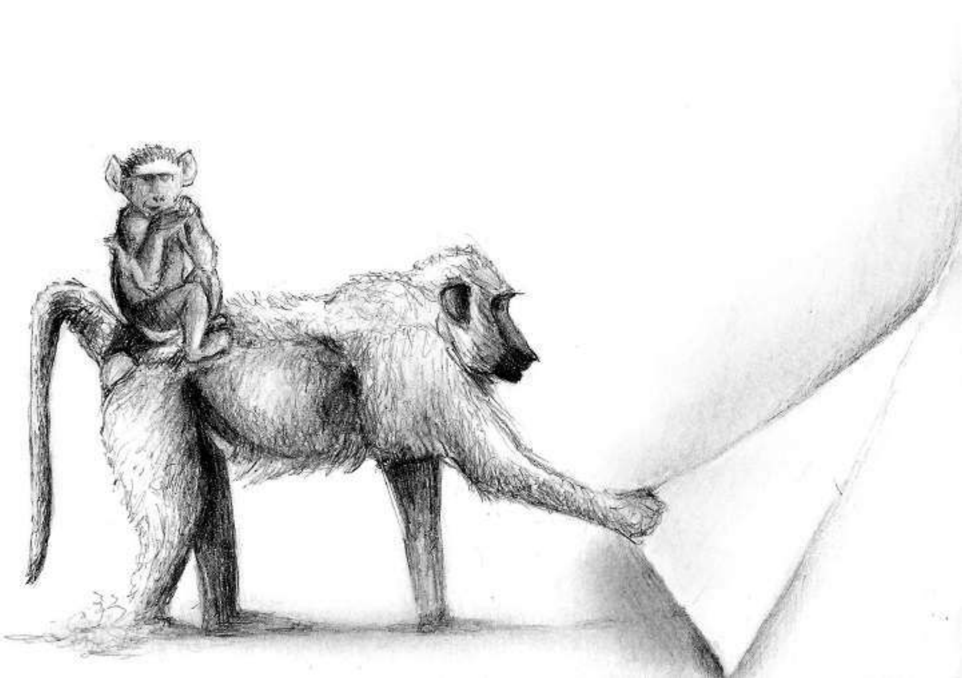

Introduction

Around two centuries ago, Alexander von Humboldt – described as the lost hero of ecological science – revolutionised the way we perceived the natural world, as Andrea Wulf explains beautifully in her book *The invention of nature* [368]. Humboldt observed patterns, similarities and connections everywhere, prompting him to write "In this great chain of causes and effects, no single fact can be considered in isolation". The web of life, the concept of nature as we know it today, was invented for the first time. Concomitantly, nature's vulnerability became obvious because pulling on one thread would cause the whole tapestry to unravel. Ernst Haeckel, greatly inspired by Humboldt's evocative writing [368], named this new discipline: *Oecologie.* In his book *Generelle morphologie* [132], Haeckel wrote "All the Earth's organisms belonged together like a family occupying a dwelling; and like the members of a household they could conflict with, or assist, one another. Organic and inorganic nature made a system of active forces".

Biocoenosis, the importance of community ecology

In ecological studies, biocoenosis is the emphasis on relationships between species co-occurring at a given time and space. These relationships are considered in addition to the interaction of each species with the physical environment [234]. All organisms exist as an intrinsic component of a community, and yet relatively few experiments investigate the web of species interactions within the context of multi-species coexistence [187, 308, 323]. The significance of the community context is highlighted by the observation that the intensity and often the direction of the interactions between a set of species may vary in the presence of others [323]. John Lawton said, in a commonly cited paper, "community ecology is a mess" and "why [do] ecologists continue to devote so much time and effort to traditional studies in community ecology?" [187]. Natural communities are indeed extremely complex and understanding the processes governing them often requires tedious and laborious elaboration of details, often not transferable to broadly similar systems [134, 186].

Community ecology investigates the nature of the biological interactions between organisms, their origins and their ecological, as well as evolutionary, outcomes [60]. To achieve these objectives, one must take account not only of the dynamics of the target species and/or process, but also of the variations within the biotic and abiotic environments. This requires studies, which cover larger geographical areas than are usually done and which emphasise the role of historical factors in order to consider evolution in the community assembly process [6, 60, 63].

Most of the conservation issues which ecologists are called on to help resolve are essentially about ecological communities; it is therefore crucial to pursue and advance ecological studies at various scales and to analyse community assembly and structure over space and time [98, 112, 308].

Camera trap, a revolutionary tool

Accessing a large amount of ecological data about animal communities, collected unobtrusively over vast spatial and temporal scales, has always been a consequential challenge for ecologists. Observing wildlife without interfering with it was an activity first developed by hunter-gatherers who constructed blinds and other smokescreens aiming to conceal themselves. Today, the desire for undisturbed observations of wildlife is still highly sought-after, both for recreation and aesthetic appreciation of nature, and for scientific understanding of animal populations and their relationships to their environment [252]. Today, modern photographic devices, camera-triggering systems and compact power sources allow us unequalled, non-invasive access into wildlife habitats using automated digital camera traps.

Wildlife photography became famous in the late nineteenth century, and the first animal-triggered photograph was that of a galloping horse, taken in 1877 with a dozen of cameras triggered by breaking strings [129]. Other successful attempts to have animals taking their own pictures took place during the first decades of the twentieth century. Using trip wires and a flash system, George Shiras photographed a myriad of North-American wild species, and developed innovative methods, sometimes using bait and sometimes positioning cameras at strategic places with frequent animal movement [302–304]. Shiras' methods were then adapted by the German Carl Georg Schillings to photograph the Eastern African wildlife, which produced striking photographs of leopards *Panthera pardus*, black-backed jackals *Canis* *mesomelas*, spotted hyenas *Crocuta crocuta*, African lions *Panthera leo*, black rhinoceros *Diceros bicornis*, all taken by the subjects themselves [296, 297].

Figure 1: Camera trap photographs of George Shiras
Five of the 74 published photographs of George Shiras, father of wildlife photography, showing the North American fauna. Shiras, who began photographing in 1889, was the first to use camera traps and flash photography when photographing animals.

It did not take long before this newly developed photographic tool attracted the attention of scientists wishing to document the species diversity of a specific area. For example, in 1927, using trip wires and bait, Frank M. Chapman photographed ocelots *Leopardus pardalis*, mountain lions *Puma concolor* and white-lipped pecaries *Tayassu pecari* among many other species on the Barro Colorado Island in Panama [62]. He also used the photographs to make inferences about animal behaviour and to attempt individual identification.

Since the earliest models that used traditional film and a one-shot trigger function, the remote cameras advanced significantly. The trip wire fell into disuse and the camera trigger evolved, becoming a treadle placed in runways, before turning into a beam of deep red light activating the photographic device once interrupted by animals [72, 259]. The practicability of remote cameras improved with thriving technology; they became digital, portable, affordable, easy to use, long lasting and reliable. Weather and water-proof housings were designed to protect the equipment from damage and to camouflage it for minimal disturbance [127]. Remote photography has a deep-seated background in ecological research [72]. It is the development, in 1991, of infrared-triggered camera systems – which are described as digital and automatic photographic devices, employing a pulsed infrared beam as a triggering device [59] – that induced its use to surge. Remote camera systems for detecting wildlife, also called camera traps, became so attractive that from 1993 onwards, they matured into commercially available products [182].

Ecological studies benefited greatly from the use of camera trap systems. The primary advantage was the large savings in time and money by forgoing labor-intensive direct observations, the ability to gather information in inclement weather as well as throughout the night [68, 99], and to record data in inaccessible locations and rugged terrain [54, 202]. These benefits became all the more profitable when the research was conducted on multiple sites [265, 321]. Chronic mechanical problems (battery failure and programming errors) could however cause data loss, especially because it often took time for the investigator to become aware of the issue [278]. Remote photographic systems also enabled ecologists to collect reliable data and to get insights into the ecology of rare, secretive and sometimes aggressive species [202], which would have been challenging to observe otherwise. However, several scientists highlighted the possibility for camera traps to alter animal behaviour [148, 207, 221, 261, 358]. Initially lacking, the number of surveys attempting to evaluate the impacts of camera trapping on animals increased and provided guidelines on how to minimise the risks of bias [141, 278]. Through the years, the variety of camera traps exploded; they differed in terms of their aspect, zones of detection, sensitivity and performances under contrasting environmental conditions [330]. As camera traps kept developing, their reliability increased and their disturbance became minimal [3, 41, 128]; they alleviated problems associated with observer bias, making the study of rare, protected and sensitive species, feasible.

Camera traps have received wide exposure in both the scientific and popular literature because they bring opportunities to collect a colossal amount of data where little information was previously available and because they provide engaging images useful for education and promotion [166, 331]. In a purely scientific framework, camera traps were employed to investigate animal activity patterns [8,59,72,77,127,128,288,348], nest ecology [67,185,207], habitat preferences [83, 172, 312, 315], species richness [1, 44, 279], as well as species abundance and density [33, 137, 203–205, 314, 349]. Camera traps can be utilised to address far-reaching questions in community ecology by collecting systematic data on an assemblage of wide-ranging species [331]. Remaining continuously on and being deployed across large areas, camera trap networks offer opportunities to evaluate spatial and temporal inter-species dynamics [2, 331].

Camera traps and statistical ecology

Scientific and technical jargon define camera traps as 'proximity detectors' [29], meaning that they have the potential to register the animals' presence and identity without any animal detention. The surge in mass camera trap development provided the scientific scene with a new tool, which led researchers to revisit commonly used ecological methods such as capture-mark-recapture. Bringing technology into the ecological framework made the field of statistical ecology a flourishing discipline. Among the myriad of statistical developments, one stands out: Spatially-Explicit Capture-Recapture (SECR) models [89]. SECR is a newly-developed statistical analysis which provides reliable population density estimates from camera trap data, and which is used worldwide to gain insights into the population ecology of wide-ranging and elusive species; often those of the greatest conservation concern [33,55,84,137,171]. While conventional capture-recapture methods provides abundance estimates, the SECR approach takes account of the spatial history of the photo-captures and skips the intermediate step of estimating an Effective Trapping Area (ETA) to access density estimates [90].

The Little Karoo, a unique landscape

The mingling of unsustainable consumption in developed countries and unceasing poverty in developing nations is threatening the natural world with non-reversible species extinction, proceeding at an ever-increasing pace, exceeding greatly conservation resources [231, 241]. In developing countries, the Critical Ecosystem Partnership Fund (CEPF) safeguards, by promoting working alliances and circumventing effort duplications as well as *ad hoc* actions, the internationally recognised hotspots: places where outstanding concentrations of endemic species are undergoing phenomenal loss of habitat [70, 241].

The Little Karoo of South Africa is a semi-arid inter-montane basin falling into the Cape Floristic Region [Appendix 1A], where succulent Karoo (dwarf, succulent shrublands), subtropical thicket (discreet bush clumps) and fynbos (fire-prone shrublands and heathlands) [199] – three globally-recognised biodiversity hotspots – intermingle [230, 231, 240]. The succulent Karoo biome is one of two international biodiversity hotspots located in arid regions [230]. In South Africa, although these semi-arid rangelands contain some of the most biodiversity rich landscapes in the country, they are also some of the least conserved spaces; falling under the national average of 6% of their area under protection [253].

The bedrock of biodiversity conservation strategies has been the use of statutory conservation areas; it is however becoming increasingly clear that this global network alone is not going to be adequate to reach its goal of comprehensively conserving biodiversity [47, 238, 247, 289]. Alternative recourses for biodiversity conservation merit closer attention.

From the 1730s onwards, the European settlement subjected the Little Karoo ecosystem to major anthropomorphic forces. The main form of land use was extensive livestock husbandry with ostriches, sheep and goats, due to unfertile landscapes [144]. The region has since experienced a regression of the agricultural economy because of substantial actual and perceived economic losses due to livestock depredation, which has been to the benefit of tourism and second-home industries. The Little Karoo is sparsely populated and the landscape is now a mosaic of extensive farms, small protected areas, and secondary properties. Being rugged, scenic and one of the least productive agricultural system [34, 270] of the Cape landscape, it makes for an extensive grazing/browsing area with a substantial wild mammal presence, despite few statutory conservation areas [115].

Embryonic research motivations and collateral benefits

Landowners, especially farmers and nature enthusiasts, show a keen interest in knowing their property and understanding its biological functioning. Throughout the years and generations, they learnt to read the signs that nature leaves behind: spoors, droppings, pastings, etc. Nowadays, it is fairly common to see them use camera traps as an additional source of information [183]. All the knowledge gathered in this way is shared, discussed and debated within the local community; it is nonetheless lost to science and conservation, despite an ever-increasing effort to develop open-access atlas projects where data can be submitted and explored by anyone, from anywhere at anytime [81, 307, 342]. The camera trap survey that was led as part of this PhD study, was initially motivated by the desire to investigate and document the potential presence of the brown hyena *hyaena brunnea* in the western section of the Little Karoo. No mammal atlases remotely mentioned the presence of the species in this area, although multiple local farmers were convinced of its occurrence. The data collected enabled to identify at least 18 individuals and to record the population within the Red List of mammals of South Africa, Lesotho and Swaziland [369], which was revised in 2016 by EWT (Endangered Wildlife Trust), SANBI (South African National Biodiveristy Institute), IUCN (International Union of Conservation of Nature) and MammalMAP (African Mammal Atlas Project).

The camera trap survey also documented the presence of a rare species, one of the most endangered mammal in the world, the riverine rabbit *Bunolagus monticularis*. Three unknown sites, located in riverine vegetation adjacent to seasonal rivers, were revealed. The information was passed on to CapeNature – the statutory institution with responsibility for biodiversity conservation in the Western Cape – so that it gets incorporated into the Western Cape Biodiversity Assessment report.

On a less positive note, the survey also revealed the presence of non-native species, such as warthog *Phacochoerus africanus* and fallow deer *Dama dama*, most likely introduced to the ecosystem by landowners themselves. The observation of bushpigs *Potamochoerus larvatus* was unexpected and could be explained by a gradual migration of the species from the Eastern Cape region of South Africa.

Timeline of research fieldwork

Given the vastness of the study area (4,327 km^2), the camera trap study was conducted as a series of six three-month long surveys. The initial scientific design for camera trap deployment was to use a regular grid and rotate it so that the number of camera stations falling onto roads, river beds and animal paths was maximised. The first camera trap survey was conducted using this design and camera grids placed at random locations provided few to no data at all. However, camera stations located on roads and major animal paths were successful, providing large datasets with a rich species diversity. Camera stations located along river beds were not nearly as successful as that on roads, both in terms of capture frequency and capture diversity.

On the 6th of January 2014, two months after initial deployment of the field equipment, the Little Karoo was hit by the worst flooding since the terrible 1981 flood that then wiped out half the buildings in nearest towns. This time, the water level did not rise as dramatically as it used to 35 years earlier, but roads were washed away and 20 camera traps (a third) were never to be found again.

The first survey led to redraw the scientific design and camera trap deployment protocol of the project. Camera trap stations were then all deployed on roads and animal paths, with a density of two camera trap stations per 50 km^2. Although the first survey should be considered to be a preliminary stage of the study, valuable data were gathered and included into the analysis as well as into the thesis whenever it was relevant. The sixth survey of the series consists of a replicate of the first, using the newly chosen and standardised protocol which was then used throughout the project.

Research rationale and thesis overview

Considering the ever-increasing pace at which biodiversity erosion is happening, and the expectation for continued increase in pressure on the natural world, it is crucial to gain insights into the mechanisms behind species responses to their environment, so that we can effectively manage biodiversity in a rapidly changing environment, where all biological equilibrium is jeopardised. Camera trapping technology has led to a surge in the collection of animal information, which provides an unmissable opportunity to help resolve numerous of the burning ecological questions that are essentially dealing with ecological communities. This thesis aims to develop new analytical methods enabling to explore large camera trap datasets and to attain deeper knowledge of the mammal community assembly and structure, over space and time, in the Little Karoo, in South Africa.

The thesis is built as a series of stand-alone chapters, which explains the redundancies in the introduction and method sections.

Chapter 1: *Understanding the role of topographic relief in the sympatry of mammal species.*
This chapter first develops – for 27 species within the mammal community – a quantitative approach to relate species distribution to roughness of the terrain in the Little Karoo. Using the Jacob's Index, the species preference/avoidance for all gradual ruggedness levels is estimated on a scale ranging from −1 (strict avoidance of this habitat) to +1 (strict preference, the species is always found in this habitat). Values close to zero indicate that the habitat is used in proportion to its availability. The Jacob's preference index is then used to produce chloropleth maps: shaded graphical representations showing the preferred habitat maps for 27 mammal species. Then, using Non-metric Multi-Dimensional Scaling (NMDS), I estimate the dissimilarities of habitat preferences in relation to terrain ruggedness for each pair of species within the mammal community. The output of the analysis is summarised into a two-dimensional graphical display, gathering species with similar habitat preferences, and keeping away those that demonstrate opposite trends.

Chapter 2: *Seasonal plasticity of mammalian diel activity rhythms: patterns and control.*
This chapter initially searches for seasonal shifts in species activity patterns by comparing the diel activity rhythms of 25 mammal species between the winter and summer seasons. These rhythms are estimated for every

species, using circular kernel density functions. A bootstrap analysis is used to test whether any seasonal change in species' diel activity rhythm was observed. This process was repeated, using three different time metrics to build three density functions for every species, with the objective to test whether seasonal shifts in diel activity rhythms are a consequence of photoperiodism alignment. Variations in diel activity rhythms were then quantified throughout the 24-hour cycle, and compared among all species of the community by running an NMDS dissimilarity analysis.

Chapter 3: *Multivariate analyses enable visualisation of temporal ressource partitioning in local mammal communities.*
This chapter uses circular kernel density functions to describe – for 27 mammal species with the mammal community – the species' diel activity rhythm averaged throughout the year. Using three multivariate analyses, the rhythms are compared among all species of the mammal community to differentiate species strategies on how they use the different periods of the 24-hour sleep-wake cycle, and to describe the partitioning of temporal resources among sympatric species.

Chapter 4: *Estimating leopard population density in relation to terrain ruggedness with spatially explicit capture-recapture models.*
This chapter uses newly-developed likelihood-based statistical methods to estimate the population density of Cape mountain leopards in the Little Karoo. Several submodels are built; each allows model parameters to vary with a different combination of covariates. Relative goodness of fit is assessed using model averaging. Using additional habitat information, predictable density maps are plotted from the model estimates having received heaviest weight.