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# Optimizing small mammal relative abundance measures using non-invasive sampling and assessment of its contribution to occupancy modelling of small carnivores in a dry woodland savannah of South Africa

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*"If I have ever seen magic, it has been in Africa."*

John Hemingway

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## Preface

The present study is part of a larger project of the University of Venda, Limpopo, South Africa, entitled "Large carnivore mediated ecosystem service change". It focuses on understanding the influence of the presence or absence of large carnivores on the trophic chains and how this can ultimately influence the risk of zoonoses transmissions through mesocarnivore release.

# Abstract

Small mammals of the Order Rodentia represent a large portion of small carnivores' diet, influencing their distribution, densities and activity patterns. However, small carnivore studies based on camera-trapping do not include small mammals' relative abundance as prey covariate, mainly because of the large effort and cost associated with live-trapping at large scales. Alternatively, ink-tracking tunnels are a non-invasive, inexpensive and a low effort sampling method that can be used to monitor fluctuations in small mammals' relative abundance across sites and time. I implemented ink-tracking tunnels in a y-design to understand its efficiency when compared to live-trapping and the utility of the track index as prey covariate in a carnivore distribution study across a landscape gradient of human disturbance. Tracks were successfully divided into functional groups according to track size and consequently rodents' biomass. Track index of these groups was highly correlated with live-trapping abundance index, despite this correlation being abundance dependent, as the method is better at detecting large fluctuations of abundance when the group is very abundant than for low abundant species.

I applied the track index of the rodent functional groups as prey covariates to a single species – single season occupancy model for African small carnivore species, along with habitat and disturbance as alternative covariates. Results showed no preference for prey size and neither were prey covariates important for most combinations of species and areas. The only exception was the large-spotted genet at the highest level of disturbance, but only when prey was combined with habitat and disturbance variables. Therefore, the importance of prey covariates is species and context dependent, and it can be discarded from generalist multi-species distribution studies. However, prey should be considered together with habitat variables in studies of carnivore species that are rodent specialists or that rodents represent a large percentage of their diet.

Keywords: ink-tracking tunnels, rodents, track index, occupancy model, disturbance

# Resumo

Os pequenos mamíferos são essenciais para a estrutura e funcionamento dos ecossistemas pelo papel que desempenham na dispersão de sementes, ciclo de nutrientes e como principal fonte de alimentos de diversos predadores de superfície e voadores. Enquanto presas, as flutuações na sua abundância de acordo com a disponibilidade de alimento e temperatura, influenciam os padrões de ocupação do espaço, as densidades e os padrões de atividade dos seus predadores. Contudo, e apesar de constituírem uma importante fonte de alimento para muitos pequenos carnívoros, os estudos acerca da distribuição destes são limitados pela não utilização de medidas de abundância das suas presas, em particular os roedores. Esta falha deve-se muito a limitações e constrangimentos dos métodos de amostragem para avaliação de abundância. O método de captura-recaptura por armadilhagem, largamente usado em estudos de roedores, além de invasivo requer um esforço amostral muito elevado, visto que as armadilhas devem ser verificadas duas vezes ao dia para evitar a morte indesejada de indivíduos, acarreta um elevado custo e necessita de licença de captura e manuseamento de animais selvagens. Estes fatores impedem o seu uso em estudos de larga escala, tais como estudos de distribuição de carnívoros. Como alternativa, os túneis de tinta são um método de amostragem que permite a estimativa de abundância relativa de pequenos mamíferos através das suas pegadas, sendo, portanto, não invasivo e evitando a necessidade de licença, têm reduzido baixo custo e, principalmente, são de fácil colocação e não requerem controlo diário.

Sendo objetivo da presente tese avaliar os padrões de distribuição dos pequenos mamíferos numa savana seca da África do Sul, numa primeira fase este estudo procurou avaliar a eficácia da amostragem de roedores com túneis de tinta para estimar a sua abundância relativa, comparativamente a um índice de abundância relativa obtido por armadilhagem. Numa segunda fase testou-se a utilidade do uso do índice de pegadas obtido com túneis de tinta como medida de abundância de presas no estudo da distribuição de pequenos carnívoros. A amostragem dividiu-se assim em duas etapas. Numa primeira etapa, em 19 locais selecionados num gradiente de perturbação antropogénica (Reserva Natural de Phinda, fazendas e comunidades rurais), os túneis de tinta foram colocados num desenho em Y de 3 x 3 com 10 m de distância entre si, lado a lado com uma grelha de 7 x 7 armadilhas Sherman. Na segunda etapa, os túneis foram colocados com o mesmo desenho em redor de cada uma das 192 câmaras de foto-armadilhagem para os pequenos carnívoros, dispostas em grelha (1311 m de distância média entre câmaras), cobrindo o mesmo gradiente de perturbação.

Considerando que os carnívoros podem mostrar preferência por presas de diferentes tamanhos de acordo com as suas necessidades energéticas, ainda que nas análises se tenham considerado os roedores no geral (variável presas), pegadas foram ainda divididas em grupos funcionais de acordo com o seu tamanho, refletindo consequentemente o tamanho dos roedores: roedores pequenos, médios e grandes. A partir desta divisão foi estimado o índice de pegadas por grupo funcional, que consiste numa proporção de túneis por local com pegadas de cada grupo. Ao comparar este índice com o índice de abundância obtido através da armadilhagem, foi possível observar uma forte correlação entre ambas as medidas, a qual é dependente da abundância local de roedores. Ou seja, o método é mais eficaz a capturar grandes diferenças na abundância relativa quando os roedores se encontram em elevada abundância, do que quando a sua abundância é reduzida. É de referir que os túneis de tinta não permitem uma estimativa rigorosa da abundância das populações, mas são úteis na monitorização de flutuações de abundância, permitindo uma comparação entre locais ou ao longo do tempo.

Os resultados previamente obtidos sustentaram a aplicação do método dos túneis de tinta para avaliação da abundância relativa de presas no estudo de foto-armadilhagem de pequenos carnívoros ao longo do referido gradiente de perturbação antropogénica. Os índices de pegadas de roedores pequenos e médios, e de roedores em geral, foram incorporados no processo de modelação da ocupação pelos pequenos carnívoros, juntamente com variáveis de habitat e perturbação. Os roedores grandes não foram considerados devido ao reduzido número de deteções. Os resultados mostraram que para os carnívoros em estudo a abundância relativa dos roedores (global ou por grupo funcional) não é um fator decisivo na sua distribuição. A única exceção foi registada relativamente à geneta-malhada, na paisagem com mais alto nível de perturbação (comunidades rurais), mas apenas quando as variáveis de presas foram combinadas com variáveis de habitat e perturbação. Assim, é possível concluir que a importância de roedores depende da espécie e do contexto, podendo a sua utilização ser pouco relevante no estudo da distribuição de espécies de carnívoros generalistas, no entanto, deve ser considerada juntamente com variáveis de habitat em estudos de carnívoros especialistas em roedores ou cuja dieta integre uma elevada percentagem de roedores.

Palavras-chave: abundância relativa, roedores, túneis de tinta, armadilhagem, modelo de ocupação

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CHAPTER 1 – *GENERAL INTRODUCTION*

**Predators and their effect on ecosystems**

Predation is an antagonistic interaction where a predator kills and consumes an individual of another species – the prey –, constituting a strong selection process that leads to physical and behavioural changes in both predator and prey (Abrams, 2000; Fleischer, TerHorst & Li, 2018). During top-down regulation, predators (and predation rates) can deeply influence prey populations, ultimately impacting broader communities by, for example, influencing prey distribution and consequently the competition interactions within prey species that can cascade through the trophic levels (Belgrad & Griffen, 2016). In a stable community, processes induced by predators are as important as those induced by resource availability (Ruiz-Capillas, Mata & Malo, 2013). In contrast, during bottom-up processes, predator activity patterns, densities and distributions are affected by prey availability and distribution (Fuller & Sievert, 2001). Fluctuations in the abundance and biomass of prey populations, and their geographical distribution, play an important role in the viability of carnivorous populations, both in terms of reproduction and mortality from food shortages (Fuller & Sievert, 2001; Owen-Smith & Mills, 2008).

**Factors affecting predator densities**

Prey abundance therefore remains a key factor affecting the population densities of carnivores species (Fuller & Sievert, 2001; Balme, Hunter & Slotow, 2007; Červinka et al., 2013). For the vast majority of the carnivores' species, short and long-term changes in their prey abundance, availability and distribution, are the most impactful forces on population viability, distribution and abundance (Fuller & Sievert, 2001).

Such variation in resource (prey) abundance is specifically pronounced in specialist carnivores (Andersson & Erlinge, 1977; Hanski et al., 2001). Specialist predators are adapted to hunt a specific type of prey, e.g. rodents, and their abundance is highly influenced by the prey availability (Andersson & Erlinge, 1977). Even though specialists can consume other food resources when their primary prey (e.g. rodents) is scarce (e.g. switching to insects), their ability to catch other types of prey is often limited. Therefore, their population is influenced by rodents abundance fluctuations (Andersson & Erlinge, 1977; Hanski, Hansson & Henttonen, 1991). In contrast, generalist predators can feed on different types of food sources (e.g. from rodents to insects or birds), where predation is most likely affected by resource availability. Thus, in habitats with a wide diversity of potential prey, generalist carnivores are little influenced by fluctuations in rodent density, while in habitats with limited alternatives, these predators abundance can oscillate with the abundance of rodents (Andersson & Erlinge, 1977).

Even though prey plays an important role in carnivore densities, studies have highlighted the impact of large carnivores on smaller carnivore densities (Caro & Stoner, 2003; de Satgé, Teichman & Cristescu, 2017; Ramesh, Kalle & Downs, 2017; Rich et al., 2017). Small carnivores are particularly vulnerable to the presence of larger carnivores (Caro & Stoner, 2003; de Satgé et al., 2017), due to competition for resources (Caro & Stoner, 2003; de Satgé et al., 2017), interspecific killing not necessarily by predation (Caro & Stoner, 2003; Ramesh et al., 2017) or simply harassment that can injure the smaller carnivores (Ramesh et al., 2017). This pressure influences small carnivores densities and distribution, often leading them to ponder a trade-off between food resources and avoidance of large carnivores (de Satgé et al., 2017; Ramesh et al., 2017; Rich et al., 2017).

**Small carnivores**

Given the importance of large carnivores in shaping terrestrial communities (Ramesh et al., 2017), their conflict with humans (Schuette et al., 2013) and low densities (Caro & Stoner, 2003), it is no surprise that the majority of research interest and funding is directed to large carnivores (Ray, Hunter & Zigouris, 2005). However, small carnivores (e.g. Families Ailuridae, Eupleridae, Herpestidae,

Mephitidae, Mustelidae, Nandiniidae, Procyonidae, Viverridae) (Schipper *et al.*, 2008), often constitutes the majority of carnivore species in ecosystems (Roemer, Gompper & Valkenburgh, 2009) Their "lower risk" conservation status and a belief that they are common and widespread leads to low funding and research interest which makes them among the less studied carnivore species (Schipper *et al.*, 2008; San *et al.*, 2013). Even though this group is quite common and diverse, there is a tendency to underestimate their ecosystem importance. In fact, small carnivores fulfil important ecological roles which includes regulating the structure of small mammal and invertebrate communities (San et al., 2013), seed dispersal and seed predation (Guimarães, Galetti & Jordano, 2008; Roemer *et al.*, 2009) scavenging and carrion removal (DeVault *et al.*, 2011), and rodent pest control (Williams *et al.*, 2018).

Small mammals are a key prey item for the majority of African small carnivores (Williams *et al.*, 2018). Given the importance of prey in shaping carnivore abundance and distribution, it is surprising that the majority of small carnivore studies focus on habitat characteristics and human disturbance in addressing small carnivore distributions (Vanthomme *et al.*, 2013; Widdows & Downs, 2015; Widdows, Ramesh & Downs, 2015). Diet and prey information is only included in diet studies, and not as factors shaping small carnivore distribution and abundance (Avenant & Nel, 1997; Atkinson, Macdonald & Kamizola, 2002; Klare *et al.*, 2010; Ramesh & Downs, 2015). Hence, such studies incorporating small mammal abundance in small carnivore distribution models are still lacking.

**Importance of small mammals**

Incorporating small mammals into diversity and density studies is challenging since small mammals have such a great diversity (Caro, 2001; IUCN/SSC Small Mammal Specialist Group, 2019), have strong seasonal population signals (Krebs & Myers, 1974) and have fine scale habitat associations, which makes it very costly to effectively survey and quantify (Datiko, Bekele & Belay, 2007; Habtamu & Bekele, 2008; Kasso, Bekele & Hemson, 2010; Avenant, 2011). Small mammals (especially rodents) are key ecosystem components, affecting landscape architectures through their diet and faecal activity, which influences the distribution and occurrence of plant species. Their daily activity, such as construction of burrows, may offer shelter to other vertebrates and invertebrates (Ryszkowski, 1975; Hawkins & Nicoletto, 1992). They also provide a biocontrol to plant growth (e.g. seed predation), although they can become pests to certain habitats such as agriculture and pastures, where food is extremely abundant (Ryszkowski, 1975; Fischer *et al.*, 2018). In fact, some studies in protected areas, indicate a higher rodent abundance in surrounding areas with medium disturbance and high food availability in comparison to pristine areas (Caro, 2001; Rautenbach, Dickerson & Schoeman, 2014). Moreover, the majority of small mammals are inserted in a trophic level that represents the link between many primary producers and secondary consumers of the ecosystem, as they are a key food resource for many avian, mammalian and reptilian predators (Ryszkowski, 1975).

**Methods to estimate small mammals' relative abundance**

Estimating and monitoring small mammal relative abundances is largely divided into two different estimation techniques: mark-recapture and signals observation (Cavia, Cueto & Suárez, 2012). The most robust method is the mark-recapture technique through live-trapping (Wiewel, Clark & Sovada, 2007). The robust estimates from mark-recapture methods are due to the fact that it can accommodate individual physical traits (e.g. sex, age, ectoparasites) to deal with capture heterogeneity (King & Edgar, 1977; Wiewel *et al.*, 2007). However, in large-scale studies, it becomes very time consuming and labour intensive as it requires monitoring every twelve hours (Glennon, Porter & Demers, 2002; Wiewel *et al.*, 2007; Wilkinson *et al.*, 2012; Chiron *et al.*, 2018), may disturb the populations (Wilkinson *et al.*, 2012) and is dependent on animal ethics authorization due to the manipulation of individuals (Chiron *et al.*, 2018). As such non-invasive methods that estimate relative

abundance indexes are popular to investigate small mammal relative abundances, allowing a comparison between species and sites rather than a number of individuals or individual traits (Wilkinson *et al.*, 2012). These include monitoring burrow system activity, detection of tracks and droppings, hair tubes, camera-trapping and ink-tunnels (Chiron *et al.*, 2018). The use of ink-tunnels in particular seems to be a good non-invasive alternative method to live-trapping to monitor rodent relative abundances (King & Edgar, 1977; Wilkinson *et al.*, 2012). Ink-tracking tunnels allow a permanent record of small mammal tracks and are inexpensive, easy to install and require low effort which allows covering a large area (King & Edgar, 1977; Glennon *et al.*, 2002; Palma & Gurgel-Gonçalves, 2007; Wiewel *et al.*, 2007; Wilkinson *et al.*, 2012; Mills, Godley & Hodgson, 2016). Although this method can be used to monitor relative abundance, its use in distribution modelling is still untapped.

**Study objectives**

Applying a cheap, non-invasive method to estimate the distribution and abundance of small mammals will address the lack of prey covariates in small carnivore distribution models (Burton *et al.*, 2012). In this study I therefore tested the feasibility to use ink-tracking tunnels as a sampling method to capture heterogeneity in small mammals' relative abundance. I then compared relative abundance measures from tracking-tunnels with well-established mark-recapture studies from live-trapping. Finally, I tested the use of ink-tracking tunnels relative abundance measures as prey covariates in small carnivore camera-trapping studies. The study therefore addresses two main questions:

1. Can ink-tracking tunnel surveys be an efficient sampling method to assess relative abundance of small mammals in a woodland savannah?
2. Are small prey relative abundance measures derived from ink-tracking tunnels sampling important predictors of small carnivore distribution studies?

CHAPTER 2 – *STUDY AREA*

**Study sites**

Due to the high species richness and abundance of small carnivores in Africa and the increase of anthropogenic pressure (San *et al.*, 2013), this study was conducted in the Maputaland region of northern KwaZulu-Natal in South Africa (Figure 2.1). Sampling occurred on a landscape gradient of human disturbance, which included: a protected area, farmlands and rural communities. By choosing a landscape gradient of disturbance it allowed to investigate responses of different carnivore species to prey in different landscapes, which allowed to quantify the context dependent aspects of predation on prey. For the lowest level of human disturbance, sampling was done at Phinda Private Game Reserve (hereafter Phinda) (27°40′S–27°55′S; 31°11′E–32°26′E), situated in the North-eastern point of KwaZulu-Natal at approximately 30 Km from the Indian Ocean shore (Balme *et al.*, 2007; Rautenbach *et al.*, 2014). At intermediate levels of human disturbance, sampling was done on a matrix of game farms on the south border of Phinda. At the highest level of human disturbance, sampling was done in a matrix of rural small holding farming and peri-urban Zulu communities on the eastern border of Phinda (Mduku and Nibela communities).
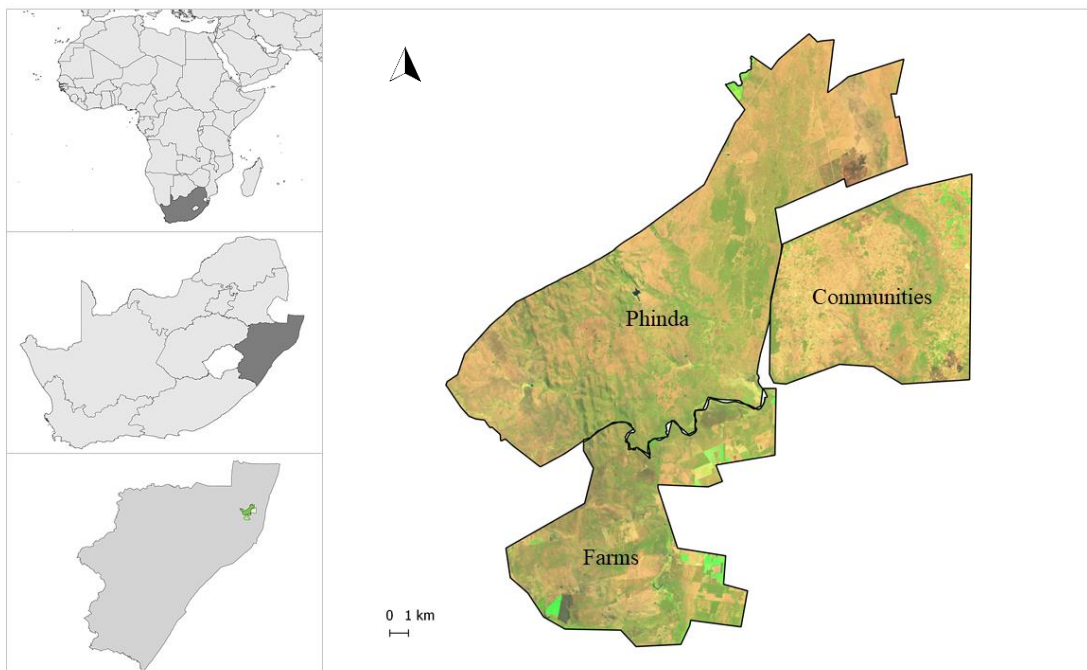


Figure 2.1: Surveyed areas: Phinda Private Game Reserve, Farms and Rural communities, which are located in KwaZulu-Natal province of South Africa, in the southern tip of the African continent.

**Climate**

This region experiences a hot and humid subtropical climate, with a dry winter from April to September and hot rainy summer from October to March (Balme *et al.*, 2007). The average rainfall is about 510 mm per year, with its majority occurring in the summer. The temperature has an average of 30 °C in summer and can drop down to 10 °C in winter (Rautenbach, 2013).

**Landscape**

Geologically, Phinda has an altitude range between 50 m and 340 m which results from the Lebombo Mountains that run through the south-west side of the reserve. It has two seasonal rivers, the main one is the Mun-Ya-Wana river that divides the reserve in two at the middle (Phinda North and Phinda South), and the Mzinene river that makes a boundary in the South (Hunter, 1998). These characteristics have huge influence on the climate and consequently on the type of vegetation, resulting

in an heterogenous landscape. It encompasses multiple vegetation types (Balme *et al.*, 2007; Van Rooyen & Morgan, 2007), but is essentially dominated by savannah woodlands of *Acacia* and *Terminalea* species, grassland and wooded grasslands (Van Rooyen & Morgan, 2007)

**Land-use**

Phinda was established as a conservation area in 1990. The land previously consisted in different private lands used for plantations, livestock or as small game farms usually associated with recreational hunting (Hunter, 1998). To date, Phinda has re-introduced an array of different mammal groups, ranging from ungulates to elephants, rhinoceros, and large carnivores and is specially known for the successful re-introduction of cheetahs. With big efforts from the conservation team, sponsors, anti-poaching units, and all the people involved, Phinda is now an expanding reserve with 270 $Km^2$ and well stablished populations of African animals and vegetation. Since it has re-introduced dangerous species, the whole reserve is surrounded by electrified game fencing, as prescribed by the country's law, which means most of the large species cannot go beyond the limits of the reserve (Hunter, 1998). The carnivore species confirmed as present are the African lion (*Panthera leo* (Linnaeus, 1758)), cheetah (*Acinonyx jubatus* (Schreber, 1775)), leopard (*Panthera pardus* (Linnaeus, 1758)), spotted hyena (*Crocuta crocuta* (Erxleben, 1777)), large-spotted genet (*Genetta maculata* (Gray, 1830)), white-tailed mongoose (*Ichneumia albicauda* (G. Cuvier, 1829)), side-striped jackal (*Canis adustus*, Sundevall, 1847), banded mongoose (*Mungos mungo* (Gmelin, 1788)), common slender mongoose (*Herpestes sanguineus* (Rüppell, 1835)), honey badger (*Mellivora capensis* (Schreber, 1776)), striped polecat (*Ictonyx striatus* (Perry, 1810)) and marsh mongoose (*Atilax paludinosus* (G. Cuvier, 1829)).

On the surrounding farms, vegetation is similar to Phinda, while the topographical relief is less pronounced. The carnivore species expected are mainly the same except for the lion which is restricted by the electrical fencing. The game farms consist in extensions of natural vegetation where humans exist in low densities. While they are mainly use for game, some can have a mixed regime with domestic cattle.

On the Zulu tribal authority lands, vegetation is less diverse, and the terrain is mostly plain. Only small carnivores are expected to occur on this area due to the high level of human disturbance. The communities consist in scattered households, small crops, livestock and a semi-natural vegetation. Besides humans, domestic predators (i.e. cats and dogs) and other domestic animals (i.e. cows, goats, sheep, chickens) are very abundant throughout the whole area.

**Small mammal species**

Small mammals constitute a group that includes rodents, shrews and eulipotyphlans that weight less than one kilogram (Lim & Pacheco, 2016). According to the IUCN SSC Small Mammal Specialist Group (2019), there are more than 2800 species around the globe, of which 437 are considered threatened by the International Union for the Conservation of Nature. For this study, I identified the small mammal species that occur or may occur on the study area based on information from live-trapping studies (using both literature and field experience) (Table 2.1).

Table 2.1: List of species present or possibly present in the study area divided by size groups and their mean head to body length in mm (HB), hindfoot length in mm (HF) and weight in g (WT), with the two most abundant in bold (Kingdon *et al.*, 2013; Rautenbach *et al.*, 2014).

| Functional Group | Species | Common name | HB | HF | WT | Reference |
|---|---|---|---|---|---|---|
| **Small rodents** | ***Mus minutoides*** | **African pygmy mouse** | 54.4 | 12.5 | 6.2 | Monadjem 2013a |
| | *Dendromus mystacalis* | Chestnut climbing mouse | 57.5 | 17.1 | 8 | Monadjem 2013b |
| | *Dendromus melanotis* | Grey climbing mouse | 69 | 17.5 | 7.2 | Monadjem 2013c |
| | *Dendromus mesomelas* | Brants' climbing mouse | 75 | 20 | 11.3 | Monadjem 2013d |
| | *Steatomys pratensis* | Fat mouse | 94 | 16 | 32.9 | Monadjem 2013e |
| **Medium rodents** | ***Mastomys natalensis*** | **Natal multimammate mouse** | 107 | 22 | 36.4 | Leirs 2013 |
| | *Grammomys dolichurus* | Woodland mouse | 113 | 24 | 32.9 | Happold 2013 |
| | *Aethomys namaquensis* | Namaqua rock mouse | 113 | 26 | 48 | Kesner et al. 2013 |
| | *Saccostomus campestris* | Pouched mouse | 114 | 21 | 48.5 | Perrin 2013 |
| | *Lemniscomys rosalia* | Single-striped grass mouse | 126.3 | 26 | 54.2 | Monadjem 2013f |
| | *Gerbilliscus leucogaster* | Bushveld gerbil | 128.6 | 33.5 | 69.8 | Dempster 2013 |
| | *Gerbilliscus brantsii* | Highveld gerbil | 134.6 | 35 | 79.9 | Dempster 2013b |
| | *Thallomys paedulcus.* | Sundevall's acacia rat | 140.3 | 25.3 | 72.3 | Perrin 2013b |
| | *Aethomys ineptus* | Tete veld rat | 147 | 30 | 83 | Linzey et al. 2013 |
| **Large rodents** | *Mystromys albicaudatus* | White-tailed mouse | 153.5 | 26.5 | 76.5 | Perrin 2013c |
| | *Otomys irroratus* | Southern African vlei rat | 161 | 32 | 144 | Taylor 2013 |
| | *Dasymys incomtus.* | Common shaggy rat | 165 | 33 | 158 | Pillay 2013 |
| | *Rattus rattus* | Black rat | 165.3 | 31.7 | 132 | Happold 2013b |
| | *Petrodromus tetradactylus* | Four-toed elephant shrew | 192.9 | 54.8 | 198.3 | Rathbun 2013 |

**Small carnivore species**

Southern Africa is endowed with a rich diversity of small, medium and large carnivores. The diversity includes over 80 carnivore species (Kingdon *et al.*, 2013), ranging from the iconic lion to the slender mongoose. South Africa, in particular, is widely known for its high number of predatory species that co-exist in protected and non-protected areas. This study was focused on the small carnivore species detected on the camera-traps, which included: large-spotted genet, white-tailed mongoose, side-striped jackal, banded mongoose, common slender mongoose, honey badger and striped polecat. Although generalist, these species have different prey preferences. The large-spotted genet and the side-striped jackal feed primarily on rodents (Atkinson *et al.*, 2002; Angelici & Luiselli, 2005), while the banded mongoose, striped-polecat and white-tailed mongoose prefer insects as main resource (Taylor, 1972; Rood, 1975; Rowe-Rowe, 1978; Waser & Waser, 1985; Larivière, 2002; Otali & Gilchrist, 2005; Hoffmann & Taylor, 2013), on the other hand, the honey badger's primarily ingest reptiles (Begg *et al.*, 2003).

*CHAPTER 3 – **EFFICIENCY OF INK-TRACKING TUNNELS AS A METHOD TO ESTIMATE RELATIVE ABUNDANCE OF SMALL MAMMALS IN KWAZULU-NATAL (SOUTH AFRICA)***

# Ink-tracking tunnels sampling method to estimate small mammals' relative abundance in a dry woodland savannah

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## Abstract

Assessing small mammals' relative abundance is important to understand what drives their population dynamics and the impact of its fluctuations in the ecosystem. To this end, the most common sampling method is live-trapping. However, its high cost and intensive labour makes its use in large-scale studies unfeasible. As an alternative, ink-tracking tunnels can monitor population abundance fluctuations and are non-invasive, inexpensive and require low effort. To evaluate ink-tracking tunnels efficiency to assess rodents' relative abundance comparing to the live-trapping method, I implemented tunnels in a 3 x 3 y-design sampling in relation to a 7 x 7 grid of live-traps. I tested two measures of abundance: number of individual track records and proportion of tunnels with track records (track index), from which I tested a functional group division based on track size. As the automatic counting of particles showed a very low correlation to the actual number of tracks, it was immediately discarded. The group division in small rodents, medium rodents and large rodents proved to be well established, as the correlation with the live-trapping abundance index was high for medium rodents and rodents in general, and moderate for small rodents. The track index was better at capturing large fluctuations in relative abundance between sites, rather than small differences. However, this efficiency is abundance dependent, detecting better fluctuations for high abundant groups than for low abundant ones.

Keywords: rodents, fluctuations, live-trapping, functional group, track index

## Introduction

### Importance of assessing small mammals' relative abundance

Small mammals from the Order Rodentia, comprise nearly 40 % of all the known mammal species and exist in a wide diversity of habitats, which makes it the most diverse and abundant mammal group in the world (Datiko *et al.*, 2007). The distribution and abundance of rodents is primarily driven by food availability and vegetation cover (Datiko *et al.*, 2007). Therefore, rodents' abundance fluctuates seasonally ultimately due to rainfall and temperature (Rautenbach *et al.*, 2014), achieving the peak in the wet season when resources availability is higher (Delcros, Taylor & Schoeman, 2015). This susceptibility to weather conditions to breed and increase abundance, renders rodents as good indicators of ecosystem conditions and climate change (Rautenbach *et al.*, 2014; Delcros *et al.*, 2015).

Small mammals are key components of the ecosystem, playing important roles such as seed dispersal, population regulation, cycling of nutrients through urine and faeces, and food sources of multiple terrestrial and volant predators (Ryszkowski, 1975; Delcros *et al.*, 2015; Fischer *et al.*, 2018). As prey of several species of carnivores, birds and reptiles, the fluctuations in rodent abundance can also influence the dynamics of its predators, depending on the level of specialization and mobility of the predator species (Andersson & Erlinge, 1977). Regarding predator-prey ecology, prey preferences can vary with the biomass and energy income of the prey (e.g. larger mice comparing to smaller mice),

hence it is important to account for heterogeneity of rodent's biomass as a response to the different metabolic needs of predator species, instead of relative abundance of rodents *per se* (Mukherjee *et al.*, 2004).

These facts highlight the importance of monitoring rodent abundance and understand their distribution patterns to better assess their ecosystem role and ultimately help the development of small carnivore conservation strategies (Widdows & Downs, 2015). Moreover, it can also aid in finding the best solutions for pest control (Williams *et al.*, 2018).

**Non-invasive small mammal sampling**

Mark-recapture and signals observation have been the two most used techniques related to the estimation and monitorization of small mammals relative abundance and distribution (Cavia *et al.*, 2012). The mark-recapture technique through live-trapping is known to be the most reliable method (Wiewel *et al.*, 2007). This methodology produces more robust results due to individual physical traits accommodation (King & Edgar, 1977; Wiewel *et al.*, 2007). However, daily monitoring (Glennon *et al.*, 2002; Wiewel *et al.*, 2007; Wilkinson *et al.*, 2012; Chiron *et al.*, 2018), potential population disturbance (Wilkinson *et al.*, 2012) and animal ethics (Chiron *et al.*, 2018) increases the time consumption and the labour intensity, more predominant in large scale studies.

The use of non-invasive camera-trapping sampling methods in the estimation of abundance of terrestrial mammals has grown in the last years since it provides permanent data on elusive species (Mills *et al.*, 2016). While this method is effective in detecting large mammalian species, small species are plagued by low detection rates (Hofmeester *et al.*, 2019). This is largely due to the field deployment method that differs between species (e.g. camera height) (Hofmeester *et al.*, 2019). Therefore, the majority of studies that involve carnivores underestimate the presence and abundance of small mammals (Burton *et al.*, 2012). Non-invasive methods that include observation of signs can also be used and are generally cheaper, from hair tubes and monitoring of burrow system activity to ink-tracking tunnels (Chiron *et al.*, 2018).

**The ink-tracking tunnel sampling method**

An alternative method less technical demanding to assess rodents' relative abundance is the ink-tracking tunnel method (King and Edgar 1977). Essentially, in this method a rodent enters a baited tube, walks over a ink-pad which then leaves tracks on the paper when the rodent exits (King & Edgar, 1977). It has several advantages comparing to live-trapping, as it can be left uninspected in the field for days, is inexpensive, non-invasive, user friendly, reduces the risk of infection with zoonoses as there is no animal interaction (Glennon *et al.*, 2002; Wiewel *et al.*, 2007), allows sampling of several areas at the same time (King & Edgar, 1977; Glennon *et al.*, 2002), can be used to study any kind of animal that fits inside the tunnel (e.g. small mammals, insects, reptiles) (King & Edgar, 1977) and leaves clear and permanent records (Palma & Gurgel-Gonçalves, 2007). By recording the tracks of individuals that enter the tunnel, this method enables monitoring studies such as distribution, habitat preferences and abundance fluctuations through time and space (King & Edgar, 1977; Glennon *et al.*, 2002; Blackwell, Potter & Mclennan, 2006; Wiewel *et al.*, 2007; Wilkinson *et al.*, 2012).

There seems to be a strong correlation between ink-tunnels relative abundance and live-trapping estimates (Wilkinson *et al.*, 2012). The correlation strength, however, depends on the sampling season, showing promising results to detect large fluctuations of abundance through time when the relative abundance is average in all sampling sites, and to detect differences between sites in the same sampling

season when relative abundance is low. However, the ink-tracking tunnels measures fail to record small fluctuations of abundance and to estimate relative abundance in seasons with low food availability, as rodents will be more attracted to the bait, whether its abundance is low or high (Wilkinson *et al.*, 2012). Even though the method does not provide information on the individuals of the population as the live-trapping method, on monitoring studies and large-scale samplings, the ink-tracking tunnels are convenient and efficient by capturing significant differences in relative abundance of small mammals between sites and seasons (Wilkinson *et al.*, 2012).

In Africa, ink-tracking tunnels advantages have not yet been explored. Given the high diversity of small carnivores that incorporate rodents in their diet (San *et al.*, 2013) the use of ink-tunnels can be a convenient method to incorporate large-scale rodent distribution and relative abundance in small carnivore distribution models (Burton *et al.*, 2012).

**Study objectives**

The main objective of this study is to assess the efficiency of ink-tracking tunnels as a sampling method to estimate relative abundance of small mammals in a woodland savannah compared to live-trapping abundance estimations. To achieve this, the study was divided in two sub-objectives:

1. Assess small mammals' relative abundance using two different measures (track index and number of tracks)
2. Comparison between ink-tracking tunnels relative abundance measures and live-trapping relative abundance indexes

# Methods

## Sampling design

The field work was conducted in the North of the KwaZulu-Natal province of South Africa, specifically in Phinda Private Game Reserve (hereafter Phinda) and surrounding areas such as the farmlands in the southern border and the rural communities in the eastern border of the reserve, during August of 2017. Sampling sites were selected to provide the same habitat heterogeneity, which led to ten sites in Phinda – five (replicates) in the South and five in the North of the reserve. A similar sampling approach was followed for the farming area (five sampling replicates) and the rural settlement area (four sampling replicates) (Figure 3.1).
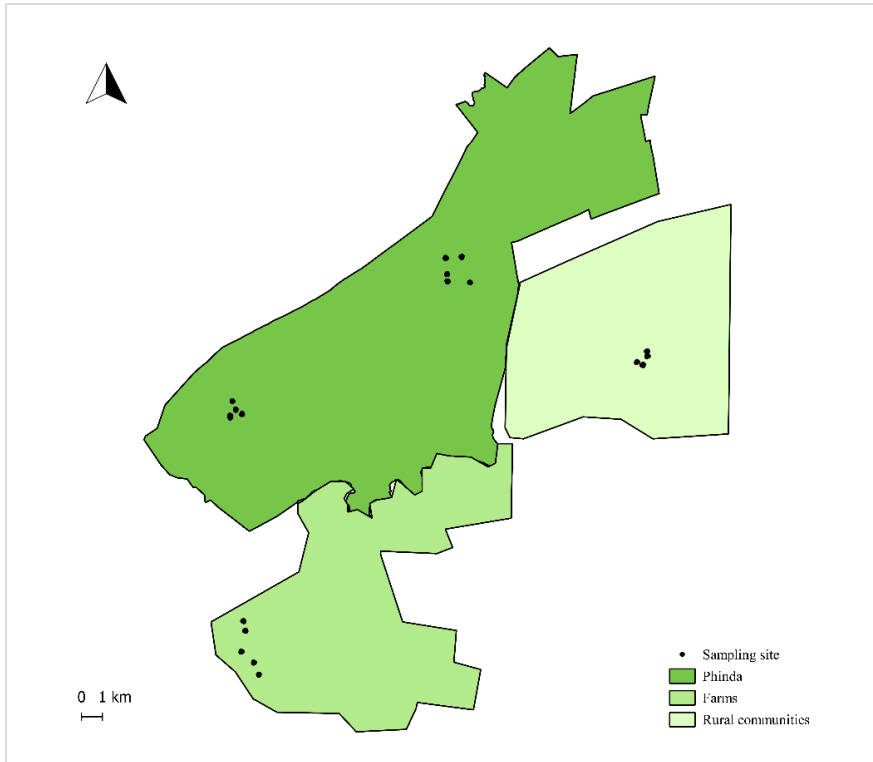
Figure 3.1: Sampling sites in the three areas, with 5 sites in the Farms, 10 sites in Phinda and 4 sites in the Rural communities.

In each sampling site I followed standard live-trapping method and deployed 49 Sherman traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) in a 7 x 7 grid approximately 10 meters apart. Simultaneously, 9 ink-tracking tunnels (King & Edgar, 1977) were placed with a 3 x 3 y-design, also 10 m apart (Figure 3.2). Ink-tracking tunnels were sampled for four consecutive nights, while live-trapping sampling nights oscillated between five to seven. The y-design was chosen in order to simplify the sampling effort and therefore allow a larger sampling scale.

Both live-traps and tunnels were baited with peanut butter and oats. The live-traps were checked every morning. In contrast, the ink-tracking tunnels were not disturbed during the entire sampling period (4 nights).
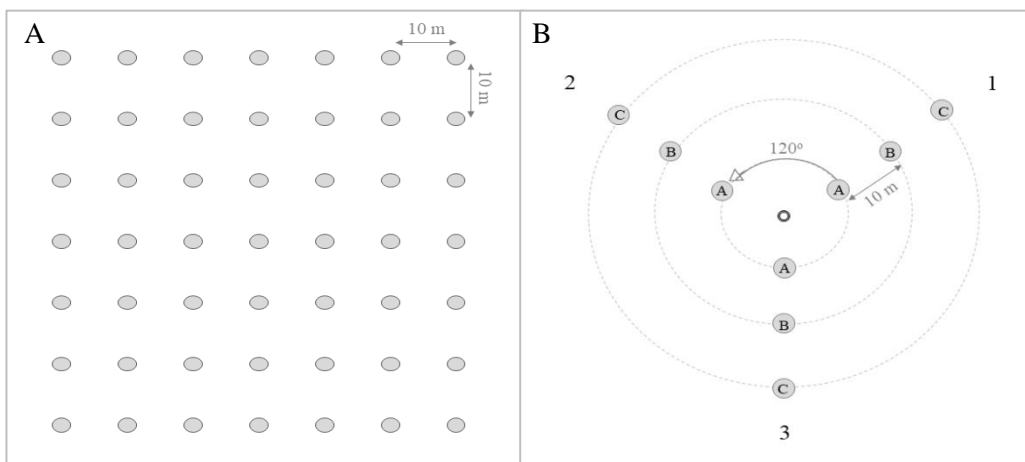


Figure 3.2: A- sampling design of the live-traps with 7 x 7 grid, 10 m apart from each trap; B- sampling design of the ink-tracking tunnel in a 3 x 3 y-design also 10 m apart from each tunnel, numbers identify the line and letters identify the circumference around the unoccupied centre.

The ink-tracking tunnels used in this study were made of robust corrugated plastic, measuring 55 x 10 x 10 cm with both entries open, a size that allows small mammals to get inside, from small rodents to elephant shrews, but not small carnivores. On the sides, the six tabs with holes allowed metal stakes to be attached to the ground, preventing its dislocation. Inside the tunnel, a folded paper was placed measuring 55 x 10 cm, covering the base length of the tunnel. In the centre of the paper, a 12 x 10 cm card was stapled to it and used as the recipient for the ink (Figure 3.3). Since this card was waterproof, it allowed the ink to last longer and was able to be reutilized. The ink used was a long lasting, environmentally friendly and animal safe black ink, enabling its stay on the field during the sampling period without drying up. Above the ink-pad, a small PVC tube was attached to the tunnel as a container for the bait. At the end of the sampling, all papers from the ink-tunnels were photographed with a scale and an android mobile phone with the same height and light conditions.
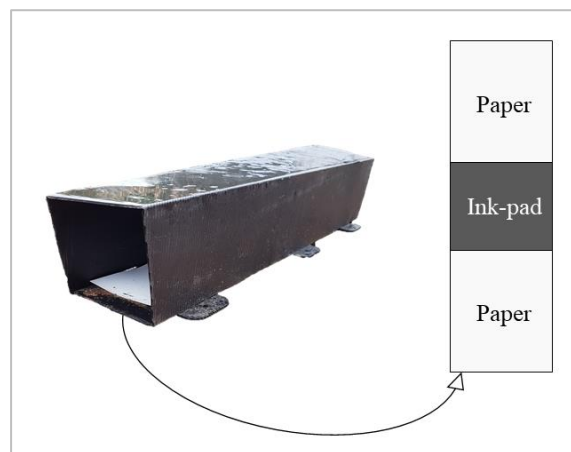


Figure 3.3: The ink-tracking tunnel outside design and the inserted tracking card.

## Relative abundance measures from ink-tracking tunnels

In ink-tracking tunnel studies, the proportion of the tunnels with records (track index; TI) is often used as a measure for rodent abundance (Wilkinson *et al.*, 2012). However, to know if it is possible to obtain more information on rodent abundance from the number of individual tracks per tunnel, I also tested an automatic counting method to count individual tracks.

### Functional grouping and track index

Track size can be an indication of rodent size (Palma & Gurgel-Gonçalves, 2007), and hence add some extra information on rodent relative abundance. This can be important for predator studies, because carnivore species have different metabolism and energy income needs, and available energy is associated with prey biomass and consequently with size. Rather than trying to identify rodent tracks, I opted to group tracks into functional size groups (Mukherjee *et al.*, 2004). To achieve this, I compiled a list of potential species present in the area (Table 2.1) (Kingdon et al., 2013; Rautenbach et al., 2014). Based on species body-length we consider three possible functional groups – small rodents (54.4 to 94 mm), medium rodents (107 to 147 mm) and large rodents (which may include sengi) (153.5 to 192.9 mm). I obtained hindfoot sizes for each group from published morphological data (Kingdon et al., 2013) and assigned front and hind track measured on track plates to each group.

I measured one forefoot and one hindfoot track for each functional group in a random sample of 100 track papers using ImageJ software, applying a scale where 1 cm equals 200 pixels. Only footprints in good conditions were considered for measuring (e.g. no missing fingers). For each track I measured the length and width to nearest mm, however most tracks were incomplete, so measurements excluded heel pads as shown in Figure 3.4. Each track was then assigned to either a small, medium or large rodent (Figure 3.5).
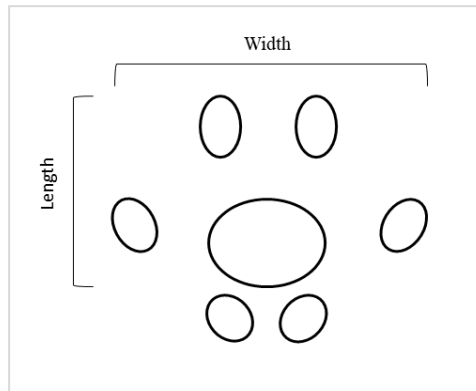


Figure 3.4: Measuring method used to measure the 100 random tracks.
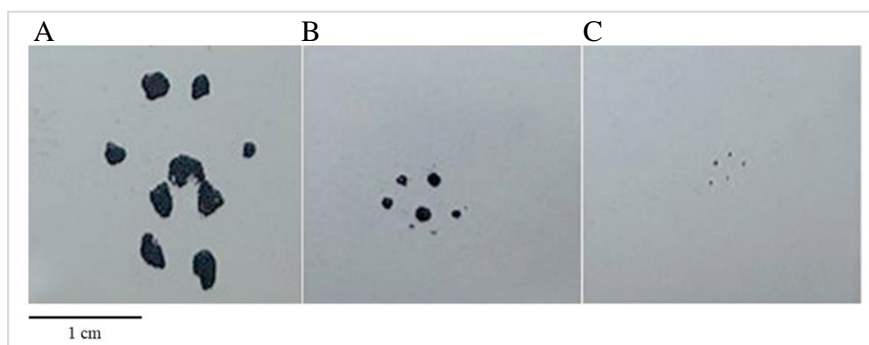


Figure 3.5: Example of forefeet tracks of the three functional groups: A-Large rodents, B-Medium rodents, C-Small rodents.

I then tested for differences in foot track length and width to validate the classification of the functional groups. Considering the small dataset, normality and homoscedasticity were tested using Shapiro-Wilk and Levene tests, respectively (Razali & Wah, 2011; Kim & Cribbie, 2018). Data for both width and length did not meet the ANOVA assumptions. I then used Kruskal-Wallis test (Ostertagová, Ostertag & Kováč, 2014; Ali & Bhaskar, 2016) for differences in track length and width for each functional group using IBM SPSS Statistics 25 (IBM, 2007).

I derived track index (TI) based on the proportion of tunnels with small mammal tracks (Wilkinson *et al.*, 2012) of the three different functional groups plus general rodents (i.e. prey) per site.


**Number of individual track records**

To estimate the number of tracks per paper I used an automatic counting method, implemented by a particle analysis tool (Image processing software ImageJ 1.51j8; (Abràmoff et al. 2004). By transforming an image to 8-bit and adjusting its threshold, the software turns the image to black and white. The particle analysis tool image analysis (software settings) is dependent on the minimum pixel size and circularity of the particles (Hoeks, n.d.). Because resulting counts depend on the software

settings used (i.e. threshold, pixel size, and circularity), I first manually counted the number of individual tracks and compared it with automatically counted particles to derive the best software settings.

As the automatic method does not distinguish tracks, but only particles, the manual counts considered tracks of rodents in general. I randomly selected papers (using a Random File Picker 1.2 (Szeniak, 2015)) until reaching 100 papers with tracks, which resulted in a total of 157 papers. I then set up 56 different image software setting combinations (i.e. threshold, pixel size, and circularity which was used to count the tracks. The settings were chosen based on a step-by-step selective process and observation of correlation values. (see Supplemental Information I, Table I.1). These automated particle counts were then compared to the manual counts using a Pearson's correlation test.

Since the automatic image processing can be affected by how dark the image is (e.g. high density of tracks), I also divided the papers in three groups according to the number of manual counted tracks. These include from 0 to 100 tracks, 100 to 300 tracks and more than 300 tracks. I then applied a Pearson's correlation test between the manual counts in each group to the automated counts.

**Baseline relative abundance estimates from live-trapping**

The live-trapping abundance index was calculated by dividing the number of captured animals by the number of trap nights. Since the low number of recaptures did not allow to use capture-recapture estimates. The trap nights parameter was estimated by multiplying the number of sampling nights by the number of traps set up per site, as not all sites had the same sampling effort.

**Comparison between ink-tracking tunnels (Track Index; TI) and live-trapping relative abundance indexes (Abundance Index; AI)**

To understand the efficiency of ink-tunnels to describe small mammal relative abundance indexes, I compared the track index (TI) with the live-trapping relative abundance index (AI) obtained using the sampling design described before (Figure 3.2). A Pearson correlation was performed between the track index and the abundance index of small rodents, medium rodents and rodents in general captured per site (19 sites). The large rodents' group was not considered since the live-traps were smaller than the ink-tracking tunnels and therefore some larger individuals may not be captured by the live-traps. For the correlation, all species of the medium rodents and small rodents captured were considered, with an evaluation of the most abundant species per group. Statistical tests were performed on IBM SPSS Statistics 25 software (IBM, 2007), while scattered plots were performed on R software using package *graphics* 3.6.0 (R Core Team, 2017).

# Results

## Relative abundance measures from ink-tracking tunnels

### Number of individual track records

The Pearson correlation between the different settings of the automatic counting method and the manual counting (see Supplemental Information I, Table I.1) of the 157 random papers resulted in low correlation coefficients ranging from 0.04 to 0.31, however, when focusing on the $r^2$, values were null. The setting "55_15_0.90" (threshold, pixel size and circularity respectively) returned the best correlation coefficient ($r^2 = 0.098$, n = 157, p = 0.000), followed by "55_15_0.80" ( $r^2 = 0.081$, n = 157, p = 0.000), and the third best setting was "55_10_0.90" ( $r^2 = 0.063$, n = 157, p = 0.001). Different thresholds for the same pixel size and circularity resulted in the same particle counts and therefore same correlation value.

Focusing on the null relationship between the automatic counting (using the best settings) and the manual counting, (Figure 3.6), in papers with approximately 500 tracks, the automatic method didn't count as many particles as it would be expected. At lower densities this method shows higher accuracy, although there are also some outliers, where the automatic method counted multiple particles on the papers when in fact there are few tracks.
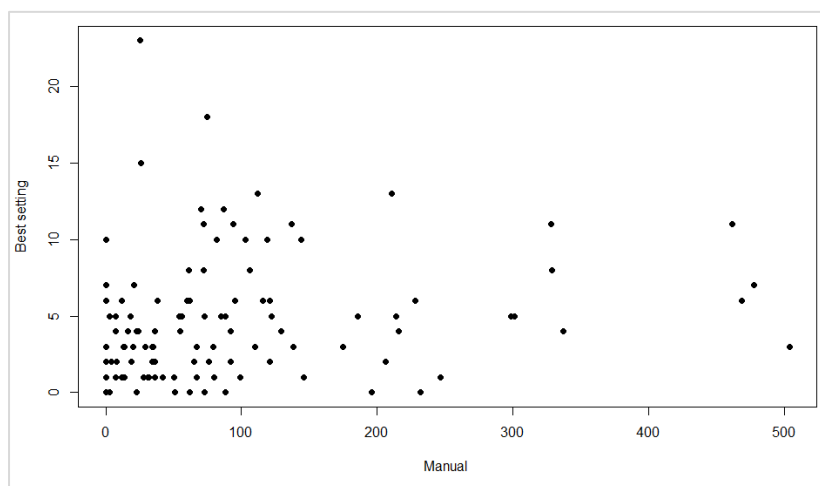


Figure 3.6: Relationship between the best setting ("55_15_0.90") and the manual counts.

By dividing the papers in three groups of track density (Figure 3.7), correlation values with the manual counting varied. From 0 to 100 tracks the coefficient is very low ($r^2 = 0.133$, n = 124, p = 0.000), from 100 to 300 tracks the coefficient is also very low ($r^2 = 0.112$, n = 25, p = 0.102), and more than 300 tracks has a null correlation ($r^2 = 0.014$, n = 8, p = 0.781).
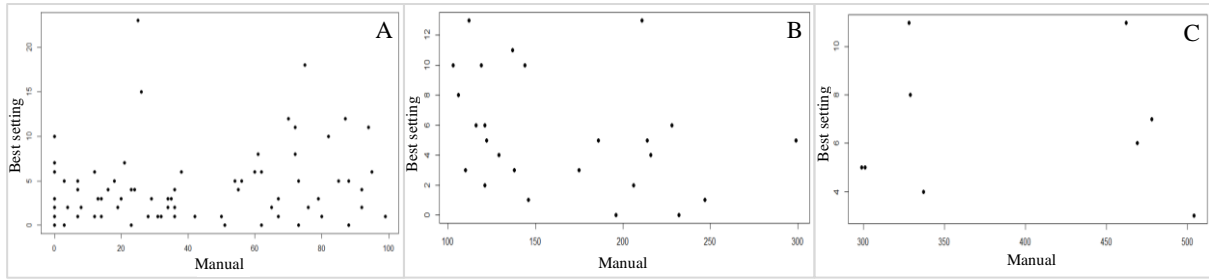
Figure 3.7: Relationship between the best setting ("55_15_0.90") and the manual counting of three groups of track density: A: 0-100 tracks, B: 100-300 tracks, C: more than 300 tracks.

## Functional grouping

The three groups have distinct means for both length and width on the forefeet and hindfeet (Table 3.1). On the forefeet, small rodents have a length range from 1.57 to 2.41 mm and width range of 2.63 to 4.35 mm, medium rodents have a length range from 3.45 to 6.18 mm and a width range from 5.14 to 9.71 mm, and large rodents have a length range from 11.14 to 12.75 mm and a width range from 13.14 to 15.14 mm. On the hindfeet, small rodents have a length range from 2.06 to 4.35 mm and a width range from 2.63 to 4.91 mm, medium rodents have a length range from 4.52 to 8.74 mm and width range from 5.70 to 10.11 mm, and large rodents have a length range from 13.65 to 14.68 mm and a width range from 14.15 to 17.71 mm.

Table 3.1: Measures in mm, with respective mean, standard deviation, minimum and maximum of forefeet (FF) and hindfeet (HF) length and width for the three functional groups division proposed: small rodents (n = 45), medium rodents (n = 57) and large rodents (n = 5), measured for 100 random ink-tracking tunnel papers.

| Measure (mm) | Functional group | FF | | | | HF | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SD | Min. | Max. | Mean | SD | Min. | Max. |
| **Length** | Small rodents | 1.955 | 0.186 | 1.570 | 2.410 | 3.331 | 0.663 | 2.060 | 4.350 |
| | Medium rodents | 4.597 | 0.642 | 3.450 | 6.180 | 6.696 | 0.938 | 4.520 | 8.740 |
| | Large rodents | 11.700 | 0.625 | 11.140 | 12.750 | 14.058 | 0.422 | 13.650 | 14.680 |
| **Width** | Small rodents | 3.560 | 0.363 | 2.630 | 4.350 | 3.691 | 0.544 | 2.630 | 4.910 |
| | Medium rodents | 6.961 | 1.096 | 5.140 | 9.710 | 7.731 | 1.070 | 5.700 | 10.110 |
| | Large rodents | 14.326 | 0.902 | 13.140 | 15.140 | 15.832 | 1.314 | 14.150 | 17.710 |

According to Shapiro-Wilk test applied to the measures, data is normally distributed in all cases (p-value > 0.05) with exception for medium rodents forefoot length and small rodents hindfoot length (FF length: small rodents $p = 0.964$, medium rodents $p = 0.154$, large rodents $p = 0.175$; FF width: small rodents $p = 0.739$, medium rodents $p = 0.005$, large rodents $p = 0.244$; HF length: small rodents $p = 0.050$, medium rodents $p=0.056$, large rodents $p=0.5$; HF width: small rodents $p=0.920$, medium rodents $p = 0.361$, large rodents $p = 0.877$). Levene's homogeneity of variances test resulted in $p = 0.019$ for hindfoot length and $p = 0.000$ for the rest, meaning variances are heterogeneous (Razali & Wah, 2011). By failing one of the ANOVA assumptions, the Kruskal-Wallis non-parametric test was applied (Ali & Bhaskar, 2016), whose results showed a significant difference ($p = 0.000$) between the three groups for all measures and both feet (Ostertagová, Ostertag & Kováč, 2014).

Small rodents' forefoot length and width are smaller, do not vary much in length and a have a little more variation in width (Figure 3.8). Medium rodents have more heterogeneity of length and width, showing it englobes footprints of smaller and bigger sized rodents. Large rodents' footprints are notably larger than all the other groups.

Hindfoot length and width appear to be more heterogeneous for small rodents comparing to their forefeet (Figure 3.8). Medium rodents, similarly to their forefeet, have a large range of footprint sizes. Large rodents have much larger measures than the other groups.
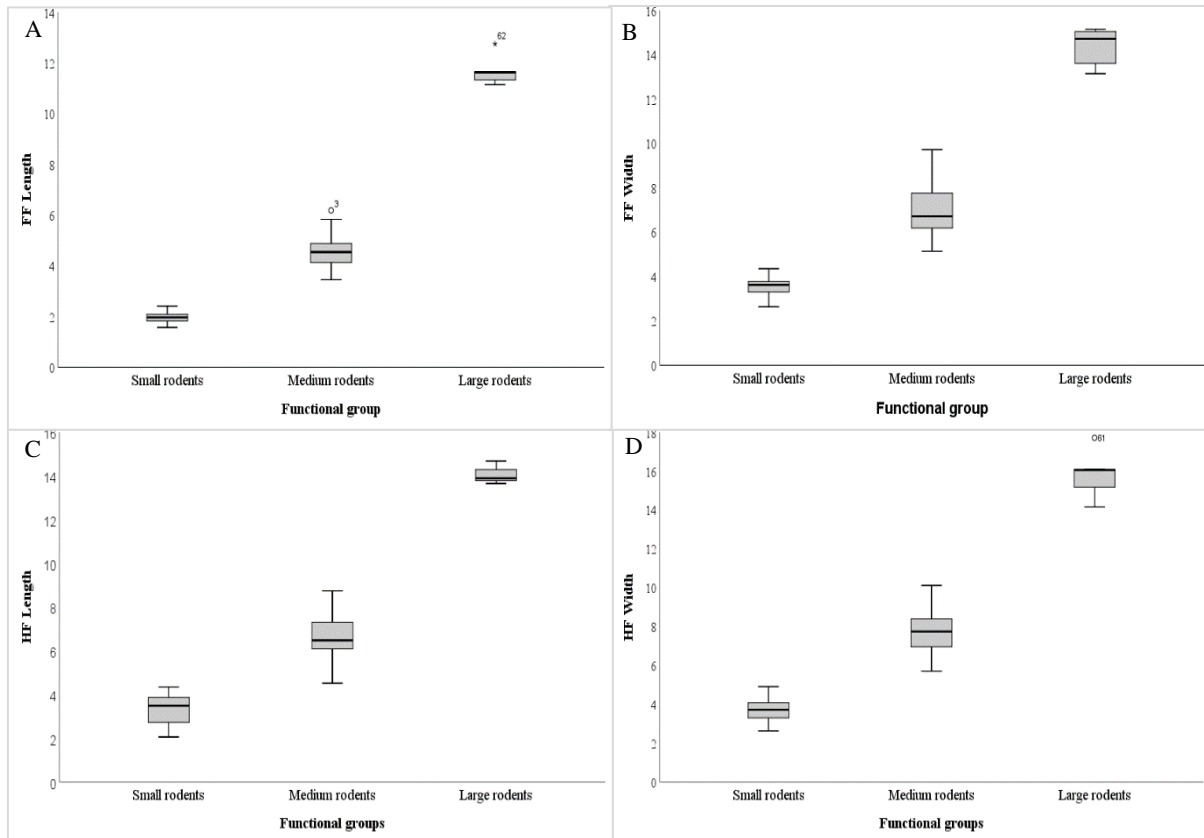


Figure 3.8: Track measures in mm of the three functional groups: A – forefoot (FF) length, B – forefoot width, C –hindfoot (HF) length, D – hindfoot width.

**Live-trapping**

A total of 305 rodents were captured during the study. The highest number of rodents were captured on the Farms, followed by Phinda and then the Rural communities (Figure 3.9). Live captures comprehended a total of 10 species (see Supplemental Information II). In terms of functional groups, medium sized rodents were dominated by *Mastomys natalensis* (Smith, 1834), while small rodents were dominated by *Mus minutoides* Smith, 1834 (Figure 3.9).
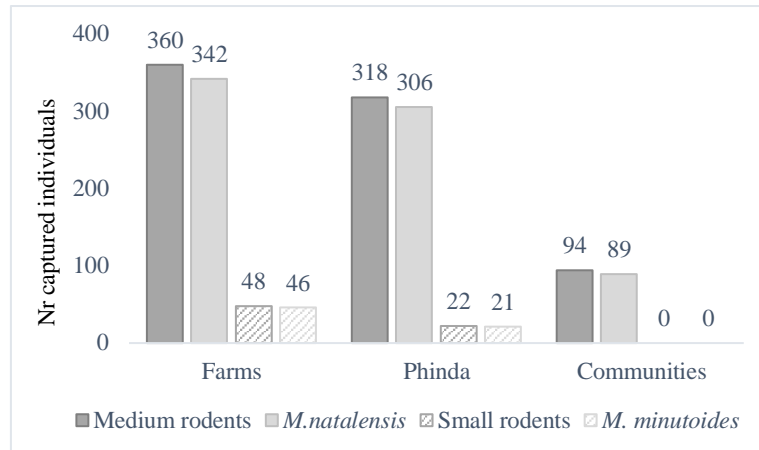
Figure 3.9: Number of individuals of medium rodents, *Mastomys natalensis*, small rodents and *Mus minutoides* captured by the live-trapping sampling method on the three surveyed areas.

## Comparison between ink-tracking tunnels and live-trapping relative abundance indexes

There is a high and significant positive correlation ($r^2 = 0.728$, n = 19, p = 0.000) between medium rodents' abundance index and medium rodents track index, as does for rodents in general although lower ($r^2 = 0.516$, n = 19, p = 0.001). Small rodents have a positive low correlation between measures, although it is not significant ($r^2 = 0.245$, n = 19, p = 0.031) (Havlicek & Peterson, 1976).

The relationship between medium rodents' track index and abundance index (Figure 3.10) shows that at low abundance, the track index can be low or medium, as some sites with null and low abundance index indicated a track index up to 0.4 (on a scale of 0 to 1). At medium and high abundance index, the track index was high.

For the small rodents, there are more discrepancies, as sites with the low and null abundance indexes resulted in low to high track indexes. For rodents in general, at low abundance index sites the track index was low to average, with an outlier where the track index was high. At medium to high abundance sites, the track index was high.
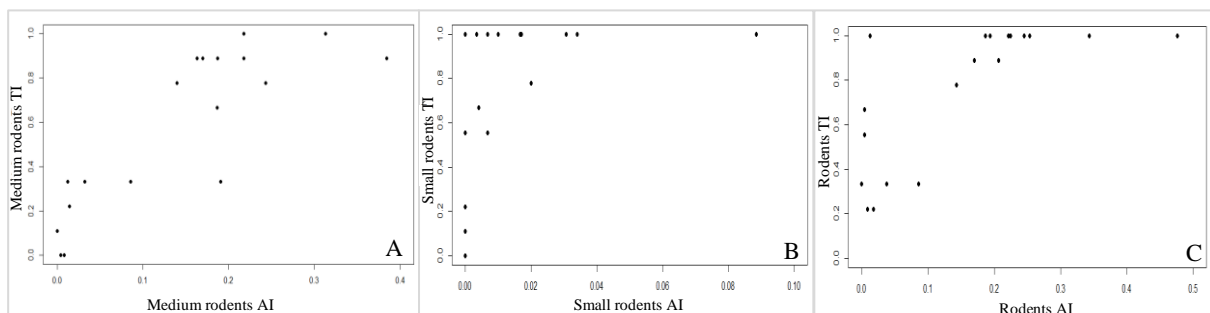


Figure 3.10: Relationship between abundance index (AI) and track index (TI): A- medium rodents, B- small rodents, C- rodents in general.

# Discussion

Of the two relative abundance measures tested, only the track index obtained from the proportion of tunnels with tracks was reliable and therefore compared with the live-trapping index. As the automatic particle counting was not able to represent the actual number of tracks, and counting the track of all tunnels was unfeasible, there was no confidence in using it as a measure of rodents' abundance.

Dividing the rodents into functional groups was successful, providing more information that can be relevant when studying predators with different energy requirements (Mukherjee *et al.*, 2004). Nevertheless, the high heterogeneity of medium rodent track sizes suggests that it may be possible to subdivide this group. The significant correlation between track index and abundance index of the medium rodents' group and rodents in general is understandable (Glennon *et al.*, 2002; Wiewel *et al.*, 2007), as for groups that are more frequent contrasting, differences in abundance through the sites can be more easily detected (e.g. very abundant site versus least abundant site). There was however a lower correlation between small rodents' track index and small rodents' abundance index. This low correlation may not be due to low abundance index but rather low trapability. Considering that species may have different behaviours, it is possible that small rodent species are trap shy, avoiding live-traps but not ink-tunnels (Glennon *et al.*, 2002). The higher abundance of rodents captured by ink-tunnels frequently compared to live-trapping, can be related not only to trap shyness, but also to the fact that live-traps are limited to one entry while the tunnels can be visited by multiple species (Glennon *et al.*, 2002). Moreover, the proximity between ink-tunnels, imposed by the need to minimize the risk of encounter with large predators, can overestimate abundance as the same animal may enter several tunnels.

Combined, these results suggest that the track index is better at detecting large relative abundance differences between sites of high abundant groups, which does not completely agree with Wilkinson *et al* (2012) study that showed better detections at average abundance, rather than low or high. However, Wilkinson's study focused on one single species in a relatively small area.

Moreover, the fact that track index detects rodents in sites where the live-trapping did not, shows that when rodents abundance reduces, ink-tracking tunnels perform better than live-traps to detect species presence. Suggesting that ink-tracking tunnels are a better option for sampling species presence than the live-trapping method (Palma & Gurgel-Gonçalves, 2007; Wiewel *et al.*, 2007).

This study opted for the y-design instead of the 7 x7 grid commonly used in ink-tunnel studies (Glennon *et al.*, 2002; Wiewel *et al.*, 2007; Wilkinson *et al.*, 2012). The strong correlations obtained indicate that the simpler sampling effort applied can be used with confidence in small mammals monitoring studies. Although the 10m distance between each tunnel may cause pseudo-replication, since the same rodent can cross multiple tunnels, larger distances can reduce the accuracy of the track index (Blackwell *et al.*, 2006; Wilkinson *et al.*, 2012).

On the division of functional groups, the anatomical measurements of head to body and hindfoot length seems to show low relationship (e.g. as some smaller species have larger hind feet than some larger species), the results from ink-tunnels did indeed show positive group differentiation as expected (Palma & Gurgel-Gonçalves, 2007). This can be due to the fact that in anatomical studies, measurements were taken from ankle to the tip of the longest finger (Kingdon *et al.*, 2013), while in this study measurements were taken from the tip of the longest finger to the palm edge. The different measurement approach causes better grouping, as rodents total hindfoot can vary between size groups adding heterogeneity. Suggesting that fingers/palm length and width (track size) of both forefeet and hindfeet

may be more related to individual size than the total hindfoot, especially considering the large differences between the trapped tracks.

On the automatic counting method, different thresholds for the same pixel size and circularity resulted in the same particle counts, meaning that threshold has little impact on the particle counting. Circularity appears to have more influence on the particle counts, followed by minimum pixel size and at last the threshold. However, this novel approach which could yield more robust relative abundances, did not produce reliable results. Even though I obtained "55_15_0.90" as the best setting, its ability to capture the real number of tracks is so low that it could not be used to compare with the live-trapping abundance index. The failure to accurately capture track density can have multiple explanations. First, the size and shape similarity of insect tracks with particles from rodents' tracks. For example, smaller rodents have small tracks (and therefor small particles) that are easily mistaken by the software, with large insect tracks (e.g. cockroaches) (Hasler *et al.*, 2004). Secondly, as rodents walk by the ink-pad, sometimes splashes of ink close to the pad can occur, which depending on the shape, may also be detected by the software. Besides these, overlap of tracks can result in particles that do not fit the dimension settings. Thus, under high track density conditions, the ImageJ software tends to underestimate the particle counts (Hoeks, n.d.). Yet, to better understand the effect of track density, it would be crucial to increase the dataset to obtain statistical significance.

Shrews were not considered in the study as neither live-traps nor ink-tunnels were able to capture them. It is most likely that the track index relative abundances reflect abundance variation of *Mus minutoides* and *Mastomys natalensis* for small rodents and medium rodents respectively, according to the live-trapping. These two species are generalists with a high tolerance to disturbance and habitat types, which facilitates their reproduction and territorial expansion (Rautenbach *et al.*, 2014). The significant higher abundance of *M. natalensis* in contrast with other species, even *M. minutoides*, may be related to the high rainfall that occurred in May of 2017 ("South African Weather Service"). This happens because the *M. natalensis* reproduction rates are strongly affected by fluctuations in rainfall and consequently food availability (Leirs, Verhagen & Verheyen, 1994; Leirs *et al.*, 1996). Even though *M. natalensis* breeding decreases as the dry season approaches, when heavy rains occur, the breeding season can be extended during the following three months (Leirs *et al.*, 1994, 1996). Hence, occasional heavy rain can induce an outbreak in *M. natalensis* abundance (Leirs *et al.*, 1994; Caro, 2002). On the other hand, *M. minutoides* abundance is expected higher during the winter, but as both *M. natalensis* and *M. minutoides* can occur simultaneously in several habitat types, it can lead to interspecific competition and the small *M. minutoides* may suffer from the pressure of the high abundance of *M. natalensis* (Rautenbach, 2013).

Live-trapping still remains as the best method to estimate small mammals' relative abundance (Wiewel *et al.*, 2007). However, this does not exclude ink-tracking tunnels which offer many advantages in monitoring fluctuations in abundance across sites and time. Especially considering its low effort, cost and impact on the individuals, and the enhanced possibility to sample large areas at the same time, that live-traps lack of. But a first correlation test between ink-tunnels and live-trapping abundance index should be done to increase the confidence on the obtained data (Blackwell *et al.*, 2006). Moreover, groups' identification based on size is easy and of lower effort than species identification, which also favours large-scale studies that do not require advanced tracking recognition knowledge. However, on areas with higher species diversity, a group division may be more complicated.

While indirect methods like track tunnels show promise for non-invasive small mammal monitoring (this study, Glennon et al., 2002; Wiewel et al., 2007; Wilkinson et al., 2012), there are several caveats that need to be considered. First, like any relative abundance metric, the track index and number of tracks do not necessarily mean more rodents. This is because the same rodent can visit several

ink-tunnels causing pseudo-replication (Blackwell *et al.*, 2006; Wilkinson *et al.*, 2012). Secondly, the struggle in identifying species tracks on a large-scale study, limits the possible ecological studies (e.g. density, species home range) (Palma & Gurgel-Gonçalves, 2007). The lack of individual characteristics (e.g. sex, age) withdraws mark-recapture history which leads to less robust relative abundance measures (Glennon *et al.*, 2002).

In terms of the automated counting methods, there is also some caveats and technical issues to be considered. First, automated methods can only work where the software can identify morphological differences, which will depend on the quality of images processed (Palma & Gurgel-Gonçalves, 2007; Russell *et al.*, 2009). The track data is inherently low quality since several species can cross the tunnels which can contaminate the tracks (e.g. insects). Also, the same rodents may walk inside the same tunnel several times, increasing the number of track while there was only one rodent. Hence, without a footprint identification and potentially individual identification through previous markings, this method is too unreliable to be considered.

### Conclusions

In the present work I was able to determine the efficiency of ink-tracking tunnels to assess relative abundance of small mammals across different sites in a woodland savannah using a simpler sampling design. I was also able to optimize relative abundance measures from this method. Track index remains as the most successful method to obtain relative abundance measures from the ink-tunnels (Wilkinson *et al.*, 2012) and it can be used for a functional group division identification based on track size and consequently small mammals' body size. Track index is better at capturing contrasting differences in relative abundance than small differences. However, this efficiency is abundance dependent, detecting better fluctuations for high abundant groups or species than for low abundant ones.

In conclusion, the sampling using ink-tracking tunnels on a 3x3 y-design and track index obtained from a group division based on track size can be used to monitor spatial heterogeneity in rodents' abundance across sites and arises as a reliable method to sample small mammals in large-scale studies and an added value in predator-prey ecology studies.

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CHAPTER 4 – *APPLICATION OF SMALL PREY RELATIVE ABUNDANCE MEASURES DERIVED FROM INK-TRACKING TUNNELS SAMPLING AS COVARIATE FOR SMALL CARNIVORE DISTRIBUTION STUDIES*

# Small mammals track index as covariate for small carnivore distribution studies

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## Abstract

Carnivores' distribution is mainly driven by prey availability, habitat characteristics and competitive interactions. Due to the sampling effort challenges associated with assessing rodents' relative abundance at a large-scale study, small carnivore camera-trapping studies often discard the small prey abundance covariate. To integrate this covariate, I set the low effort and non-invasive ink-tracking tunnels sampling method in a y-design around camera-traps across a landscape gradient of human disturbance. I applied a single species – singles season occupancy model to small African carnivore species integrating track index measures of small rodents, medium rodents and rodents in general, and alternative covariates of habitat and disturbance. Small prey covariates were not important for most species, except for the large-spotted genet at the highest disturbance level, but only when combined with habitat and disturbance variables. Hence, the importance of prey relative abundance depends on the species diet and disturbance context. On distribution studies including multiple generalist species, prey variables can be discarded without major impact. But it should be considered together with ecologically relevant habitat variables for rodent specialist species or species that feed mainly on rodents.

Keywords: rodents, relative abundance, ink-tracking tunnels, occupancy model, disturbance

## Introduction

### Factors influencing small carnivore distribution

Mammalian carnivore communities are driven by food availability, habitat heterogeneity, and competitive interactions (Burton *et al.*, 2012; Rich *et al.*, 2017). Competition between similar carnivores for resources leads to spatial and temporal partitioning where subordinate species face a trade-off between needed resources and the presence of more dominant predators (Rich *et al.*, 2017). Particularly small carnivores which are vulnerable to interspecific competition (Caro & Stoner, 2003), under natural conditions a species distribution and abundance is a result of such niche partitioning (Schuette *et al.*, 2013; Kheswa *et al.*, 2018). Carnivores worldwide are exposed to increased anthropogenic disturbance with resulting habitat loss, fragmentation and lower prey availability (Pettorelli *et al.*, 2010; Burton *et al.*, 2012; Schuette *et al.*, 2013). Therefore, understanding the drivers of carnivore distribution and abundance becomes important for conservation and management efforts (Pettorelli *et al.*, 2010; Rich *et al.*, 2017).

While there is a good understanding in factors affecting African large carnivore distributions and abundances (Pettorelli *et al.*, 2010; Schuette *et al.*, 2013; Rich *et al.*, 2017), little work has been done on African small carnivores (Pettorelli *et al.*, 2010; Widdows & Downs, 2015; Ramesh *et al.*, 2017). A key challenge has been to include small carnivore prey into distribution models (Petersen *et al.*, 2019). This is important since a large percentage of Africa's small carnivores often incorporate small mammals in their diet (Williams et al., 2018). The response of small carnivores to changes in small mammal

abundance, will largely depend on the species feeding strategy and mobility (Hanski *et al.*, 1991). For specialist predators adapted to hunting rodents, fluctuations in rodents' abundance will play a crucial role in the small carnivore abundance (Hanski *et al.*, 2001). In contrast, generalist predators which can switch between prey, will be less affected by the fluctuations in the rodents abundance (Andersson & Erlinge, 1977). On the other hand, during low rodent abundance periods, resident predators (e.g. mustelids) increase their movements inside the territory in search for rodents or other prey (Begg, Begg & Kingdon, 2013). Meanwhile, nomadic predator species (e.g. avian predators) respond to the low prey abundance by performing large relocations (e.g migration) in search for rodents (Andersson & Erlinge, 1977). Hence, small mammal population cycles and distribution can be key drivers in small carnivore population densities and distribution.

Rodent abundance and distribution are largely affected by bottom up processes (Datiko *et al.*, 2007). However, there seems to be an asymmetric productivity - diversity relationship, where highest diversity and abundances often peaks in moderately low resource levels – the heterogeneity hypothesis (Tilman, 1982; Caro, 2001; Rautenbach *et al.*, 2014). In addition, increasing evidence has suggested that top down regulation can affect small carnivore distribution and abundances (Jiménez *et al.*, 2019). Small carnivores therefore have to adjust trade-offs between large carnivore predation, habitat heterogeneity and avoid degraded landscapes (Martinoli *et al.*, 2006).

Despite the importance of rodent abundance in small carnivores ecology, most studies investigate habitat variables (Burton *et al.*, 2012; Rich *et al.*, 2017), presence of top predators and competitors (Rich *et al.*, 2017), but prey species are only considered in diet studies (Martinoli *et al.*, 2006). In small carnivore distribution models, spatial variation in rodent abundance is often not considered in (Blackwell *et al.*, 2006). This is due to rodent abundance being estimated with intensive and logistically limiting live-trapping methods, which limits its applicability over larger spatial scales (Glennon *et al.*, 2002; Wiewel *et al.*, 2007; Wilkinson *et al.*, 2012; Chiron *et al.*, 2018).

**Ink-tracking tunnels sampling method**

Camera-trapping is a common method to study habitat preferences and distribution patterns of carnivore species (Kelly & Holub, 2008; Hofmeester *et al.*, 2019). It is non-invasive and suitable for the study of elusive and nocturnal species, simultaneously capturing data on a large diversity of species (Burton *et al.*, 2015; Porfirio *et al.*, 2018; Hofmeester *et al.*, 2019). In large carnivore distribution studies, camera-trapping data is used to infer spatial and temporal variation in ungulate biomass (O'Brien *et al.*, 2010; Linkie *et al.*, 2013; Willcox *et al.*, 2015). Concurrent, prey measures are usually obtained from camera-traps, either by using raw capture rates or by modelling the distribution/abundance of prey species. However, the conditions under which camera-traps are set to sample carnivores is inadequate for sampling small mammals (Hofmeester et al., 2019) and rodent abundances are often underestimated (Burton et al., 2012; Rich et al., 2017). Therefore, as camera-trapping cannot be used to simultaneously sample carnivores and rodents with confidence (Burton et al., 2012; Hofmeester et al., 2019), smaller prey studies need specific parallel surveys. This demands an extra cost added to the project, for data to be used as a predictor. Commonly used for this purpose, live-trapping is a method that requires intensive labour, is very time consuming, expensive and invasive (Glennon *et al.*, 2002; Wiewel *et al.*, 2007; Wilkinson *et al.*, 2012; Chiron *et al.*, 2018). Importantly, this method is usually conducted at small scales while camera-trap surveys span large survey areas. Matching these scales would be very expensive, time consuming and would require more labour. As an alternative, the non-invasive ink-tracking tunnels method (King & Edgar, 1977), has been proven valuable in assessing distribution, habitat preferences and fluctuations in small mammal' relative abundance across sites and time (King & Edgar, 1977; Glennon *et al.*, 2002; Blackwell *et al.*, 2006; Wiewel *et al.*, 2007; Wilkinson *et al.*, 2012). Since ink-tunnels can be deployed over a larger scale,

require less investment and effort, it can be a valuable method to address the spatial variation of rodent abundance and its importance for small carnivore distribution.

**Study objectives**

The main aim of this study is to investigate the viability of including relative rodent abundance as derived from ink-tunnels into small carnivore camera-trapping studies. Furthermore, to investigate the context dependence of rodents in small carnivore distribution, rodent relative abundance was derived across a gradient of human disturbance. To unravel whether prey or other factors are affecting distribution, alternative covariates of habitat and disturbance were also considered.

# Methods

## Study area

The sampling of this project was conducted in the Maputaland region of the KwaZulu-Natal province of South Africa. Sampling occurred on a landscape gradient of anthropogenic disturbance: Phinda Private Game Reserve (hereafter Phinda) (27°40′S–27°55′S; 31°11′E–32°26′E) as the lowest level of disturbance, game farms on the South border of the reserve as the intermediate level of disturbance, and Zulu rural communities on the East border of the reserve as the highest level of disturbance.

### Camera-trapping carnivore surveys

We placed Cuddeback Professional white-flash camera-traps (CT) at 192 stations across the three areas from August to November of 2017 (Figure 4.1). Camera-trapping stations were set at a minimum average distance of 1311 m, without bait and at animal trails and gravel roads to increase its detectability of animal movements (Cusack *et al.*, 2015). In order to obtain data on different sized animals, camera-traps were set on trees or metal stakes at 30 cm height from the ground to increase detection rates (Meek, Ballard & Falzon, 2016), at 2 to 3 meters distance from the trail and angled to focus the crossing zone (Cusack *et al.*, 2015). Cameras were programmed to photograph with minimum delay, which corresponds to one second with day light and 30 seconds during the night due to the flash use. Camera-trapping data was managed using *camtrapR* package (Niedballa *et al.*, 2016), considering an independence interval of 30 min between each record of the same species.
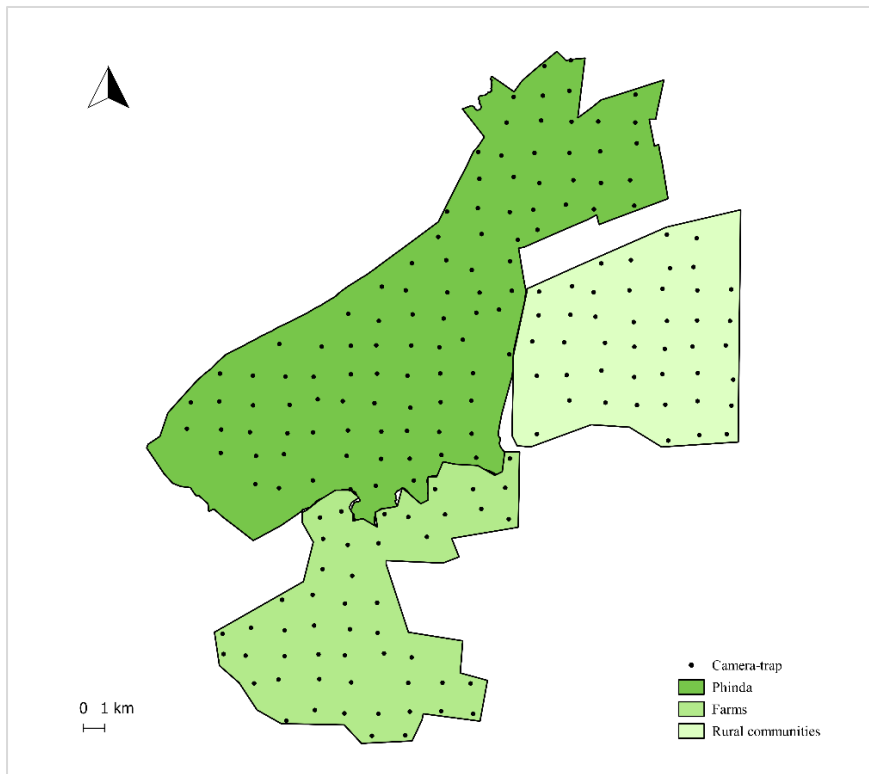
Figure 4.1: Camera-trapping grid across the three surveyed areas, with 98 CTs in Phinda 50 CT in the Farms and 44 in the Rural communities.

**Ink-tracking tunnel small mammal surveys**

During the months of October and November 2017, ink-tracking tunnels were placed in a 3 x 3 y-design around each camera-trap (Figure 4.2) (192 CTs make a total of 1728 tunnels) with 10 m distance between tunnels, during four consecutive nights. The tunnels were baited and inked the night before of the placement. This deployment resulted in an effort of 6 912 ink-tunnel tracking nights.

Estimations of rodents' abundance were obtained through a proportion of tunnels with records of tracks (track index). Track index was assessed not for rodent species but for functional groups based on track size to assess the relevance of prey biomass: small rodents, medium rodents and rodents in general, since it was proven to be significant (Rosa, Beatriz P., 2019).
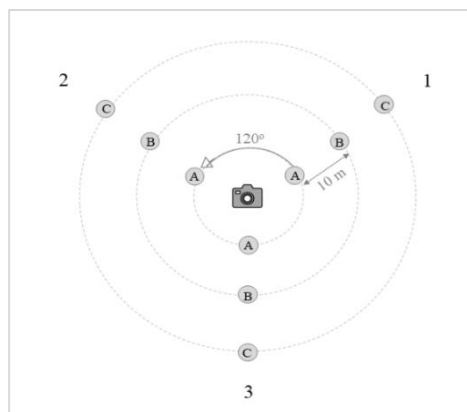


Figure 4.2: Sampling design of the ink-tracking tunnel in a 3 x 3 y-design 10 m apart from each tunnel, numbers identify the line and letters the circumference around the camera-trap at the centre.

## Occupancy modelling

To understand how the probability of a small carnivore species occurring in a site is influenced by the spatial heterogeneity in relative small mammal abundance, I applied a single species - single season occupancy model to a set of carnivore species using ink-tracking tunnels track indexes as prey covariates (MacKenzie *et al.*, 2002). This hierarchical model accounts for imperfect detections (i.e. false absences) to reduce the error and biases. Thus, the model integrates two independent processes: a detection (p) and an ecological process of site being occupied (occupancy - ψ) (MacKenzie *et al.*, 2002). The replicated observations across sites during the sampling time provides a series of detection or non-detection information which results in the probability of detection (i.e. detectability) (MacKenzie *et al.*, 2002). This hierarchical approach by simultaneously addressing detection and occupancy in the same model formulation, including site-specific variables (e.g. habitat), recognises species-covariates' relationships while reducing detection error.

Detection histories were collapsed for a 10-day period to reduce the number of zeros which cause over dispersion in model fitting (MacKenzie & Bailey, 2004). Since the model formulation accounts for both detection and occupancy, I followed a two-step approach in model fitting. First, I modelled detection as a function of trail width, as trail width preference may be associated with species size (Cusack *et al.*, 2015), and contrasted this model to a null model without any detection covariates (see Supplemental Information IV). In these detection models the occupancy parameter was kept constant. Secondly, using the best detection variable for each species and context, z-scored covariates were added to the occupancy parameter, avoiding highly correlated covariates (see Supplemental Information III).

Covariates correlation analysis was performed on R software using package *stats* 3.6.0 (R Core Team, 2017). The single-species single-season occupancy model was applied using *Unmarked* package of R software (Fiske & Chandler, 2011; R Development Core Team, 2011).

## Covariates

To estimate prey importance on small carnivore's distribution, I incorporated track index of the functional groups obtained from the ink-tracking tunnels survey as covariates in the occupancy parameter. To understand the full importance of prey covariates, first they were compared to the null model to see if they themselves were important, then habitat and disturbance covariates (Table 4.1), were added to see if prey covariates are still important when accounting for the effect of alternative drivers.

Tree cover (TC) was chosen as a proxy for habitat, since small carnivore richness and distribution has been described to be correlated with habitat structure (Rich *et al.*, 2017). Tree cover was based on a 30 m resolution MODIS continuous field of tree cover dataset (Sexton *et al.*, 2013). Since the carnivore species in this study have different home ranges and previous studies use different buffer sizes (Widdows *et al.*, 2015; Ramesh *et al.*, 2016; Rich *et al.*, 2017), we conducted a previous scale-optimization analysis and used the top ranked species-specific scale among 30 m, 100 m, 150 m, 250 m and 500 m (see Supplemental Information V). Distance to the closest waterbody (DistW) was added since the literature refers to a positive relationship between waterbodies and carnivore distribution (Rich *et al.*, 2017). Waterbodies (from small lagoons to dams and rivers) were marked on Google Earth and distance was measured in ArcGIS v10.6.1 (ESRI, 2018). The anthropogenic disturbance covariates used were independent records of cow abundance (cow) obtained from the camera-trapping sampling (Blaum,

Tietjen & Rossmanith, 2009), and distance to houses (DistH) (Kalle *et al.*, 2013) which were also marked on Google Earth and distance measured in ArcGIS.

Table 4.1: List of covariates used in the occupancy modelling, their brief description, the area they were applied to and range.

| Variable | Description | Area | Range (min-max) |
|---|---|---|---|
| **Main Covariates** | | | |
| | **Prey** | | |
| **SR** | Proportion of tunnels with footprints of small rodents (footprint sizes Table 3.1) | Farms Phinda Rural | 0 – 1 |
| **MR** | Proportion of tunnels with footprints of medium rodents (footprint sizes Table 3.1) | Farms Phinda Rural | 0 – 1 |
| **Rodents** | Proportion of tunnels with footprints of rodents in general (footprint sizes Table 3.1) | Farms Phinda Rural | 0 – 1 |
| **Alternative Covariates** | | | |
| | **Detection** | | |
| **TrailW** | Trail mean width in meters of three measured points of the trail or road at each camera station. | Farms Phinda Rural | 0.47 – 6.37 |
| | **Habitat** | | |
| **TC** | Percentage of tree cover with 30 m resolution at the best buffer around the camera previously estimated for each species, between 30 m, 100 m, 150 m, 250 m and 500 m. | Farms Phinda Rural | 0 – 100 |
| **DistW** | Distance in meters of the camera to the nearest waterbody. | Farms Phinda Rural | 0 – 2897.95 |
| | **Disturbance** | | |
| **Cow** | Relative abundance of cows per station, using camera-trapping data. | Farms | 0 – 3.17 |
| **DistH** | Distance in meters of the camera to the nearest house. | Rural | 38 – 98676.88 |

## Model selection

To avoid saturating the model and decreasing its fit (MacKenzie & Bailey, 2004), the number of covariates must be carefully selected. Consequently, to assess the best candidate model for each species and area and the importance of the small prey on carnivore space-use, I applied three sets of candidate models to the three areas: one using small rodents (SR) as prey covariate, a second one using medium rodents (MR), and a third one using rodents in general as prey covariate, in order to see which of the prey covariates is more relevant. Using combinations of covariates, I had a total of seven candidate models per set and per area (Table 4.2).

Table 4.2: Candidate models by area. The detection probability and the tree cover area used were the ones previously optimized by species and area. Prey is related to small rodents, medium rodents or rodents in general.

| Area | | |
| --- | --- | --- |
| **Farms** | **Phinda** | **Rural communities** |
| p(*) Ψ(Prey) | p(*) Ψ(Prey) | p(*) Ψ(Prey) |
| p(*) Ψ(Prey+TC) | p(*) Ψ(Prey+TC) | p(*) Ψ(Prey+TC) |
| p(*) Ψ(Prey+Cow) | p(*) Ψ(Prey+DistW) | p(*) Ψ(Prey+DistH) |
| p(*) Ψ(Prey+TC+Cow) | p(*) Ψ(Prey+TC+DistW) | p(*) Ψ(Prey+TC+DistH) |
| p(*) Ψ(TC) | p(*) Ψ(TC) | p(*) Ψ(TC) |
| p(*) Ψ(Cow) | p(*) Ψ(DistW) | p(*) Ψ(DistH) |
| p(*) Ψ(.) | p(*) Ψ(.) | p(*) Ψ(.) |

To scan the importance of small prey covariates, I calculated the difference between each small prey covariate and the null model (ΔAIC). Then I compared the prey covariates with the best candidate model in the set. Along with the relative importance in model selection exercise, I considered the effect signal and size by looking at the beta coefficient of prey covariates which can have a positive, negative or neutral influence on the carnivore space-use. For this section, I focused on values of ΔAIC under 2, since it indicates that the candidate model is highly supported (Fabozzi *et al.*, 2014). Prior to the analysis, all covariates were standardized to *z* scores. Covariate correlations were assessed on R software using package *stats* 3.6.0 (R Core Team, 2017). Highly correlated covariates (correlation coefficient > 0.5) were discarded, with exception of prey covariates. AIC ranking indicates the best model among the candidate models chosen to explain the species occurrence, but it does not inform on how adequate the covariates are. To acknowledge this, global model fit was assessed using Pearson chi-square statistic with a parametric bootstrap of 1000 samples in order to obtain the over-dispersion factor (ĉ, hereafter c-hat) (MacKenzie & Bailey, 2004). Where c-hat value should be approximately 1, values below 1 show low variation, higher values show overdispersion and much higher values are associated with lack-of fit (MacKenzie & Bailey, 2004).

## Results

The camera-trapping survey captured seven species of small carnivores over 60 to 90 effective trapping days: large-spotted genet, white-tailed mongoose, side-striped jackal, banded mongoose, common slender mongoose, honey badger and striped polecat. However, only species by area with significant number of independent records, naïve occupancy and null model detection were selected to be included in the analyses (Table 4.3).

The species by area selected to model were: large-spotted genet (LSG) in the Farms, Phinda and Rural communities; white-tailed mongoose (WTM) in the Farms, Phinda and Rural communities; banded mongoose (BDM) in the Farms; side-striped jackal (SSJ) in Phinda; honey badger (HNB) in Phinda; and side-striped polecat (STP) in the Rural communities. Since these have a minimum of five records, a naïve occupancy above 0.10 and null detect model of 0.15, they were selected as thresholds for modelling considering the data obtained. Making a total of ten applied occupancy models (Table 4.3).

The large-spotted genet was the most captured species, followed by the white-tailed mongoose. While the less captured species was the striped polecat. Phinda had the highest number of records, followed by Farms, while Rural communities had the lowest numbers and even absence of some species.

Table 4.3: Number of records, naïve occupancy and null model detection estimation for all species and areas. In bold are the combinations of species and areas selected to model.

| Area | Species | Number of Records | Naïve Occupancy | Null Model Detect |
|---|---|---|---|---|
| **Farms** | **Large-spotted genet** | **38** | **0.76** | **0.50** |
| **Farms** | **White-tailed mongoose** | **23** | **0.46** | **0.22** |
| Farms | Side-striped jackal | 5 | 0.10 | 0.08 |
| **Farms** | **Banded mongoose** | **16** | **0.32** | **0.16** |
| Farms | Slender mongoose | 9 | 0.18 | 0.05 |
| Farms | Honey badger | 7 | 0.14 | 0.02 |
| Farms | Striped polecat | 1 | 0.02 | 0.00 |
| **Phinda** | **Large-spotted genet** | **79** | **0.81** | **0.37** |
| **Phinda** | **White-tailed mongoose** | **54** | **0.55** | **0.229** |
| **Phinda** | **Side-striped jackal** | **33** | **0.34** | **0.20** |
| Phinda | Banded mongoose | 10 | 0.10 | 0.07 |
| Phinda | Slender mongoose | 11 | 0.11 | 0.01 |
| **Phinda** | **Honey badger** | **20** | **0.20** | **0.08** |
| Phinda | Striped polecat | 10 | 0.10 | 0.03 |
| **Rural** | **Large-spotted genet** | **11** | **0.25** | **0.34** |
| **Rural** | **White-tailed mongoose** | **5** | **0.11** | **0.32** |
| Rural | Side-striped jackal | 1 | 0.02 | 0.00 |
| Rural | Banded mongoose | 0 | 0.00 | NaN |
| Rural | Slender mongoose | 5 | 0.11 | 0.07 |
| Rural | Honey badger | 0 | 0.00 | NaN |
| **Rural** | **Striped polecat** | **5** | **0.11** | **0.32** |

## Heterogeneity in detection probability

The detection optimization (see Supplemental Information IV) showed that the importance of covariates is species and area specific. For the banded mongoose, large-spotted genet, side-striped jackal and white-tailed mongoose in Phinda and Rural communities, the best model for the detection parameter was the null model. On the other hand, for the honey badger, large-spotted genet in the Farms and Rural communities, striped-polecat and white-tailed mongoose in the Farms, the best covariate for detectability is the trail width. Trail width had a negative effect on most combinations of species by area, except for white-tailed mongoose in the Rural communities, honey badger in Phinda and striped polecat in the Rural communities.

## Ink-tunnel measures of prey relative abundance as drivers of carnivore occupancy

Considering the global model fit results obtained (see Supplemental Information VI), I found lack of fit for the large-spotted genet in Phinda, side-striped jackal, white-tailed mongoose in Phinda and Rural communities. Hence, theses combinations of species by area were removed from the analysis.

Model selection results for candidate models with $\Delta AIC \leq 2$ are depicted in Table 4.4. Univariate prey candidate models were ranked higher than the null models for 5 of the 18 model sets applied (Figure

4.3). However, this higher ranking comparing to the null model is only well supported with a $\Delta AIC \leq 2$ for 3 of the 18 models. Specifically, medium rodents for white-tailed mongoose in the Farms, and rodents in general for the large-spotted genet and white-tailed mongoose both in the Farms. Although, considering that values higher than zero indicate the variable adds information to the null model, but only when there is a minimum difference of 2 ($\Delta AIC$) between each other, none of the prey candidate models added information.
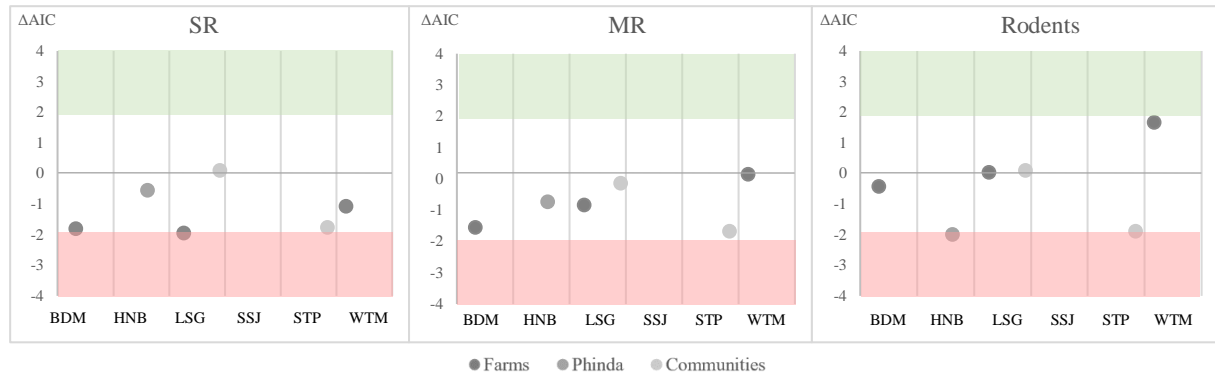


Figure 4.3: The difference between the null model AIC and small rodents, medium rodents and rodents in general, where the zero corresponds to the null model. Each vertical line separates the carnivore species: BDM – banded mongoose, HNB – honey badger, LSG – large-spotted genet, SSJ – side-striped jackal, STP – striped polecat, WTM – white-tailed mongoose. The green area indicates well supported candidate models.

When combined with alternative covariates (Table 4.4), prey appeared high ranked for 10 of the 18 model sets, of which there was a difference of at least 2 from the null model for 9 model sets.

Analysing only the combinations of species by area with a significant difference from the null model $\Delta AIC \geq 2$. For the banded mongoose, cow was the best candidate model for the three model sets. Followed by a combination of prey and cow, which had a difference superior to 2 ($\Delta AIC$) to the null model, while prey by itself was worse then the null model. For the honey badger, tree cover is the best candidate model for the three model sets. Followed by a combination of prey and tree cover, which is significantly different from the null model ($\Delta AIC \geq 2$), while prey by itself is worse than the null model.

The large-spotted genet in the Rural communities, for the small rodents' model set, the best candidate model is the tree cover followed by a combination of small rodents and tree cover. The difference to the null model is significant for the combination, except for small rodents' model is very close to the null model. For the medium rodents, the best candidate model is a combination of medium rodents and tree cover, followed by a combination of medium rodents, tree cover and distance to houses. However, independently, they are all very bad with an $\Delta AIC$ much higher than 2 and, with exception for tree cover, very close to the null model. For the rodents in general model set, the results were similar to the medium rodents set.

Table 4.4: Candidate models with $\Delta AIC \leq 2$ by species and area for the three model sets (SR, MR and Prey) using the previously optimized detection and tree cover scale.

| Area | Species | Model set | Candidate model | $\Delta AIC$ | AICw |
|---|---|---|---|---|---|
| **Farms** | Banded mongoose | SR | p(*) Ψ(Cow) | 0 | 0.4835 |
| | | | p(*) Ψ(**SR**+Cow) | 1.08 | 0.282 |
| | | MR | p(*) Ψ(Cow) | 0 | 0.557 |
| | | | p(*) Ψ(**MR**+Cow) | 1.91 | 0.214 |
| | | Rodents | p(*) Ψ(Cow) | 0 | 0.525 |
| | | | p(*) Ψ(**Rodents**+Cow) | 1.89 | 0.204 |

| | | | Model | ΔAIC | w |
|---|---|---|---|---|---|
| | | SR | p(*) Ψ(.) | 0 | 0.402 |
| | | | p(*) Ψ(TC) | 1.88 | 0.157 |
| | | | p(*) Ψ(**SR**) | 1.95 | 0.152 |
| | | | p(*) Ψ(Cow) | 1.97 | 0.15 |
| | Large-spotted genet | MR | p(*) Ψ(.) | 0 | 0.313 |
| | | | p(*) Ψ(**MR**) | 0.83 | 0.206 |
| | | | p(*) Ψ(TC) | 1.88 | 0.122 |
| | | | p(*) Ψ(**MR**+TC) | 1.94 | 0.119 |
| | | | p(*) Ψ(Cow) | 1.97 | 0.117 |
| | | Rodents | p(*) Ψ(**Rodents**) | 0 | 0.253 |
| | | | p(*) Ψ(.) | 0.043 | 0.248 |
| | | | p(*) Ψ(**Rodents**+TC) | 1.067 | 0.149 |
| | | | p(*) Ψ(**Rodents**+Cow) | 1.789 | 0.104 |
| | | | p(*) Ψ(TC) | 1.919 | 0.097 |
| | | SR | p(*) Ψ(.) | 0 | 0.336 |
| | | | p(*) Ψ(**SR**) | 1.06 | 0.198 |
| | | | p(*) Ψ(TC) | 1.51 | 0.158 |
| | | | p(*) Ψ(Cow) | 2 | 0.123 |
| | White-tailed mongoose | MR | p(*) Ψ(**MR**) | 0 | 0.274 |
| | | | p(*) Ψ(.) | 0.16 | 0.252 |
| | | | p(*) Ψ(TC) | 1.67 | 0.119 |
| | | | p(*) Ψ(**MR**+Cow) | 1.69 | 0.118 |
| | | | p(*) Ψ(**MR**+TC) | 1.98 | 0.102 |
| | | Rodents | p(*) Ψ(**Rodents**) | 0 | 0.348 |
| | | | p(*) Ψ(**Rodents**+Cow) | 1.42 | 0.171 |
| | | | p(*) Ψ(.) | 1.67 | 0.151 |
| | | | p(*) Ψ(**Rodents**+TC) | 1.82 | 0.14 |
| **Phinda** | Honey badger | SR | p(*) Ψ(TC) | 0 | 0.433 |
| | | | p(*) Ψ(**SR**+TC) | 0.31 | 0.371 |
| | | MR | p(*) Ψ(TC) | 0 | 0.569 |
| | | | p(*) Ψ(**MR**+TC) | 1.99 | 0.21 |
| | | Rodents | p(*) Ψ(TC) | 0 | 0.615 |
| | | | p(*) Ψ(**Rodents**+TC) | 1.95 | 0.232 |
| | Large-spotted genet | SR | p(*) Ψ(TC) | 0 | 0.445 |
| | | | p(*) Ψ(**SR**+TC) | 1.01 | 0.268 |
| | | MR | p(*) Ψ(**MR**+TC) | 0.000 | 0.634 |
| | | | p(*) Ψ(**MR**+TC+DistH) | 1.500 | 0.300 |
| | | Rodents | p(*) Ψ(**Rodents**+TC) | 0 | 0.5936 |
| | | | p(*) Ψ(**Rodents**+TC+DistH) | 1.92 | 0.2275 |
| **Rural** | | SR | p(*) Ψ(.) | 0 | 0.323 |
| | | | p(*) Ψ(TC) | 1.03 | 0.193 |
| | | | p(*) Ψ(DistH) | 1.43 | 0.158 |
| | | | p(*) Ψ(**SR**) | 1.75 | 0.134 |
| | Striped-polecat | MR | p(*) Ψ(.) | 0 | 0.365 |
| | | | p(*) Ψ(DistH) | 1.43 | 0.179 |
| | | | p(*) Ψ(**MR**) | 1.67 | 0.159 |
| | | | p(*) Ψ(TC) | 1.9 | 0.141 |
| | | Rodents | p(*) Ψ(.) | 0 | 0.329 |
| | | | p(*) Ψ(TC) | 1.03 | 0.196 |
| | | | p(*) Ψ(DistH) | 1.43 | 0.161 |
| | | | p(*) Ψ(**Rodents**) | 1.89 | 0.128 |

The effect of small prey covariates on the small carnivores at 95 % of confidence (Figure 4.4) showed that the confidence interval overlaps zero for all combinations of species and areas. However, some are better supported, such as the white-tailed mongoose in the farms that shows a for a positive effect of the three prey covariates. For the other species/areas there is little confidence in the effect of the prey covariates.
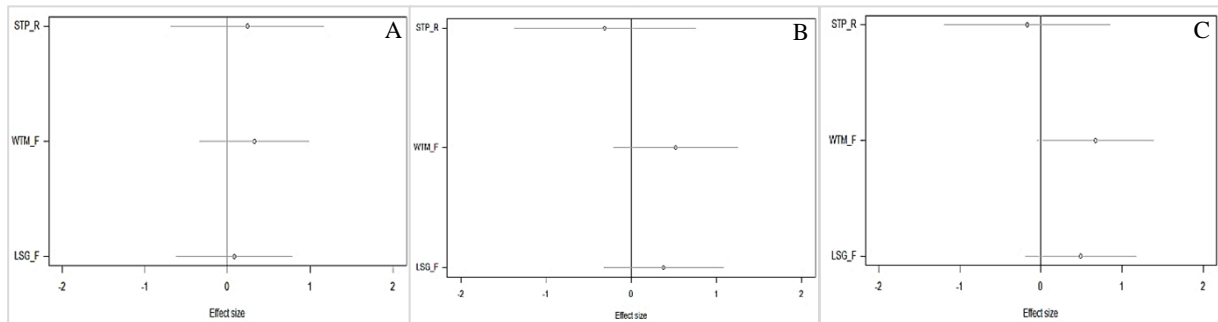


Figure 4.4: Effect of prey covariates on small carnivores' occupancy for models with ΔAIC ≤ 4 by area. A- small rodents, B- medium rodents, C- rodents in general.

## Discussion

The ink-tracking tunnels rodent survey was successfully implemented concurrent to a very large camera-trapping effort (192 CTs), highlighting its feasibility for large-scale studies. However, the small prey measures obtained (track index of small rodents, medium rodents and rodents in general) did not have a meaningful contribution to the modelling of the local small carnivore species.

When combined with alternative covariates, prey variables appeared to add information to the null model, however, on most of the cases it was a by-product of the explanatory power of the alternative variable. On combinations that were top ranked, prey was always very close to the null model or worse than it, while the alternative variable was high ranked with a significant difference from the null model. Which enables the conclusion that prey was valorised by the presence of the alternative variable. This was the case for the banded mongoose in the Farms, which was most influenced by cows, showing an avoidance of areas where cows were more abundant. The honey badger in Phinda was more influenced by the tree cover and the large-spotted genet for the small rodents set, was also more influenced by the tree cover. Although, observing the case of the large-spotted genet for the medium rodents and prey sets in the Rural communities, all the covariates independently were not important nor added information, but together were the most important and significantly different from the null model, especially prey and tree cover. Thus, in these cases prey was in fact relevant and added explanatory information to the tree cover and to the distance to houses.

Hence, I can infer that even though tree cover has a great impact on small carnivores' distribution, the abundance of small prey can be an important driver as well when the two are combined. Therefore, when using prey covariates, tree cover and other ecologically important habitat covariates should be considered together in the modeling process.

Large-spotted genet was the most influenced by small prey relative abundance, however only in the Rural communities. Which leads to the conclusion that the distribution of the *G. maculata* is positively associated with rodents' abundance in the highest level of anthropogenic disturbance. It would be important to rethink the modelling approach with this species to understand the role of prey

abundance in other levels of disturbance. However, the result obtained meets the diet information that places rodents as a main food resource for the species (Angelici & Luiselli, 2005). For this reason, in future studies of this species, it will be important to account for prey relative abundance as a driver for their distribution in human degraded habitats.

The overall weak effect of small mammals' relative abundance on small carnivores' distribution is not surprising, as the studied species have a generalist feeding behaviour and even though rodents comprehend a large portion of their diets, they can feed on other prey, such as insects (Taylor, 1972; Rood, 1975; Rowe-Rowe, 1978; Waser & Waser, 1985; Atkinson *et al.*, 2002; Larivière, 2002; Begg *et al.*, 2003; Angelici & Luiselli, 2005; Otali & Gilchrist, 2005; Hoffmann & Taylor, 2013). Moreover, the low response may be also related to sampling limitations. The ink-tracking tunnel survey measured small mammals' relative abundance in a 30 m buffer which is a very small portion for carnivores' movements, especially considering cameras were spaced by over 1 Km. Moreover, track index was obtained over four nights of sampling comparing to the three months of camera-trapping survey. This is particularly important as rodents' abundance may have changed during the three months. Therefore, it would be important to increase the sampling time. Instead of increasing the number of trapping nights, because of over-tracking, it could be interesting to consider replicating the prey sampling throughout the camera-trapping sampling (e.g. four nights per sampling month). On the other hand, prey studies may be improved by sampling small prey at a large-scale adjusted to their specific ecology, to better understand proxies or to model the distribution of small prey abundance that can then be summarised in variables for the use in carnivore studies.

### Conclusions

In summary, ink-tracking tunnels as a method to sample small mammals' relative abundance at a large-scale study and its measures (i.e. track index) can be used in carnivore camera-trapping studies as prey covariates. However, the prey measures were not relevant in the context of this study. The track index does not need to be separated into functional groups as small carnivores did not show a preference for the body mass of rodents. Consequently, studies including prey availability do not need the effort of identifying the rodent tracks, but rather should consider them as prey in general. The effect of small mammals' relative abundance on small carnivores' distribution is species and context specific, so in studies where the species are food resources generalist, this covariate may not have an impact. Nevertheless, it should be considered on studies focused on species that are either rodent specialists or feed mainly on rodents (i.e. large-spotted genet), or in studies focused on prey relevancy.

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CHAPTER 5 – *FINAL CONSIDERATIONS*

This research showed that ink-tracking tunnels are a reliable alternative to live-trapping to capture spatial heterogeneity in small mammals' relative abundance, enhancing its applicability on a large-scale study due to the low sampling effort associated. To extract information in a simple way, tracks can be successfully divided according to size in small rodents, medium rodents and large rodents, from which track index can be obtained through a proportion of tunnels with tracks of each group per site. Track index is therefore strongly correlated with live-trapping abundance index and allows to capture large fluctuations on rodents' abundance across sites for species or groups that are very abundant. Even though live-trapping gives more information on the individuals traits, ink-tunnels advantages, especially the low sampling effort, make it a feasible alternative for studies where robust measures are not required. Moreover, ink-tunnels can even be better than live-trapping for presence studies, by contouring trap shyness and single-entry issues.

At last, ink-tracking tunnels sampling method is feasible to implement at large-scale studies and can be useful in small carnivore camera-trapping studies, depending on the target species dietary needs and landscape disturbance context.


## Conservation applications


Although small carnivores are a diverse group, and data deficient status has been decreasing (9%), their current population trend is declining (40%) or unknown (35%), with only 2% increasing. Some small carnivore species have proven resilient and adaptable to various threats, even capable to recolonise areas or recover from low populations. However, the 35% of "unknown" situations solidifies the need to understand populational fluctuations and presence/absence. When evaluating the conservation actions to take and postulating proper management recommendations (Zaw *et al.*, 2008), it is important to access with precision and accuracy the knowledge of the species status (Schipper *et al.*, 2008).

Ink-tracking tunnels can serve a variety of purposes and can be very important in the management and conservation of species and ecosystems. When comparing with other methods with the same purposes (i.e. accessing population data), mainly with live-trapping, it presents several advantages. Its non-invasiveness, low cost and low complexity ease the sampling efforts, allowing therefore an increase of the data obtained and ensuring a much higher efficiency (King & Edgar, 1977; Glennon *et al.*, 2002). Moreover, it reduces the mortality rate and induced stress by avoiding capturing animals (Glennon *et al.*, 2002).

The method's capability to estimate the relative abundance of rodents (King & Edgar, 1977) is of great importance for monitoring populations at risk (e.g. *Peromyscus polionotus*) (Wilkinson *et al.*, 2012) or species dependent on these populations, many of which are also at risk. Realizing the influence of prey abundance on the distribution of carnivores through this method, and using their data in carnivorous occupation models, enables the application of ink-tunnels to projects that focus on assessing the current situation of a carnivorous mammal species, providing conservation measures through the management of their prey. Moreover, the possibility of comparing the relative abundance of small prey between different locations with different habitats also allows assessing the effectiveness of the natural reserve design and the impact of the surrounding matrix, allowing the adaption of implemented measures.

The fact that it is possible to detect fluctuations in the abundance of populations promotes their application in assessing the situation of species considered to be potential pests. Consequently, this will possibly allow population control of these rodent species in agricultural fields, whose socio-economic

impact is very high (Cavia *et al.*, 2012). And also the possibility of controlling diseases that may arise from the high abundance of rodents near dwelling areas (Lovera, Soledad & Regino, 2015; Williams *et al.*, 2018).

## Study limitations and future research

Sampling in a Big Five game reserve requires safety measures, including the distance to the car. Considering the camera-traps were set on animal trails where the car could not reach, tunnels had to be set 10 m apart to shorten the distance to the car in the case of animal encounter. The fact that tunnels distance was shortened, increased the possibility that the same rodent entered multiple tunnels, influencing relative abundance assessment (Blackwell *et al.*, 2006; Wilkinson *et al.*, 2012).

Regardless of the large dataset and site with high abundance of rodents, the fail to create a track guide using the species trapped with the live-trapping method, withdraw the possibility of identifying species tracks that could be for future studies on rodents ecology. The tunnels that were moved, attacked or the papers that were eaten, were not accounted for the track index. However, a previous study shows that when using track index, the lack of tunnels does not influence the result (Wilkinson *et al.*, 2012).

To try to work around the model fit problem it would be important to study the influence of prey availability on carnivores' distribution using more complex models such as the multi-species occupancy model to better understand what drives their distributions.

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*SUPPLEMENTAL INFORMATION*

# I. Automatic particle counting analysis

Table I.1: The 56 different settings (threshold, pixel size, circularity respectively) from the automatic particle counting analysis tested. In bold are the three best ones.

| Settings | | | |
|---|---|---|---|
| 45_10_0.6 | **50_15_0.9** | 55_10_1 | 60_10_0.6 |
| 45_10_0.7 | 55_05_0.6 | 55_15_0.6 | 60_10_0.7 |
| 45_10_0.8 | 55_05_0.7 | 55_15_0.7 | 60_10_0.8 |
| 45_10_0.9 | 55_10_0 | **55_15_0.8** | **60_10_0.9** |
| 45_15_0.6 | 55_10_0.05 | **55_15_0.9** | 60_15_0.7 |
| 45_15_0.7 | 55_10_0.1 | 55_15_1 | **60_15_0.8** |
| **45_15_0.8** | 55_10_0.2 | 55_20_0.6 | **60_15_0.9** |
| **45_15_0.9** | 55_10_0.3 | 55_20_0.7 | 65_10_0.6 |
| 50_10_0.6 | 55_10_0.4 | 55_20_0.8 | 65_10_0.7 |
| 50_10_0.7 | 55_10_0.5 | 55_20_0.9 | 65_10_0.8 |
| 50_10_0.8 | 55_10_0.6 | 55_30_0.6 | **65_10_0.9** |
| 50_10_0.9 | 55_10_0.7 | 55_30_0.7 | 65_15_0.7 |
| 50_15_0.7 | 55_10_0.8 | 55_30_0.8 | **65_15_0.8** |
| **50_15_0.8** | 55_10_0.9 | 55_30_0.9 | **65_15_0.9** |

Table I.2: The three best correlation scores between the best settings (threshold, pixel size, circularity respectively) and the manual counting.

| Settings | Pearson correlation | p-value |
|---|---|---|
| **55_15_0.90** | **0.313427** | **0.000** |
| 50_15_0.90 | 0.313427 | 0.000 |
| 60_15_0.90 | 0.313427 | 0.000 |
| 65_15_0.90 | 0.313427 | 0.000 |
| 45_15_0.90 | 0.313427 | 0.000 |
| **55_15_0.80** | **0.284637** | **0.000** |
| 50_15_0.80 | 0.284637 | 0.000 |
| 60_15_0.80 | 0.284637 | 0.000 |
| 65_15_0.80 | 0.284637 | 0.000 |
| 45_15_0.80 | 0.284637 | 0.000 |
| **55_10_0.90** | **0.251459** | **0.001** |
| 50_10_0.90 | 0.251459 | 0.001 |
| 60_10_0.90 | 0.251459 | 0.001 |
| 65_10_0.90 | 0.251459 | 0.001 |
| 45_10_0.90 | 0.251459 | 0.001 |

# II. Captured species

Table II.1: Species captured during live-trapping surveys and respective number of captured in the three sampled areas.

| Species | Area | | |
|---|---|---|---|
| | Phinda | Farms | Communities |
| *Saccostomus campestris* | 5 | 15 | 1 |
| *Aethomys namaquensis* | 1 | - | - |
| *Thallomys paedulcus* | - | - | 1 |
| *Gerbilliscus brantsii* | 3 | - | 2 |
| *Grammomys dolichurus* | 1 | - | - |
| *Lemniscomys rosalia* | 3 | 3 | 1 |
| *Mus minutoides* | 22 | 46 | 1 |
| *Mastomys spp* | 316 | 353 | 96 |
| *Steatomys pratensis* | - | 2 | - |
| *Otomys irroratus* | - | - | 3 |

# III.   Covariates correlations

Table III.1: Correlation between the different covariates for the Farms, including tree cover scale optimization variables.

| | TrailW | SR | MR | Rodent | TC30 | TC100 | TC150 | TC250 | TC500 | DistW | EVI250 | EVI500 | Cow | DistH | Human | Dog |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **TrailW** | 1.000 | -0.325 | -0.057 | -0.114 | -0.146 | -0.137 | -0.120 | -0.119 | -0.135 | -0.118 | -0.109 | -0.095 | 0.181 | -0.012 | 0.130 | -0.231 |
| **SR** | -0.325 | 1.000 | 0.383 | 0.516 | -0.117 | -0.115 | -0.155 | -0.180 | -0.222 | -0.046 | -0.260 | -0.270 | 0.177 | 0.027 | -0.184 | 0.117 |
| **MR** | -0.057 | 0.383 | 1.000 | 0.917 | -0.469 | -0.435 | -0.478 | -0.523 | -0.584 | -0.323 | -0.507 | -0.507 | 0.401 | 0.355 | -0.308 | 0.064 |
| **Rodents** | -0.114 | 0.516 | 0.917 | 1.000 | -0.395 | -0.432 | -0.477 | -0.533 | -0.553 | -0.274 | -0.477 | -0.470 | 0.397 | 0.312 | -0.247 | 0.137 |
| **TC30** | -0.146 | -0.117 | -0.469 | -0.395 | 1.000 | 0.926 | 0.919 | 0.862 | 0.844 | 0.559 | 0.770 | 0.747 | -0.395 | -0.160 | 0.222 | -0.054 |
| **TC100** | -0.137 | -0.115 | -0.435 | -0.432 | 0.926 | 1.000 | 0.989 | 0.957 | 0.905 | 0.606 | 0.799 | 0.806 | -0.384 | -0.150 | 0.193 | -0.001 |
| **TC150** | -0.120 | -0.155 | -0.478 | -0.477 | 0.919 | 0.989 | 1.000 | 0.975 | 0.923 | 0.648 | 0.811 | 0.817 | -0.378 | -0.164 | 0.188 | -0.021 |
| **TC250** | -0.119 | -0.180 | -0.523 | -0.533 | 0.862 | 0.957 | 0.975 | 1.000 | 0.962 | 0.633 | 0.826 | 0.840 | -0.380 | -0.171 | 0.198 | -0.007 |
| **TC500** | -0.135 | -0.222 | -0.584 | -0.553 | 0.844 | 0.905 | 0.923 | 0.962 | 1.000 | 0.553 | 0.807 | 0.854 | -0.364 | -0.207 | 0.206 | -0.027 |
| **DistW** | -0.118 | -0.046 | -0.323 | -0.274 | 0.559 | 0.606 | 0.648 | 0.633 | 0.553 | 1.000 | 0.472 | 0.505 | -0.199 | -0.301 | 0.121 | 0.064 |
| **EVI250** | -0.109 | -0.260 | -0.507 | -0.477 | 0.770 | 0.799 | 0.811 | 0.826 | 0.807 | 0.472 | 1.000 | 0.944 | -0.387 | -0.086 | 0.317 | 0.055 |
| **EVI500** | -0.095 | -0.270 | -0.507 | -0.470 | 0.747 | 0.806 | 0.817 | 0.840 | 0.854 | 0.505 | 0.944 | 1.000 | -0.350 | -0.167 | 0.367 | 0.047 |
| **Cow** | 0.181 | 0.177 | 0.401 | 0.397 | -0.395 | -0.384 | -0.378 | -0.380 | -0.364 | -0.199 | -0.387 | -0.350 | 1.000 | 0.318 | -0.198 | 0.104 |
| **DistH** | -0.012 | 0.027 | 0.355 | 0.312 | -0.160 | -0.150 | -0.164 | -0.171 | -0.207 | -0.301 | -0.086 | -0.167 | 0.318 | 1.000 | -0.149 | 0.086 |
| **Human** | 0.130 | -0.184 | -0.308 | -0.247 | 0.222 | 0.193 | 0.188 | 0.198 | 0.206 | 0.121 | 0.317 | 0.367 | -0.198 | -0.149 | 1.000 | -0.113 |
| **Dog** | -0.231 | 0.117 | 0.064 | 0.137 | -0.054 | -0.001 | -0.021 | -0.007 | -0.027 | 0.064 | 0.055 | 0.047 | 0.104 | 0.086 | -0.113 | 1.000 |

| > 0.40 | > 0.50 | > 0.70 |
|---|---|---|

Table III.2: Correlations between the different covariates for Phinda, including tree cover scale optimization variables.

| | TrailW | SR | MR | Rodent | TC30 | TC100 | TC150 | TC250 | TC500 | DistW | EVI250 | EVI500 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **TrailW** | 1.000 | -0.194 | -0.073 | -0.181 | 0.322 | 0.351 | 0.363 | 0.342 | 0.299 | -0.158 | 0.061 | 0.033 |
| **SR** | -0.194 | 1.000 | 0.139 | 0.662 | 0.010 | -0.007 | 0.006 | 0.022 | 0.083 | -0.025 | 0.042 | 0.109 |
| **MR** | -0.073 | 0.139 | 1.000 | 0.705 | -0.402 | -0.442 | -0.436 | -0.429 | -0.415 | 0.171 | -0.420 | -0.386 |
| **Rodent** | -0.181 | 0.662 | 0.705 | 1.000 | -0.202 | -0.258 | -0.253 | -0.232 | -0.159 | 0.117 | -0.276 | -0.182 |
| **TC30** | 0.322 | 0.010 | -0.402 | -0.202 | 1.000 | 0.911 | 0.886 | 0.858 | 0.807 | 0.059 | 0.499 | 0.471 |
| **TC100** | 0.351 | -0.007 | -0.442 | -0.258 | 0.911 | 1.000 | 0.983 | 0.946 | 0.875 | 0.110 | 0.572 | 0.551 |
| **TC150** | 0.363 | 0.006 | -0.436 | -0.253 | 0.886 | 0.983 | 1.000 | 0.981 | 0.917 | 0.093 | 0.604 | 0.598 |
| **TC250** | 0.342 | 0.022 | -0.429 | -0.232 | 0.858 | 0.946 | 0.981 | 1.000 | 0.967 | 0.102 | 0.640 | 0.652 |
| **TC500** | 0.299 | 0.083 | -0.415 | -0.159 | 0.807 | 0.875 | 0.917 | 0.967 | 1.000 | 0.096 | 0.648 | 0.697 |
| **DistW** | -0.158 | -0.025 | 0.171 | 0.117 | 0.059 | 0.110 | 0.093 | 0.102 | 0.096 | 1.000 | 0.139 | 0.142 |
| **EVI250** | 0.061 | 0.042 | -0.420 | -0.276 | 0.499 | 0.572 | 0.604 | 0.640 | 0.648 | 0.139 | 1.000 | 0.939 |
| **EVI500** | 0.033 | 0.109 | -0.386 | -0.182 | 0.471 | 0.551 | 0.598 | 0.652 | 0.697 | 0.142 | 0.939 | 1.000 |

| > 0.40 | | > 0.50 | | > 0.70 |
|---|---|---|---|---|

Table III.3: Correlations between the different covariates for the Rural communities, including tree cover scale optimization variables.

| | TrailW | SR | MR | Rodent | TC30 | TC100 | TC150 | TC250 | TC500 | DistW | EVI250 | EVI500 | Cow | DistH | Human | Dog |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **TrailW** | 1.000 | 0.014 | 0.036 | 0.154 | -0.231 | -0.260 | -0.236 | -0.194 | -0.111 | 0.003 | 0.032 | 0.096 | 0.360 | -0.087 | 0.253 | 0.014 |
| **SR** | 0.014 | 1.000 | -0.062 | 0.595 | -0.134 | -0.163 | -0.245 | -0.256 | -0.264 | -0.150 | -0.251 | -0.208 | 0.345 | -0.275 | 0.120 | 0.312 |
| **MR** | 0.036 | -0.062 | 1.000 | 0.719 | 0.341 | 0.362 | 0.266 | 0.312 | 0.342 | 0.053 | -0.094 | -0.062 | -0.225 | 0.339 | 0.036 | 0.081 |
| **Rodent** | 0.154 | 0.595 | 0.719 | 1.000 | 0.121 | 0.146 | 0.035 | 0.086 | 0.121 | -0.093 | -0.220 | -0.168 | 0.140 | 0.088 | 0.115 | 0.265 |
| **TC30** | -0.231 | -0.134 | 0.341 | 0.121 | 1.000 | 0.885 | 0.834 | 0.715 | 0.542 | 0.412 | 0.538 | 0.417 | -0.422 | 0.161 | -0.122 | -0.036 |
| **TC100** | -0.260 | -0.163 | 0.362 | 0.146 | 0.885 | 1.000 | 0.955 | 0.899 | 0.717 | 0.326 | 0.551 | 0.444 | -0.468 | 0.227 | -0.167 | -0.115 |
| **TC150** | -0.236 | -0.245 | 0.266 | 0.035 | 0.834 | 0.955 | 1.000 | 0.943 | 0.781 | 0.364 | 0.633 | 0.555 | -0.489 | 0.248 | -0.204 | -0.194 |
| **TC250** | -0.194 | -0.256 | 0.312 | 0.086 | 0.715 | 0.899 | 0.943 | 1.000 | 0.911 | 0.288 | 0.585 | 0.547 | -0.456 | 0.376 | -0.202 | -0.187 |
| **TC500** | -0.111 | -0.264 | 0.342 | 0.121 | 0.542 | 0.717 | 0.781 | 0.911 | 1.000 | 0.190 | 0.480 | 0.514 | -0.415 | 0.440 | -0.233 | -0.212 |
| **DistW** | 0.003 | -0.150 | 0.053 | -0.093 | 0.412 | 0.326 | 0.364 | 0.288 | 0.190 | 1.000 | 0.659 | 0.699 | -0.073 | 0.086 | 0.120 | -0.099 |
| **EVI250** | 0.032 | -0.251 | -0.094 | -0.220 | 0.538 | 0.551 | 0.633 | 0.585 | 0.480 | 0.659 | 1.000 | 0.886 | -0.097 | 0.003 | 0.049 | -0.171 |
| **EVI500** | 0.096 | -0.208 | -0.062 | -0.168 | 0.417 | 0.444 | 0.555 | 0.547 | 0.514 | 0.699 | 0.886 | 1.000 | -0.062 | -0.036 | 0.165 | -0.113 |
| **Cow** | 0.360 | 0.345 | -0.225 | 0.140 | -0.422 | -0.468 | -0.489 | -0.456 | -0.415 | -0.073 | -0.097 | -0.062 | 1.000 | -0.194 | 0.351 | 0.168 |
| **DistH** | -0.087 | -0.275 | 0.339 | 0.088 | 0.161 | 0.227 | 0.248 | 0.376 | 0.440 | 0.086 | 0.003 | -0.036 | -0.194 | 1.000 | -0.371 | -0.311 |
| **Human** | 0.253 | 0.120 | 0.036 | 0.115 | -0.122 | -0.167 | -0.204 | -0.202 | -0.233 | 0.120 | 0.049 | 0.165 | 0.351 | -0.371 | 1.000 | 0.780 |
| **Dog** | 0.014 | 0.312 | 0.081 | 0.265 | -0.036 | -0.115 | -0.194 | -0.187 | -0.212 | -0.099 | -0.171 | -0.113 | 0.168 | -0.311 | 0.780 | 1.000 |

| | > 0.40 | | > 0.50 | | > 0.70 |
|---|---|---|---|---|---|

# IV. Detection optimization

Table IV.1: ΔAIC and AIC weight of the detection model ranking procedures.

| Area | Candidate model | Species | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | BDM | | HNB | | LSG | | SSJ | | STP | | WTM | |
| | | ΔAIC | AICw | ΔAIC | AICw | ΔAIC | AICw | ΔAIC | AICw | ΔAIC | AICw | ΔAIC | AICw |
| Farms | p(.) Ψ(.) | 0.000 | 0.710 | - | - | 6.09 | 0.05 | - | - | - | - | 2.46 | 0.23 |
| | p(TrailW) Ψ(.) | 1.780 | 0.290 | - | - | 0.00 | 0.96 | - | - | - | - | 0.00 | 0.77 |
| Phinda | p(.) Ψ(.) | - | - | 3.77 | 0.13 | 0.00 | 0.55 | 0 | 0.71 | - | - | 0.00 | 0.56 |
| | p(TrailW) Ψ(.) | - | - | 0 | 0.87 | 0.42 | 0.45 | 1.74 | 0.29 | - | - | 0.44 | 0.44 |
| Rural | p(.) Ψ(.) | - | - | - | - | 0.26 | 0.47 | - | - | 0.95 | 0.38 | 0.00 | 0.66 |
| | p(TrailW) Ψ(.) | - | - | - | - | 0.00 | 0.53 | - | - | 0 | 0.62 | 1.36 | 0.34 |

# V. Tree cover optimization

Table V.1: ΔAIC and AIC weight of the tree cover scale optimization for all species and areas, using the best previously selected detection covariate.

| Area | Candidate model | Species | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | BDM | | HNB | | LSG | | SSJ | | STP | | WTM | |
| | | ΔAIC | AICw | ΔAIC | AICw | ΔAIC | AICw | ΔAIC | AICw | ΔAIC | AICw | ΔAIC | AICw |
| Farms | p(*) Ψ(TreeC_30) | 0.084 | 0.020 | - | - | **0** | **0.2** | - | - | - | - | 0.28 | 0.2 |
| | p(*) Ψ(TreeC_100) | 0.342 | 0.200 | - | - | 0.011 | 0.2 | - | - | - | - | 0.49 | 0.18 |
| | p(*) Ψ(TreeC_150) | 0.070 | 0.200 | - | - | 0.026 | 0.2 | - | - | - | - | 0.49 | 0.18 |
| | p(*) Ψ(TreeC_250) | 0.006 | 0.200 | - | - | 0.117 | 0.19 | - | - | - | - | 0.19 | 0.21 |
| | p(*) Ψ(TreeC_500) | **0.000** | **0.200** | - | - | 0.039 | 0.2 | - | - | - | - | **0** | **0.23** |
| Phinda | p(*) Ψ(TreeC_30) | - | - | **0.000** | **0.399** | 0.711 | 0.17 | 9.630 | 0.005 | - | - | **0** | **0.504** |
| | p(*) Ψ(TreeC_100) | - | - | 2.140 | 0.137 | 1.001 | 0.15 | 6.150 | 0.028 | - | - | 2.12 | 0.174 |
| | p(*) Ψ(TreeC_150) | - | - | 1.460 | 1.920 | 0.49 | 0.19 | 1.700 | 0.255 | - | - | 2.37 | 0.154 |
| | p(*) Ψ(TreeC_250) | - | - | 1.530 | 0.185 | 0.092 | 0.24 | **0.000** | **0.598** | - | - | 2.81 | 0.124 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | p(*) Ψ(TreeC_500) | - | - | 3.040 | 0.087 | **0** | **0.25** | 3.310 | 0.114 | - | - | 4.87 | 0.044 |
| **Rural** | p(*) Ψ(TreeC_30) | - | - | - | - | 6.36 | 0.031 | - | - | **0.000** | **0.280** | 0.291 | 0.19 |
| | p(*) Ψ(TreeC_100) | - | - | - | - | 6.19 | 0.033 | - | - | 0.890 | 0.180 | 0.303 | 0.19 |
| | p(*) Ψ(TreeC_150) | - | - | - | - | 5.29 | 0.053 | - | - | 0.970 | 0.170 | 0.433 | 0.18 |
| | p(*) Ψ(TreeC_250) | - | - | - | - | 3.3 | 0.142 | - | - | 0.890 | 0.180 | 0.059 | 0.22 |
| | p(*) Ψ(TreeC_500) | - | - | - | - | **0** | **0.741** | - | - | 0.870 | 0.180 | **0** | **0.22** |

# VI.   Global model fit

Table VI.1: Global model fit estimates of p-value and c-hat for all species per area, for the three tested model sets: small rodents, medium rodents and rodents in general.

| Area | Model set | BDM | | HNB | | LSG | | SSJ | | STP | | WTM | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | p-value | c-hat | p-value | c-hat | p-value | c-hat | p-value | c-hat | p-value | c-hat | p-value | c-hat |
| **Farms** | SR | 0.146 | 1.4 | - | - | 0.885 | 0.87 | - | - | - | - | 0.571 | 0.76 |
| | MR | 0.118 | 1.36 | - | - | 0.935 | 0.85 | - | - | - | - | 0.585 | 0.63 |
| | Rodents | 0.132 | 1.45 | - | - | 0.959 | 0.85 | - | - | - | - | 0.623 | 0.68 |
| **Phinda** | SR | - | - | 0.286 | 0.74 | 0.000 | 2.39 | 0.087 | 1.87 | - | - | 0.002 | 9.89 |
| | MR | - | - | 0.202 | 0.47 | 0.001 | 2.27 | 0.086 | 1.71 | - | - | 0.001 | 10.25 |
| | Rodents | - | - | 0.215 | 0.65 | 0.000 | 2.28 | 0.102 | 1.68 | - | - | 0.000 | 10.3 |
| **Rural** | SR | - | - | - | - | 0.819 | 0.56 | - | - | 0.767 | 0.39 | 0.09 | 1.76 |
| | MR | - | - | - | - | 0.922 | 0.41 | - | - | 0.737 | 0.36 | 0.068 | 2.36 |
| | Rodents | - | - | - | - | 0.877 | 0.44 | - | - | 0.765 | 0.38 | 0.102 | 1.99 |