 (± 0.57) for cameras located off trails, and 0.23 (± 0.65) for cameras deployed on trails. Initial occupancy has a mean probability of 0.03 (± 0.74), while extinction probability has a mean value of 0.08 (± 0.69). Regarding colonization probabilities, a mean value of 0.07 (± 0.73) was obtained for colonization inside the fence, and 0 outside the fence (Table 14).

Table 14. Estimated values of common elands' probabilities of initial occupancy ψ , colonization γ inside and outside the fenced area, extinction, ε and detection p by cameras located on trails and of trails. $\hat{\beta}$ – untransformed model-averaged coefficient; SE – standard error; CI95- 95% confidence interval.

<i>Process</i>	<i>Parameter</i>	$\hat{\beta}$ (<i>SE</i>)	<i>CI95</i>
<i>Ecological</i>	ψ	0.03 \pm 0.74	[0; 0.2]
	γ (inside fence)	0.07 \pm 0.73	[0.01; 0.34]
	γ (outside fence)	0 \pm 1	[0; 1]
<i>Detection</i>	ε	0.08 \pm 0.69	[0.02; 0.29]
	p (off trail)	0.05 \pm 0.57	[0.03; 0.09]
	p (on trail)	0.23 \pm 0.65	[0.08; 0.5]

d) Proportion of occupied area over time

Common eland shows a constant increasing in occupation area since the first period. Elands revealed a constant growth of occupied area over time (Figure 13), with 12% by the end of the sampling period, a value that is much lower than the ones obtained for plains zebra and black-faced impala.

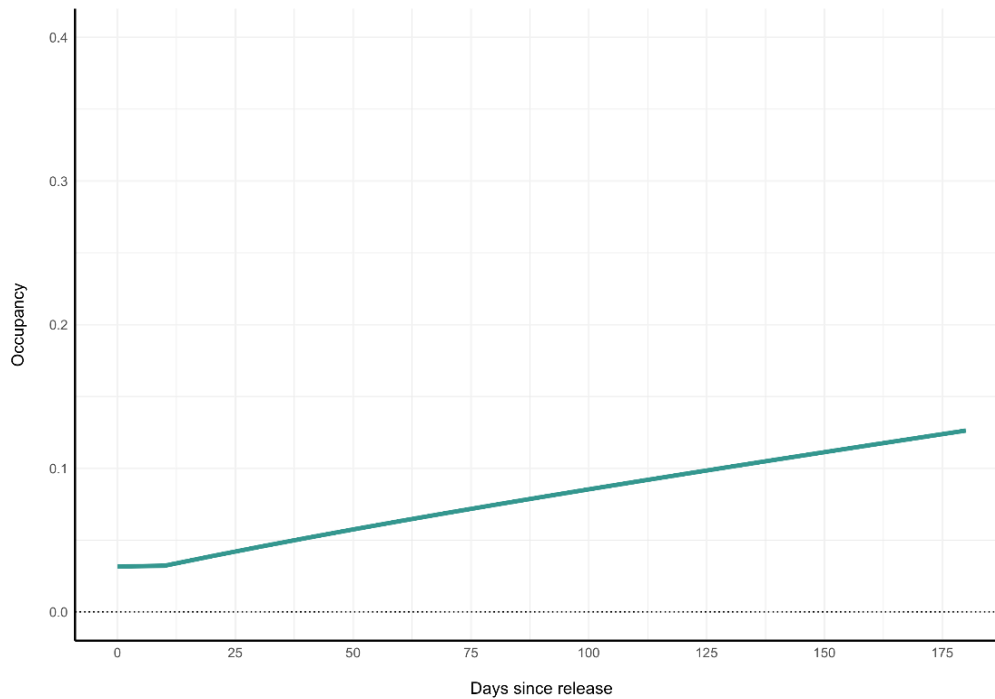


Figure 13 . Proportion of occupied area by common eland population in Cuatir private reserve. The period corresponds to the number of days since the release date, and occupancy values represent the proportion of area occupied at each period.

3.2.4. Greater kudu

a) Model selection

Twelve models were obtained with $\Delta AIC < 7$, and for all models, the position of the camera on trails explains the detection probabilities of this species. The four best-supported models comprise an AIC weight of 0.61 and consider position inside the fence as a driver of the colonization probabilities for greater kudu. The second best-supported model includes the temporal trend for colonization probability, whereas distance to the last colonized site and distance to boma are included in the third and fourth best-supported models (Table 15).

Table 15. Selection of models with substantial support - $\Delta AIC < 7$ - for colonization (γ) and detection (p) of greater kudu, *Tragelaphus strepsisceros*. The colonization covariates considered are the location of a camera in the fenced area – fenced, distance to last colonized site – dcol, distance to boma- dboma, and the detection covariate is the position of a camera on a trail– trail. The model information contains number of model parameters -K, log-likelihood – logLik, the value of the information criterion used – AIC; the delta- ΔAIC , the “Akaike weight” – ω_i and the cumulative “Akaike weight” – $Cum\omega_i$.

<i>Model</i>	<i>loglik</i>	<i>K</i>	<i>AIC</i>	ΔAIC	ω_i	<i>Cumω_i</i>
$\psi (.) \gamma (fenced) \mathcal{E} (.) p (trail)$	227.45	6	466.91	0.00	2.59	0.25
$\psi (.) \gamma (fenced+trend) \mathcal{E} (.) p (trail)$	227.02	7	468.04	1.12	1.47	0.40
$\psi (.) \gamma (fenced+dcol) \mathcal{E} (.) p (trail)$	227.34	7	468.68	1.77	1.07	0.51
$\psi (.) \gamma (fenced+dboma) \mathcal{E} (.) p (trail)$	227.42	7	468.84	1.92	9.92	0.61
$\psi (.) \gamma (.) \mathcal{E} (.) p (trail)$	229.75	5	469.51	2.59	7.08	0.68
$\psi (.) \gamma (dcol) \mathcal{E} (.) p (trail)$	228.82	6	469.64	2.72	6.65	0.75
$\psi (.) \gamma (fenced+dboma+trend) \mathcal{E} (.) p (trail)$	226.96	8	469.93	3.01	5.75	0.80
$\psi (.) \gamma (fenced+dcol+trend) \mathcal{E} (.) p (trail)$	227.00	8	470.01	3.09	5.51	0.86
$\psi (.) \gamma (dboma) \mathcal{E} (.) p (trail)$	229.22	6	470.45	3.53	4.43	0.90
$\psi (.) \gamma (trend) \mathcal{E} (.) p (trail)$	229.39	6	470.78	3.86	3.76	0.94
$\psi (.) \gamma (dcol+trend) \mathcal{E} (.) p (trail)$	228.64	7	471.29	4.38	2.90	0.97
$\psi (.) \gamma (dboma+trend) \mathcal{E} (.) p (trail)$	228.80	7	471.60	4.69	2.48	1.00

b) Covariates effects

Results for greater kudu showed that the covariate “fenced” is the only informative colonization covariate, with a negative effect on colonization probabilities of -1.10 (± 0.54) (Table 16). Greater kudus were detected in seven cameras outside the fence, meaning that either the released individuals were able to cross the fence, or the detected animals were already in the area before releases. Regarding the detection covariate, the estimated effect of the position of a camera on a trail on the detection probability of greater kudu is 2.62 (± 0.50), but the wide confidence interval supports that the effect of this covariate is not significant (Table 16).

Table 16. Untransformed estimates of probabilities of initial occupancy, ψ extinction, ε , colonization, γ , and detection, p , estimated for greater kudu, and respective effect of tested colonization and detection covariates. $\hat{\beta}$ – untransformed model-averaged coefficient; SE – standard error; CI95- 95% confidence interval; *dboma*- distance to release site (boma); *dcol* – distance to last colonized site; *fenced* – effect of the fence; *trend* – effect of time trend; *trail* – effect of the position of a camera on a trail.

	$\hat{\beta}$ (SE)	CI95
ψ	-6.04 (23.01)	[-51.15; 39.06]
γ	-2.35 (0.74)	[-3.81; -0.89]
ε	-0.93 (0.86)	[-2.63; 0.76]
p	-3.55 (0.47)	[-4.48; -2.61]
<i>dboma</i>	-0.62 (1.12)	[-2.83; 1.57]
<i>dcol</i>	-1.78 (2.35)	[-6.40; 2.83]
<i>fenced</i>	-1.10 (0.54)	[-2.17; -0.023]
<i>trend</i>	1.15 (1.37)	[-1.53; 3.84]
<i>trail</i>	2.62 (0.50)	[1.63; 3.60]

c) Colonization-extinction, and detection probabilities

The detection probability of greater kudu in cameras located on trails has a mean value of 0.28 (± 0.7), and 0.03 (± 0.62) for cameras outside trails. Initial occupancy was 0, while extinction probability has a mean value of 0.28 (± 0.7). Colonization probability inside the fence has a mean value of 0.09 (± 0.68), and 0.03 (± 0.09) outside the fence (Table 17).

Table 17. Estimated values of greater kudu's probabilities of initial occupancy ψ , colonization γ inside and outside the fenced area, extinction, ε and detection p by cameras located on trails and of trails. $\hat{\beta}$ – untransformed model-averaged coefficient; SE – standard error; CI95- 95% confidence interval.

Process	Parameter	$\hat{\beta}$ (SE)	CI95
Ecological	ψ	0 \pm 1	[0; 1]
	γ (inside fence)	0.09 \pm 0.68	[0.02; 0.29]
	γ (outside fence)	0.03 \pm 0.78	[0; 0.28]
Detection	ε	0.28 \pm 0.7	[0.07; 0.68]
	p (off trail)	0.03 \pm 0.62	[0.01; 0.07]
	p (on trail)	0.28 \pm 0.73	[0.05; 0.73]

d) The proportion of occupied area over time

Initial occupancy of greater kudu was of approximately 4% and increased gradually since the first period. The portion of occupied area by this species started to stabilize around three months after the release date, and the highest value obtained was 16% (Figure 14).

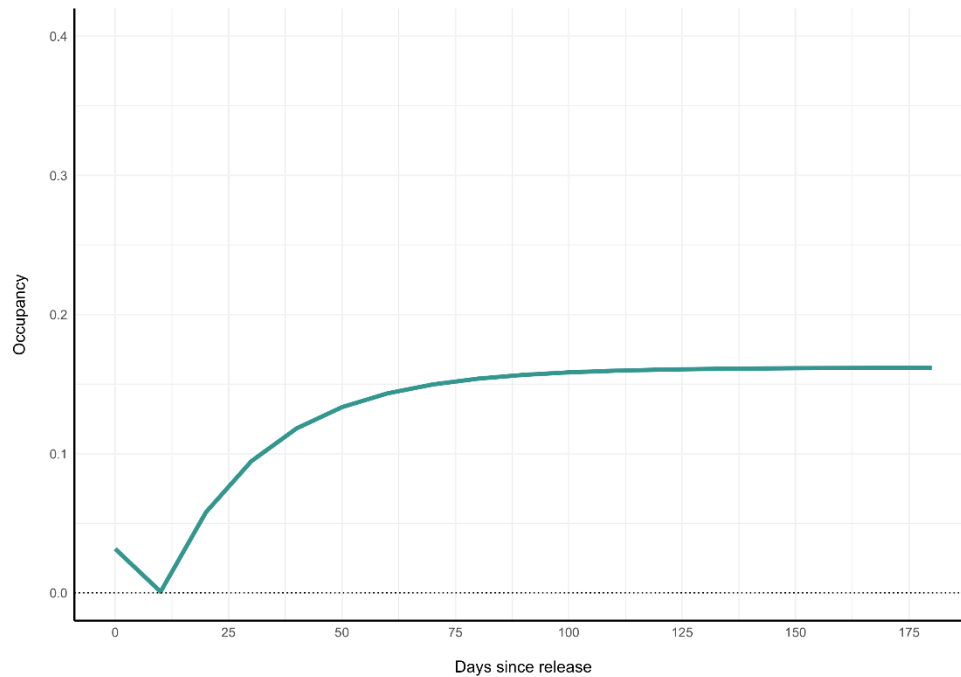


Figure 14. Proportion of occupied area by greater kudu population in Cuatir private reserve. The period corresponds to the number of days since the release date, and occupancy values represent the proportion of area occupied at each period.

4. Discussion

4.1. General discussion

In the present study, camera trapping allowed for the collection of data not only from all target species but also from many others, and the estimation of vital rates for the target populations.

Besides camera trapping, several methods could have been used to monitor the translocated species. Direct field observations (Schneider et al., 2019), and aerial or ground surveys (Rowcliffe, 2017) are traditional methods to survey wildlife, but these bring the disadvantage of requiring strong human participation (Latham et al., 2014).

Other methods such as searching for field signs, i.e., scats or foraging marks, are also used to detect the presence of species and may be applied in monitoring programs, but such methods do not apply to all species and are not accurate to estimate colonization rates, since detection probabilities are usually not accounted for (Janečka et al., 2011). Non-invasive genetic techniques can also be used to assess populations' colonization trends, allow the estimation of population parameters, and acquire information that might not be easily assessed with camera traps, such as accurate individual and sex identifications (Balestrieri et al., 2021). However, such methods often imply expensive and time-consuming laboratory manipulations, as well as constraints due to the degradation of genetic material (Murphy et al., 2019).

Tracking animals with GPS collars has also been used to evaluate the same kind of questions that are targeted in this study, since they are suitable to acquire specific spatial and temporal data for many species, including elusive mammals, and allow to collect of data regarding animal movement and location with high accuracy (Hebblewhite & Haydon, 2010). For this study, such devices could have been used to monitor the dispersal of the translocated species with high precision, and infer if the released greater kudu, for instance, crossed the fence. Despite their many advantages, GPS collars also have constraints. These include the high cost, potentially biased estimates due to inference to the whole population drawn from tracking data from only a few individuals, and direct negative effects on the animals that have to be captured and manipulated (Borquet, 2020). Several studies revealed atypical behavioral traits in tracked animals (Brooks et al., 2008; Nussberger & Ingold, 2006), and other adverse effects such as increased energy expenditure (Lear et al., 2018; Rosen et al., 2018) and even decreased survival rate of marked versus non-marked conspecifics (Severson et al., 2019).

Overall, camera trapping brings many advantages due to its low invasiveness, and capacity to capture images through any environmental and habitat conditions (Wern & Glover-Kapfer, 2019). In this particular study, this technique could have been

complemented by tagging the animals before their release – through neck collars or ear tagging - not only to obtain more accurate data regarding species dispersal along the release area but also to identify individuals and to distinguish between translocated and native ones.

Regarding the number of independent detections obtained for the different species, a higher number was obtained for camera CBR-F4 (Table 3), probably due to its' proximity to the release site (Figure 10). Among the target species, black-faced impala collected the highest number of independent detections (127, Table 4), which can be due to a higher population size. Moreover, black-faced impala and kudu were the only species detected outside the fenced area (Table 4), confirming that black-faced impalas were able to cross the fence. Furthermore, carnivores including leopard and cheetah were also detected inside the fence (Table 5), which might have influenced the target species colonization-extinction dynamics due to anti-predator behaviors.

4.2. Ecological and detection processes

4.2.1. Colonization-extinction probability

Colonization is one of the most important parameters to consider when addressing reintroductions since individuals should occupy the space in the new environment and make use of the available resources (Nichols & Armstrong, 2012).

The basal colonization probabilities outside the fenced area were estimated for black-faced impalas and the greater kudu, resulting in very similar values (Tables 11 and 17). Black-faced impalas' colonization probability in the open area was higher than inside the fenced area of Cuatir, suggesting that the individuals moved towards that area after their release. Other studies investigating the habitat use of black-faced impalas have shown that the species tends to occupy ecotones and edge areas that share grassland and woodland, while avoiding open areas (Matson et al., 2005, 2006). Ecotones have a high variety of vegetation, which is important for impalas' usual changes in dietary preferences (Jarman, 1973), but also because woodlands provide shelter in escape situations, while grasslands offer visibility to threats such as predators (Matson et al., 2005). Since potential predators of this species, i.e., leopard and cheetah, were detected by cameras located inside and outside the fenced area (Table 5), is possible that black-faced impalas chose to move towards the ecotones outside the fenced area, to enhance both their vigilance and flight capacity.

Regarding the colonization inside the fence, plains zebras showed the higher value of basal colonization probability, followed by greater kudu, common elands, and black-

faced impalas. This indicates that zebras have a stronger capacity to disperse and colonize the hosting area (Wang et al., 2021) than the remaining target species.

Extinction probabilities correspond to the odd of a location not being occupied by a species during a sampling season, given that it was occupied by that species in the previous season (MacKenzie et al., 2003). In this study, greater kudu showed the higher values of basal extinction probability, followed by black-faced impalas, common elands, and plains zebras, that showed the lowest values.

Habitat features and climate conditions play a major role in influencing extinction rates (Yackulic et al., 2015). Plains zebras' basal extinction probability contrasts with their high values of colonization, and these values, together with the rates of the proportion of occupied area over time, implies that zebras occupied the area evenly, and did not stop using a given site after colonizing it. This pattern suggests that zebras could find suitable habitat throughout the fenced area of Cuatir (Franken & Hik, 2004), and might also be related to this species' big home ranges (Klingel, 1969).

Contraly, black-faced impalas' extinction probability was higher than their colonization probability, and this disparity is explained by their departure from the fenced area towards the open area of Cuatir. By doing so, black-faced impalas left the sites that were initially colonized inside the fenced area, increasing the basal extinction probability (MacKenzie et al., 2003).

A small population of greater kudu was already present in Cuatir before the performed releases and occurs both in the fenced and in the open areas. Hence, the individuals are dispersed through a larger area when compared to the remaining target species, explaining the high extinction probabilities (Hofmeester et al., 2019). Moreover, greater kudu establish home ranges of approximately 22 km² (Du Toit, 1990), which can lead to higher local extinction probabilities while individuals move along Cuatir.

Regarding common elands, their extinction and colonization probabilities presented very similar values, which is illustrated by their constant proportion of occupied area over time. Elands' movement behavior is typical of herds, moving in a group from place to place (Pappas, 2002). These slow and gradual movements might underly the obtained similarity between basal extinction and colonization probabilities that were obtained for this species.

4.2.2. Detection probability

Many factors can underly a species detection probability, essentially related to habitat use and/or behavior, environmental conditions, or camera settings (Gjelland & Hedger, 2013; Hofmeester et al., 2019). Animal features such as species home range, daily range, population density, and behavior (Hofmeester et al., 2019; Neilson et al., 2018), and environmental elements – resource availability, time of the day, or weather – might as well influence detection (Hofmeester et al., 2019). Hofmeester et al (2019) proposed that realized detection probability results from a combination of three conditional probabilities: i) the probability that an animal moves in front of a camera, ii) the probability that the animal triggers the sensor of the camera given that it went in front of it, and iii) the probability that it can be identified in the image.

The detection probabilities outside trails resulted in small differences among the target species. However, the differences between species detection probabilities on trails are more marked. Plains zebra was the species with the lowest detection probabilities on trails out of the four species, whereas the greater kudu was the one with the highest values for this variable. Black-faced impala and common eland had similar intermediate values. These results were concordant with those obtained in a camera-trapping study performed in Mlawula Nature Reserve and Mbuluzi Game Reserve (Swaziland), where plains zebra was also the species with lower detection probability values ($0.05 \pm (0.03)$), followed by impala ($0.08 \pm (0.04)$) and the greater kudu ($0.09 \pm (0.04)$) (Soto-Shoender et al., 2018). In this study, the different detection probabilities were associated with the denseness of the vegetation and the level of visual obstruction in the areas where the species were detected, two factors that can also be responsible for the different detection probabilities obtained in this study (Hofmeester et al., 2019).

The results of this work suggest that the frequency with which a species uses a given area may explain the detection probabilities of the four species. Plains zebras tend to move frequently (Pedersen et al., 2018) and establish large home ranges (Klingel, 1969). Therefore, zebras may be less likely to revisit a camera, resulting in lower detection probabilities (Hofmeester et al., 2019). However, black-faced impala, the greater kudu, and common eland have smaller home ranges when compared with plains zebra (Du Toit, 1990; Lorenzen et al., 2010) which contributes to more frequent use of the same area and the higher detection probabilities obtained for these species, when compared with plains zebras.

Furthermore, Colyn et al (2018) suggested that animal body size influences its' detection probability, whereas bigger animals have a higher probability of being detected.

However, our results do not support this suggestion. Instead, the obtained results agree with the ones described by Silveira et al (2003), where the species body size presented a negative correlation with detection probabilities. This pattern can however be related to low population densities in each study site (Colyn et al., 2018).

4.3. Effects of detection and colonization covariates

The group of best-supported models ($\Delta AIC < 2$) for the four target species shows similarities, but also several disparities. The colonization covariate “fence” is included in all the best-supported models for all species, strongly suggesting that this structure influences animal movements. The distance to the release site (boma) is also included in a few best-supported models for the four species, but it has more impact on common elands’ colonization probabilities than on the remaining species as it is present in two best-supported models while only in one for the other species. The distance to the last colonized site is included in one of the best-supported models for each species suggesting some influence of this variable in colonization. The covariate “temporal trend” is included in all the best-supported models for impala, in two models for common eland, and one model for plains zebra and greater kudu, suggesting a variable effect of time since release date on species colonization rates.

4.3.1. Detection covariate

The observed effects of the location of the camera on a trail on the detection probabilities confirm that the four species are using human trails as a travel route more often than other pathways. This is in agreement with other studies that also observed a positive association between the deployment of cameras in human trails and the detection probabilities of several species (Balme et al., 2009; Karanth, 1995; Kolowski & Forrester, 2017; Mann et al., 2015; O’Connell et al., 2011; Soisalo & Cavalcanti, 2006). Such results can have several explanations. First, often mammals prefer to move on trails because these travel routes are more energy-efficient than thickly vegetated environments (Kolowski & Forrester, 2017; Rafiq et al., 2020). In Yellowstone National Park, bison prefer to travel through groomed roads during winter since those paths allow a lower energy cost to cross than natural routes covered in snow (Bruggeman et al., 2007). Moreover, paths are associated with a more efficient territory marking and intra-specific communication for some species, e.g., the Eurasian lynx (*Lynx lynx*) (Krofel et al., 2017). This species shows higher rates of marking in paths, particularly on roads,

than in natural habitats, and Eurasian lynx populations are even suggested to have their community networks increased when traveling through roads (Krofel et al., 2017).

Large carnivores show a tendency to use trails and roads as travel routes, and some prey species adopt the same travel strategies, which could eventually lead to higher predation rates (O'Connell et al., 2011). Usually, leopards and cheetah – carnivore species inhabiting Cuatir- tend to avoid preying on larger species like plains zebra, kudu, and eland (Hayward et al., 2006a, 2006b; Stein et al., 2015). Therefore, the low predation risk for these species may result in their higher tendency to use trails for locomotion. Regarding the use of trails by black-faced impala in Cuatir, which is potential prey for both leopard and cheetah (Hayward et al., 2006a, 2006b; Melin et al., 2016), it is plausible to assume that this species is still naïve to the presence of predators in the new habitat (Ruxton, 1995), not avoiding trails as an anti-predator behavior. In addition, wildlife locomotion strategies usually rely on the best cost-benefit ratio (Carnahan et al., 2021), considering environmental parameters like travel speed, facility of movement, and danger (Luo et al., 2019). Hence, higher probabilities of detecting black-faced impala on trails suggest that the trade-off of facing higher predation rates by sharing the paths with predators may be, compensated by the energy that is saved while using trails as a travel route.

Another justification for the obtained results is the potential low density of predators of these species in Cuatir, or the presence of smaller predators such as caracal, which shows no threat LH (Braczkowski et al., 2012; Grobler, 1981), and shows no preference for small ungulates like a black-faced impala (Avenant & Nel, 2002).

4.3.2. Colonization covariates

4.3.2.1. Camera position concerning the fence

The colonization probabilities of the four species seem to be strongly influenced by the position of a particular area regarding the fence. The effect of this covariate could not be accurately quantified for plains zebras and common elands, because both were only detected inside the fenced area. As observed for other ungulates, such as the pronghorn antelope (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*), or elk (*Cervus elaphus*), a reduced number of pictures across a fenced area indicate reluctance or even incapacity on crossing fences (Scott, 1992). Likewise, the species under study likely face some difficulties in crossing the fence present in Cuatir. The difficulty of crossing can also be directly related to the characteristics of the fence (Connolly et al., 2009; Pirie et al., 2017), since fences over 2.4 m are known to be

effective in containing common eland's, greater kudu's, and impala's movements (Lindsey et al., 2012).

The black-faced impala and greater kudu were detected outside the fenced area, therefore the effect of the fence on colonization probability was more accurately estimated for these species (Tables 10 and 16, respectively), being negative for both. As black-faced impalas were absent from Cuatir before the reintroductions, the detections of this species across the fenced area support two distinct scenarios: either the fence is partially permeable to this species or black-faced impalas were able to move around it through the floodplains. In any case, the colonization probabilities in the unfenced area were low (Table 11). It is not possible to conclude if the greater kudus detected beyond the fenced area were released or resident individuals – that is, if they were able to cross the fence, or if those detections correspond to the individuals that already existed in Cuatir, outside the core conservation area.

4.3.2.2. Temporal trend

Common elands did not exhibit a temporal trend in colonization rates. Conversely, black-faced impalas increased the probability of colonization with time since release. Greater kudus and plains zebras' colonization rates showed a similar pattern, with a tendency to increase the colonization probability over time. The different responses to temporal trends are reflected in the distinct occupation dynamics between species and can be related to several features.

a) Species mobility and habitat suitability

Habitat suitability and species mobility are the two most important parameters in colonization: generally, a site is more likely to be colonized if having suitable conditions for a given species, while species with more mobility capacity have higher probabilities of colonizing a site (Yalcin & Leroux, 2018).

Plains zebras perform long and frequent movements (Regassa, 2013; Pedersen et al., 2018), which explains this species' higher colonization probability. Moreover, reintroduced plains zebras use their mobility and accurate sense of orientation to move towards quality resources (Mandlate et al., 2019), which seems to have been the case in Cuatir.

Regarding habitat suitability, the abundance of resources that fulfill species-specific needs does not seem to condition the target species' colonization rates, since species

with distinct needs have similar tendencies – greater kudu and plains zebras (Roque et al., 2021) – , while species with shared requirements – common eland and black-faced impala (Roque et al., 2021) - revealed distinct patterns. This has two distinct explanations: on one hand, this study was performed during the wet season (Huntley et al., 2019), where water and vegetation that provide quality forage are abundant and do not limit species movements. On the other hand, the preference for the habitat with specific features is not expected in the first months following the releases, since the animals are in an initial exploration phase where they don't know the area and its' resources (Berger-Tal & Saltz, 2014).

b) Neophobia

Neophobia is a reaction of fear produced by contact with a new situation or stimuli (Schaffer et al., 2021), and shapes the ecology and behavior of several wild populations (Crane & Ferrari, 2017). It can be manifested in different ways, but spatial and predation neophobic responses (Crane et al., 2020) are particularly interesting for this study. Many species exhibit spatial neophobia when put in new or unknown areas (Crane et al., 2020), since the habitat and its potential dangers are unknown, and the resultant behaviors can cause less frequent or slower movements and migration rates, resulting in more time needed to start exploring a new environment (Crane & Ferrari, 2017).

In this study, is suggested that all species have exhibited spatial neophobia. However, the time necessary to overcome these tendencies was shorter for plains zebras and greater kudu, while black-faced impalas took more time to do so. However, the patterns of common elands' colonization suggest that they were not able to overcome neophobia in the first six months following their release in Cuatir.

c) Distinct predation risks

Different predation pressures across species tend to follow a pattern related to body size, where smaller species are often preyed with higher frequency and by more predator species (Schaffer et al., 2021). Hence, smaller animals adopt more cautious behaviors as a measure of defense against predation (Crane & Ferrari, 2017).

The target species colonization trends follow a similar pattern. Black-faced impalas have a smaller body size than the remaining species (Roque et al., 2021), and have higher predation by the carnivores inhabiting Cuatir (Matson et al., 2006). Therefore, they adopt increased vigilant behaviors when recently exposed to natural predators, as was

observed in a study regarding the occupation of the area of released black-faced impalas in Etosha National Park (ENP), in Namibia (Matson et al., 2005, 2006).

In Cuatir, plains zebras do not seem to avoid areas covered in dense vegetation, which is an important part of this species anti-predator behavior (Chen et al., 2021; Riginos, 2015; Valeix et al., 2011). Moreover, plains zebra showed strong exploratory behavior, similar to the observed for the reintroduced American bison in Europe (Schmitz et al., 2015), and is a feature of less cautious/neophobic animals (Schaffer et al., 2021). Greater kudu showed a similar pattern, but more caution is manifested because kudus' populations form groups of females, juveniles, and subadults, while males are separated (Du Toit, 1995), and female greater kudu and calves are potential prey for leopards (Kandume, 2012; Mills, 1993).

Elands are very large animals (Roque et al., 2021), but seem to keep their prudent movements, apparently being an exception to the association between animal size and degree of cautiousness towards predators (Crane et al., 2020). This can be due to the fact of elands being very shy animals (Mastin, 2000).

d) Thermoregulation

Solar radiation and high temperatures often affect species daily activity (Jarman & Jarman, 1974). Black-faced impalas, greater kudu, and common elands are generally less exposed to such environmental conditions since these species prefer areas with thicker vegetation cover (Roque et al., 2021). Plains zebras, however, prefer grasslands (Roque et al., 2021), where the foliage does not provide considerable protection against solar radiation.

Due to their small size, black-faced impalas rely on keeping under the shadow provided by vegetation (Jarman & Jarman, 1974) as a thermoregulation mechanism, to be less exposed to solar radiation and warm temperatures, therefore moving less in the first weeks after their release (Veldhuis et al., 2019). The larger species, however, rely on sweating to lose heat, and not on seeking protection under shade (Veldhuis et al., 2019), which clarifies the lower occupation rates obtained for black-faced impalas in comparison to the larger species in the first weeks following their release.

4.3.2.3. Distance to release site (boma)

Estimating the effect of the distance to release site on colonization allows to infer the fidelity of species to the release site, rates of expansion, among other information

(Yott et al., 2011), and the tendency of an individual to stay close to the release site is important for the success of the translocation (Rogers, 1988; Yott et al., 2011).

In this study, the effect of the distance to the release site was not significant for any of the four species. However, it was included in two of the best-supported models for common eland, and was the colonization variable with better-estimated values for this species, suggesting a negative effect on the colonization of this species. Moreover, elands showed a slow rate of occupancy in the new environment, and a lower proportion of occupied area compared to the other species (Figure 13). These results indicate that elands had a tendency to maintain their occupation range close to the release site and colonized the area slowly. These occupancy patterns suggest that the habitat can provide the necessary resources for this species and that elands might move less to enjoy those resources and save energy (Berger-Tal & Saltz, 2014; Stamps & Swaisgood, 2007). However, these results can also rely on shy or neophobic behaviors, as well as weak exploratory tendencies (Crane et al., 2020).

4.3.2.4. Distance to the last colonized site

Although informative, the effect of the distance to the last colonized site was not significant for any of the target species, although it was included in one of the best-supported models for each one. It is expected that the occupancy status of close sites has more influence on other site colonization and persistence than distant sites (Bled et al., 2011). Indeed, according to both the metapopulation paradigm for fragmented landscapes and the invasion theory, the probability of one site being colonized is higher for lower distances from the closer previously occupied sites (Bled et al., 2011; Davies et al., 2018), as shown in different studies (Kolar & Lodge, 2001; Lockwood et al., 2005). Yet, the results from this study did not support this pattern.

Plains zebras' home ranges vary between 80 to 250 km² (Klingel, 1969), while common elands have home ranges that are beyond 50 km² (Lorenzen et al., 2010). Greater kudu and black-faced impala's home ranges are smaller, being around 22 km² (Du Toit, 1990), and 6,81 km² (Du Toit, 1990), respectively. Hence, the distances between different sampling units (2 km) are low when compared to the animals' home ranges and their mobility, and these are capable of colonizing distances that are much bigger than the ones between two neighbor sampling sites, justifying the obtained results.

5. Conclusions

The performed reintroductions of Angolan giraffe, plains zebra, and black-faced impala returned these species into the Angolan province of Cuando-Cubango, and the population reinforcements increased the number of common elands and greater kudus in the region, which are the main contributions of these translocations. This study provides relevant information regarding the colonization-extinction dynamics of four of the ungulate populations released in the Cuatir Conservation Area, and the respective rates of occupation of the new environment along the first six months after the releases. Moreover, it brings insights regarding the factors underlying the colonization process for each species, and how they vary with time.

The main conclusion of this study is that all the target species were able to colonize the new hosting habitat, suggesting that the performed conservation translocations have been successful in the first six months.

Regarding the species-specific colonization-extinction dynamics and resultant occupation rates, these generally agree with the patterns obtained in other studies and show some variation among species. Such differences are mainly related to distinct biologic and ecological features i.e., preference for specific landscape features, thermoregulation, or different predation risks, but the obtained results suggest that behavior – in particular neophobic and exploratory tendencies - plays an important role in colonization as well. Moreover, these features can also explain the distinct effects of time on the colonization rates of the target species.

Regarding the analyzed colonization covariates, the absence of significant effect of the analyzed distance covariates implies that the released species can disperse from the release site, and that exists efficient habitat connectivity in CCA. Moreover, the quick occupation of almost the entire fenced area by the target species suggests that the extension of the region might be too small when related to species home ranges.

My results also suggest that the fence constraints the movements of large herbivores, but smaller species such as black-faced impalas and others can cross it, which was already expected due to the fence's height and the fact that it is not buried in the ground. The fenced area can be considered a useful acclimatization zone for newly released individuals, not only by preventing their escape but also by protecting them from hunters.

Regarding the detection process, my results strongly suggest that all the target species prefer to travel through human trails, which intensifies the efficacy of these

structures as energetically efficient travel routes when compared to more natural environments.

Finally, by performing this study I concluded that camera trapping techniques are quite useful to monitor wild populations and to monitor conservation translocations as well. Despite some disadvantages i.e., bad quality factors and exhaustive analysis of camera trapping data, this technique allowed to obtain unequivocal data from all the target species in this study, and to estimate the parameters of interest using dynamic occupancy models, which were the main goals of this project.

Overall, these translocations and respective monitoring provided useful knowledge regarding the target species ecology, biology, and behavior, following their release in a new environment, and this can be implemented in future conservation translocations of this species or similar ones (Cochran-Biederman et al., 2015).

6. Future perspectives

Reintroductions and population reinforcements are very important contributors to restoring and stabilizing wild populations, and their monitoring is a key factor to understand how the released individuals adapt and occupy a new habitat. Regarding this project, the results for the first six months after release are promising, and continuous monitoring is recommended to verify how the species occupation rates vary along longer periods and apply adequate measures if necessary.

Furthermore, it would be interesting to verify how the species colonization-extinction dynamics change during the dry season since this can be marked by the existence of fewer food resources and water. Also, with the potential decrease of the water levels of Cuatir river, large herbivores could be able to cross this natural barrier and colonize the open area. Hence, future surveys in CCA aim to infer the eventual colonization rates of the open area.

In future similar studies, using data collected over more time after the release, including more detection and colonization covariates will be useful to gain more insight regarding the main forces behind the colonization and extinction processes. Habitat selection by the target species was not expected in the first six months after release, but such starts to occur later. Hence, the effects of distinct vegetation cover, distance to water sources, environmental conditions, and other factors on the colonization-extinction rates of these species could provide valuable knowledge.

Moreover, future analyses could include individual and sex identification, to estimate population sizes and sex ratios, which are important parameters to verify population stability and allow appropriate management.

Finally, upcoming translocations performed into CCA should consider marking the animals previously to the releases, to enhance individual identification and in the case of population reinforcements, distinguish between translocated and native individuals. This procedure would have been useful in this study, for instance, to infer if the released greater kudu colonized the open area.

Furthermore, species home ranges must be considered for future similar procedures, and the dimension of the fenced area adjusted accordingly.

7. References

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