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Conservation science for Common ground: developing the necessary tools to manage livestock grazing pressure in Bale Mountains National Park, Ethiopia.

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Abstract

One of the greatest proximate threats facing biodiversity is habitat change as a result of the combined effects of agricultural development and livestock grazing. Extensive livestock systems are increasingly competing with wildlife for access to land and natural resources in African rangelands. Ethiopia has the highest numbers of livestock in Africa with most livestock production taking place in highland systems. The Bale Mountains contain the largest extent of afroalpine habitat in Africa and are the most important conservation area in Ethiopia as one of thirty-four Conservation International Biodiversity Hotspots. The Bale Mountains National Park was established forty years ago to protect the endemic, and rodent-specialist Ethiopian wolf (*Canis simensis*) and the afroalpine habitats upon which they depend.

I use a 21 year time-series of livestock counts in the park to detect changes in the Oromo traditional livestock production system or *godantu*. I show that a seasonal transhumant livestock production regime, akin to *godantu*, only appears to persist in the Web valley today and I also find some evidence that the type of livestock is changing with smaller stock, such as sheep and goats, being more frequently kept. Despite reportedly growing numbers of households in the Web valley, I do not detect an overall increase in livestock numbers, suggesting that the area may have reached its carrying capacity in terms of livestock. In contrast, the number of livestock on the Sanetti Plateau increased over the monitoring period, including the remote and inhospitable western section of the plateau. Furthermore, I detect an increase in the risk of contact and disease transmission between Ethiopian wolves and free-roaming dogs in wolf optimal habitats. I subsequently estimate, through the use of transects, the densities of livestock in the Web valley, Morebawa and Sanetti and calculate the ratio of observed to maximum sustainable livestock density (based on rainfall and vegetation productivity). The conservative results suggest that the Web valley and Morebawa are overstocked given the rangeland predicted productivity for those areas, and that the problem of overstocking is at its worst during the dry season.

I then establish critical relationships between vegetation conditions, livestock grazing pressure and rodent populations (*Tachyoryctes macrocephalus*, *Lophuromys melanonyx* and *Arvicanthis blicki*) in the afroalpine, under both natural and controlled experimental conditions. Rodent biomass declines as the livestock index increases along a natural grazing gradient, but rodents' body condition, use of the habitat or breeding ecology and most vegetation variables measured do not significantly vary across the

livestock grazing gradient. Rodent populations do respond to the experimental removal of livestock inside exclosures, although this response is site and species-specific, and I find some evidence that these responses are concurrent with changes in the vegetation. Grazed plots have higher plant species richness and diversity compared to the exclosure sites which harbour reduced bareground cover and taller vegetation. Differences among rodent species in their responses to grazing may be mediated by interaction between the direct effects of grazing on habitat quality and species-specific habitat requirements, although the specific mechanism of this interaction could not be tested. Livestock may negatively affect rodents by increasing their predation risk (through removing vegetation cover), by reducing the soil suitability for maintaining burrow systems (through trampling) or, less likely, by competing for food resources.

A series of simple dynamic food chain models are developed to explore the interactions between Ethiopian wolves, rodents and vegetation and how they may be affected by increasing levels of livestock grazing. I also explore how predictions made about these trophic dynamics are affected by the type of functional response linking the different levels. The models suggest that the pastures of the Web valley and Morebawa are likely to be incapable of maintaining wolves at current livestock densities, while the Sanetti plateau may be able to sustain only slight increases in livestock density before tipping into a trophic configuration unable to sustain wolves. This model is a first step in assessing the seriousness of conflict between pastoralists and wildlife in BMNP.

Resource selection functions are developed and validated for cattle and sheep/goats grazing in the Bale afroalpine in an attempt to understand some of the drivers behind the heterogeneous use of the landscape by livestock. Habitat use by livestock is focused on lower-lying pastures in the vicinity of water sources (rivers or mineral springs). Only cattle strongly select for/against particular vegetation types. The probability of habitat use is also linked to the distance from the nearest villages. The models developed highlight a strong association between livestock use and rodent biomass in Morebawa and Eastern Sanetti, suggesting that livestock grazing poses a threat to Ethiopian wolves' persistence in marginal habitats in which rodent availability is already limited. Furthermore, the concentration of livestock around water sources has serious implications for the degradation of the park's hydrological system and the livelihoods and food security of the millions of people living in the dependent lowlands.

Integrating research and practice is a fundamental challenge for conservation. I discuss how the methodological tools developed and the insights gained into the dynamics of the afroalpine system can contribute to the management of livestock grazing pressure in Bale Mountains National Park and highlight gaps in the knowledge of the afroalpine ecosystem where more research is needed.

Author's Declaration

I declare that the work recorded in this thesis is entirely my own, except where otherwise stated, and that it is also of my own composition. Much of the material included in this thesis has been produced in co-authorship with my supervisors, and my personal contribution to each chapter is as follows:

Chapter 2. Resubmitted to *African Journal of Ecology* as Vial, F., Sillero-Zubiri, C., Marino, J., Haydon, D.T. and Macdonald, D.W.: The changing face of pastoralism and the implications for Ethiopian wolves in the Bale Mountains National Park, Ethiopia. Data collection and compilation by the Ethiopian Wolf Conservation Programme, facilitated by CS and JM. Initial concept developed by FV, CS and JM. Analysis conducted and manuscript drafted by FV. Final draft enhanced by DT, CS, JM and DW.

Chapter 3. In preparation for submission as: Vial, F., Haydon, D.T. and Macdonald, D.W.: Estimating livestock densities inside Ethiopian wolf ranges in the Bale Mountains: a comparison of direct and indirect methods. Data collection by FV. Initial concept developed by FV and DH. Analyses conducted and manuscript drafted by FV. Final draft enhanced by DH and DW.

Chapter 4. In preparation for submission as: Vial, F., Macdonald, D.W., Sillero-Zubiri, C., and Haydon, D.T. Responses of three endemic afroalpine rodents to habitat modification by livestock. Data collection by FV. Initial concept developed by FV. Analysis conducted and manuscript drafted by FV. Final draft enhanced by DH, CS and DW.

Chapter 5. In preparation for submission as: Vial, F., Haydon, D.T., Sillero-Zubiri, C. and Macdonald, D.W.: Responses of afroalpine vegetation and rodents to the removal of livestock grazing pressure. Data collection by FV. Initial concept developed by FV. Analysis conducted and manuscript drafted by FV. Final draft enhanced by DH, CS and DW.

Chapter 6. Resubmitted to *Journal of Applied Ecology* as: Vial, F., Macdonald, D.W. and Haydon, D.T.: Limits to exploitation: Modelling the impact of livestock grazing on Ethiopian wolves (*Canis simensis*) and their prey in the Bale Mountains, Ethiopia. Initial concept developed by DH and FV. Modelling conducted by FV and manuscript drafted by FV. Final draft enhanced by DH and DW.

Chapter 7. In preparation for submission as: Vial, F., Tallents, L., Beyer, H., Macdonald, D.W. and Haydon, D.T.: Modelling livestock habitat use of afroalpine grasslands inside a protected area. Data collection by FV and LT. Initial concept developed by FV, HB and DH. Analyses conducted by FV with input from HB, manuscript drafted by FV. Final draft enhanced by DH, LT, HB and DW.

I further declare that no part of this work has been submitted as part of any other degree.

Flavie Vial

University of Glasgow

February 2010

Acknowledgements

I would certainly say that my first trip in Ethiopia in September 2006 with Dan Haydon, Hawthorne Beyer and Juan Morales is in many ways a very good analogy to the journey that was to lead me to the completion of this thesis. After a couple of days in Addis Ababa, we embarked on a 2 days car journey to the Simien Mountains National Park where we would spend a few days trekking before flying back to Addis. Six hours after the start of our car journey, we ground to a halt as we watched one of the car's front wheel roll down the road in front of us. We all looked around us, perhaps in the hope of finding out that we were hallucinating, and realised that we were stuck in the middle of a dirt road, itself in the middle of nowhere. An unlikely hero, in the shape of a 10 year-old boy armed with a stone and a chisel miraculously sorted out the wheel axle and we found ourselves on the road again an hour later. Just like for the journey through my PhD, I soon found out that another obstacle will be thrown my way, and as I silently cursed my supervisor for misplacing the plane tickets back to Addis. I learned a few basic life lessons at the end of those four weeks: not to leave Dan in charge of travelling arrangements again, and not to underestimate the intrinsic capacity of things to somewhat work themselves out. I finished that particular trip (and my PhD!) with a feeling of relief but with a newly-found belief that it is the people you meet along the way that make any journey worthwhile.

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1 General introduction

According to the Millennium Ecosystem Assessment, one of the greatest proximate threats facing biodiversity is habitat change as a result of the combined effects of agricultural development and livestock grazing (2005). While the ultimate threats, such as increasing human populations and expanding global markets, are the root causes of biodiversity loss, they are generally beyond the scope of conservation planning. However, it is essential that the diverse array of goods and services provided by ecosystems (from biodiversity to carbon sequestration) are managed, at the regional or local scales, in ways that sustain human populations, not only meeting their food requirements but also a variety of other environmental, social and economic needs. In the framework of sustainable development as a guideline for environment protection (The five IUCN Park world congresses from 1962 to 2003; UNESCO's Man and the Biosphere Programme 1974; World Conservation Strategy WWF/UICN/PNUE 1980; World Commission for Protected Areas 1992; UN Conference for Environment and Development 1992; United Nations Millennium Development Goals 2000) most natural resource management programmes aim to integrate conservation and development issues, involving local stakeholders in the management of protected areas.

The global livestock sector is growing faster than any other agricultural sub-sector, providing livelihoods to about 1.3 billion people and contributes about 40 percent to global agricultural output (FAO, 2008). As a result of growth in human population and increased demand for meat in developing nations, the world's population of cattle has increased from 720 million in 1950 to about 1.5 billion in 2001, with a concomitant increase in sheep and goat (caprines) numbers from 1.04 billion to 1.75 billion (FAO, 2006). Despite the substantial rate of growth, livestock is not a major force in the global economy, generating just under 1.5 percent of total Gross Domestic Product (GDP). However, the livestock sector is locally economically, socially and politically very significant in developing countries: it provides food and income to 1.3 billion of the world's poor, especially in dry areas, where livestock are often the only source of livelihoods (Figure 1.1). The rangelands that result from grazing and browsing are an important natural resource, managed for a variety of agricultural, forestry, hunting, recreation and conservation objectives (Gordon et al., 2004).

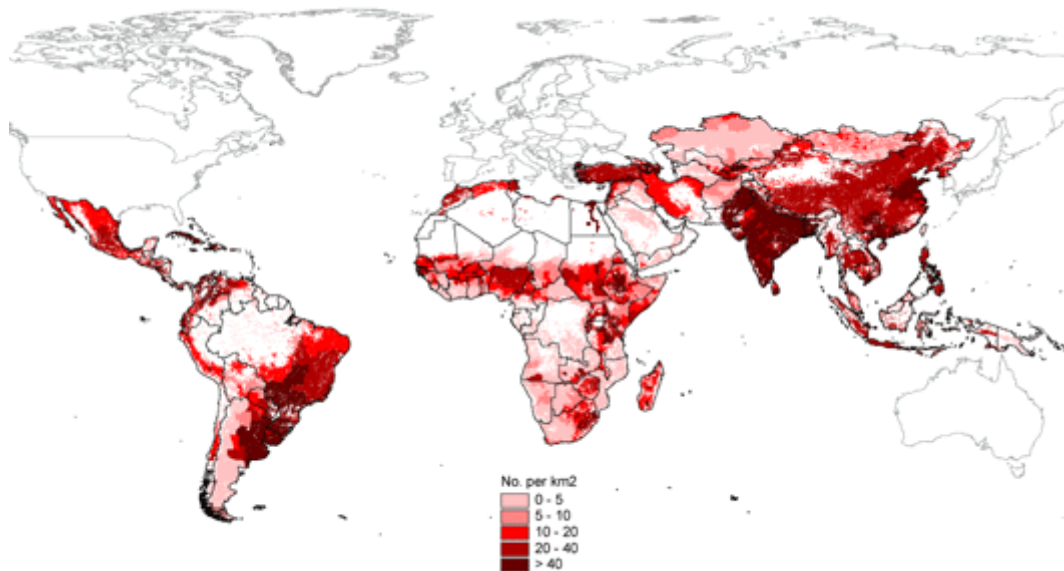


Figure 1-1: Map of livestock densities in the developing world (Thorton et al., 2002).

Densities are expressed in tropical livestock units/km² (Boudet and Riviere, 1968), a unit that quantifies the total density of livestock by combining the numbers of individuals of the different species present.

The impact of livestock on the environment is substantial with 26% of the earth's terrestrial surface used for livestock grazing and 33% of global arable land used to grow feed grain (FAO, 2008), contributing to extensive land and habitat degradation (Dodd, 1994, Ibaneza et al., 2007, Rietkerk et al., 1997, Asner et al., 2004). The link between deforestation and livestock production is strong in South America where, by the year 2010, cattle are projected to be grazing on 24 million hectares of Neotropical land that was forest in 2000 (Wassenaar et al., 2007). Another area where livestock have fuelled habitat degradation is in rangelands. Rangeland degradation results from an imbalance between livestock density and the capacity of the pasture to support grazing and trampling. Such mis-management occurs most frequently in the less resilient arid and semi-arid rangelands, characterised by a relatively erratic biomass production (Campbell et al., 2006, Kaine and Tozer, 2005, Illius and O'Connor, 1999), and leads to the fragmentation of the herbaceous cover, desertification (increase in bare soil) and woody encroachment (Milchunas and Lauenroth, 1993, van de Koppel et al., 1997, Fuhlendorf et al., 2001). Such processes affect a multitude of key ecosystem functions such as decomposition, nutrient cycling, biomass production and soil and water conservation (Savadogo et al., 2007, Mwendera and Saleem, 1997, Derner and Hart, 2007, Hiernaux et al., 1999).

1.1 Livestock production & livelihoods in Africa

It would be difficult to find any substantial area entirely unaffected by the activities of men and their herds of domestic stock in Africa, with some 230 million cattle, 246 million sheep and 175 million goats on the continent today. Most of the present-day livestock entered Africa from Asia, and did not become a major part of the ecosystem until the last 4-5,000 years when sizeable nomad herds of cattle, sheep, goats and donkeys built up and reliance on domestic stock restricted the pastoralist to areas of good grazing, with access to water and free of tsetse flies (Pratt and Gwynne, 1977). As a result of inter-tribal warfare and conquest of territories, the land soon became divided into areas of high rainfall and better grazing, where pastoralists became more sedentary and arid areas where nomadism remains a requirement of survival and efficient land use. Indigenous resource tenure systems have evolved to meet the constraints of local, often difficult, environments and to facilitate the operation of complex spatial and temporal land use patterns (Behnke et al., 1993).

Pastoralists depend wholly upon their livestock for food and other necessities. Of the edible products – milk, meat and blood- only milk can be obtained daily and regularly. Because milk is the pastoralist's basic need, herds are composed very differently to that of the commercial rancher. Nomadic pastoralists therefore strive to maintain as many female individuals as possible (50-60% herd) (Pratt and Gwynne, 1977) leading to herds with an inherent capacity for very rapid increase when conditions are favourable. If rainfall is very erratic, as in most rangelands, rapid increase in good conditions leads to over-population in the bad years which follow. In tropical countries with no other means of preserving meat than by sun-drying, the meat-producing animals (caprines) must be fairly small and numerous. In terms of standard stock units (450kg), a pastoral family (8 people) needs at least 20 units, made up of cattle, sheep and goats, to survive from one year to another (Pratt and Gwynne, 1977). From this, it follows that, in any given area, only a limited number of human beings can survive by pastoralism alone. Overstocking, which can lead to rangeland degradation, is the direct result of increasing human biological needs, coupled with the livestock capacity for rapid increase under good environmental conditions. The first arises when the human population is excessive; the second arises when pastoralists, reluctant to sell their surplus animals, accumulate more livestock than is needed for subsistence. The difference between these two causes has clear management implications.

Extensive livestock systems are increasingly competing with wildlife for access to land and natural resources in African rangelands. Extensive production systems and wildlife have intermingled for millennia in the dry lands of Africa. Both forms of land use used to be compatible as the high mobility of pastoralists limited their impact on resources and competition over access to common resources was low (Binot et al., 2006). However, with the extension of protected areas (today, representing 13% of the land in sub-Saharan African) and the spread of crop farming, extensive production systems are progressively deprived of pastures, increasing the risk of conflict (FAO, 2006). Protected areas and their surroundings are under great pressures as they are often comparatively rich in water and fodder resources and competition between wild herbivores and livestock has escalated. Habitat change and depredation have resulted in 84 of the 175 species of large herbivores alive at the end the 20th century to be listed as critically endangered, endangered or vulnerable in the 2002 edition of Red Data Book (IUCN, 2002).

Many studies in East African protected areas and rangelands have looked at the dynamics of wild herbivores in the presence of livestock. Grevy's zebra, *Equus grevyi*, have undergone one of the most substantial reductions of range of any African mammal (Moehlman et al., 2008). Historically, ranging through most of Kenya, Somalia, Djibouti Eritrea and Ethiopia, Grevy's zebras range is now limited to northern Kenya with a few isolated populations in southern Ethiopia. Extensive spatial and temporal overlap between livestock and Grevy's zebra has been shown throughout parts of its Kenyan range (Low et al., 2009). There is evidence that competition with livestock for water negatively affects foal survival (Williams, 1998) and that individuals actively select for areas free from competition or disturbance by livestock. A 15-years time series of resident and migratory grazers in the Maasai Mara National Reserve in Kenya has recently revealed that five out of seven species of wild ungulates monitored between 1989 and 2003 (Topis *Damaliscus korrigum*, Coke's hartebeests *Alcelaphus busephalus cokii*, warthogs *Pharcocoerus africanus*, impalas *Aepyceros melampus*, and giraffes *Giraffa camelopardalis*) decreased significantly as the number of *bomas* (huts where livestock are kept at night) increased inside the reserve (Ogutu et al., 2009). The role played by livestock in structuring wild herbivore assemblages is not limited to African rangelands. The introduction of livestock and intensification of grazing in the Indian Trans-Himalaya has resulted in the local extinction of four of the seven species of wild ungulates originally present in the area (Mishra et al., 2002), a pattern that has been observed on other continents too (Harris et al., 2009).

1.2 Pastoralism in the Bale Mountains, Ethiopia: past, present and threats.

Ethiopia has the highest numbers of livestock in Africa (Solomon et al., 2003), estimated for the year 2007 as follows: 43 million cattle, 2.3 million camels, 48 million caprines and 2.2 million transport animals (horses, mules and donkeys) (FAO, 2007a). According to government estimates, the livestock sector contributes 12-16% of the total GDP and 30-35% of the agricultural GDP (Halderman, 2005). The Ethiopian highlands, with their diverse physical and biological environments, make up 40% of the total land mass of the country and dominate the national economy. Most livestock production (95%) in Ethiopia takes place in mixed rain-fed tropical highland systems and supports 88% of the total human population (Thorton et al., 2002). Censused at around 62 million people in 2000, the population of Ethiopia is expected to almost triple, reaching an estimated 170 million people by 2050 (Thorton et al., 2002), while cattle, with an annual growth rate of 1.1% (Solomon et al., 2003), is expected to reach 66 million head.

1.2.1 The Bale Mountains

Located in the southern highlands of Ethiopia (6°41'N, 39°03'E and 7°18'N, 40°00'E) within the National Regional State of Oromia, the Bale Mountains are the site of the second highest mountain in Ethiopia, Tullu Deemtu (4385m a.s.l.). The Bale Mountains contain the largest extent of afroalpine habitat (over 3000m) in Africa (Yalden, 1983). The main contiguous massif is 2067km², or 17.5% of African land above 3000m, and represents the most intact remnant of original highland vegetation (Brooks et al., 2004). One of the most important resources of these mountains is its hydrological system which provides water and economic benefits to 12 million downstream users in both Ethiopia and Somalia (OARDB, 2007). Furthermore, the Bale Mountains are the most important conservation area in the Ethiopian highlands and are of international significance. The Bale Mountains are part of one of 34 International Conservation International Biodiversity Hotspots (Williams et al., 2004), with 163 highland endemics (including 19 species of mammals), 27 of which are restricted to Bale itself (Williams et al., 2004, Yalden and Largen, 1992).

The Bale Mountains National Park (BMNP) was established in 1969 to protect the endemic mountain nyala (*Tragelaphus buxtoni*) and Ethiopian wolf (*Canis simensis*) and c.

2,200 km² of montane habitats upon which they depend (Hillman, 1986). Although, six isolated populations of Ethiopian wolves have been described in Ethiopia (Marino, 2003b) (Figure 1.2), over half of the remaining wolves are found in the Bale Mountains (Sillero-Zubiri et al., 2000).

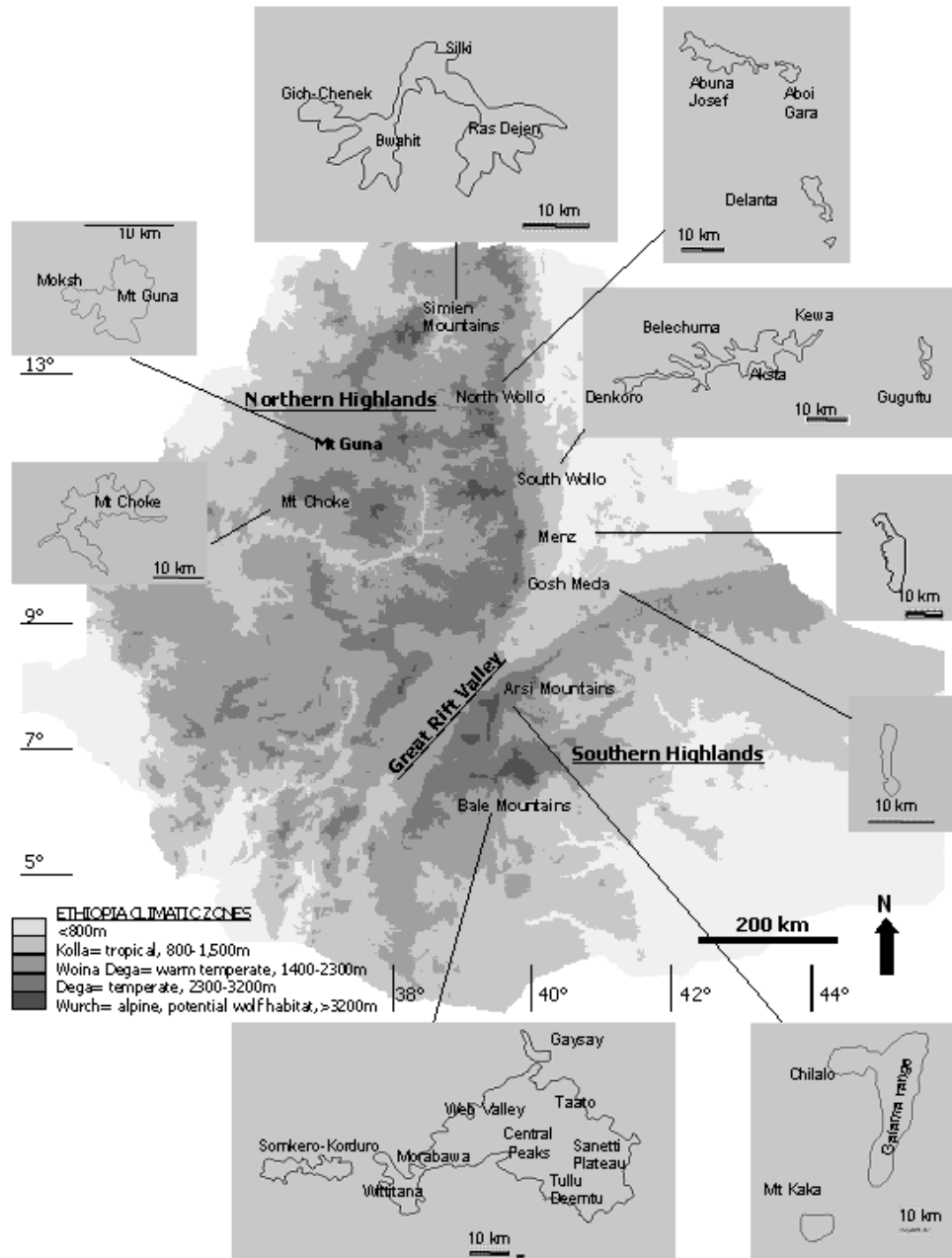


Figure 1-2: Afroalpine ranges and remaining wolf habitat in Ethiopia. Climatic zones are illustrated in a gradient of gray. The detailed maps illustrate the current distribution of suitable wolf habitats. While Ethiopian wolf remain extant in seven of these habitat islands, the populations in Mount Choke and Gosh Meda have been reported extinct (Marino, 2003b).

1.2.2 Oromo pastoralists and changes in the use of the Commons in BMNP

The Oromo pastoralists and their livestock have been an integral part of the Bale landscape for many centuries. A system of seasonal movements known as *godantu* was the traditional method of livestock management in Bale (OARDB, 2007, BMNP, 2007). The lower altitudes provided grazing during the wet season, but during the dry season livestock were trekked to the higher altitudes, in particular to high altitude forests, which provided fodder, browse and also shade. In the Hareenna Forest on the southern slopes of the Bale Mountains (Figure 1.3), influxes of pastoralists from the surrounding lowland areas occurred for 3-4 months (December-March) in the dry season (Girma, 2005). Regular census in the Web valley until 2000 (Marino et al., 2006) revealed that in the afroalpine zone, the opposite pattern of movement was observed, with livestock numbers peaking in the wetter months, when herds were kept away from the crops growing in the plains further down and highland pastures were at their most productive. Conversely, livestock numbers in the afroalpine were lowest in the dry season, as herds were taken to feed on the fields which have been left fallow. Extreme climatic conditions deterred human settlement or prolonged grazing seasons on the Sanetti Plateau (Figure 1.3), but the *Helichrysum* and ericaceous heaths along the slopes were occasionally grazed.

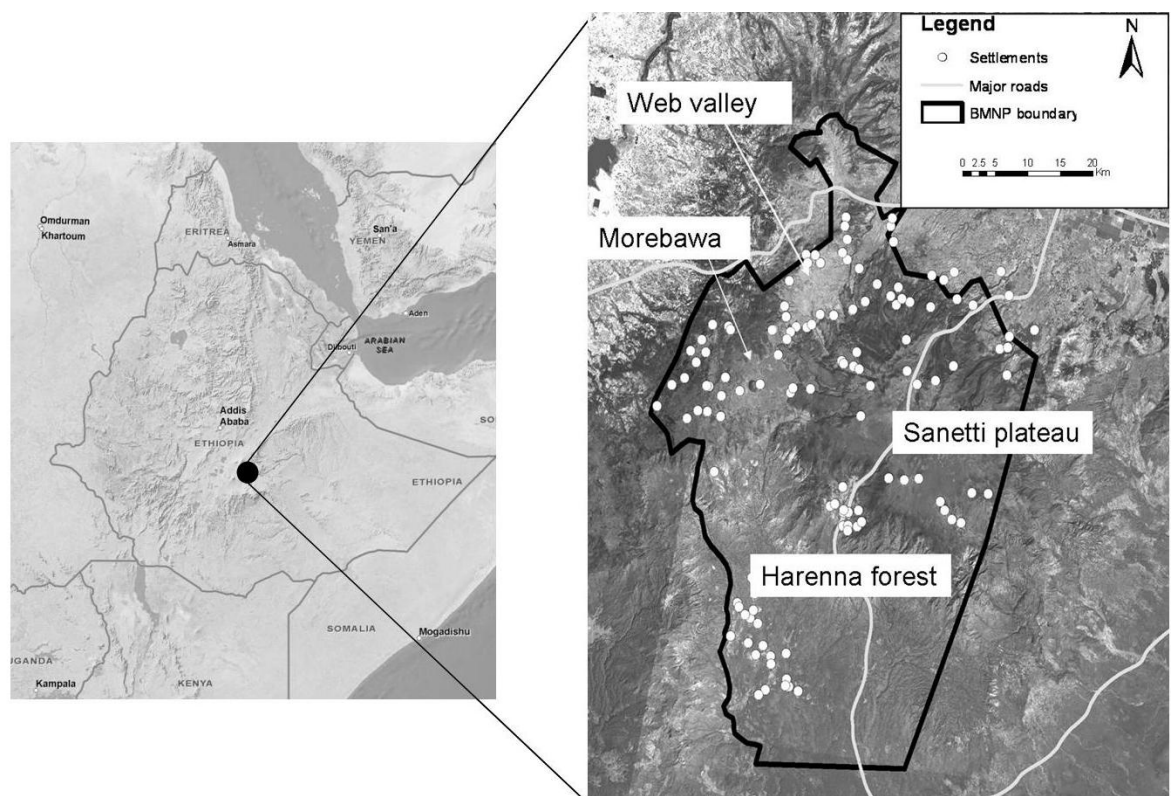


Figure 1-3: Locations of settlements within BMNP.

The BMNP has been under increasing pressure from a rapidly growing human population and the transition of transhumant and nomadic pastoralist populations to a more sedentary lifestyle. Human populations within the BMNP stood at 2,500 in 1984 rising to 7,000 in 1992 and 20,000 in 2004 (Flintan et al., 2008). The concomitant increase in livestock numbers (from 10,500 in 1986 to 168,000 in 2004) was a result of population expansion within the park and of the immigration of pastoralist communities from the lowlands. This immigration began after the fall of the socialist-military government (1974-1991) during which pastoralists had been prohibited from travelling large distances in search of forage as a result of ethnic conflicts and the government's attempt to restrict the movement of the population within the country (Jacobs and Schloeder, 2001). At the same time, increasing investment in mechanised state farms in the lowlands, established under Haile Selassie's reign (1930-1974), compelled livestock producers to shift their migration routes to the higher altitude regions. As a result, the Bale highlands, including remote and inhospitable areas of the afroalpine and Hareenna forest, have become more populated, a phenomenon amplified as Bale has long been seen as a suitable location to resettle households from food deficient areas (Flintan et al., 2008). Current estimates place the number of people living in the park permanently and seasonally at approximately 20,000 and 40,000 respectively (OARDB, 2007). Despite attempts to control livestock numbers in the past through fining and impoundment (Flintan et al., 2008), this has had little effect (Table 1-1 & Chapter 2). Today, there is little effective control at all.

Such radical changes in land use patterns have been facilitated by the common property regime the grazing land in BMNP falls under and the absence of gazetted boundaries to the national park. Common property resources are defined as a class of resources for which exclusion is difficult and joint use involves subtractability (Berkes and Farver, 1989). Common property resources are not open-access but are managed under interactive traditional resource management systems and institutions (Alcorn, 1997, Ostrom, 1991). Such institutions are local and informal, and community-based rather than government sponsored (Berkes and Farver, 1989, Ostrom, 1991). However, such institutions are under threats as the Ethiopian government strongly believes today that sedentarisation is the way forward for the majority of pastoralists in the country (Ministry of Federal Affairs, 2002)

<i>Livestock type</i>	<i>Sanetti Plateau</i>	<i>Web Valley</i>	<i>N.E. Park</i>	<i>W. of Web Valley</i>	<i>Hareenna Forest</i>			<i>Total</i>
					<i>Rira</i>	<i>W. edge</i>	<i>Hawo</i>	
<i>Cattle</i>	2,053	7,750	10,684	2,514	2,205	83,340	10,837	119,383
<i>Sheep/goats</i>	3,393	11,954	7,100	2,727	1,577	9,806	2,847	39,404
<i>Transport animals</i>	176	1,000	2,758	193	964	2,821	1,610	9,522
<i>Total</i>	5,622	20,704	20,542	5,434	4,764	95,967	15,294	168,327

Table 1-1: Number and distribution of livestock in BMNP in 2004 (adapted from Flintan et al. 2008). It is however unclear whether these numbers are estimates or came from a physical census.

1.2.3 Mounting anthropogenic threats and conservation on the Commons

A key challenge for the conservation of BMNP is the unclear legal status of the park. The Ethiopian Wildlife Conservation Organisation (EWCO) was formed in 1965 with the responsibility to “establish, develop and administer national parks for wildlife, game reserves and other conservation areas designed to provide for the better protection of the fauna and flora, and for purposes of education and scientific research” [Article 3(1) of Wildlife Conservation Order, 1970]. Under this mandate BMNP was declared a National Park in 1969 by EWCO. BMNP was never formally gazetted by parliament, but the boundary was later described (EWCO, 1974) and it was thereafter treated as a National Park. This lack of clarity in legal status has contributed to the increasingly unsustainable natural resource use in BMNP. Forty years after the creation of the park, the highest level threats are human-related threats, including agricultural expansion, wood extraction, anthropogenic fires and livestock grazing (Figure 1.4).



Figure 1-4: Anthropogenic threats in BMNP. From top to bottom: bamboo logging in Haremma forest, agricultural expansion in the afroalpine (Web valley), fire and livestock grazing (Web valley)(© Charlene Watson & Flavie Vial).

In the Hareenna forest, land has been cleared for agriculture, principally for wheat, barley and garlic production. The current rate of deforestation in Oromia is estimated at between 50,000 and 100,000 ha per annum. An area of about 10,000 ha inside BMNP is used for agriculture (ETFF, 2007). However, agricultural expansion on the afroalpine grasslands has recently been observed at 3,300m a.s.l. (Figure 1.4). Aside from the obvious problems caused by habitat loss, unmanaged expansion of cultivation leads to habitat fragmentation and increased human wildlife conflict, such as crop raiding by mountain nyalas, bush pigs (*Potamochoerus larvatus*) and Olive baboons (*Papio anubis*).

In association with settlement and agricultural expansion, demand for timber and wood increases both locally and commercially. Indigenous bamboo is used extensively in large quantities for construction materials (Figure 1.4). The most commonly collected firewood is *Euryops pinifolius*, but *Erica spp.*, *Helichrysum spp.*, *Hypericum revolutum* and *Lobelia rhynchopetalum* are collected to a lesser extent (Ashenafi, 2001).

Farmers purposely set the fires for various activities: honey collection, agricultural land preparation and burning *Erica* trees and bushes to improve forage quality and reduce retreats for leopards, *Panthera pardus*, and spotted hyaenas, *Crocuta crocuta*, suspected livestock predators. Such fires are aggravated by prolonged dry seasons and burn very large areas of the forest and afroalpine every year. While vegetation eventually recovers (Wesche, 2002), other studies have showed that rodents and other small mammals may take a long time to recolonize the area (Clausnitzer, 2003, Kasso, 2008). Furthermore, increasing grazing pressure will limit the regeneration rate of vegetation after fires.

Increasing settlements and livestock numbers in the afroalpine grasslands of BMNP are major concerns for four main reasons (Stephens et al., 2001):

1. The Bale Mountains are the source of more than 40 rivers including the five major rivers (Wabe Shebele, Genale, Welemel, Dumal, and Yadot) that are used for hydroelectric power. The major rivers originating in the Bale massif are also the only sources of perennial water for agricultural production and people occupying the arid lowlands of Eastern Ethiopia and Somalia (Sillero-Zubiri and Macdonald, 1997). Overgrazing in the highlands is likely to impact on the hydrology of these areas, threatening the livelihoods and food security of the people in the lowland areas who are highly dependent on good environmental management of the highlands (Mwendera and Saleem, 1997, Gebremeskel and Pieterse, 2006).

2. The erosive effects of livestock are visible in many areas. The occurrence of the denuded mima mounds around the lower-altitude *horas*, or mineral springs, seem to indicate that heavy livestock grazing pressure and soil poaching have acted to reduce natural vegetation cover (Tallents, 2007). Moreover, grazing in the Hareenna forest removes understorey vegetation while patches of forest are burned down regularly to increase the area of grazing land.
3. High levels of livestock have a negative impact on tourism, particularly in the Web Valley as this area is one of the greatest attractions for tourists, yet their experience is greatly impaired by the presence of thousands of livestock (Stephens et al., 2001).
4. Increased settlement and numbers of livestock are linked to a variety of threats to the wildlife, especially the mountain nyala and Ethiopian wolf. Nyalas and other antelopes compete directly with livestock for food and are usually absent from areas where livestock numbers are high (Brown, 1969). There is also some evidence to suggest that the presence of livestock is detrimental to rodent populations (Busby et al., 2006), possibly reducing the prey base of wolves and raptors in Bale.

1.2.4 Insights from other Ethiopian rangelands

The likely impacts of increased settlements in BMNP can be anticipated by looking at the environmental degradation in protected areas that have been more intensively exploited by humans in the past. The examples are numerous in Eastern Africa where reserves and national parks have often been created in areas inhabited by pastoralists and their domestic stocks.

The Simien National Park (SNP), in Northern Ethiopia, offers an interesting insight into recent changes in mountain land use. With one of the densest rural populations in Africa, the majority of habitat below the tree line (<3800 m a.s.l.) has been converted to agriculture while livestock grazing is widespread above these heights (Gotelli and Sillero-Zubiri, 1992). Busby and colleagues' vegetation survey in SNP reveals that overgrazing is widespread, with vegetation cover <5% common across the Simiens (Busby et al., 2006). Their survey also indicates that intensive grazing has caused degradation to the afroalpine ecosystem; higher grazing intensity in SNP is correlated with increased soil exposure, loss of vegetation structure, reduced vegetative species diversity, prevention of giant *Lobelia* regeneration and possibly reduced rodent abundance. Land degradation, which includes

degradation of vegetation cover, soil degradation, and nutrient depletion, as a result of grazing, is a major ecological and economic problem in Ethiopia (Hailelassie et al., 2005). It is estimated that fertile topsoil is lost at a rate of one billion cubic meters per year, resulting in massive environmental degradation and constituting a serious threat to sustainable agriculture and forestry and hence the livelihood of the agro-pastoralists themselves (Hurni, 1990, Esser et al., 2002, Anley et al., 2007).

Over the past fifty years, pastoralists and nomads living besides the Awash River in the Ethiopian Rift Valley have gradually lost access to their traditional grazing lands as a result of large-scale agricultural development and the inter-tribal conflict between the traditional rights of the Kerreyu, Afar and Itu pastoralists for dry-season grazing and access to water. Increasingly, these tribes have had to rely on the grasslands within the Awash National Park and today, more than two thirds of the park is permanently occupied by people and their livestock (Jacobs and Schloeder, 2001). In Awash National Park, encroachment and settlement led to the illegal harvest of wood for fuel and shelter, increase in illegal hunting and increased competition between wildlife and livestock which contributed to the disappearance of many wild species (Jacobs and Schloeder, 1993).

1.2.5 BMNP Ecological Management Programme

A fundamental paradox confronting conservation biologists is that the ecosystems they wish to conserve are subject to change (Burns et al., 2003). Changes can arise from endogenously induced fluctuations arising from normal ecosystem dynamics and, very often, from accumulating stresses imposed by ever increasing human demands on ecosystem resources (Ludwig et al., 1993). Distinguishing between these agents of change is a major scientific challenge (Green et al., 2005); anticipating when the limits of acceptable change might be exceeded is a conservation imperative. While essential, simply monitoring key indicators of ecosystem health or integrity is unlikely to provide the fundamental understanding necessary to predict the future consequences of mounting threats (Mace, 2005). For example, remote sensing enables broad-scale assessment of certain ecosystem components but understanding what these can tell us about ecosystem function is essential if they are to be useful indicators of future ecosystem conditions (Pettorelli et al., 2005). How ecosystems respond to different stressors will depend on their intrinsic dynamics, this is why anticipating the effects of different ecosystem stresses requires additional knowledge of intra and inter-trophic interactions.

A recurrent question relating to the protection of the Bale Mountains is how to conserve the renewable natural resources and the biotic elements of the environment in the face of changing human use patterns, given that the livelihood of thousands of people depends on the good management of the land. Before management tools can be put into place, it is crucial to determine what the threats to the ecosystems are and to quantify their impact on the resources that may require protecting. Currently, the state of knowledge of the BMNP ecological processes, species and threats is low and most management decisions have to be made with preliminary rather than detailed or expert knowledge. The ecological management programme (EMP) was designed to address this knowledge deficiency with two objectives (OARDB, 2007):

1. The first objective is the establishment of a management-orientated monitoring and research plan for BMNP. This monitoring plan aims to undertake a suite of actions to address the paucity of data and understanding of ecosystem processes in BMNP; collect baseline data on the extent of potential threats and identify ecological indicators for monitoring the achievement of the park purpose.
2. The second objective of the EMP is to feed back the information on the status of the ecosystem components and their threats to enable the design and implementation of appropriate future management actions in this and other programmes.

Livestock grazing has now been recognized as the major stress on the key ecological attributes of the afroalpine zone, and is considered an immediate priority in the Sustainable Natural Resources Management Programme (SNRMP) (OARDB, 2007, BMNP, 2007). The programme aims to convert currently unsustainable natural resource use in BMNP to sustainable levels of resource use through a participatory process where communities enter into joint natural resource management agreements with park management. SNRMP agreements will specify the type and amount of resources that can be used, by whom, and will lay out the methods, roles and responsibilities for community monitoring, regulation and resource protection. However, information is urgently required in order to initiate and implement such management activities, including quantifying levels, locations and impacts of livestock grazing.

1.3 Thesis structure

The recognition that effective conservation strategies must embrace the dynamical nature of ecosystems lies at the heart of this project. The ultimate goal of my PhD research is to inform the development of protocols within BMNP to enable the adaptive management of pastoral grazing pressure so as to ensure the stability of important trophic interactions. My research strategy has included:

1. Understanding the spatial and temporal aspects of pastoral use of the afroalpine (Chapter 2 & 7).
2. Estimating livestock densities inside three Ethiopian wolf core ranges: the Web valley, Morebawa and the Sanetti plateau (Chapter 3).
3. Establishing critical relationships between vegetation, livestock grazing pressure and rodent populations under both natural and controlled conditions (Chapter 5 & 6).
4. Carrying out broad-scale predictive modelling of the dynamics of the trophic interactions between vegetation, rodents and Ethiopian wolves as well as their response to disturbance by livestock (Chapter 4).

This research delivers a quantitative framework for managing livestock grazing, thereby contributing to the alleviation of a critical human-wildlife conflict that endangers an area of incalculable biodiversity value.

In **Chapter 2**, I use a 21 year time series (spanning the years 1986-2007) generated by the Ethiopian Wolf Conservation Programme's monitoring program in the Bale Mountains to detect changes in the Oromo traditional livestock production system. Specifically, I investigate whether the use of the afroalpine grasslands is still seasonal and driven by vegetation productivity and whether long-term trends in the numbers of livestock (cattle, caprines and transport animals), humans and domestic dogs in core Ethiopian wolf habitat can be detected.

In **Chapter 3**, I provide the first systematic livestock density estimates for each of the three main Ethiopian wolf ranges in Bale: the Web valley, Morebawa and the Sanetti plateau. First, I use distance sampling along 408 km of transects to estimate seasonal

density of livestock in those areas between July 2007 and June 2008. I then use dung counts as an indirect method of estimating livestock abundance on twenty four experimental grids in the Web valley, Morebawa and Sanetti plateau between 2007 and 2009. Dung deposition rate and decay rate are estimated seasonally for each livestock species, in different experiments, and used to convert the dung counts into a density estimate for each species. The estimates derived from both methods are compared and I make recommendations for future monitoring of livestock populations in the Bale Mountains.

Few studies have explored the interactions between livestock and small herbivores in landscape-scale experiments, and determined to what extent these interactions are mediated through changes in vegetation along a continuous grazing gradient. I use this approach across 96 experimental grids to quantify the impact of livestock grazing on the abundance and ecology of three fossorial rodent species, the giant mole rat (*Tachyoryctes macrocephalus*), Blick's grass rat (*Arvicanthis blicki*) and the brush-furred mouse (*Lophuromys melanonyx*) in **Chapter 4**. All three species are endemic to the Bale Mountains and constitute the main prey items for the endangered Ethiopian wolf. I specifically investigate the possible mechanisms through which livestock-mediated changes in the vegetation may affect rodent populations.

Exclosure studies are widely used to investigate the grazing impacts of ungulates on vegetation and animal communities by controlling ungulate access to plant resources. In **Chapter 5**, livestock are excluded from three 50x50m experimental grids in the Web Valley, an area of high human and livestock density, by the means of exclosures. The exclosures were built in March 2008, and paired with three control sites freely accessible to livestock. The purpose of this study is to establish whether afroalpine rodent populations and vegetation responded positively to the removal of livestock grazing pressure. Rodent and vegetation surveys were carried out on all sites before the construction of the exclosures and repeated regularly over a period of 14 months.

Combining results from past research conducted on the interactions between afroalpine vegetation and rodents, and rodents and Ethiopian wolves, I develop a simple dynamic food web model to explore the interactions between these trophic levels and their response to disturbance by livestock inside the three main wolf ranges in Bale (**Chapter 6**). This trophic model allows the partition of vegetation biomass into that required to sustain desired abundances of rodents and wolves, and that available for livestock grazing.

Output of this model indicates areas where vegetation biomass is insufficient to maintain acceptable trophic functioning and areas where livestock grazing could be maintained without detriment to key ecological attributes.

Visualising the distribution of the threats to endangered species is necessary for effective implementation of conservation planning. In **Chapter 7**, I develop resource selection functions for cattle and caprines inside the three main wolf ranges in BMNP to quantify the strength of selection by livestock for a number of different habitat components including, elevation, slope, distance to water and settlements, vegetation type and rodent biomass. The data collected allow for a better understanding of the patterns of habitat use by livestock in the afroalpine, as well as delimitating “ecologically sensitive” areas of both high rodent biomass and high probably of livestock use.

Applied research should be directed at providing predictive tools for risk assessment as well as decision support for managers throughout the management process. In **Chapter 8**, I summarise the findings of the present study and discuss how the methodological tools developed and the insights gained into the dynamics of the afroalpine system can contribute to the management of livestock grazing pressure in BMNP. I also highlight gaps in the knowledge of the afroalpine ecosystem and recommend future research directions.

2 The changing face of pastoralism and its implications for Ethiopian wolves in the Bale Mountains National Park, Ethiopia.

2.1 Introduction

Understanding the factors impacting an ecosystem is critical to effective and rational management. Monitoring of these factors and their impact is essential for identifying and quantifying changes that occur and which may result in the adjustment of management strategies. For example, understanding the spatio-temporal distributions of livestock is necessary for determining their impact on rangelands, and for evaluating the sustainability of grazing systems (Scoones, 1995). However, while many endangered species are closely monitored, data on the numbers of livestock being grazed inside or close to protected areas are rarely collected in a systematic manner that allows trend analyses to be performed. Here, we present the results from the analysis of a 21-year time series on livestock numbers in the Bale Mountains National park (BMNP), in the Oromia region of Ethiopia.

The BMNP conserves the largest area of afroalpine on the continent and is a centre of endemism, with the best remaining populations of Ethiopian wolves (*Canis simensis*). With approximately 500 individuals remaining, Ethiopian wolves are the rarest canid in the world, being limited to seven isolated ranges across the Ethiopian highlands (Marino, 2003). Ethiopian wolf core ranges in BMNP (Figure 2.1) are located in the Web valley (775000° N and 578000° E, 3500 m above sea level) and on the Sanetti plateau (757000° N and 596000° E, 4200 m a.s.l.). These populations have been affected by diseases spilling over from the domestic dog populations, the most immediate threat to their persistence of (Sillero-Zuberi et al., 2004, Randall et al., 2006), but by livestock grazing which affects the quality of rodent habitat, through changes in vegetation cover and composition as well as through suspected soil compaction (Chapters 5 & 6). Because of the wolves highly specialized diet (Marino et al., 2010), it is suspected that livestock grazing will have a negative effects on wolves population (Nievergelt, Good & Guttinger, 1998, Ashenafi, 2001, Stephens et al., 2001).

The BMNP has been under increasing pressure from a rapidly growing human population. In Oromia for example, the census by the Central Statistical Agency of Ethiopia reported that the region's population was estimated at 18,732,525 in 1994 versus 27,158,471 in 2007 (Central Statistical Agency of Ethiopia, 2007). This increased was mirrored inside BMNP with a human population going from an estimated 2,500 total users in 1984; to 7,000 in 1992 (OARDB, 2007) and c. 35,000 in 2009 (FZS-unpublished data). The transhumance system of Oromo pastoralists, known as godantu, follows the rainfall

pattern and has been a key feature of human use of the Bale Mountains for centuries (OARDB, 2007). Livestock comprises cattle and smaller stock such as sheep and goats (shortened to caprines). In the afroalpine zone of BMNP (> 3000m above sea level) the number of households stood at 2872 in 2009 (average household size of 6 people) including 1072 seasonal households (FZS-unpublished data). In the godantu system, livestock numbers peak on the lush highland pastures in the wetter months (April-August) and are at their lowest during the dry season.

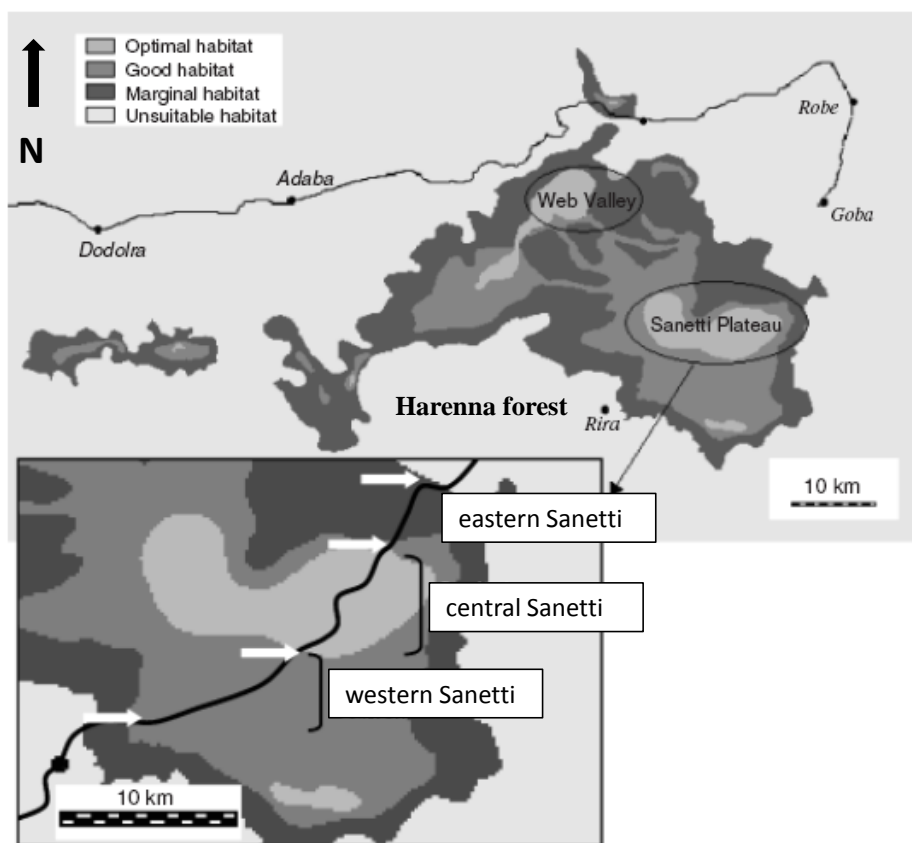


Figure 2-1: Map of the Bale Mountains showing the distribution of Ethiopian wolf habitats and study areas. The inset shows the details of Sanetti line transect along the Goba–Rira road (Marino et al., 2006).

Monitoring of livestock in BMNP was prompted in the early 80s and followed with standard methods up to present by the Ethiopian Wolf Conservation Programme (EWCP). While livestock trends up to 2000 have been analysed by Marino et al. (2006), we update the analyses up to 2007 with the following objectives:

- To identify recent and long-term trends (1980's to present) in the encounter rate of livestock and free-roaming dogs, within wolf ranges.

- To test for seasonality in the use of the afroalpine pastures by livestock and whether such use is still correlated to fluctuations in vegetation productivity.

We would expect the region-wide demographic expansion and accompanying increase in agriculture to lead to changes in pastoralist systems, from a mobile and extensive system transhumant (*godantu*) system to a more intensive non-transhumant management of livestock production, as seen on other African rangelands (Desta and Coppock, 2004, Wurzinger et al., 2009).

2.2 Methods

2.2.1 The EWCP livestock dataset: 1986-2008

Afroalpine habitats in BMNP can be classified on the basis of rodent abundance and vegetation types, and their empirical associations with wolf density (Gotelli and Sillero-Zubiri, 1992, Sillero-Zubiri, 1994):

- The Web valley and central Sanetti grasslands and meadows are “optimal” wolf habitats with high rodent biomass (~ 27kg/ha) and wolves at densities ca. 1.2/km².
- Western Sanetti is “good” wolf habitat, dominated by uniform *Helichrysum* dwarf-scrub, rodent biomass around 1/5 of that in optimal habitat and wolf at densities of ca. 0.25 /km².
- Eastern Sanetti is “marginal” wolf habitat in the ericaceous belt with rodent biomass less than 1/10 of optimal habitat.

Data collection on livestock and free-roaming dog numbers in BMNP has occurred since 1986 on the Sanetti plateau, along a transect that runs along the Goba-Rira road, crossing the plateau from east to west (Figure 2.1) and partitioning it into three areas (eastern Sanetti for 6.7 km; central Sanetti for 10km and western Sanetti for 14.3 km) as described above. Counts are conducted from a vehicle driving at c. 20km/hour by 2-4 observers (Marino et al. 2006). From 1988, EWCP initiated comparable counts along a 20km-circuit through optimal wolf habitat in the Web valley. Counts are made on horseback by 1-4 observers. Monitoring was interrupted between 1993 and 1995 due to political unrest. The frequency of surveys is shown in Table 2-1. The methodology applied permits to compare encounter rates of livestock (individuals/km of survey) across years and habitat types, after averaging by season to reduce the effect of missing months. The

seasons, known by Oromo pastoralists, follow the regime of rainfall: dry season (January to March); early wet season (April to June), mid wet season (July to September), and late wet season (October to December) (OARDB, 2007).

	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07
Sanetti Plateau	22	23	28	23	5	8	3		2	8	3	5	10	10	12	12	13	5	8	5	5	10
Web valley			2	4	5	5	6			1	3	6	11	11	12	12	12	10	7	4	7	11

Table 2-1: EWCP monitoring activity in BMNP: number of surveys per year.

2.2.2 Testing for trends in the livestock time series

We carried out the analyses of the time series in R (R Development Core Team, 2009) using the *pastecs* package (Ibanez et al., 2009). The first step was the “regulation” of the time series, to avoid the shortcomings of incompleteness. Missing values (mainly between 1993 and 1996) were extrapolated using cubic splines between observed values (Lancaster and Salkauskas, 1986). Spline interpolation was conservative for all the time series regulated (Figure 2.2). We are therefore confident that the trends detected do not result from the interpolated values but illustrate changes in the observed encounter rates during the length of the time series.

I assumed that the amplitude of both the seasonal and irregular variations in the time series did not change as the level of the trend rises or falls. The time series were therefore decomposed using a loess smoother (locally weighted polynomial regression) (Cleveland et al., 1990) into three additive components: a trend, a seasonal component and the residuals (Figure 2.3). Seasonality in the encounter rate was said to exist if the seasonal component showed an amplitude of at least 5 individuals per km of transect between seasons (Figure 2.3). After removing the seasonal component from the time series, we used a non-parametric Spearman rank correlation test (ρ) between the observations and time to examine trends across the entire dataset or across a sub-set of the dataset (2000-2007). The time series were resampled 999 times for a bootstrap test, and p values <0.05 were judged to demonstrate a significant trend in the time series. The same procedure was used to explore the trends along the time series of the ratio of cattle to caprines encounters for both the Web valley and the whole Sanetti plateau data. We removed an obvious outlier in the Sanetti dataset (Figure 2.4) prior to the analyses.

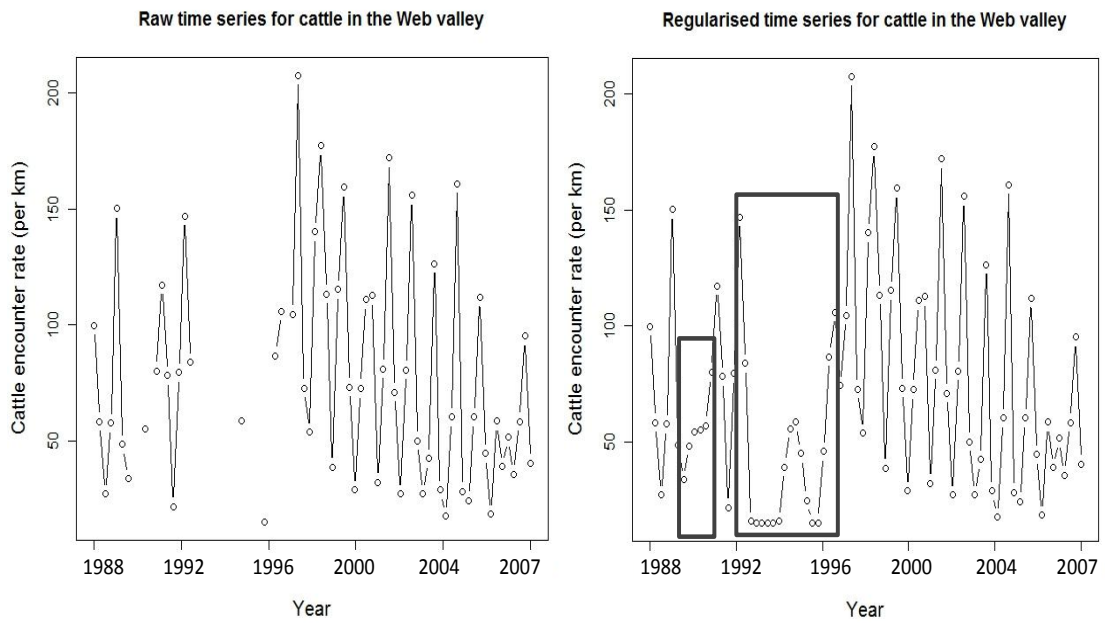


Figure 2-2: Comparison of the raw (left) and regularised time series (right) for cattle encounter rate in the Web valley. Missing values are conservatively interpolated using cubic splines between observed values as seen inside the black box.

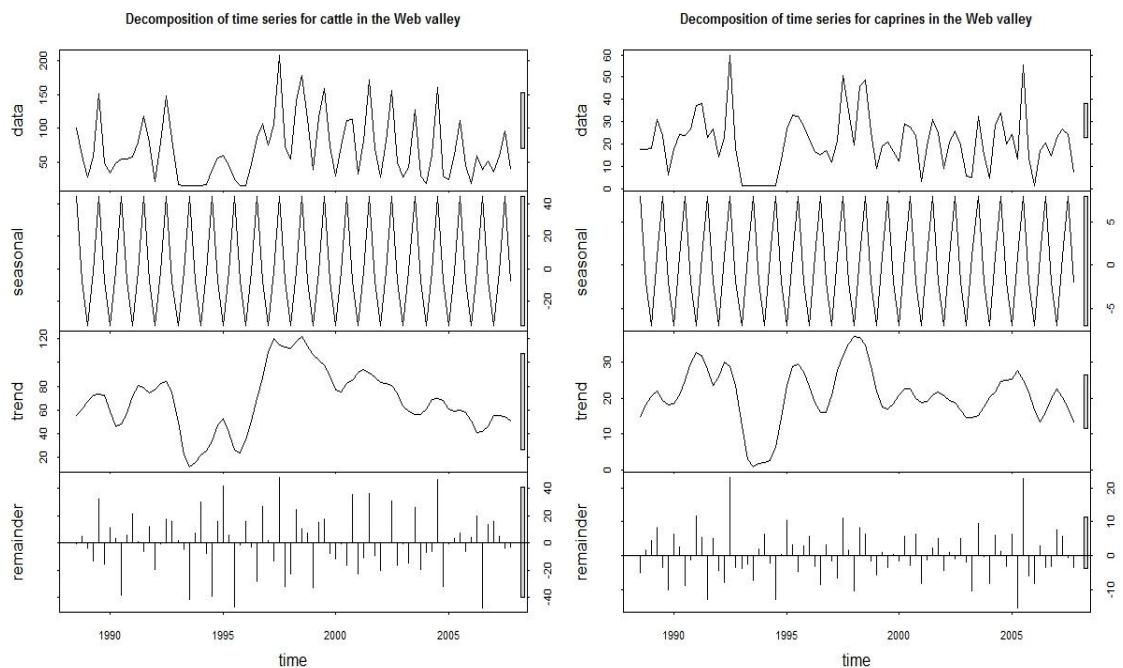


Figure 2-3: Decomposition of the regularised cattle and caprine time series for the Web valley into a seasonal component (the amplitude of which is denoted by the grey bars on the side), a trend and a residual component.

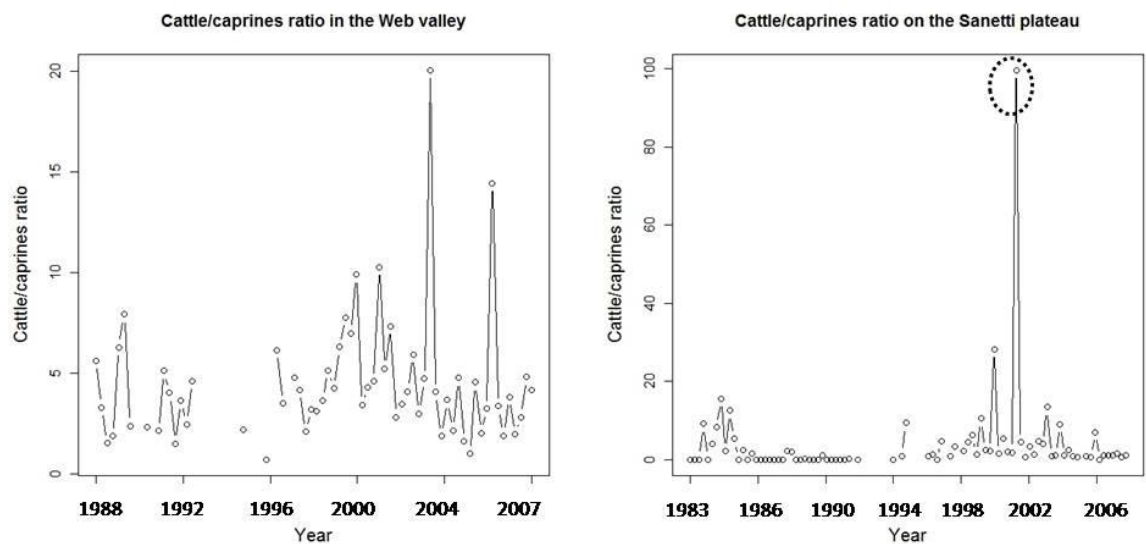


Figure 2-4: Raw time series of the ratio of cattle to caprines in the Web valley (left) and on the Sanetti plateau (right). Note that the road survey on the Sanetti plateau started in 1983 but was only sub-divided into the three wolf habitat types in 1986. An unusual high encounter of caprines in the mid-wet season 2001 on the Sanetti plateau (dotted circle) was considered as unrepresentative and removed from the time series prior to trend analysis.

2.2.3 Cross-correlating livestock and vegetation productivity time series

We derived data on plant biomass and productivity between January 2000 and December 2007 from MODIS- Normalised Difference Vegetation Index (NDVI) satellite imagery (United States Geological Survey, 2000-2007). These images were monthly composites with 1km resolution and were not adjusted for cloud cover or slope. NDVI is a proxy for green-leaf biomass and photosynthetic activity (Curran, 1982, Box et al., 1989). High values of NDVI in afroalpine areas of BMNP are likely to be a good indicator of high photosynthetic activity and rapid seasonal growth in the herb layer, as well as being a measure of biomass (Tallents, 2007). We calculated monthly average NDVI values for both the Web valley and the Sanetti plateau in ArcGIS (Environmental Systems Research Institute Inc., 2004). Satellite images could not be reliably partitioned into the three wolf habitat types present on the Sanetti plateau, and average monthly NDVI values were calculated for eastern, central and western Sanetti combined. We regularised the NDVI time series (using the same methods as described above) before computing their auto-correlation factors using the stats package in R (R Development Core Team, 2009) in order to test for seasonality in vegetation biomass and productivity. We finally examined the cross-correlation factor between the NDVI and livestock time series in order to quantify

the correlation and lag between the two time series, i.e. whether NDVI at time t_0 in a particular area was a good predictor of livestock encounter rate at time t_{+lag} (lag measured in months).

2.3 Results

In the Web valley, seasonality in the encounter rate of cattle and caprines was identified for the whole dataset (1988-2007) (Figure 2.3), with encounter rates higher during the mid-wet season (peak counts) than during the dry season (troughs) by c.70 head/km and by c.10 head/km respectively. No significant long term trends were detected for either type of livestock in the Web valley over the whole dataset (Figure 2.5 & Table 2-2). However, when partitioning the dataset pre-2000 (Marino et al. 2006) and post-2000, we observed a significant increase in cattle encounter rate pre-2000 and a close to significant decrease post-2000 (Figure 2.5 & Table 2-2). No significant trends in caprines encounter rate were detected pre-2000 or post-2000. The time series for free-roaming dogs did not present evidence of seasonality, but showed a significant decrease both post-2000 and across the whole dataset (Figure 2.6 & Table 2-2). We did not observe any significant trend in the cattle to caprines ratio ($\rho = 0.04$, $p = 0.36$) between 1988 and 2007 (Figure 2.4).

No seasonality was detected for livestock on the Sanetti plateau (eastern, central and western). The encounter rates of cattle and caprines significantly increased in all three wolf habitats between 1986 and 2007 (Figure 2.5 & Table 2-2). In most cases, the significant increase occurred both pre and post-2000, with the exception of caprines on central Sanetti which were not encountered pre-2000 (Figure 2.5 & Table 2-2). The time series for free-roaming dogs did not present evidence of seasonality in any of the three wolf habitats. No overall significant trend in the encounter rate of free-roaming dogs was detected on central and western Sanetti between 1986 and 2007. However, free-roaming dogs increased on eastern Sanetti during the same period and have increased on western Sanetti since 2000 (Figure 2.6 & Table 2-2). We observed a significant increase of the cattle to caprines ratio ($\rho = 0.27$, $p < 0.01$) between 1983 and 2007 (Figure 2.4), i.e. proportionally more cattle are being kept.

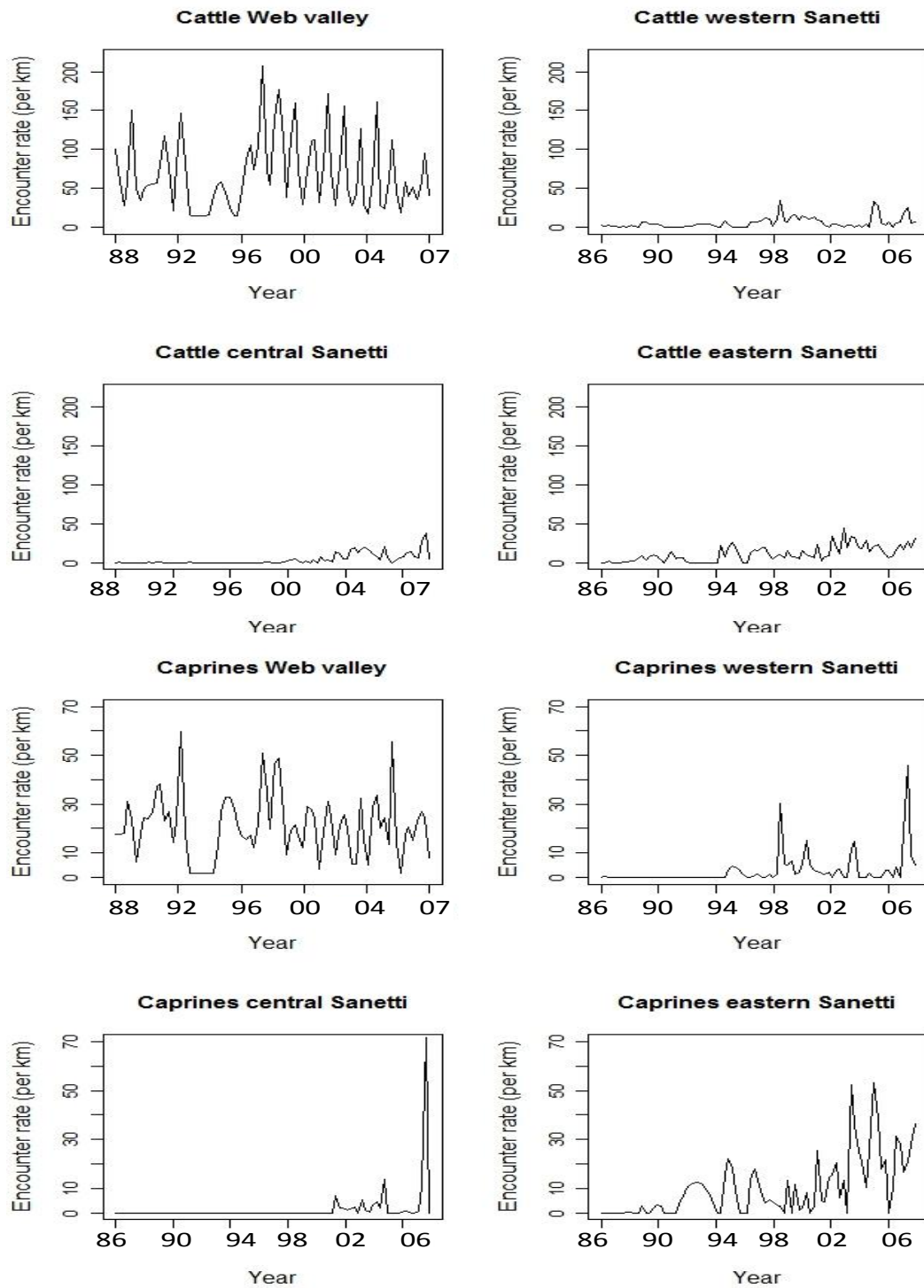


Figure 2-5: Regularised times series of the encounter rate (individuals/km survey) of cattle (top) and caprines (bottom) in the Web valley, eastern/ central and western Sanetti.

Area	Species	Seasonality (Y/N)	Trend up to 2000 (Marino et al. 2006)	Trend since 2000	Trend across whole dataset
Web valley	Cattle	Yes	Increase (p<0.01)	No (n=28, p =0.06)	No (n=78, p = 0.38)
	Caprines	Yes	No (p = 0.64)	No (n=28, p = 0.43)	No (n=78, p = 0.41)
	Dogs	No	Decrease (p = 0.03)	Decrease (n=28, p = 0.03)	Decrease (n=78, p<0.01)
eastern Sanetti	Cattle	No	Increase (p<0.01)	Increase (n=28, p = 0.05)	Increase (n=85, p<0.01)
	Caprines	No	Increase (p<0.01)	Increase (n=28, p<0.01)	Increase (n=85, p<0.01)
	Dogs	No	Only 1 dog encountered	Increase (n=28, p<0.01)	Increase (n=54, p = 0.05)
central Sanetti	Cattle	No	Increase (p<0.01)	Increase (n=85, p = 0.05)	Increase (n=85, p<0.01)
	Caprines	No	Not encountered	Increase (n=28, p = 0.05)	Increase ((n=85, p<0.01)
	Dogs	No	Only 1 dog encountered	No (n=28, p = 0.37)	No (n=54, p = 0.12)
western Sanetti	Cattle	No	Increase (p<0.01)	No (n=28, p =0.39)	Increase (n=85, p<0.01)
	Caprines	No	Increase (p = 0.02)	No (n=28, p = 0.49)	Increase (n=85, p<0.01)
	Dogs	No	Rarely encountered	Increase (n=28, p<0.01)	No (n=54, p = 0.22)

Table 2-2: Summary of seasonality and trends for livestock and free-roaming dogs. Trends were assessed after removing the seasonal signal from the time series. Counts of livestock and free-roaming dogs were started during the late wet season in 1986 and during the mid wet season in 1994 respectively on the Sanetti plateau. All counts in the Web valley were started during the mid wet season in 1988. Optimal wolf habitat is colour coded in white, good wolf habitat in light grey and marginal wolf habitat in dark grey.

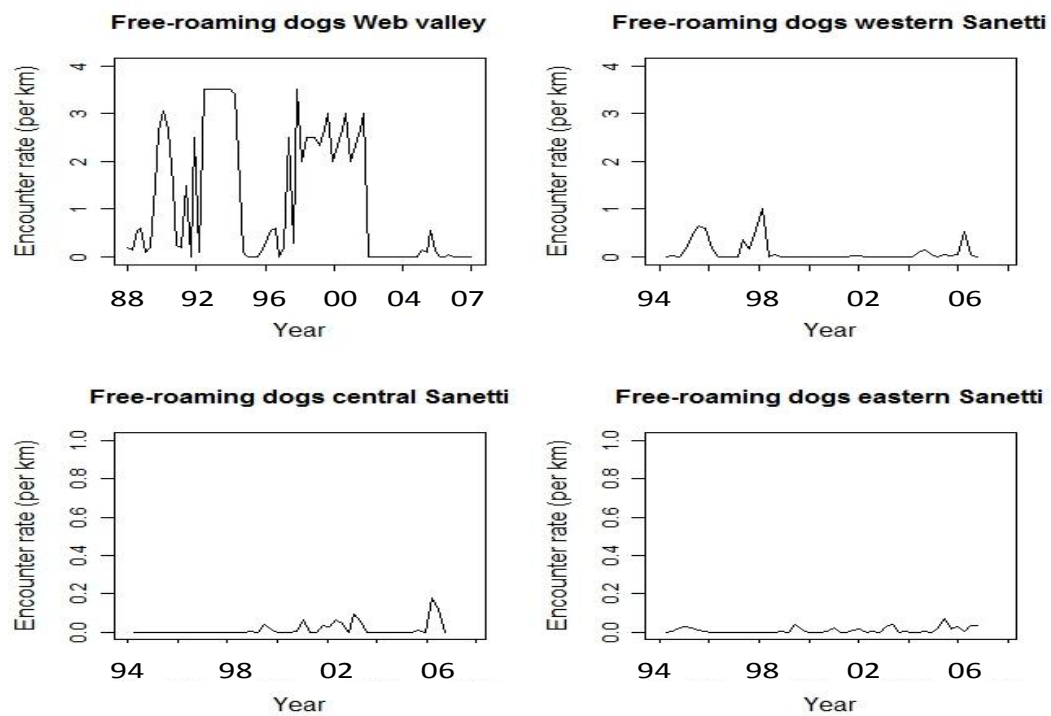


Figure 2-6: Regularised times series of the encounter rate (individuals/km survey) of free-roaming domestic dogs in the Web valley, eastern/ central and western Sanetti.

The computation of the auto-correlation for the NDVI time series revealed that vegetation biomass was highly seasonal in the Web valley, with cycles being less pronounced on the Sanetti plateau (Figure 2.7). In the Web valley, livestock (both cattle and caprines) encounter rates at time t_0 and t_{+1} were positively correlated with NDVI at time t_0 (Figure 2.8). A positive correlation between cattle encounter rate at t_{+1} and NDVI at t_0 indicates a lag of 1 month between an increase in NDVI, for example, and the subsequent increase in cattle encounter rate on the same pastures. Cattle encounter rate at time t_{+4} was negatively correlated with NDVI at time t_0 , indicating a time lag of 4 months between an increase in NDVI and a decrease in cattle encounter rate. On the Sanetti plateau (where NDVI values were combined across areas), cattle encounter rates were not correlated to NDVI at time t_0 (Figure 2.8) while caprine encounter rates at time t_0 and t_{+1} were marginally positively correlated to NDVI at time t_0 .

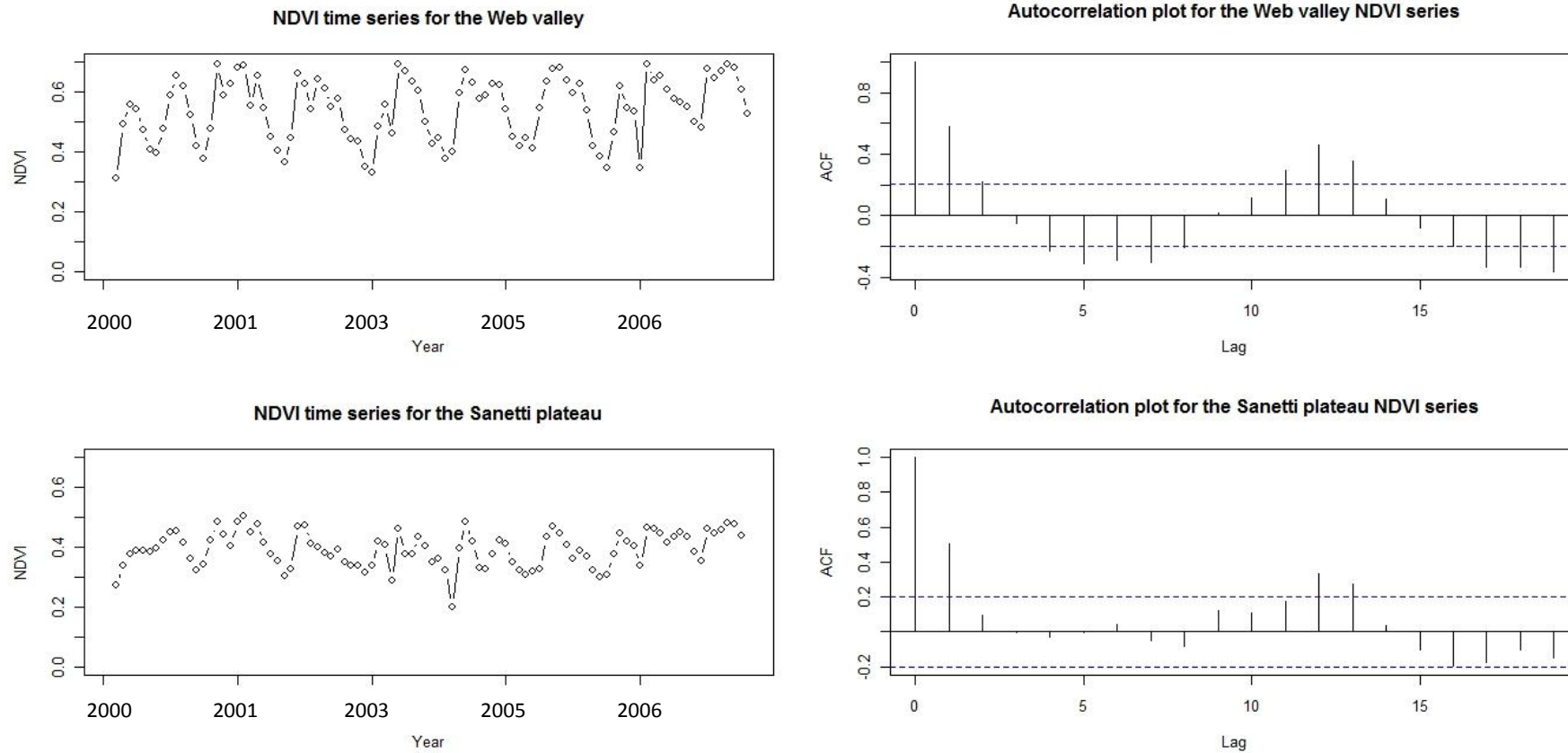


Figure 2-7: Regularised NDVI time series (left) and the corresponding auto-correlation function (right) for the Web valley (top) and the Sanetti plateau (bottom) between 2000-2007. The dotted lines represent the 95% confidence intervals for the correlation factor based on a non auto-correlated series. It follows that auto-correlation values outwith the confidence intervals denote a significant correlation at time lag $t+x$ (lag measured in months). NDVI exhibit pronounced regular cycles of 12 months in the Web valley indicative of strong seasonality in vegetation biomass, while the cycle in NDVI is less pronounced on the Sanetti plateau.

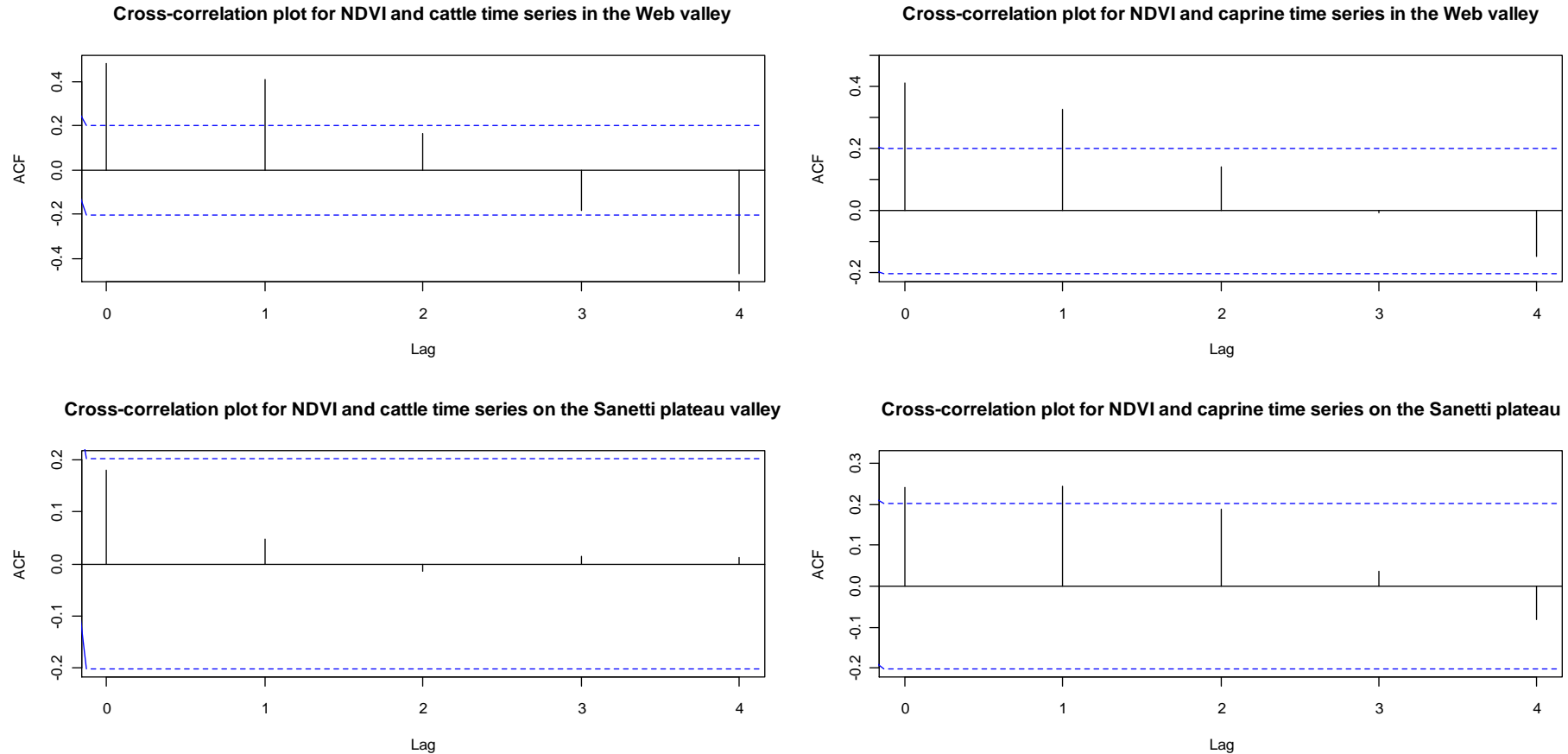


Figure 2-8: Cross-correlation factor between livestock encounter rate (seasonal and non-detrended) and NDVI for cattle (top) and caprines (bottom) in the Web valley (left) and on the Sanetti plateau (right) between 2000-2007. We are looking at the correlation between livestock encounter rate at time $t+x$ (lag measured in months) and NDVI at time t . The dotted lines represent the 95% confidence intervals for the correlation factor based on uncorrelated series. It follows that cross-correlation values outwith the confidence intervals denote a significant correlation between the two time-series at time lag t_{+x} .

2.4 Discussion

2.4.1 Trends in livestock and changes in pastoralist land use

This updated analysis of livestock trends in BMNP confirms the persistence of some trends (Marino et al., 2006) but also highlights more recent changes in afroalpine land use. The long-term stability of livestock numbers, despite increasing settlements (OARDB, 2007), in the Web Valley indicates changing livelihoods, and diminishing herd sizes, as a consequence of expanding agriculture (now commonly encountered >3000m a.s.l) and the subsequent loss of communal grazing land as observed in other parts of the region (Flintan et al., 2008). In the district of Dinsho (north of the Web Valley), for example, agriculture is now the primary activity. Most households keep livestock but the livestock to human ratio has dramatically decreased (Watson, 2007). A seasonal livestock production system, akin to the traditional godantu system, persists in the Web Valley with cattle numbers, and caprines to a lesser extent, reaching a peak during the wet season (June to September). This seasonal variation was congruent with fluctuations in primary productivity, which showed pronounced regular 12-months cycles (echoing the findings of Tallents, 2007). This may constitute a strong indication that transhumant pastoralists still follow the rainfall patterns to track productive grazing grounds during the wetter months. However, another force driving livestock transhumance today may be the lack of pastures, as most of the lowlands are cultivated during the wet season and livestock are forced out to other grazing grounds. In the dry season, some livestock return to the lowlands as the fields left fallow provide additional forage at a time when the high altitude afroalpine areas become totally dry. Other herds, in particular those belonging to permanent settlers in the Web valley, shift their habitat use from the grass meadows to the Erica covered slopes which were not represented by the fixed survey lines established in the Ethiopian wolf habitat.

In contrast, livestock strongly remains a central pillar of the livelihoods of the communities living on the Sanetti plateau, as judging by the increase in livestock numbers over the monitoring period in all three habitats, coinciding with an increase in households over the last 20 years around Rira (western Sanetti) and Goba (eastern Sanetti), just below the afroalpine belt (OARDB, 2007). The livestock production system appears less intensive there than in the Web Valley (as far as depicted by lower encounter rates) and

not seasonal. The Erica moorlands above Goba, the open grasslands of the upper plateau (central Sanetti), and the drier declivity towards Rira were used all year round for grazing, albeit at different intensity. Seasonal movements of livestock reported by people from the Goba and Dolo Mena (south of the Sanetti plateau) woredas (districts) by Flintan et al. (2008) were not reflected in the present analyses. One reason may be that the seasonal movements only involve small herds, and thus go undetected, or that the upland movement reaches up to the Hareenna forest (39°-40° E and 6°-7° N; 2000-3200 m a.s.l.) on the southern slopes of BMNP (Fig. 2.1), but not further up onto the plateau. On the Sanetti plateau, the NDVI exhibited a weaker cycle and only a marginally significant cross-correlation with the time series of caprines. Because the NDVI is less sensitive to slow-growing pubescent perennials such as the *Helichrysum* spp. that dominate the vegetation in parts of the plateau, a possible caveat is that the time series underestimated the amplitude of changes in vegetation biomass (Tallents, 2007). Otherwise, the more constant biomass would explain, at least in part, why livestock encounter appears to be a-seasonal on the Sanetti plateau.

Finally, while Flintan and colleagues (2008) presented some evidence that the types of livestock may be changing in the region, with people reducing their cattle numbers and including more caprines in their herds, we find no evidence of such changes taking place in BMNP afroalpine.

2.4.2 Implications for the Ethiopian wolf

The monitoring conducted by EWCP may not represent livestock trends in other areas of the BMNP dominated by Erica moorlands and forests, and it is limited to relative comparisons only, but its strength resides on the length of the time series. The data convincingly show increases in the grazing pressure in both optimal (central Sanetti) and marginal wolf habitat (eastern Sanetti) which constitutes an additional threat to the already uncertain future of the Ethiopian wolf.

The effects of grazing upon small mammals, and rodents in particular, in grasslands are of concern because of their top-down effects on plant communities (Manson et al., 2001), their role as ecosystem engineers (Zhang et al., 2003) and, in particular, their bottom-up effects on bird and mammal predators (Hanski et al., 1991, Korpimäki and Norrdahl, 1991, Torre et al., 2007). From independent estimations of livestock densities in

BMNP, we know the densities of cattle and caprines in the Web Valley to be c. 250 and 120 heads/km² respectively, and c. 60 and 73 head/km² on the Sanetti Plateau in 2007-2008 (Chapter 3). At this level of grazing, the first systematic study of grazing impacts in BMNP revealed some apparent vegetation changes and negative effects of livestock upon rodent biomass (Chapters 5 & 6), while another study in the central highlands showed that livestock grazing affected the composition of the rodent community in another afroalpine area (Ashenafi, 2001). In the drier and more heavily populated northern highlands, overgrazing has been suspected to affect wolves through unfavourable impacts on rodent populations for a long time (Nievergelt et al., 1998).

The second, and most imminent, threat posed by the growing human population inside the park, is the presence of free-roaming dogs. Our result indicates that the number of free-roaming dogs have increased in parts of the Ethiopian wolf range in BMNP post-2000 (eastern and western Sanetti). Domestic dogs, and in particular free-roaming ones, are the reservoir from which infectious pathogens such as canine distemper virus and rabies virus spill over into the Ethiopian wolf populations (Laurenson et al., 1998). At least three outbreaks of rabies have occurred in the Bale Ethiopian wolf population in the last 18 years (Sillero-Zuberi et al., 2004, Randall et al., 2006), each causing a devastating 50-76% mortality in affected populations and substantially increase the probability of local extinction (Haydon et al., 2002). The capacity of wolf populations to recover from these population crashes may be limited by a reduction in the wolves' prey-base as a direct consequence of livestock grazing. It is thus a matter of great concern, even if under current grazing level wolves have recovered from previous outbreaks.

3 Estimating livestock densities inside Ethiopian wolf ranges in the Bale Mountains: a comparison of direct and indirect methods.

3.1 Introduction

The Bale Mountains, part of the eastern afroalpine hotspot (Williams et al., 2004), are home to over half of the 500 Ethiopian wolves estimated to survive today in afroalpine relicts across Ethiopia (Marino, 2003b, Sillero-Zuberi et al., 2004). The BMNP is also inhabited by the pastoralist Oromo people, their livestock and dogs, which spread diseases and can interbreed with the wolves (Sillero-Zuberi and Macdonald, 1997). High levels of livestock grazing in Bale may be affecting the quality of the habitat suitable for the rodent community on which the Ethiopian wolves and other carnivores and raptors depend (Abebe, 2008, Sillero-Zuberi and Gottelli, 1995, Tallents, 2007) through a reduction in vegetation cover (Grant et al., 1982, Keesing and Crawford, 2001) and decrease in suitable food resources (Steen et al., 2005). Monitoring Ethiopian wolf populations livestock, domestic dogs and human use has been one of the core activities of the Ethiopian Wolf Conservation Programme (EWCP) in the Bale Mountains for the last twenty years. While offering an insight into the patterns of human use of the afroalpine grasslands, the EWCP dataset has limitations. Regular EWCP monitoring activities are largely confined to key Ethiopian wolf core ranges (i.e., Web valley and Sanetti plateau), and while the methodology used is appropriate for the detection of trends in livestock encounter rates (defined as number of sightings per km of transect) (Vial et al., 2009), it does not produce statistically-based and comparable density estimates.

The monitoring of populations is a crucial component in animal ecology and wildlife conservation (Blanchard et al., 2008, Collen et al., 2009, Joseph et al., 2006). The conservation and management of endangered or harvested animals necessitates understanding each population's abundance, and the impacts on it of management (Focardi et al., 2005). Information on population density can be obtained by direct or indirect methods, such as line transect surveys (Caley and Morley, 2002, Devos et al., 2008, Gross et al., 2007, Marques et al., 2001, Nomani et al., 2008), aerial surveys (Jachmann, 2002), faecal pellet counts (Guschanski et al., 2009, Hacker et al., 2002, Nchanji and Plumptre, 2001, van Vliet et al., 2008), or sign counts (Gusset and Burgener, 2005). Line transect surveys are widely used in animal population ecology (Plumptre, 2000, Marques et al., 2001) as they are an effective method to estimate animal densities over large areas within budgetary limits (Olson et al., 2005, Focardi et al., 2005). Distance sampling has become increasingly popular for the estimation of animal population densities (Caley and Morley, 2002, Devos et al., 2008, Gross et al., 2007, Marques et al., 2001, Nomani et al., 2008),

being extensively used for surveying wild ungulates by direct observation or sign counting (Trenkel et al., 1997, Buckland, 1992, Focardi et al., 2005, Marques et al., 2001, Barnes and Jensen, 1987).

I compare two methods to estimate livestock density. First, I chose distance sampling to produce systematic estimates of the densities of cattle, sheep/goats (caprines) and transport animals (horses, mules and donkeys) in the three key Ethiopian wolf ranges in Bale (Web valley, Morebawa and Sanetti plateau) over 12 months (July 2007-June 2008). I subsequently used those estimates to test for spatial and temporal variation in livestock stocking rate across Bale afroalpine range, and combined them with rainfall data for the region to assess potential overstocking.

Direct survey methods such as vantage point counts or transects allow estimation of sex-specific or age-specific abundance whereas indirect methods, usually based on dung counts, only allow estimation of overall abundance. However, the latter provide estimates of average abundance over several months, whereas the former usually yield estimates of abundance for the day of the survey, which may provide misleading information on habitat use (Marques et al., 2001). Dung methods are commonly used to estimate herbivore population density (Guschanski et al., 2009, Hacker et al., 2002, Nchanji and Plumptre, 2001, van Vliet et al., 2008) as they often yield estimates of abundance that are comparable with estimates using direct methods for a wide range of species while being cheaper and less labour-extensive (Barnes, 2001). The most commonly used method, the ‘standing crop’ method, records all detected dung on the survey plots, irrespective of age and can be conducted using quadrat sampling (Bailey and Putman, 1981, Putman, 1984), strip transect sampling (Plumptre and Harris, 1995) or line transect sampling (Barnes et al., 1995, Marques et al., 2001). I chose this method as a second approach to estimating average livestock densities inside survey grids located in Web, Morebawa and Sanetti during the wet and dry seasons of 2008/2009.

3.1.1 Study sites

Tallents (2007) produced a map of the vegetation in the afroalpine zone of the BMNP at a finer spatial scale and broader extent than had previously been achieved. Her unsupervised classification isolated 23 spectrally separable vegetation classes, 17 of which

were statistically distinct in terms of substrate, species composition, height and/or vegetation cover. However, the number of vegetation classes was too large for our purposes, and classes were merged into 3 broader categories, reflecting rodent abundance (Sillero-Zubiri, 1994, Tallents, 2007):

1. *Alchemilla*/grass pastures (A/G) with high giant molerat (*Tachyoryctes macrocephalus*) and murine rodent (*Lophuromys melanonyx* and *Arvicanthis blicki*) densities.
2. *Helichrysum/Artemisia* shrublands (H/A) with low giant molerat and murine rodent densities.
3. Bare soil/Herbs/drainage lines (H/D) with high giant molerat and intermediate murine rodent densities.

Twenty-four survey grids (40x40m) were set up in these three habitat types to establish empirical relationships between livestock grazing pressure, afroalpine vegetation and rodent diversity and abundance (Chapter 5). The locations of these grids were randomly generated in ArcGIS (Environmental Systems Research Institute Inc., 2004) subject to the following criteria:

1. Equal numbers of grids (8) in each habitat types.
2. Grids to be located inside Ethiopian wolf core ranges: Web (6 grids), Morebawa (6 grids) and Sanetti (12 grids).
3. Grids located within a 4km radius of research camps.

The survey grids were located at varying distances from both the nearest source of water and settlements (Figure 3.1). Such variation was anticipated to result in differential intensity of use by livestock, as measured by dung counts, allowing us to sample vegetation and rodents across a grazing gradient. Grazing gradients (Pickup and Chewings, 1994) provide a way to observe vegetation changes under different grazing intensities in areas where it is not possible to manipulate livestock densities. Previous studies have used the distance to a source of water (Adler and Hall, 2005, Andrew, 1988, Fernandez-Gimenez and Allen-Diaz, 2001, Gonnet et al., 2003, Nash et al., 1999) or from a livestock camp (Hoshino et al., 2009, Sasaki et al., 2008) to assess the impact of grazing on rangeland structure.

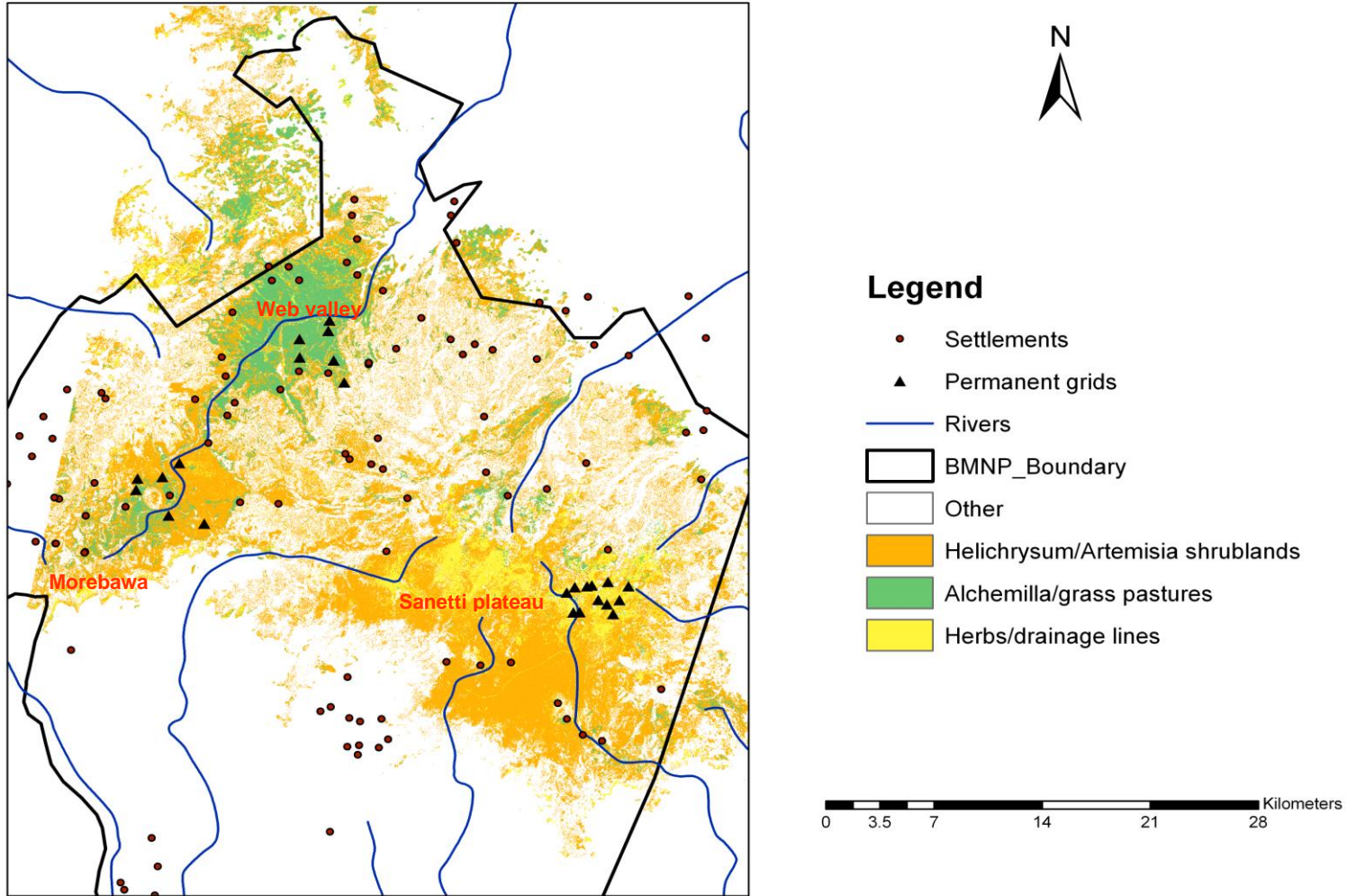


Figure 3-1: Locations of the twenty-four permanent survey grids within the three broad habitat types identified as relevant to rodents.

3.2 Methods

3.2.1 Distance sampling: transect design and model selection

I used livestock encounter rates from a previous study (Tallents, unpublished results) to calculate the total length of transect required to obtain a minimum of 60 sightings of cattle per survey in Bale, thereby allowing more precise density estimates (Buckland et al., 2001). I estimated that 100km of transects (25 transects of 4km each) were required. The number of transects in each of the three Ethiopian wolf ranges was proportional to the area of each site: 8 transect lines in Web (74km²), 6 in Morebawa (57km²) and 11 in Sanetti (110 km²). The location of these transects was determined in ArcMap using randomly generated starting points and bearings, and by discarding proposed transects that crossed rivers.

Quarterly, all transects were walked (= survey) and sightings of all i species of livestock were recorded: cattle (CT), caprines (ST) and transport animals (TA). Real search effort varied between 72 and 100km per survey depending on weather. For every livestock sighting, species and cluster size were noted. Distance from the observer to the centre of the cluster and angle of sighting were estimated and later transformed into a perpendicular distance to the transect line. Distance 5.0 (Thomas et al., 2006) was used to estimate $D_{i,k}$, the density estimate for the i^{th} species of livestock in the k^{th} region during five surveys between July 2007 and June 2008. Four parameters were needed to be able to compute density estimates: the number of clusters sighted (n_i), the estimated mean cluster size ($E(s_i)$), the transect length in km (L_k) and the probability density function evaluated at 0m distance ($f(0)_i$) (Buckland et al., 2001).

The probability density function $f(x)_i$, is derived from the probability of detecting a cluster given it is at distance x from the transect ($g(x)_i$). Sightings were pooled across geographic strata (Web /Morebawa/Sanetti), assuming no difference in the detectability of the different species in the different habitats within each survey, to yield the detection function $g(x)_i$ for each species and survey (Figure 3.2). All datasets were organized with a right-truncation (w) of observations beyond 375m (Figure 3.2). A left truncation (before 62.5m) was applied to the five datasets for which the number of observations in the first distance bin was much lower than those in the second bin. This left truncation was only applied to some of the transects walked in January 2008 by the same observers and not

under unusual weather conditions. It was therefore assumed that this “hump” in the number of sightings in the second distance bin was not the result of animals moving away from the transect line as a response of the surveyors approaching (Turnock and Quinn, 1991), but merely a result of chance which did not contradict the assumption of a uniform distribution of animals on the landscape (Buckland et al., 2001).

The selection of the most appropriate model for $g(x)_i$ was made by comparing AIC values and goodness of fit tests. The most commonly selected models for $g(x)_i$ used a half-normal key function with cosine series expansion or a hazard rate key function with a simple polynomial series expansion. The probability density function $f(x)_i$ was then computed as:

$$f(x)_i = \frac{g(x)_i}{\int_0^w g(x)_i dx} \quad \text{Equation 3-1}$$

By assumption, $g(0)_i=1$, so that $f(x)_i$ evaluated at 0 distance was:

$$f(0)_i = \frac{1}{\int_0^w g(x)_i dx} \quad \text{Equation 3-2}$$

Dependency between cluster size and distance can arise when large clusters are more easily detected than small clusters at long distances but their size can be underestimated due to the reduced detectability of individuals. Size bias in the detection can be corrected in Distance by performing a weighted linear regression of s_i against $g(x)_i$ (Figure 3.3) (Buckland et al., 2001). Mean cluster size, $E(s_i)$, was then estimated by the predicted mean size of detected clusters in the region around the line for which detection is estimated to be certain ($g(x)_i = 0$).

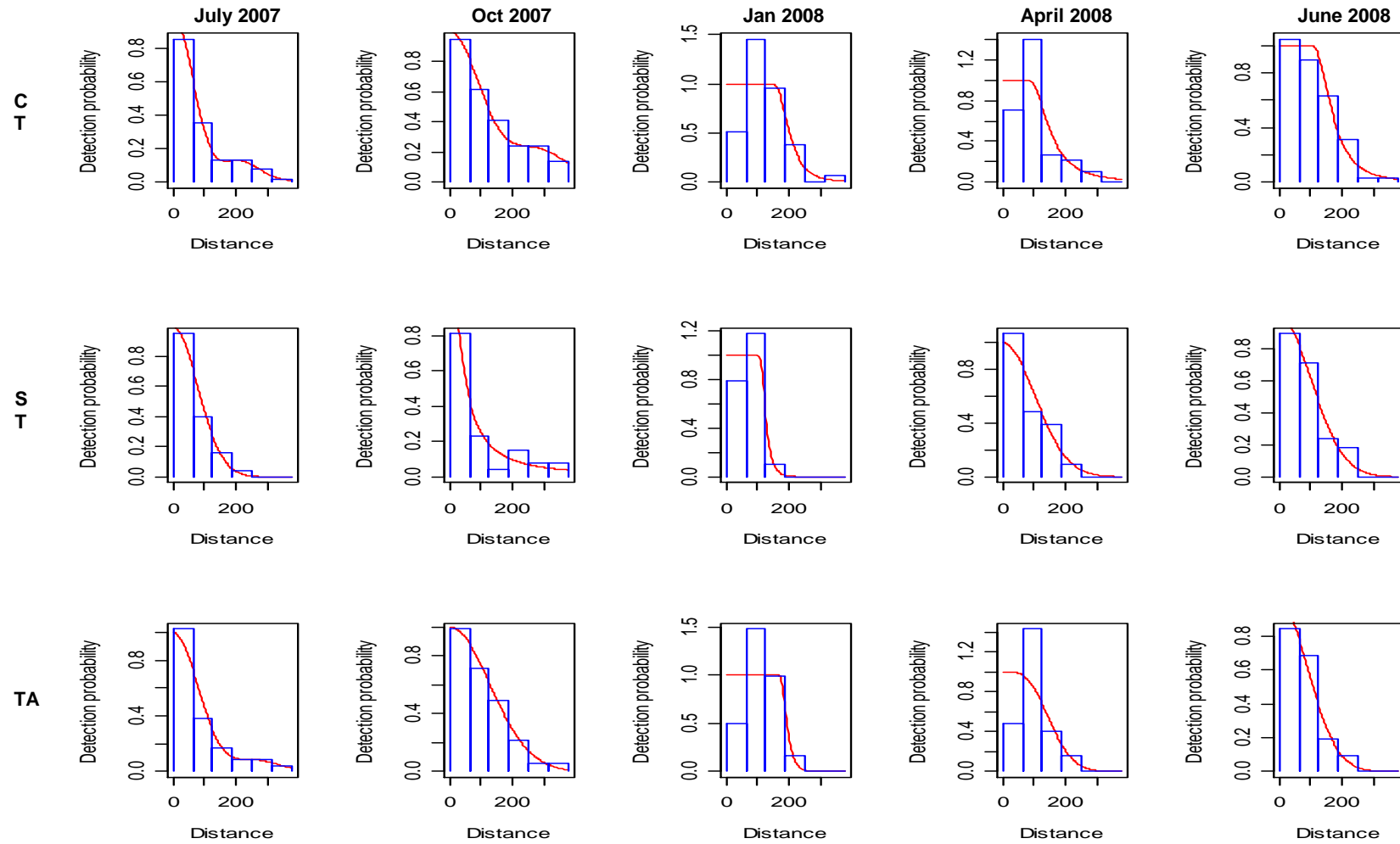


Figure 3-2: Global detection probability plots for all livestock types for the five surveys. The blue bars represent frequencies of sightings within distance bins (m) and the detection function $g(x)$ modelled, after pooling sightings across geographic strata, is shown in red.

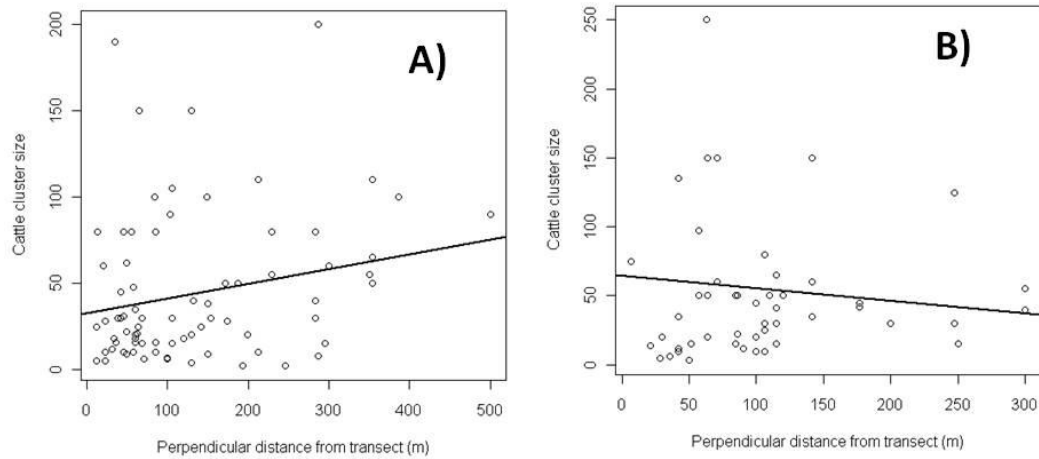


Figure 3-3: Examples of weighted linear regressions of cattle cluster sizes against the distance from the transect for A) November 2007 and B) April 2008 as performed by Distance.

The density ($D_{i,k}$) of the i^{th} species of livestock (individuals/km²), in the k^{th} region was then estimated using the following equation:

$$D_{i,k} = \frac{n_i E(s_i) f(0)_i}{2L_k} \tag{Equation 3-3}$$

The livestock density estimates thus obtained are log-normally distributed, allowing the use of Fisher’s combined probability test (Fisher, 1948) to:

1. Test for seasonality by comparing, within each area, livestock numbers in the wet (July 07, April 08 and June 08) and dry (November 07 and January 08) seasons.
2. Compare livestock densities across the three areas.

Fisher's method combines probabilities, p-values, from each independent test, into one test statistic, χ^2 , that has a chi-square distribution using the formula:

$$\chi^2_j = -2 \sum_{i=1}^j \ln p_i \tag{Equation 3-4}$$

The p-value for χ^2 is then interpolated from a chi-square table using $2j$ degrees of freedom, where j is the number of tests being combined.

Livestock density estimates obtained from the line transects in 2007/2008 were converted into TLU to allow comparisons between areas/seasons across species (Boudet and Riviere, 1968). Those estimates were then used to compute an average annual, average dry (November 2007 and January 2008) and wet (July 2007, April/June 2008) season stocking rate (D_k) for the three sites.

3.2.2 Dung counts and conversion to livestock density estimates

Counts of the number of livestock dung piles were carried out inside each of the twenty-four grids (wet/dry seasons 2008/2009 = four surveys). Dung visible on the grids represents the remains of dung deposited by livestock in the area over the period preceding the surveys. Assuming a system at steady state (McClanahan, 1986) (i.e. where the amount of dung deposited equals the amount being lost from the system), only two parameters are needed to convert dung density for the i^{th} species in the j^{th} grid of region k ($S_{i,j,k}$) into an average livestock density estimate in the k th region ($D_{i,k}$): the estimated mean time to decay of dung of the i^{th} species (r_i) and the estimated rate of production of dung by the i^{th} species (p_i) in both dry and wet seasons.

All dung piles inside the grids were counted and identified as cattle (CT), caprines (ST) or transport animal (TA) dung by two independent observers. Using a sign-test, I found no evidence of observer bias in the dung counts inside the grids ($p = 0.34$).

3.2.2.1 Estimating mean time to decay

Mean time to decay of the three different types of dung was separately estimated for the wet and the dry seasons (Barnes et al., 1997, Ellwood, 2008, Laing et al., 2003, Nchanji and Plumtre, 2001). Decay refers to the disappearance of the animal signs irrespective of the mechanism by which the process occurred. In this study, ST pellet groups were estimated to have decayed when they had been spread out over a large area by trampling making it impossible to know whether the pellets belonged to the same group or when they had organically broken down. CT and TA dungs were said to have decayed when they had broken down to an amorphous patch.

Fourteen dung degradation plots were set up and monitored in the Web valley between January 2007 and January 2009 (six and eight dry season/wet season plots respectively). Fresh livestock dung (84 CT, 72 ST and 84 TA) was collected, labelled and laid out on plots that were revisited at intervals. The estimated time to decay for each dung pile was calculated as the number of days from date of deposition to the date the dung was last observed as "visible" plus a random number of days between last "visible" and "decayed" visits. The seasonal mean time to decay (in days) for each species (r_i) was computed together with its associated standard error σ_{r_i} .

3.2.2.2 Estimating dung production rate

Dung production rates for all species were estimated from focal livestock observations on the grazing pastures around Dinsho settlement (BMNP park headquarters). Observers followed focal animals for 220 minutes (m) a day, recording the number of defecation events (q_i) taking place (31/30/8 days of observations for CT/ST/TA respectively). As dung production rate is related to forage type (Chapman, 2004), which will change to some extent with season, the above observations were carried out during both the dry and wet seasons. Assuming animals grazed for 720 minutes (z) over the course of a day, a daily dung production rate was computed for each individual as:

$$p = \frac{z\bar{q}}{m} \text{ dung. animal}^{-1} \cdot \text{day}^{-1} \quad \text{Equation 3-5}$$

and a seasonal species-specific dung production rate (p_i : dung.animal⁻¹.day⁻¹ for a given species in a given season) was computed together with its associated standard error σ_{p_i} .

3.2.2.3 Estimating livestock densities

The rate of change of dung on the pastures will depend on changes in the rate it is produced (p_i) and its decay (r_i), as described by the following equation:

$$\frac{dS_{i,k}}{dt} = p_i D_{i,k} - \frac{1}{r_i} S_{i,k}^* \quad \text{Equation 3-6}$$

If the system is in a steady state, Equation 3-6 can be set to zero and solved for $S_{i,k}^*$ (referred to as $S_{i,k}$ in the rest of the text). As $S_{i,k}$, p_i and r_i are estimated with a degree of uncertainty, a season-specific livestock density estimate ($D_{i,k}$) was computed using the delta method (Lynch and Walsh, 1998):

$$D_{i,k} = \frac{\overline{S_{i,k}}}{p_i r_i} \left(1 + \frac{\sigma^2(p_i r_i)}{(p_i r_i)^2} \right) \quad \text{individuals.km}^2 \quad \text{Equation 3-7}$$

Where $\overline{S_{i,k}}$ is the average dung density (/km²) of the i^{th} species in the k^{th} region and $\sigma^2 p_i r_i$ is the squared standard error of the product of p_i and r_i .

Assuming that p_i , r_i and $\overline{S_{i,k}}$ are independent and normally distributed, the variance $\sigma^2 D_{i,k}$ can be estimated using the following equation:

$$\sigma^2(D_{i,k}) = \left(\frac{\overline{S_{i,k}}}{p_i r_i} \right)^2 \left(\frac{\sigma^2 S_{i,k}}{(\overline{S_{i,k}})^2} + \frac{(r_i^2 \sigma^2(p_i) + p_i^2 \sigma^2(r_i) + \sigma^2(p_i) \sigma^2(r_i))}{(p_i r_i)^2} \right) \quad \text{Equation 3-8}$$

Where $\sigma^2(S_{i,k})$ is the squared standard error of $S_{i,k}$.

$D_{i,k}$ were converted into tropical livestock units (TLU) to allow comparisons across species. The TLU is a conventional stock unit of a mature zebu weighing 250kg (Boudet and Riviere, 1968). The following conversion factors were used: 1 TLU = 1.5 cattle = 11 caprines = 1.5 transport animal (Le Hou rou and Hoste, 1977). A total livestock density estimate for each k region (D_k , unit TLU.km⁻²) could then be computed as the sum of all $D_{i,k}$ for each season. I then compared the livestock density estimates computed using dung counts to the density estimates from distance sampling within all three regions and season using t-tests.

The dung count data was analysed in R (*lme4* package) using generalised linear mixed models (with a Poisson distribution of residuals) to understand the variation in dung counts within and between grids. Habitat type, season, year, distance to water and distance to settlements were treated as fixed factors, while the temporal pseudo-replication of grids was included as a random factor. Models were compared using the likelihood ratio test and the most parsimonious model was chosen.

3.2.3 Modelling maximum sustainable livestock biomass from rainfall data

The study of the relationship between annual rainfall and range production in the Sahelian tropical zones of Africa shows a close correlation between average range production and average rainfall over large areas (Le Houérou and Hoste, 1977). Le Houerou and Hoste developed regression models relating rainfall and rangeland productivity from 45 sites from eight countries in the Sahelian-Sudanian belt. Their derived relationship between the maximum rangeland sustainable livestock density (y) and rainfall (x in mm) took the following form:

$$y = 0.0004 x^{1.001} \text{ TLU.ha}^{-1}.\text{year}^{-1} \quad \text{Equation 3-9}$$

The predictions made under this growth model were closely positively correlated to the data collected in the 45 rangeland sites ($r^2=0.89$). We therefore used to determine whether or not our three afroalpine areas might be overstocked: I compared the ratio of observed to maximum sustainable livestock biomass on the basis of mean annual rainfall. Mean annual rainfall estimates for Web/Morebawa and Sanetti were not available but estimates for other parts of Bale (with similar topography and altitude) were described in Mieke and Mieke (1994) and extrapolated to our study sites (Table 3-1). However, it is important to note that both the Web valley and Morabowa are drier than their respective extrapolated values (C. Sillero-Zubiri pers. comment), resulting in over-estimated maximum rangeland sustainable livestock densities for both areas.

<i>Station recorded</i>	<i>Altitude (m a.s.l.)</i>	<i>Mean annual rainfall (mm)</i>	<i>Mean dry season rainfall (Nov/March)</i>	<i>Mean wet season rainfall (April/Oct)</i>	<i>Used as proxy for</i>
Chorchora	3500	1086	235	851	Web
Koromi	3850	1061	225	836	Morebawa
Tullu Konteh	4050	852	230	622	Sanetti

Table 3-1: Estimates of mean rainfall for the study sites as derived from Mieke and Mieke (1994).

3.3 Results

3.3.1 Estimation of livestock densities using Distance sampling

During five surveys between July 2007 and June 2008, 389 clusters of cattle (36-119 per survey), 150 clusters of caprines (20-39 per survey) and 209 clusters of transport animals (27-56 per survey) were observed (Table 3-2). A total of 408 km of transect lines were surveyed with a sampling effort ranging between 72-100 km per survey. Global (pooled across geographic areas) cluster encounter rate varied between 0.49-1.49 clusters per km of transect for cattle, 0.28-0.49 for caprines and 0.36-0.53 for transport animals (Table 3-2). Global livestock mean cluster size was variable between surveys ranging from 30.7 to 60.6 for cattle, 41.4 to 85 for caprines and 6.0 to 8.1 for transports animals (Table 3-2).

The Web valley harbours the highest densities of livestock during the wet season, with cattle being the most numerous (Figure 3.4A). Applying Fisher's combined probability test to livestock density estimates for each region, I find that the total number of livestock is not statistically different between Web and Morebawa (Figure 3.4B) ($p_{\text{cattle}} = 0.4684$, $p_{\text{caprines}} = 0.6991$, $p_{\text{TA}} = 0.0360$; $\chi_6^2 = 8.88$, NS) but there are significantly more livestock in Web ($p_{\text{cattle}} = 0.0205$, $p_{\text{caprines}} = 0.3570$, $p_{\text{TA}} = 0.0019$; $\chi_6^2 = 22.36$, $p_{\text{Fisher}} < 0.01$) or Morebawa ($p_{\text{cattle}} = 0.0172$, $p_{\text{caprines}} = 0.1044$, $p_{\text{TA}} = 0.0143$; $\chi_6^2 = 21.13$, $p_{\text{Fisher}} < 0.01$) compared to Sanetti (Figure 3.4C), which remains a marginal grazing area.

Seasonal density of cattle varied from 119.1 to 405.4 CT.km⁻² in Web, 118.7 to 345.3 CT.km⁻² in Morebawa and 23.7 to 110.6 CT.km⁻² in Sanetti. Seasonal density of caprines varied from 38.5 to 289 ST.km⁻² in Web, 62.9 to 256.9 ST.km⁻² in Morebawa and 21.5 to 109 ST.km⁻² in Sanetti. Seasonal density of transport animals varied from 12.1 to 40.6 TA.km⁻² in Web, 5 to 16.5 TA.km⁻² in Morebawa and 0.2 to 10 TA.km⁻² in Sanetti. Applying Fisher's combined probability test to the livestock density estimates for each survey, I find evidence of seasonality in the number of livestock in Web ($p_{\text{cattle}} = 0.0229$, $p_{\text{caprines}} = 0.0323$, $p_{\text{TA}} = 0.0381$; $\chi_6^2 = 20.96$, $p_{\text{Fisher}} < 0.01$) but not in Morebawa ($p_{\text{cattle}} = 0.0968$, $p_{\text{caprines}} = 0.6722$, $p_{\text{TA}} = 0.0494$; $\chi_6^2 = 11.47$, NS) or Sanetti ($p_{\text{cattle}} = 0.8534$, $p_{\text{caprines}} = 0.4522$, $p_{\text{TA}} = 0.2552$; $\chi_6^2 = 4.64$, NS).

<i>Date</i>	<i>Species</i>	<i>Sampling effort (km)</i>	<i>No. clusters</i>	<i>Cluster encounter rate</i>	<i>Mean cluster size</i>	<i>Total observations</i>
<i>July 07</i>	CT	80	119	1.49 (1.05-2.1)	30.7 (28.35-33.05)	3654
<i>July 07</i>	ST	80	39	0.49 (0.32-0.75)	85 (78.6-91.4)	3315
<i>July 07</i>	TA	80	42	0.53 (0.33-0.82)	8.1 (7.43-8.77)	341
<i>November 07</i>	CT	80	76	0.95 (0.65-1.4)	43.35 (34.7-54.2)	3485
<i>November 07</i>	ST	80	36	0.45 (0.27-0.74)	41.36 (28.95-59.09)	1489
<i>November 07</i>	TA	80	46	0.58 (0.35-0.95)	6.02 (4.66-7.77)	277
<i>January 08</i>	CT	72	45	0.63 (0.43-0.9)	44.82 (31.69-63.4)	2017
<i>January 08</i>	ST	72	20	0.29 (0.14-0.6)	60.1 (37.75-95.69)	1202
<i>January 08</i>	TA	72	38	0.53 (0.32-0.87)	6.13 (4.75-7.92)	233
<i>April 08</i>	CT	76	37	0.49 (0.34-0.7)	53.03 (38.63-72.8)	1963
<i>April 08</i>	ST	76	21	0.28 (0.17-0.46)	64.57 (41.25-101.1)	1356
<i>April 08</i>	TA	76	27	0.36 (0.23-0.55)	6.48 (4.71-8.91)	175
<i>June 08</i>	CT	100	112	1.12 (0.77-1.63)	60.55 (50.77-72.21)	6782
<i>June 08</i>	ST	100	34	0.34 (0.21-0.54)	62.35 (49.54-78.48)	2120
<i>June 08</i>	TA	100	56	0.56 (0.35-0.9)	6.89 (5.64-8.42)	386

Table 3-2: Global sampling effort, number of livestock observed, cluster encounter rates and mean cluster size across three survey regions during five transect surveys with 95% confidence intervals in brackets.

3.3.2 Modelling maximum sustainable livestock biomass from rainfall data

The simplest approach to arriving at permissible densities is to examine feed supply and demand ratios that underlie the conventional manner of determining livestock carrying capacity (de Leeuw and Tothill, 1993, Bartels et al., 1993). Winrock (1992) assessed consumable feed by zone at 0.19, 0.51, 0.72 and 0.76 tonnes of dry matter per hectare for

the arid, semiarid, subhumid and highland zones of Africa, respectively, which convert to permissible densities of 8, 22, 31 and 33 TLU. km⁻².

The average annual density of livestock was calculated as 195/149/49 TLU. km⁻² in the Web valley, Morebawa and Sanetti respectively. Since those estimates were produced with a certain degree of variance (Table 3-2 & Figure 3.4), as a result of experimental design, the conservative density estimates (lower 95% confidence limit) is also reported as 125/69/13 TLU.km⁻² in the same three sites respectively, as a measure of the minimum density of livestock or “best-case scenario”.

For the average estimated annual rainfall of 1086mm/year (Miehe and Miehe, 1994) extrapolated for Web, Le Houérou and Hoste's (1977) relationship would predict a sustainable livestock density of 44 TLU.km⁻². The predicted biomass densities for Morebawa and Sanetti were 43 and 34 TLU.km⁻² respectively (Table 3-3). These estimates are close to Winrock's (1992) permissible density for the highland zone of Africa. Given that the densities thus obtained for Web and Morebawa are likely to be slight over-estimation of the true range capacity (since both areas are drier than the stations used as proxies), the estimates are close to the one devised by Winrock (1992) on the basis of feed supply for the whole highland ecozone. The observed/sustainable ratio in Web, using the average annual density estimate, was found to be 4.4, indicating potential overstocking (Table 3-3). Similar findings were made for Morebawa, and to a lesser extent, with Sanetti with observed/sustainable ratio of 3.5 and 1.4 respectively. Using the conservative livestock density estimates for these regions, only Web and Morebawa appear to be overstocked with ratios of 2.8 and 1.6 respectively.

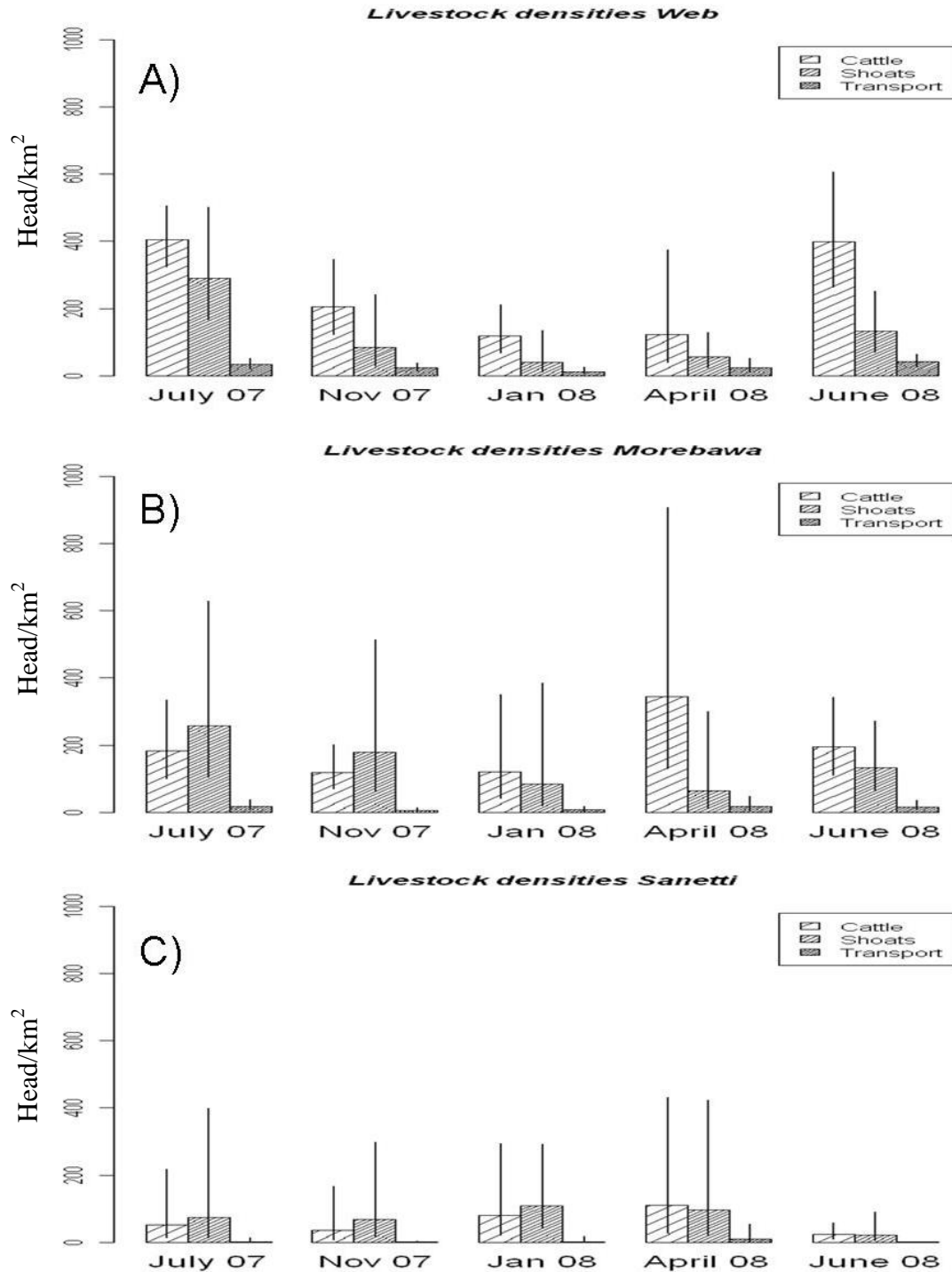


Figure 3-4: Distance-based livestock density estimates (and their 95% confidence intervals) in A) the Web valley, B) Morebawa and C) Sanetti in July 2007 (peak of wet season), November 2007 (start of dry season) , January 2008 (peak of dry season), April 2008 (end of dry season) and June 2008 (beginning wet season).

When considering average TLU densities by season, Le Houérou and Hoste's (1977) relationship predicts a biomass density of 9 TLU.km⁻² for the dry season for all three areas and 34/34/25 TLU.km⁻² for the wet season in Web, Morebawa and Sanetti

respectively. The observed/ sustainable ratio, using average annual density estimates, then becomes 13.9/10.7 and 5.2 during the dry season and 7.1/3.4 and 2 during the wet season for Web, Morebawa and Sanetti respectively (Table 3-3). The ratios obtained when using the conservative livestock density estimates for both seasons are always lower for all three areas. However, both sets of results suggest that, although herbivore densities on the pastures are much higher all year round than are likely to be sustainable from the mean annual rainfall received, pastures are more overstocked during the dry season than during the wetter months.

	Obs. annual density	Max. sustain. annual density	Ratio (annual)	Obs. dry season density	Max. sustain. dry season density	Ratio (dry season)	Obs. wet season density	Max. sustain. wet season density	Ratio (wet season)
Web	195 (125)	44	4.4 (2.8)	125 (72)	9	13.9 (7.9)	242 (160)	34	7.1 (4.7)
Morebawa	149 (69)	43	3.5 (1.6)	96 (43)	9	10.7 (4.8)	184 (86)	34	3.4 (2.5)
Sanetti	49 (13)	34	1.4 (0.38)	47 (12)	9	5.2 (1.3)	50 (13)	25	2 (0.5)

Table 3-3: Distance-based estimates of mean annual and seasonal densities of livestock (TLU.km⁻²) in the afroalpine range of the Bale Mountains (2007-2008) with conservative estimates (lower 95% confidence limit) inside the brackets. The maximum sustainable livestock density was estimated from the relationships established by Le Houérou and Hoste (1977) between herbivore biomass density and rainfall. The ratio of observed density to maximum sustainable density was computed with conservative estimates inside the brackets.

3.3.3 Livestock dung counts in the survey grids.

The highest densities of livestock dung for both seasons were recorded in the Web valley (Table 3-4). In almost all instances, the highest density of dung recorded was for cattle followed by shoat and finally transport animals. Shoat dung density was higher than cattle dung density in Morebawa during the wet season and in Sanetti during the dry season. For all species, the dung production rate and the mean time to decay were higher during the wet season (Table 3-4).

Variation in the number of livestock dung piles counted inside the grids was best explained by the additive effects of habitat type, distance to water, season and year of survey. Distance to the nearest settlement was not a significant explanatory variables ($t = -0.82$, $df = 19$, $p = 0.42$). Grids in H/A and H/D pastures had significantly less livestock dung than those in A/G pastures ($t = -4.08$, $df = 19$, $p < 0.01$ and $t = -3.32$, $df = 19$ and $p < 0.01$ respectively). Less livestock dung were recorded during the wet season ($t = -1.97$, $df = 70$, $p = 0.05$), whilst more dung was recorded in the second year ($t = 2.55$, $df = 70$, $p = 0.01$). The number of livestock dung piles in the grids slowly increased ($t = 2.62$ $df = 20$, $p = 0.02$) as the distance from the nearest source of water increased at a rate of 5.8 dung piles.km⁻² per 1m (“reverse” grazing gradient).

The season-specific livestock density estimates for each area (D_k) obtained using distance sampling and dung counts were significantly different in all cases except in Sanetti during the dry season (Table 3-5):

1. Web ($t = 2.40$, $df = 26$, $p = 0.02$ and $t = 6.15$, $df = 34$, $p < 0.01$ for dry and wet season respectively)
2. Morebawa ($t = 4.84$, $df = 22$, $p < 0.01$ and $t = 11.15$, $df = 28$, $p < 0.01$ for dry and wet season respectively)
3. Sanetti ($t = 0.798$, $df = 44$, $p = 0.44$ and $t = 6.24$, $df = 55$, $p < 0.01$ for dry and wet season respectively)

			$\overline{S_{i,k}}$ (dung/km ²)	p_i (dung/animal/day)	r_i (days)
Web	Dry	Cattle	$\overline{S_{i,k}} = 20885.42$ $\sigma = 4105.32$	$p_i = 8.4$ $\sigma = 1.08$	$r_i = 9.83$ $\sigma = 2.86$
		Caprines	$\overline{S_{i,k}} = 19270.83$ $\sigma = 4003.87$	$p_i = 14.05$ $\sigma = 1.84$	$r_i = 9.33$ $\sigma = 2.06$
		TA	$\overline{S_{i,k}} = 7187.5$ $\sigma = 1514$	$p_i = 9.17$ $\sigma = 1.50$	$r_i = 9.2$ $\sigma = 3.5$
	Wet	Cattle	$\overline{S_{i,k}} = 14635.42$ $\sigma = 2527.47$	$p_i = 11.40$ $\sigma = 0.85$	$r_i = 15.63$ $\sigma = 6$
		Caprines	$\overline{S_{i,k}} = 12135.42$ $\sigma = 4699.32$	$p_i = 14.62$ $\sigma = 1.19$	$r_i = 15.75$ $\sigma = 5.53$
		TA	$\overline{S_{i,k}} = 5312.5$ $\sigma = 1475.90$	$p_i = 12.02$ $\sigma = 3.22$	$r_i = 11$ $\sigma = 3.67$
Morebawa	Dry	Cattle	$\overline{S_{i,k}} = 3437.5$ $\sigma = 1058.46$	$p_i = 8.4$ $\sigma = 1.08$	$r_i = 9.83$ $\sigma = 2.86$
		Caprines	$\overline{S_{i,k}} = 2291.67$ $\sigma = 1151.34$	$p_i = 14.05$ $\sigma = 1.84$	$r_i = 9.33$ $\sigma = 2.06$
		TA	$\overline{S_{i,k}} = 520.83$ $\sigma = 263.87$	$p_i = 9.17$ $\sigma = 1.50$	$r_i = 9.2$ $\sigma = 3.5$
	Wet	Cattle	$\overline{S_{i,k}} = 7239.58$ $\sigma = 1954.96$	$p_i = 11.40$ $\sigma = 0.85$	$r_i = 15.63$ $\sigma = 6$
		Caprines	$\overline{S_{i,k}} = 9218.75$ $\sigma = 3859.19$	$p_i = 14.62$ $\sigma = 1.19$	$r_i = 15.75$ $\sigma = 5.53$
		TA	$\overline{S_{i,k}} = 1305.08$ $\sigma = 854.10$	$p_i = 12.02$ $\sigma = 3.22$	$r_i = 11$ $\sigma = 3.67$
Sanetti	Dry	Cattle	$\overline{S_{i,k}} = 6953.13$ $\sigma = 2363.91$	$p_i = 8.4$ $\sigma = 1.08$	$r_i = 9.83$ $\sigma = 2.86$
		Caprines	$\overline{S_{i,k}} = 8489.58$ $\sigma = 2620.49$	$p_i = 14.05$ $\sigma = 1.84$	$r_i = 9.33$ $\sigma = 2.06$
		TA	$\overline{S_{i,k}} = 26.04$ $\sigma = 26.04$	$p_i = 9.17$ $\sigma = 1.50$	$r_i = 9.2$ $\sigma = 3.5$
	Wet	Cattle	$\overline{S_{i,k}} = 2812.5$ $\sigma = 715.78$	$p_i = 11.40$ $\sigma = 0.85$	$r_i = 15.63$ $\sigma = 6$
		Caprines	$\overline{S_{i,k}} = 0$ $\sigma = 0$	$p_i = 14.62$ $\sigma = 1.19$	$r_i = 15.75$ $\sigma = 5.53$
		TA	$\overline{S_{i,k}} = 0$ $\sigma = 0$	$p_i = 12.02$ $\sigma = 3.22$	$r_i = 11$ $\sigma = 3.67$

Table 3-4: Season-specific estimates of dung density, dung production rate and mean time to decay ($\overline{S_{i,k}}$, p_i and r_i respectively) for all species in all regions.

	Season	Dung counts	Distance sampling
Web	Dry	$D_k = 266.22$ $\sigma = 67.53$	$D_k = 126.24$ $\sigma = 3.70$
	Wet	$D_k = 98.87$ $\sigma = 26.50$	$D_k = 241.98$ $\sigma = 4.06$
Morebawa	Dry	$D_k = 37.08$ $\sigma = 12.63$	$D_k = 95.97$ $\sigma = 4.74$
	Wet	$D_k = 42.80$ $\sigma = 13.89$	$D_k = 185.7$ $\sigma = 4.99$
Sanetti	Dry	$D_k = 68.39$ $\sigma = 26.27$	$D_k = 46.65$ $\sigma = 3.79$
	Wet	$D_k = 12.15$ $\sigma = 4.93$	$D_k = 49.78$ $\sigma = 3.69$

Table 3-5: Summary of dung-based and Distance-based livestock density estimates (D_k) in TLU.km⁻², and standard deviations of the estimated means (σ) obtained from distance sampling and dung counts in the three wolf ranges during the dry and wet season of 2007/2008.

3.4 Discussion

3.4.1 Is the Bale afroalpine overstocked?

Much evidence exists for a relationship between mean rainfall and pasture production (Coe et al., 1976, Deshmukh, 1984, Le Houérou and Hoste, 1977). In tropical and sub-tropical areas, rainfall is correlated with a number of other climatic factors such as rain variability, number of rainy days, length of dry and rainy seasons and potential evapotranspiration which all partly contribute to the determination of pasture production. The ratio of observed annual livestock density to that maximum sustainable density on the basis of mean rainfall was 4.43:1, 3.47:1 and 1.44:1 (or 2.8:1, 1.6:1 and 0.4:1 under the conservative scenario) for the Web valley, Morebawa and Sanetti respectively. The conservative results suggest that the Web valley and Morebawa are overstocked given the rangeland predicted productivity for those areas and that Sanetti has ratio < 1 suggesting that range production may be enough to sustain the current livestock population. Both sets of results indicate that overstocking is more prominent during the dry season than during the wetter months, an important consideration given that both Web and Morebawa are drier

than the ranges used as proxies for rainfall and that the conservation ratios may still slightly underestimate the extent of overstocking.

3.4.2 Are dung counts reliable enough to estimate livestock densities?

The livestock density estimates inside each wolf range, as derived from the dung counts, were almost always significantly different from the ones derived from distance sampling, however not in a biased way. There is, of course, the issue of temporal variability affecting “snap-shot” estimates based on line transects as compared to dung counts which integrate over longer time periods. However, based on the sample size and on the estimated standard error for those estimates, I would argue that the livestock density estimates derived from distance sampling are more reliable and realistic. It is, however, difficult, to justify why the livestock density estimates derived from both the direct and indirect methods are almost invariably significantly different. While estimating $\overline{S_{i,k}}$ was relatively straightforward, I observed a bigger degree of uncertainty (standard error) in our estimates of seasonal dung production rate (p_i) and, to a larger extent, in dung mean time to decay (r_i). This may have contributed to the larger standard errors associated with our livestock density estimates ($D_{i,k}$) from dung counts. For the above reasons, I will use the density of livestock dung (and not livestock density estimates), as an index of livestock presence (Brooker et al., 2006, Lange, 1969), in our analyses in Chapter 5. I would recommend more trials on estimating accurate r_i and p_i before establishing dung counts as a monitoring method for livestock populations in BMNP.

3.4.3 On the cautious use of grazing gradients

Many studies use the distance gradient from a livestock camp to assess the impact of grazing on rangeland structure (Hoshino et al., 2009, Sasaki et al., 2008). Our results suggest that, at least in Bale, the distance from the nearest settlement is not a significant predictor of livestock use of an area as revealed by livestock dung counts in our survey grids. Many more studies have used the distance to the nearest source of water (Adler and Hall, 2005, Andrew, 1988, Blanco et al., 2008, Fernandez-Gimenez and Allen-Diaz, 2001, Gebremeskel and Pieterse, 2006, Gonnet et al., 2003, Nash et al., 1999, Solomon et al., 2006). These studies not only often assume that the probability of livestock use of an

area decreases as the distance from the nearest source of water increases, but also assume that this grazing gradient operates on a very small spatial scale (sometimes less than 50m away from water). However, these assumptions are rarely tested. Our results suggest that in Bale, factors such as habitat type contribute significantly to the variation in habitat use by livestock and our results imply that the timing of the survey (wet/dry season) is a factor that should be taken into consideration. First livestock movements and use of pastures is likely to be dependent on rainfall and the onset of the wet season. Second, livestock may aggregate around sources of water during the drier months but may range more widely on the pastures during the wet season when access to water is not limited. Finally, in our case, heavy rains may accelerate the decay of livestock dung on which I based our livestock use index. The distance to the nearest source of water is a significant predictor of livestock use of an area, however, contrary to other systems, I seem to observe a “reverse” grazing gradient, with the number of livestock dung observed increased as the observer moves away from water. I also find that this “reverse” grazing gradient operates on a very large spatial scale with an increase of 5.8 dung pile.km⁻² per 1m (equivalent to +9 dung pile/grid per 1000m). I would therefore recommend that future studies, using the grazing gradient concept to measure livestock impact, test for the significance of distance to water or settlements in explaining the variation in the intensity of use of the pastures by livestock, especially in semi-arid or non-arid rangelands where water may not be a limiting resource all year-long.

4 Responses of three endemic afroalpine rodents to habitat modification by livestock.

4.1 Introduction

Livestock grazing has major impacts on native biodiversity throughout the world (Scimone et al., 2007, De Vries et al., 2007). Grazing has both a direct and an indirect impact on plants, influencing their growth, survival and reproduction (Diaz et al., 2007, Milchunas and Lauenroth, 1993, van de Koppel et al., 1997, Fuhlendorf et al., 2001), and the abundance and distribution of animal communities inhabiting grasslands (Wheeler, 2008, Kruess and Tschardtke, 2002, Schmidt et al., 2005, Bakker et al., 2009, Coppedge et al., 2008). Small mammals are especially relevant in grasslands because of their top-down effects on plant communities (Brown and Heske, 1990, Manson et al., 2001) and their bottom-up effects on bird and mammal predators (Korpimäki and Norrdahl, 1991, Hanski et al., 1991b, Torre et al., 2007). Many rodent species are also ecosystem engineers, increasing landscape heterogeneity and species diversity by creating unique patches of habitat that differ from the surrounding landscape (Bagchi et al., 2006, Zhang et al., 2003, Olofsson et al., 2008, Murdoch et al., 2009). Rodents generally have pronounced species-specific habitat preferences, influenced by the distribution and abundance of habitat resources such as food and location of burrows and/or plant-community physiognomy making them highly sensitive to habitat change (Mapelli and Kittlein, 2009, Rosi et al., 2009, Olayemi and Akinpelu, 2008, Layme et al., 2004).

Surveys on distributions of small mammals demonstrate that patterns of population change associated with the disturbance of habitat are complex and difficult to assess since the specific requirements of most species are largely unknown (Heroldova et al., 2008). This suggests that several mechanisms are operating within a particular ecosystem and that an experimental approach beyond a comparison of “grazed versus ungrazed” is needed to test hypotheses on the impact of livestock grazing on the rodent community as a whole. While a few studies compare the effect of light/heavy grazing on rodent communities (Steen et al., 2005, Jones and Longland, 1999), very few have tried to establish empirical relationships between a continuous measure of livestock grazing and rodent populations (Blaum et al., 2007). Grazing gradients provide a way to observe changes in vegetation and animal populations under different grazing intensities, with previous studies using the distance to water (Fernandez-Gimmenez and Allen-Diaz, 2001, Gonnet et al., 2003) or to livestock camps (Hoshino et al., 2009, Sasaki et al., 2008) to establish gradients in livestock grazing pressure in rangelands.

4.1.1 The afroalpine and rodents of the Bale Mountains

The Bale Mountains lie between 06°41'N, 39°03'E and 07°18'N, 40°00'E, in the southern highlands of Ethiopia. They represent the largest area of afroalpine habitat over 3000m in Africa (Yalden, 1983), and form part of Conservation International's Eastern afroalpine hotspot (Brooks et al., 2004), harbouring a diverse array of endemic and range-restricted species. The Bale Mountains National Park (BMNP) was established in 1969 to protect the endemic mountain nyala (*Tragelaphus buxtoni*) and Ethiopian wolf (*Canis simensis*) and c. 2,200 km² of afroalpine habitats upon which they depend (Hillman, 1986). Although, six isolated populations of Ethiopian wolves have been described in Ethiopia, over half of the estimated 500 remaining wolves are found in the Bale Mountains (Marino, 2003b).

The giant mole rat (GM, *Tachyoryctes macrocephalus*), Blick's grass rat (AB, *Arvicanthis blicki*) and the brush-furred mouse (LM, *Lophuromys melanonyx*) are endemics restricted to the southern highlands of Ethiopia (Yalden, 1988) (Figure 4.1). These fossorial diurnal rodents are of great ecological importance as the dominant wild herbivores within the afroalpine ecosystem (Sillero-Zubiri et al., 1995a, Sillero-Zubiri et al., 1995b). They are important components of the diet of a diverse guild of diurnal raptors which inhabit the Bale massif (Clouet et al., 2000). However, these rodents have been most closely studied as the main prey of the endangered Ethiopian wolf representing an estimated 47%, 27% and 16% of the wolves' diet (by volume) respectively (Sillero-Zubiri and Gottelli, 1995). These rodents, in turn, feed principally on grasses, leaves and stems of flowering plants, occasionally eating arthropods (Yalden, 1988). GM also have an important secondary role in the afroalpine as ecosystem engineers (Jones et al., 1994). The prevalence of GM in habitats with large expanses of bare soil (Tallents, 2007) is partly indicative of their role as ecosystem engineers as they eject soil from their burrow systems, creating mima mounds, in the course of the excavation of their burrows. They also heavily graze the area around each entrance, and gather vegetation for bedding material, further denuding the landscape, maintaining pioneer stages and playing an important role in soil formation processes (Yalden, 1985, Sillero-Zubiri et al., 1995a, Sillero-Zubiri et al., 1995b).



Figure 4-1: Rodent study species: *Arvicanthis blicki* (left), *Tachyoryctes macrocephalus* (top right) and *Lophuromys melanonyx* (bottom right)(©Flavie Vial).

In the tropics, where rainfall is seasonal, many rodent species show a peak in their reproductive activity towards the end of the rainy season (Delany, 1972). Rain is accompanied by vegetation growth, which in turn influences reproductive output. In the Simien Mountains, an ecosystem similar to that of Bale with 75% of the annual rainfall falling between June and September, Müller (1977) found that the largest proportion of pregnant females of *Stenocephalemys albocaudata*, *Otomys typus* and *Lophuromys flavopunctatus* occurred during and just after the rainy season. In Bale, although pregnant females are seen throughout the year, reproduction in LM and AB is also documented to be most intense during the first half of the wet season for the former and the mid to late wet season for the latter. Fewest females show signs of pregnancy during the dry season (Sillero-Zubiri, 1994). Nothing is known about the reproductive cycle and population dynamics of the GM.

The study of small mammal assemblages in the Ethiopian highlands has mostly concentrated on distributions and population dynamics associated with geographical features like altitude and rainfall (Yalden, 1988) or vegetation (Tallents, 2007). Few studies in Africa have been conducted on the effects of human habitat use on rodent

communities (Clausnitzer, 2003, Keesing, 1998, Keesing and Crawford, 2001, Eccard et al., 2000), despite the importance of rodents in the ecosystems either as pest or prey (Davis et al., 2008, Holt et al., 2006, Rabui and Rose, 2004).

The purpose of this study was to establish empirical relationships between livestock grazing, afroalpine vegetation and rodents in BMNP. Specifically, I propose and test the following hypotheses regarding the impact of livestock grazing on the diurnal afroalpine rodent population using a grazing gradient approach. As grazing pressure increases, I expect a decrease in overall rodent density (H1), body weight (H2), and reproductive success (H3) with a concomitant increase in home range size (H4). I also investigate whether these impacts on rodent populations are concurrent with changes in vegetation structure and test the following hypotheses: As grazing pressure increases, I expect an increase in bareground cover (H5), a decrease in cover of *Alchemilla* spp., grass and other common plant species (H6) with a concomitant increase in shrub cover (H7), a decrease in vegetation species diversity and evenness (H8) and a decrease in the height of *Alchemilla* spp. and grass spp (H9).

4.2 Materials and methods

4.2.1 Study sites

I merged 23 afroalpine vegetation classes based on Tallents' (2007) unsupervised classification of Bale afroalpine vegetation into 3 habitat categories, reflecting rodent abundance (Sillero-Zubiri, 1994):

1. *Alchemilla* and grass pastures (A/G) with high rodent densities.
2. *Helichrysum/Artemisia* shrublands (H/A) with low rodent densities.
3. Bare soil/ Herb pastures/drainage lines (H/D) with high giant molerat and intermediate LM and AB densities.

Twenty-four survey grids (40x40m) were set up in these three habitat types to establish empirical relationships between livestock grazing pressure, afroalpine vegetation and rodent diversity and abundance (Chapter 3, Figure 3.1). The locations of these grids

were randomly generated in ArcGIS (Environmental Systems Research Institute Inc., 2004) subject to the following criteria:

1. Equal numbers of grids (8) in each habitat type.
2. Grids to be located inside Ethiopian wolf core ranges: Web valley (6 grids), Morebawa (6 grids) and Sanetti (12 grids).
3. Grids located within a 4km radius of the campsites.

The survey grids thus obtained were located at varying distances from both the nearest source of water and settlements. Such variation was anticipated to result in differential intensity of use by livestock, as measured by dung counts, allowing us to sample vegetation and rodents across a grazing gradient. Surveys of rodents and vegetation cover took place during the wet and dry seasons in both 2007/2008 and 2008/2009, giving us a sample size of ninety six sampling events (24 grids x 2 seasons x 2 years).

4.2.2 Livestock grazing index

I calculated the density of livestock dung inside each grid prior to vegetation and rodent surveys and converted the density estimates for each livestock species (cattle, sheep/goats and transport animals) into tropical livestock units (TLU) (Boudet and Riviere, 1968), using the following conversion factors: 1 TLU=1.5 cattle=11 sheep/goats= 1.5 transport animal (Le Houérou and Hoste, 1977). I then used the density of livestock dung (TLU dung.km⁻²), as an index of the livestock grazing pressure exerted on the experimental grids (Brooker et al., 2006).

4.2.3 Rodent field surveys

The number of GM open burrows correlates closely with minimum population size estimated from individuals surfacing simultaneously and can be used as an index of GM abundance (Tallents, 2007, Sillero-Zubiri et al., 1995b). On each grid, 25 folding Sherman live-traps (H. B. Sherman Traps, Florida, USA; model LFATDG, 12”) were arranged at 10m intervals for live-trapping of LM and AB over four consecutive days. Traps were set up at dawn, baited with a mixture of peanut butter and flour, checked at midday and at dusk when they were closed. Animals were given individual marks by fur clipping on their

abdomen, weighed, sexed and the trap in which they were captured recorded. Reproductive condition (signs of lactation, pregnancy or hymen perforation; testes size and position) was also recorded. Only non-pregnant adult rodents were used to calculate the average weight of LM and AB individuals within each grid. The proportion of LM and AB adult females (PFLMP and PFABP respectively) that were pregnant was also calculated. Tables 4-1 and 4-2 provide summaries of the number of captures/recaptures for each species, of the estimated GM densities and of the age and sex distribution of both LM and AB populations. The distributions of the weights recorded for adult LM and AB are shown in Figure 4-2. For every recapture event, I calculated the distance between the most widely separated traps where the individual was captured, also known as the observed range length (ORL-distribution shown in Figure 4-3) (Pelikan and Holisova, 1969), and the distance moved between recaptures (DRC). Both have been shown to provide a reliable index of home-range size in small mammals (Moorhouse et al., 2008, van der Ree and Bennett, 2003). I then estimated an average ORL and DRC for LM and for AB on each grid.

	LM		AB		GM
	Total captures	Recaptures	Total captures	Recaptures	Density (/km ²)
October 2007	333	135	50	12	800.85
February 2008	485	233	142	51	415.72
November 2008	408	167	117	50	423.19
February 2009	302	133	64	31	197.12

Table 4-1: The number of total captures (first capture and recaptures) and recaptures for LM and AB, alongside the estimated GM density across all survey grids for each trapping season. Note: No other species were caught with the exception of two shrews (*Crocidura fumosa*).

	LM		AB	
	Sex ratio (F:M)	Age ratio (A:SA:J)	Sex ratio (F:M)	Age ratio (A:SA:J)
October 2007	0.58 : 0.42	0.94 : 0.05 : 0.01	0.26 : 0.74	0.86 : 0.11 : 0.03
February 2008	0.70 : 0.30	0.92 : 0.05 : 0.03	0.40 : 0.60	0.96 : 0.04 : 0
November 2008	0.60 : 0.40	0.85 : 0.1 : 0.05	0.28 : 0.72	0.96 : 0.04 : 0
February 2009	0.53 : 0.47	0.93 : 0.07 : 0	0.20 : 0.80	0.94 : 0.06 : 0

Table 4-2: The sex ratio (F : M) and age ratio (A- adult, SA- subadult and J- juvenile) for LM and AB across all survey grids for each trapping season.

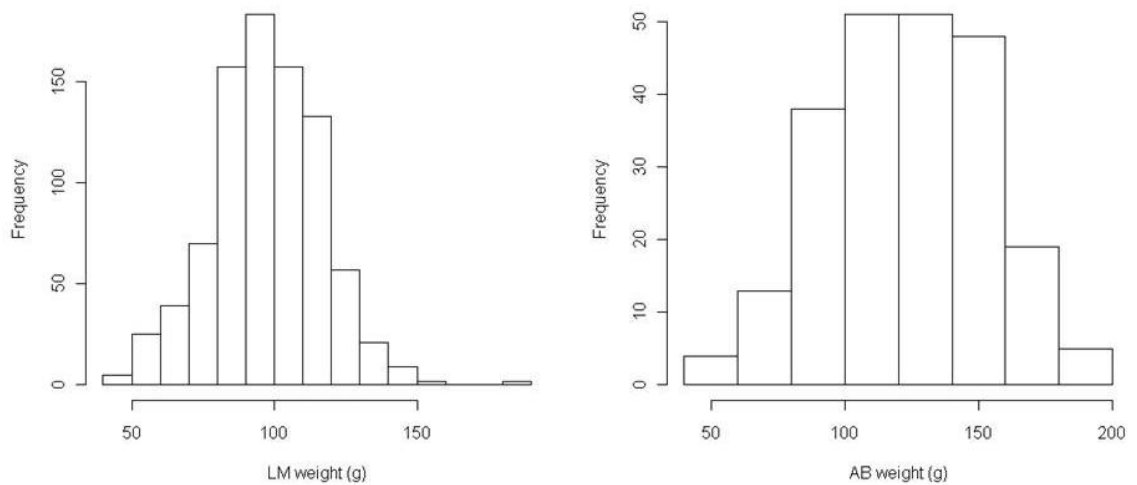


Figure 4-2: Distribution of rodent weights (in g): adult LM (left, n = 860) and AB (right, n = 229) across all grids.

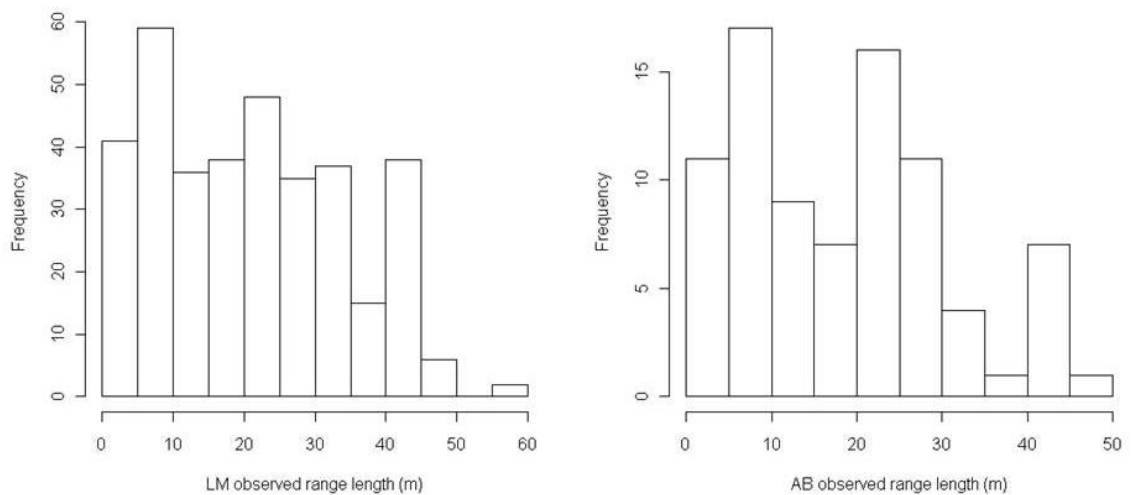


Figure 4-3: Distribution of the observed range lengths (in m) for LM (left, n = 355) and AB (right, n = 84) across all grids.

4.2.4 Modelling rodent abundance

I used Tallents (2007) equations to extrapolate minimum GM abundance (A) from the total number of open burrows (D) recorded at time C (hours after midnight):

$$A = 0.370 \times (-3.445 + 0.634 \times C - 0.025 \times C^2) \times D \quad \text{Equation 4-1}$$

The average trapping success was 9% (0-38%) with 1107 individuals LM and AB trapped and 462 recapture events observed, giving an average recapture probability of 23.8% (0-62.5%). LM and AB population sizes were estimated from minimum number known alive (MNKA). To reduce the negative bias inherent in this population estimate, a correction factor was applied based on closed capture estimates for grids with a recapture probability of at least 25% (n = 33) using Recapture (Baillargeon and Rivest, 2007). A strong relationship existed between MNKA and these closed capture estimates ($p < 0.001$, $r^2 = 0.83$, n = 33); and MNKA was multiplied by 1.44 (95% CI: 1.20-1.68) to provide bias-corrected estimates for all grids.

The effective trapping area was calculated by adding a boundary strip equivalent to half the mean distance moved between successive captures (Otis et al., 1978). The mean distance moved by rodents between recaptures was 18.97 m (n = 462, 95% CI 18.92-19.02) making the effective trapping area for each grid 2448.76 m². Population densities for LM and AB (individuals.km⁻²) were calculated using the bias-corrected population estimates for each species and the size of the effective trapping area. Overall rodent biomass for all three species combined was calculated using the density estimate for each species and the mean body mass. Mean body masses of AB and LM were 128.59g ± 22.66 SD (n = 115), and 100.31g ± 8.85 SD (n = 571) respectively. Mean body mass for GM was taken from Sillero-Zubiri (1994): mean 618g ± 190 SD (n = 11).

4.2.5 Vegetation field surveys

Twenty 1m² quadrats were randomly placed inside each grid and all plant species were identified. The flower structures necessary for identification of grasses were often not present, so all grasses were split into two categories only: wetland sedges and other grasses (referred as grasses from this point on). The height of all species was estimated using a 1-5 scale (1 = 0/10 cm, 2 = 10/20 cm, 3 = 20/30 cm, 4 = 30/40 cm and 5 = >40cm). The

percentage cover for all species and bareground (Figure 4-4) was calculated, using the mid-point coverage for each Braun-Blanquet scale (Braun-Blanquet, 1932), inside each random quadrat and averaged over all the quadrats to calculate the mean percentage cover for each grid. The same was done with height measurements. I then used the cover estimates to calculate Shannon diversity (H') and evenness (J) indices (Shannon, 1948). Species density was also computed (Figure 4-4).

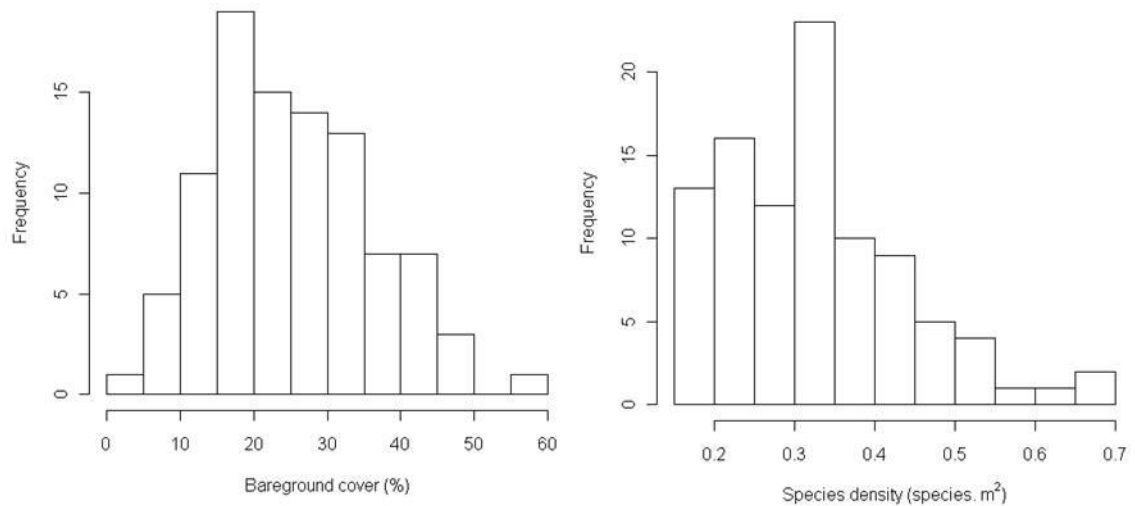


Figure 4-4: Distribution of some vegetation variables : percentage bareground cover (left, n=96) and plant species density (right, n=96) across all grids.

Within each habitat type, I computed the list of the five most common species and found that *Alchemilla* spp. (*A. abyssinica* and *A. rothii*) and grasses dominated the composition in all three habitats, followed by *Helichrysum* shrubs (*H. citrispinum* and *H. gofense*) and *Euryops prostratus* in H/A and H/D grids or by *Haplocarpha rueppellii* and *Salvia merjame* in A/G grids (Figure 4-5). I used these species as indicators for the changes in vegetation cover for inclusion in the models. Changes in the vegetation structure were modelled using the height data from the three most common vegetation species group: *Alchemilla* spp., grasses and *Helichrysum* spp.

4.2.6 Data analysis and model selection

Proportion and percentage data were arcsine transformed before being analysed. The data were analysed with the “nlme” package in R (Pinheiro et al., 2009) using general linear mixed models based on a repeated measures design with habitat type, season, year and the livestock grazing index as fixed factors, while the temporal replication of grids was

included as a random factor. Nested models were compared using the likelihood ratio test. P-values larger than 0.05 were judged to demonstrate non-significance.

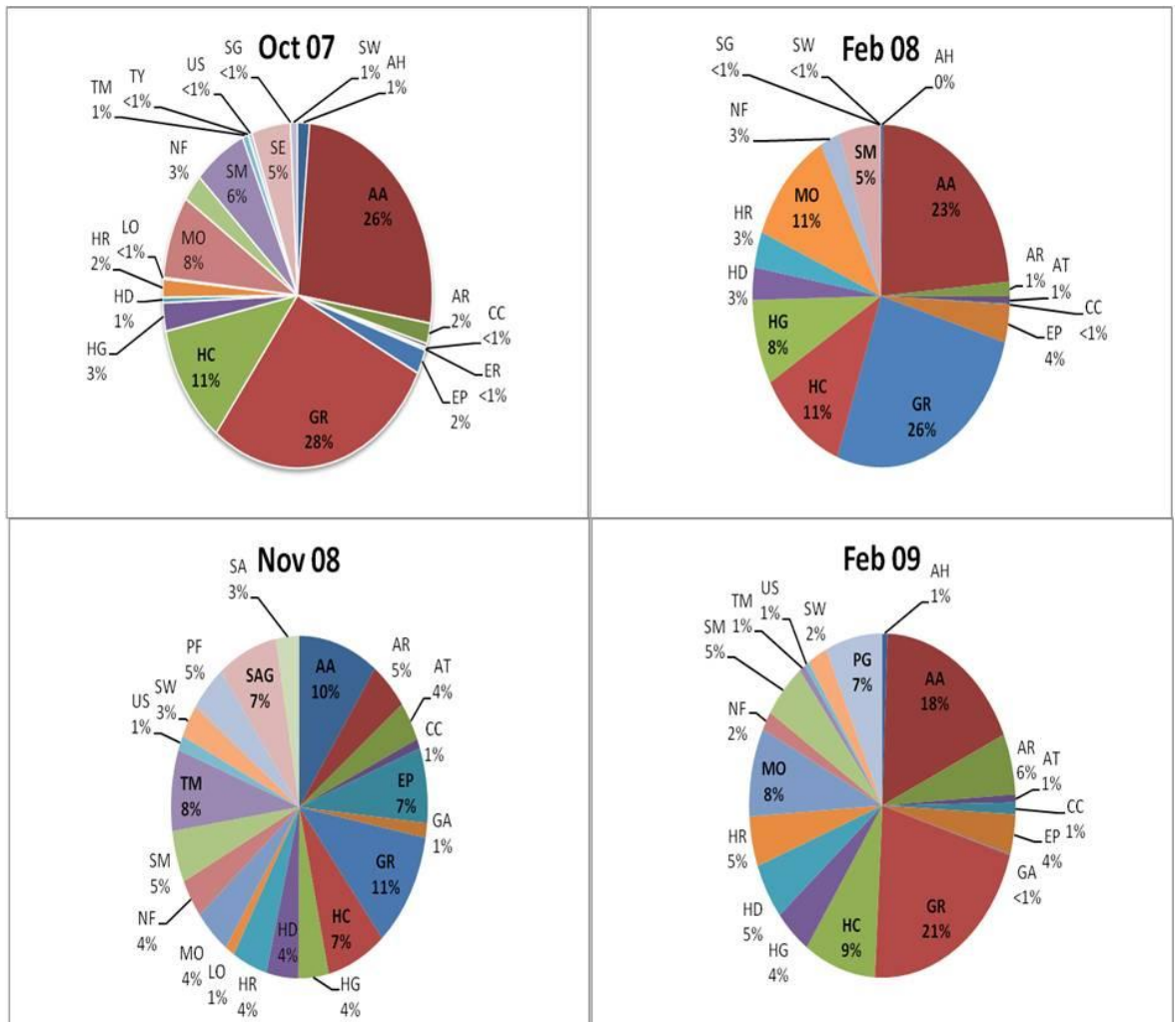


Figure 4-5: Vegetation composition (% cover) of all the grids surveyed in October 2007, February 2008, November 2008 and February 2009. The bigger the area occupied by a species inside the pie chart, the more common the species.

4.3 Results

4.3.1 Rodent analyses

4.3.1.1 Rodent abundance

When not correcting for a season or for a year effect, overall rodent biomass declined at a rate of 1 kg .km⁻² for every 59 extra TLU dung.km⁻² (Figure 4-6A). This trend was mostly driven by the changes in LM and GM densities. Variation in the overall rodent biomass was best explained by a model containing a 3-way interaction between season,

year and livestock grazing index (Table 4-3 M1). Livestock's impact on rodent biomass was negative during the wet seasons ($t = -2.19$, $p = 0.03$) and worse during year 2 ($t = -3.00$, $p < 0.01$), although there was a significant positive relationship between the number of livestock dung and rodent biomass during the wet season of year 2 ($t = 3.94$, $p < 0.01$).

When not correcting for a season or for a year effect, LM density declined at a rate of 1 individual.km⁻² for every 11 extra TLU dung.km⁻² (Figure 4-6B). The variation in LM density was also best explained by a 3-way interaction between season, year and livestock grazing index (Table 4-3 M2). Livestock's impact on LM was negative during the wet season of year 1 ($t = -2.16$, $p = 0.04$) but once again positive during the wet season of year 2 ($t = 0.71$, $p < 0.01$). I found that livestock had a negative impact on GM populations during the wet seasons (Table 4-3 M4 & Figure 4-6). The sample size of AB trapped may have been too small to reveal any significant impact of livestock grazing on population density (Table 4-3 M3: $2\Delta LL = 0.72$, 1df, $p = 0.39$).

4.3.1.2 Body weight, reproductive success and home range

The livestock grazing index did not significantly account for variation observed in the weight of adults LM (Table 4-3 M5: $2\Delta LL = 0.19$, 1df, $p = 0.67$) and adults AB (Table 4-3 M6: $2\Delta LL = 0.27$, $p = 0.60$), or the proportion of female LM (Table 4-3 M7: $2\Delta LL = 0.42$, 1df, $p = 0.52$) and female AB (Table 4-3 M8: $2\Delta LL = 0.80$, 1df, $p = 0.37$) that were pregnant (Figure 4-7). ORL (Table 4-3 M9: $2\Delta LL = 1.49$, 1df, $p = 0.22$) and DRC (Table 4-3 M11: $2\Delta LL = 2.43$, 1df, $p = 0.12$) for LM were not affected by the livestock grazing index. I drew the same conclusions for ORL (Table 4-3 M10: $2\Delta LL = 0.22$, 1df, $p = 0.64$) and DRC (Table 4-3 M12: $2\Delta LL = 0.25$, 1df, $p = 0.62$) for AB (Figure 4-8).

Model	Response variable	Best model	Significant explanatory variables
M1	Overall rodent biomass	Livestock* Season* Year	Season (wet) * Livestock: $t = -2.19$, $p = 0.03$ Year (2) * Livestock: $t = -3$, $p < 0.01$ Season (wet) * Year (2) * Livestock: $t = 3.94$, $p < 0.01$
M2	Density LM	Livestock* Season* Year	Season (wet) * Livestock: $t = -2.16$, $p = 0.04$ Season (wet) * Year (2) * Livestock: $t = 2.71$, $p < 0.01$
M3	Density AB	Null	
M4	Density GM	Habitat + Year + Season * Livestock	Habitat (H/A): $t = -2.60$, $p = 0.02$ Habitat (H/D): $t = -2.11$, $p = 0.05$ Year (2) : $t = -2.61$, $p = 0.01$ Season (wet) * Livestock: $t = -1.88$, $p = 0.05$
M5	Weight LM	Year + Season	Year (2) : $t = -2.49$, $p = 0.02$ Season (wet) : $t = 2.51$, $p = 0.02$
M6	Weight AB	Null	
M7	(Arcsine) PFLMP	Null	
M8	(Arcsine) PFABP	Null	
M9	ORL LM	Null	
M10	ORL AB	Season	Season (wet) : $t = 3.09$, $p < 0.01$
M11	DRC LM	Null	
M12	DRC AB	Season + Year	Year (2) : $t = -237$, $p = 0.03$ Season (wet) : $t = 2.61$, $p = 0.02$

Table 4-3: Summary of the models adopted for the rodent analyses along the grazing gradient. All models were fitted in R and all parameters estimated in relation to the intercept for Habitat A/G during the dry season of year 1. Models with interactions contain the components of the interactions as main effects. A null model ($Y = \text{intercept}$) was fitted when no explanatory variable significantly explained part of the variation in the response variable.

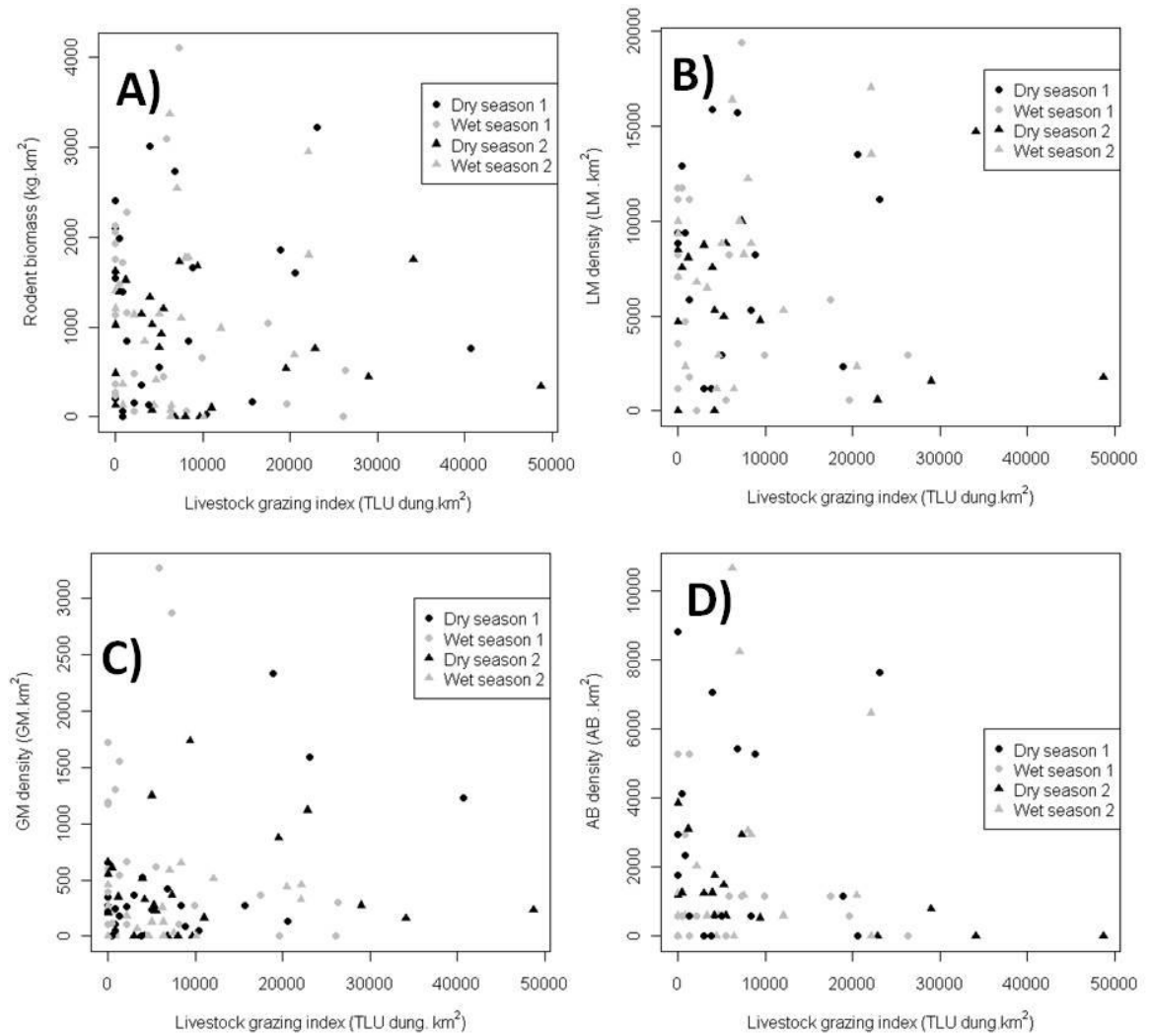


Figure 4-6: Relationships between the livestock index and rodent response variables .Season and year-specific rodent biomass (A) LM density (B) GM density (C) and AB density (D) plotted against the livestock grazing index for all grids. The data is colour-coded by season (grey-wet season, black-dry season) and by year (circle-year 1, triangle- year 2).

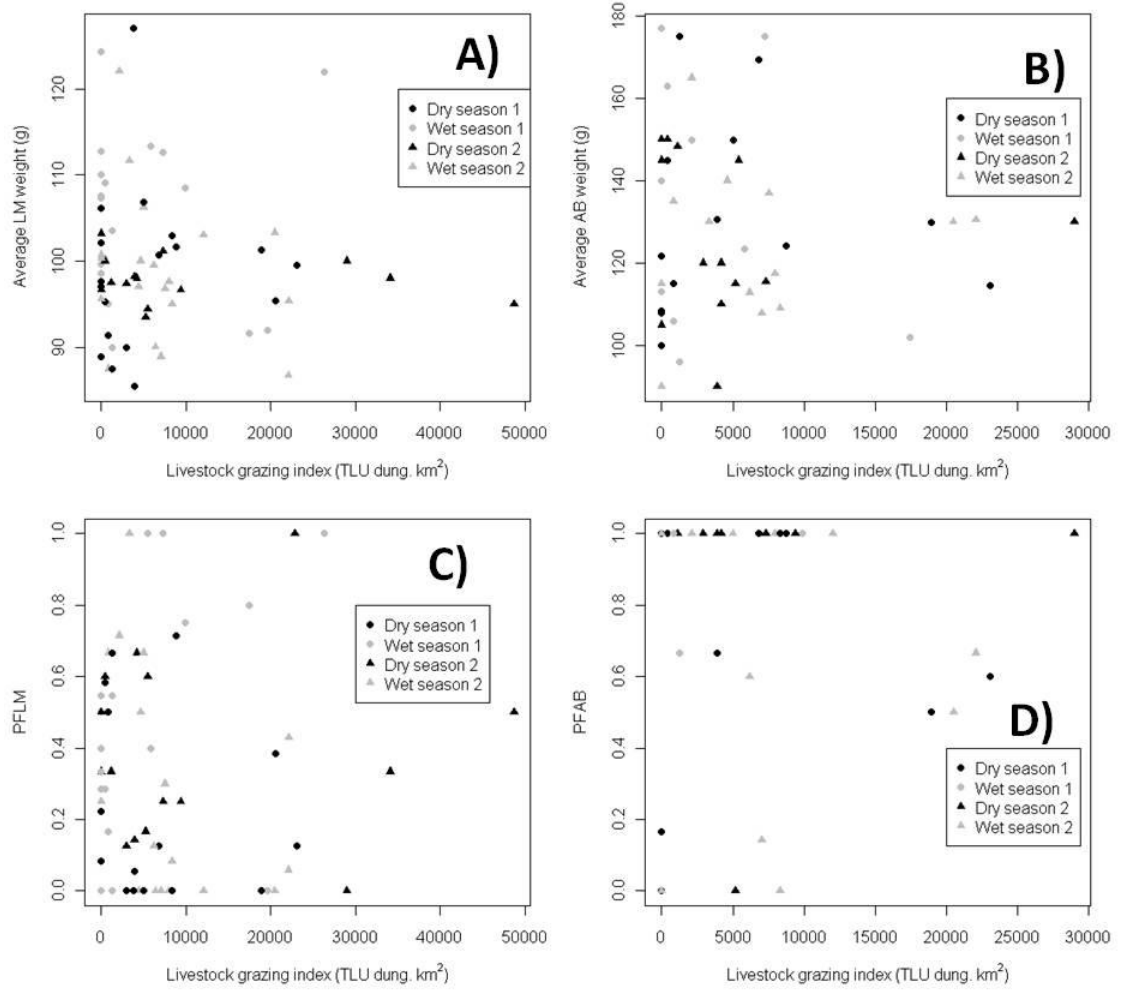


Figure 4-7: Relationships between the livestock index and rodent response variables (2). Season and year-specific LM weight (A) AB weight (B) PFLMP (C) and PFABP (D) plotted against the livestock grazing index for all grids. The data is colour-coded by season (grey-wet season, black-dry season) and by year (circle- year 1, triangle- year 2).

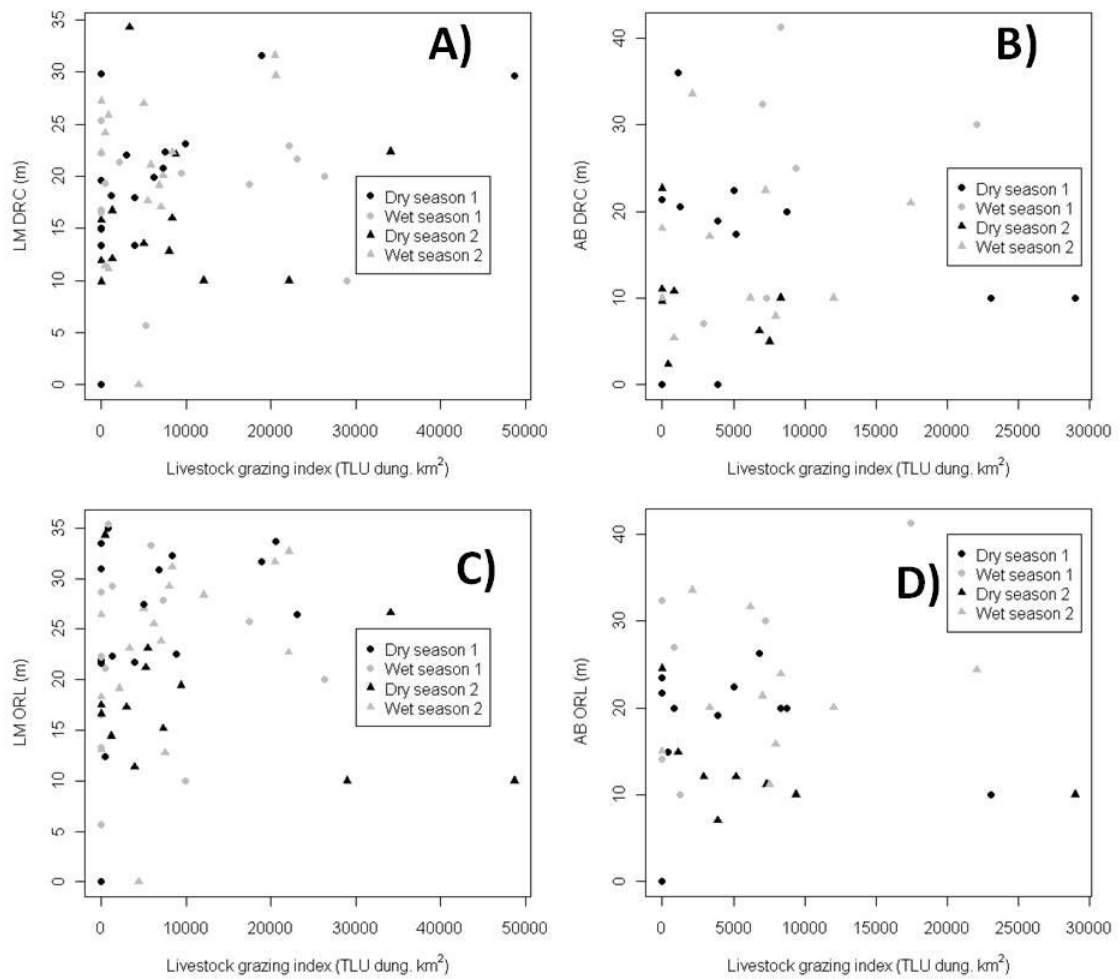


Figure 4-8: Relationships between the livestock index and rodent response variables (3). Season and year-specific LM DRC (A) AB DRC (B) LM ORL (C) and AB ORL (D) plotted against the livestock grazing index for all grids. The data is colour-coded by season (grey-wet season, black-dry season) and by year (circle-year 1, triangle- year 2).

4.3.2 Vegetation analyses

4.3.2.1 Species density, diversity and evenness

The livestock grazing index had a small but highly significant positive effect on plant species density (Table 4-4 M13 & Figure 4-9A), but did not significantly account for the variation observed in vegetation diversity (Table 4-4 M14: $2\Delta LL = 2.85$, 1df, $p = 0.09$) or evenness (Table 4-4 M15: $2\Delta LL = 0.01$, 1df, $p = 0.90$) (Figure 4-9B and C).

4.3.2.2 Vegetation cover & height

The livestock grazing index had a small but highly significant negative effect on bareground cover (Table 4-4 M16 & Figure 4.9D) and a positive effect on *H. rueppellii* cover (Table 4-4 M20 & Figure 4-10B). The livestock grazing index did not significantly account for the variation observed in the cover of *Alchemilla* spp. (Table 4-4 M17: $2\Delta LL = 1.93$, 1df, $p = 0.17$), grass spp. (Table 4-4 M18: $2\Delta LL = 0.0003$, 1df, $p = 0.99$), *Helichrysum* shrubs (Table 4-4 M22: $2\Delta LL = 1.08$, 1df, $p = 0.30$), *E. prostratus* (Table 4-4 M19: $2\Delta LL = 0.55$, 1df, $p = 0.46$) or *S. merjame* (Table 4-4 M21: $2\Delta LL = 0.02$, 1df, $p = 0.88$)(Figures 4-9 and 4-10).

Livestock significantly decreased the height of grasses during the wet seasons (Table 4-4 M24 & Figure 4-11D). However, the livestock grazing index did not significantly account for the variation observed in the height of *Alchemilla* spp. (Table 4-4 M23: $2\Delta LL = 0.01$, 1df, $p = 0.92$) or *Helichrysum* shrubs (Table 4-4 M25: $2\Delta LL = 0.79$, 1df, $p = 0.37$)(Figure 4-11).

Model	Response variable	Best model	Significant explanatory variables
M13	(Log) Species density	Livestock + Season + Year	Season (wet) : $t = 2.61$, $p < 0.01$ Year (2): $t = 4.06$, $p < 0.01$ Livestock: $t = 2.50$, $p = 0.02$
M14	Diversity	Habitat * Season * Year	Year (2): $t = 3.82$, $p < 0.01$ Habitat (H/D) * Season (wet) : $t = -3.80$, $p < 0.01$ Habitat (H/A) * Year (2): $t = -1.96$, $p = 0.05$ Habitat (H/D) * Year (2): $t = -2.46$, $p = 0.02$ Habitat (H/D) * Year (2) * Season (wet): $t = 4.20$, $p < 0.01$
M15	Evenness	Season * Year	Season (wet) : $t = -4$, $p < 0.01$ Year (2) * Season (wet): $t = 4.12$, $p < 0.01$

Table 4-4: Summary of the models adopted for the vegetation analyses along the grazing gradient. All models were fitted in R and all parameters estimated in relation to the intercept for Habitat A/G during the dry season of year 1. A null model ($Y = \text{intercept}$) was fitted when no explanatory variable significantly explained part of the variation in the response variable (continues).

Model	Response variable	Best model	Significant explanatory variables
M16	(Arcsine) % bareground cover	Livestock + Season + Year	Season (wet) : t = 5.16, p<0.01 Year (2): t = 4.55, p<0.01 Livestock: t = -2.63, p = 0.02
M17	(Arcsine) % <i>Alchemilla</i> cover	Season + Year	Season (wet) : t = -3.15, p<0.01 Year (2): t = 6.04, p<0.01
M18	(Arcsine) % grass cover	Habitat + Season	Habitat (H/D): t = -3.09, p<0.01 Habitat (H/A) : t = -2.96, p<0.01 Season (wet) : t = 2.11, p = 0.04
M19	(Arcsine) % <i>E. prostratus</i> cover	Year	Year (2): t = 3, p<0.01
M20	(Arcsine) % <i>H. rueppellii</i> cover	Livestock + Year	Year (2): t = 2.73, p<0.01 Livestock: t = 3.30, p<0.01
M21	(Arcsine) % <i>S. merjame</i> cover	Habitat + Season + Year	Habitat (H/D): t = -2.38, p = 0.03 Season (wet) : t = 2.44, p = 0.02 Year (2): t = 3.46, p<0.01
M22	(Arcsine) % <i>Helichrysum</i> shrub cover	Habitat	Habitat (H/A) : t = 3.06, p<0.01
M23	Height <i>Alchemilla</i> spp.	Habitat + Season	Habitat (H/A) : t = 2.12, p = 0.05 Season (wet) : t = 2.14, p = 0.04
M24	Height grass spp.	Livestock * Season	Season (wet) : t = 3.87, p< 0.01 Livestock * Season (wet) : t = -2.83, p< 0.01
M25	Height <i>Helichrysum</i> shrubs	Null	

Table 4-4 (continued).

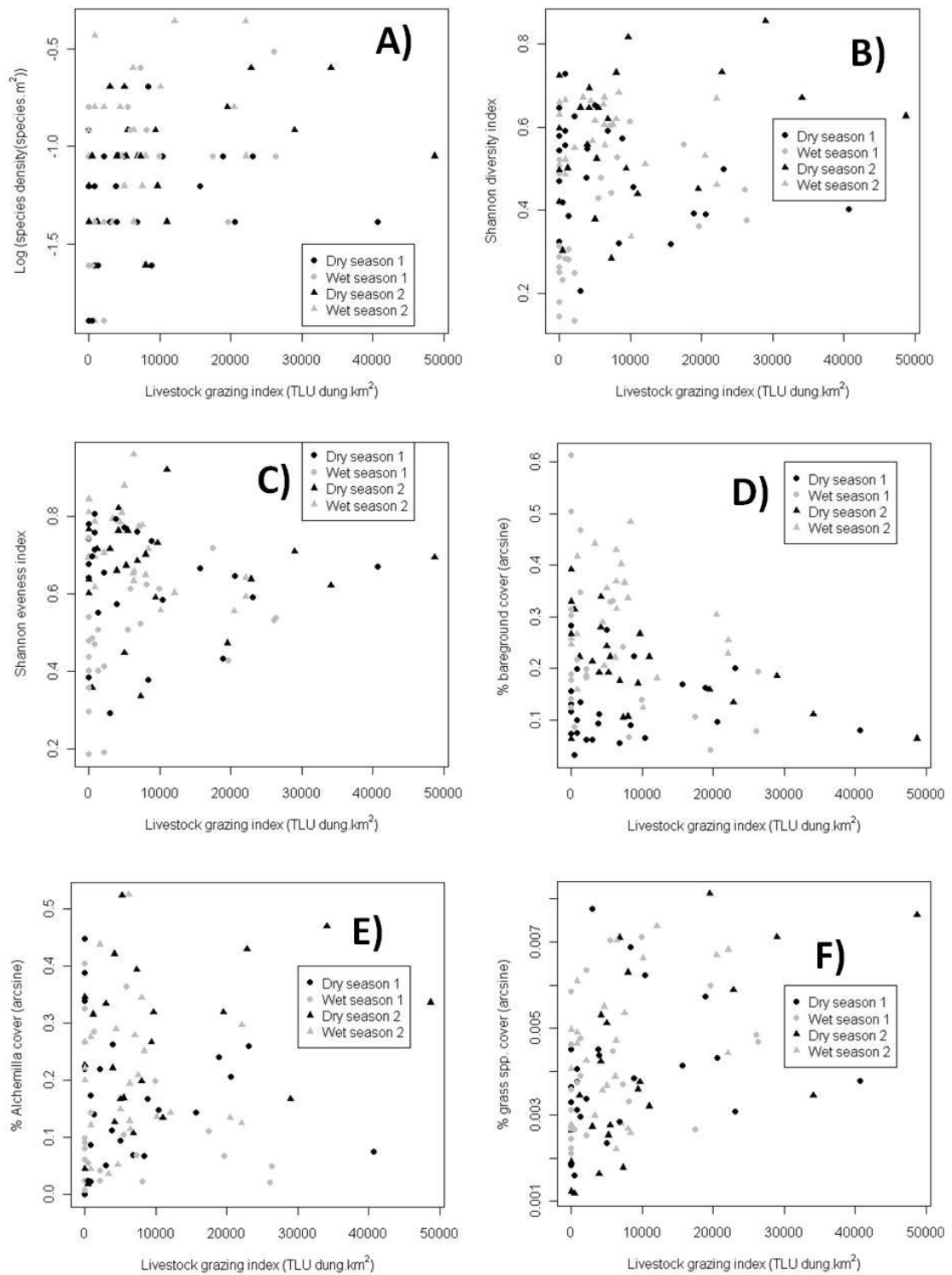


Figure 4-9: Relationships between the livestock index and vegetation response variables A) vegetation species density; B) Shannon diversity index; C) Shannon evenness index; D) bareground % cover; E) Alchemilla % cover and F) grass spp. % cover regressed against the livestock grazing index for all grids. The data is colour-coded by season (grey-wet season, black-dry season) and by year (circle- year 1, triangle- year 2).

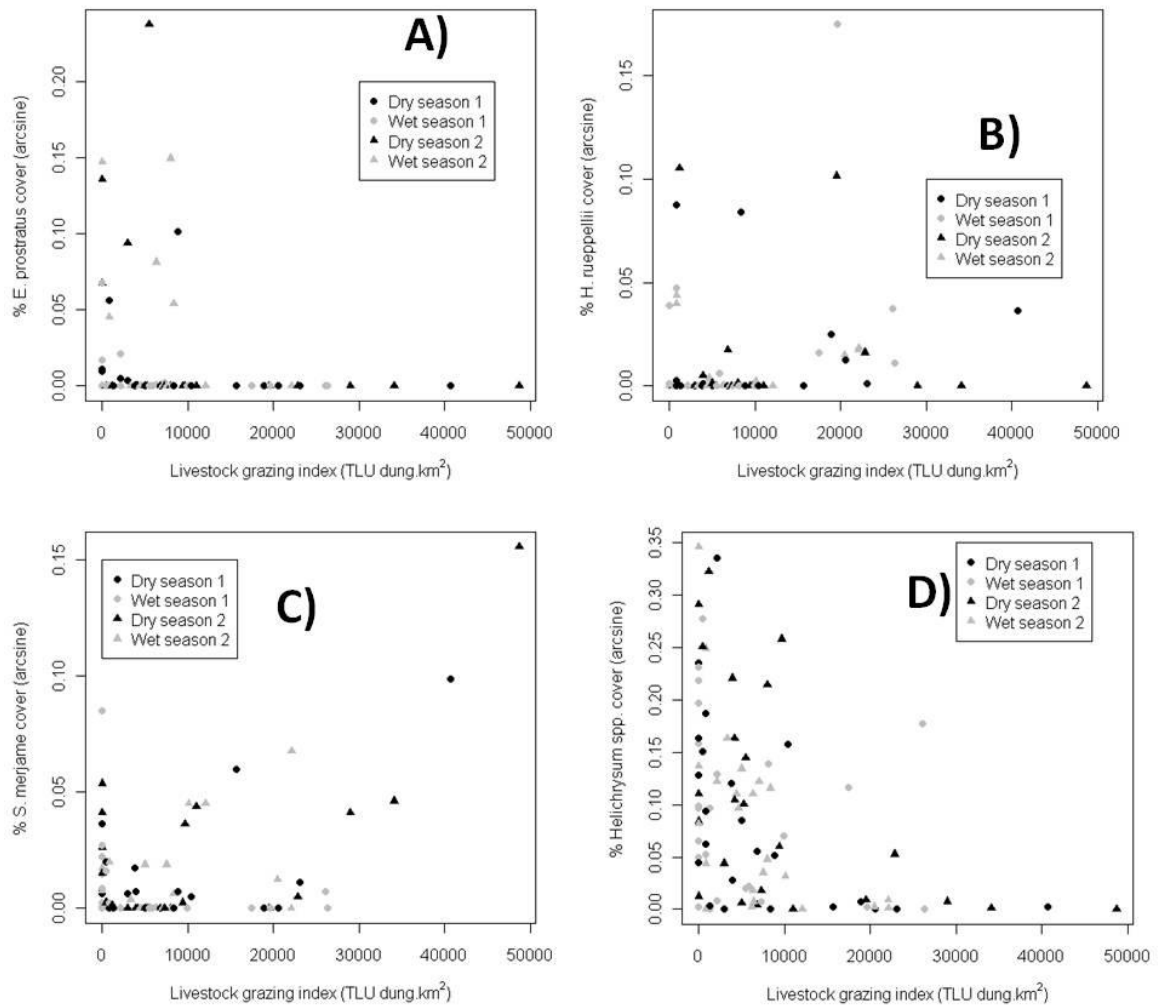


Figure 4-10: Relationships between the livestock index and vegetation response variables (2) A) *E. prostratus* % cover; B) *H. rueppellii* % cover; C) *S. merjame* % cover and D) *Helichrysum spp.* % cover regressed against the livestock grazing index for all grids. The data is colour-coded by season (grey-wet season, black-dry season) and by year (circle-year 1, triangle- year 2).

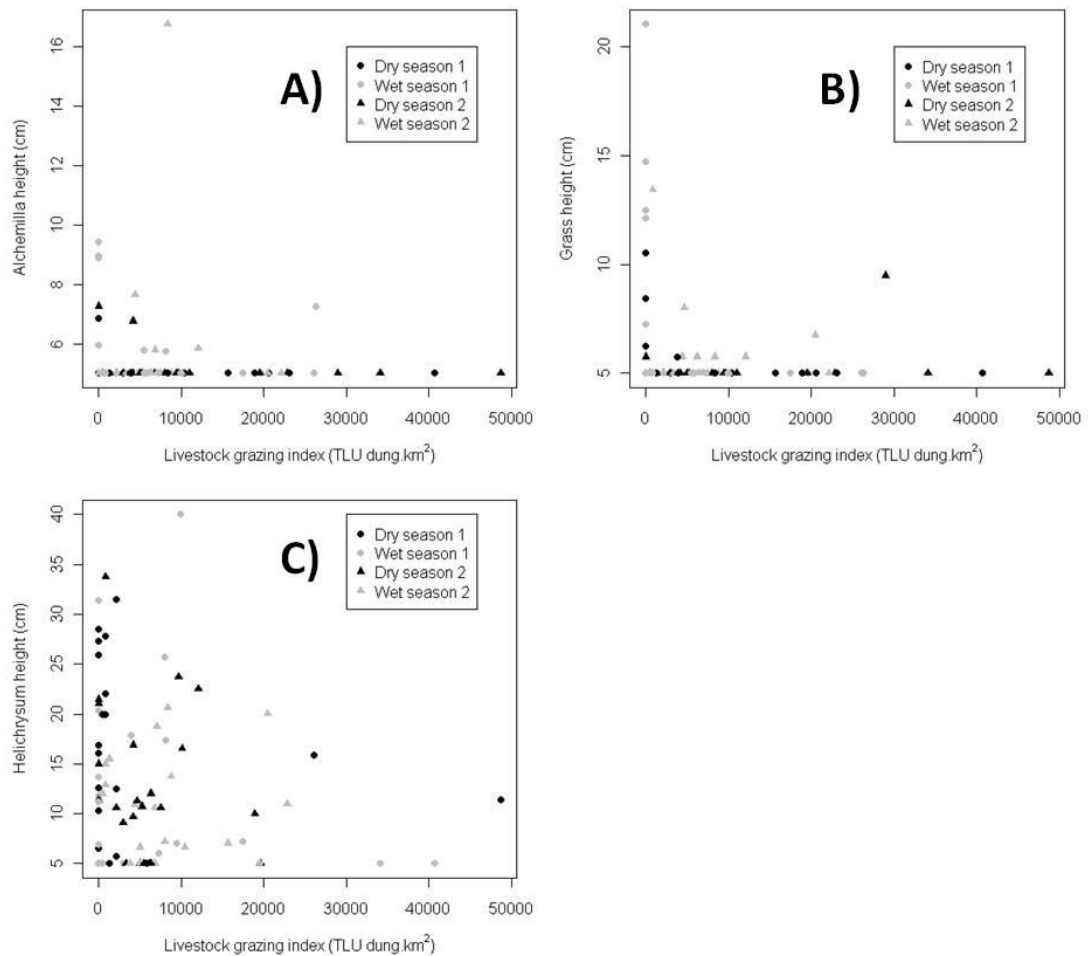


Figure 4-11: Relationships between the livestock index and vegetation response variables (3) A) *Alchemilla spp.* height; B) *grass spp.* height and C) *Helichrysum spp.* height regressed against the livestock grazing index for all grids. The data is colour-coded by season (grey-wet season, black-dry season) and by year (circle- year 1, triangle- year 2).

4.4 Discussion

4.4.1 Competition, facilitation or predation?

Livestock grazing, through its effects on vegetation, has the potential to affect rodent populations through three main pathways: competition, facilitation and predation. The likelihood of the existence of exploitation competition between livestock and rodents increases as habitat and diet overlap, and given that the shared resources are in limited supply (Tokeshi, 1999, Keesing, 2000). Should exploitative competition exist between livestock and diurnal rodents in Bale, I would expect: a decrease in abundance of all three

rodent species (H1), a decrease in their body weight (H2), and reproductive success (H3) and an increase in their home range size as rodents have to forage further out for food (H4). Such processes could be mediated through a decrease in the biomass of forage available (H5, H6 & H9) in parallel with an increase in unpalatable species such as shrubs (H7) and an overall decrease in species richness, diversity and evenness (H8). Our data brings little support to these hypotheses. The densities of LM and GM do decrease as the livestock grazing pressure on the system increases (but densities of AB don't). This provides evidence for the existence of negative interactions between some members of the two groups (H1 partially supported) although these interactions can be season and year-specific. However, livestock grazing pressure was not found to have an impact on either the body condition, reproductive success or habitat use by LM and AB (H2, H3 & H4 rejected), results supported by similar findings in common shrews subjected to high levels of livestock grazing (*Sorex araneus*) (Schmidt et al., 2009). This leads us to conclude that the negative interactions between livestock and LM are unlikely to result from exploitative competition, or from a decrease in the quality of forage.

Indeed, looking at the concomitant changes in the vegetation composition and structure, I find little evidence that those interactions are mediated by changes in the vegetation congruent with the competition hypothesis. I did not find that increasing grazing pressure led to lower cover of the five dominant species group recorded on the grids (H6 rejected), or increased bareground (H5 rejected) and shrub cover (H7 rejected) (latter supported by data from other Ethiopian rangelands (Abule et al., 2007b, Tefera et al., 2007b)). I found no evidence of livestock grazing affecting vegetation diversity or evenness. However, our H' and J estimates would be improved by the identification of grass species, as they may vary significantly in their acceptability to grazing herbivores, not only due to differences in palatability but also due to phenological differences (Tefera et al., 2007a) and grass species composition and diversity is an important indicator of rangeland condition (Abule et al., 2007a). I found some evidence of reduced vegetation biomass in the form of the decreased height of grasses when moving up the grazing gradient, but not so for *Alchemilla* spp., the preferred forage for rodents (Abebe, 2008) (H9 partially supported).

Another hypothesis is that livestock, through removal of vegetation, may benefit rodents by facilitating access to forage of a suitable height or quality (Gordon, 1988, Arsenault and Owen-Smith, 2002). I found no evidence of facilitation in our system, since

two of the rodent species respond negatively to increases in the number of livestock. However, I did find that increased grazing pressure was linked to higher overall vegetation cover, as the extent of bareground was reduced, and increased species richness. Our results may highlight the role livestock can play in maintaining grassland vegetation by spatial and temporal dispersion of readily germinating seeds and nutrient by means of manure (Woldu and Saleemb, 2000, Taddese et al., 2003), or by favouring the creation of niches for colonising species (Olf and Ritchie, 1998, Veen et al., 2008). It is also likely that livestock are attracted to patches with more vegetation resulting in a higher recorded number of dungs in areas with fuller vegetation cover. The decrease in bareground cover at higher livestock densities could also be the result of the reduction in the amount of burrow excavation taking place when rodent density is on the decrease (especially GM).

Finally, the reduction in vegetation biomass by livestock grazing may induce changes in habitat structure that affect the detection and avoidance of predators by rodents (Hayward et al., 1997, Smit et al., 2001, Schmidt et al., 2005). I find some evidence supporting this final hypothesis as the height of grasses was reduced at higher grazing intensities and the concomitant decrease in bareground cover may enhance the predators' (Ethiopian wolves and raptors) ability to detect the brownish/grey rodents on a greener background.

4.4.2 Soil compaction?

Trampling and soil compaction by livestock may affect the habitat quality for the rodents by reducing the soil suitability for building and maintaining burrow systems (Torre et al., 2007). Heavy grazing pressures are known to increase surface run-off and soil loss and reduce the infiltrability of the soil on other Ethiopian rangelands (Taddese et al., 2002b, Tefera et al., 2007a). Changes in soil compaction in turn can result in vegetation changes, the impact of which may be delayed for small mammal populations (Mwenedera et al., 1997). I suggest that evidence for such a mechanism be tested in afroalpine ranges in Bale in the light of the lack of evidence I have found of exploitative competition between livestock and rodents. Soil compaction along with increased predation risk may both be important to explain the indirect effect of livestock grazing on the rodent population in Bale.

Differences among rodent species in their responses to grazing do exist and may be mediated by interactions between the direct effects of grazing on habitat quality and species-specific habitat requirements or abilities to respond to spatial heterogeneity at different spatial scales (Milchunas et al., 1998, Jones and Longland, 1999, Hayward et al., 1997). The first species to disappear are usually those that are least abundant within the community, or those that specialise on particular vegetation types (Tabeni et al., 2007). However, in Bale I found that LM suffered more than AB from increasing grazing pressure despite being the most abundant and having a more insectivorous diet (Yalden, 1988).

The lack of significant differences in most of the studied vegetation variables could be attributed to the fact that grazing disturbance has already exceeded a certain threshold of degradation. Mean bareground cover in Bale (21.2%) is higher than that recorded in other Ethiopian rangelands, albeit non-alpine ones, such as Awash (5.3%) (Abule et al., 2007a) and Borana (5/8%) (Tefera et al., 2007a). However, such lack of significance could support the assertion that moderate livestock grazing is not always harmful to vegetation as supported by research results from other parts of Ethiopia (Taddese et al., 2002a). There is indeed a widespread notion that African grazing systems can be intrinsically resilient, because they have persisted for decades or more despite large and frequent environmental fluctuations (Ellis and Swift, 1988, Belsky, 1992, Milchunas et al., 1988). Vegetation changes in such systems may be mainly governed by rainfall variations, which determine plant productivity, and life-history attributes of species that place regenerative plant parts out of their reach (Sullivan and Rohde, 2002). The relative contribution of grazing and climatic variability to vegetation change is difficult to assess because both may produce complex interactive effects (Fuhlendorf et al., 2001). Although I found no evidence that rainfall or temperature determined the patterns of afroalpine vegetation observed in Bale over two years of experimental work (F. Vial, unpublished data), a longer time-series of vegetation patterns would be needed to test appropriately for correlations.

4.4.3 What are the implications for biodiversity conservation?

Even in areas with a long history of grazing such as Bale, domestic livestock may still constitute a threat to biodiversity and ecosystem functioning when their density is much higher than in the past (Vial et al., 2009). Stationery domestic grazers may have replaced more mobile wild ungulates (Fankhauser et al., 2008, Shrestha and Wegge, 2008a), although this is not the case in Bale, and other human activities such as burning

may also perturb the vegetation (Wesche, 2002, Veen et al., 2008). Our results suggest that increasing livestock number in BMNP may pose a threat to the long-term persistence of the endangered GM (Corti and Lavrenchenko, 2008), a species only ever recorded in the Bale Mountains, now existing as isolated local populations in a highly fragmented habitat and probably experiencing a high risk of extinction (Harrison, 1991). Ecosystems are complex and species interactions can have non-intuitive outcomes on community organization and ecosystem processes (Brown et al., 2001), such that it is important to consider the combined effects of multiple species (Davidson and Lightfoot, 2008). By modifying soil properties and plant communities through their burrowing activities, many rodent species facilitate resource exploitation for other species including birds (Arthur et al., 2008) and pollinating insects (Yoshihara et al., 2009). Through its direct effect on vegetation and indirect effect on burrowing rodents, high-intensity livestock grazing is likely to decrease habitat suitability for a range of other wildlife species. Furthermore, livestock is known to have the potential to alter the feeding ecology of carnivores by indirectly forcing them to display different functional responses to variation in prey availability (Pia et al., 2003, Eide et al., 2004, Farias and Kittlein, 2008). In Bale, the contribution of different species of prey to the diet of the Ethiopian wolf has already been shown to correlate with the abundance of prey (Sillero-Zubiri and Gottelli, 1995). Circumstantial evidence also suggests that wolves may predate more frequently on livestock (Marino, 2003b), or become crepuscular or nocturnal when human interference is severe in densely populated areas (Yalden and Largen, 1992). Our work has highlighted one of the facets of likely conflict between resident pastoralist communities and important trophic chains in the Bale Mountains, possibly affecting long-term conservation goals for the park's flagship species, the Ethiopian wolf.

5 Responses of afroalpine vegetation and endemic rodents to the removal of livestock grazing pressure.

5.1 Introduction

Livestock grazing is considered a powerful driver of plant population dynamics as well as plant community succession (Diaz et al., 2007, Milchunas and Lauenroth, 1993, van de Koppel et al., 1997, Fuhlendorf et al., 2001), and influences the abundance and distribution of the animal communities inhabiting grasslands (Wheeler, 2008, Kruess and Tscharrntke, 2002, Schmidt et al., 2005, Bakker et al., 2009, Coppedge et al., 2008). Small mammals are especially relevant in grasslands because of their top-down effects on plant communities (Brown and Heske, 1990, Manson et al., 2001) and their bottom-up effects on bird and mammal predators (Korpimäki and Norrdahl, 1991, Hanski et al., 1991b, Torre et al., 2007). Many rodent species are also ecosystem engineers, increasing landscape heterogeneity and species diversity by creating unique patches of habitat that differ from the surrounding landscape (Bagchi et al., 2006, Zhang et al., 2003, Olofsson et al., 2008, Murdoch et al., 2009).

5.1.1 *The afroalpine and rodents of the Bale Mountains*

The Bale Mountains lie between 06°41'N, 39°03'E and 07°18'N, 40°00'E, in the southern highlands of Ethiopia. They represent the largest area of afroalpine habitat over 3000m in Africa (Yalden, 1983), and form part of Conservation International's Eastern afroalpine hotspot (Brooks et al., 2004), harbouring a diverse array of endemic and range-restricted species. The giant molerat (GM, *Tachyoryctes macrocephalus*), Blick's grass rat (AB, *Arvicanthis blicki*) and the brush-furred mouse (LM, *Lophuromys melanonyx*) are endemics restricted to the southern highlands of Ethiopia (Yalden, 1988). These fossorial diurnal rodents are of great ecological importance as the dominant wild herbivores within the afroalpine ecosystem (Sillero-Zubiri et al., 1995a). They are important components of the diet of a diverse guild of diurnal raptors which inhabit the Bale massif (Clouet et al., 2000). However, these rodents have been most closely studied as the main prey of the endangered Ethiopian wolf (*Canis simensis*) representing an estimated 47%, 27% and 16% of the wolves' diet (by volume) respectively (Sillero-Zubiri and Gottelli, 1995). These rodents, in turn, feed principally on grasses, leaves and stems of flowering plants, occasionally eating arthropods (Yalden, 1988). GM also have an important secondary role in the afroalpine as ecosystem engineers (Tallents, 2007, Yalden, 1985).

The Bale Mountains National Park (BMNP) was established in 1969 to protect the endemic mountain nyala (*Tragelaphus buxtoni*) and Ethiopian wolf and c. 2,200 km² of montane habitats upon which they depend (Hillman, 1986). Although, six isolated populations of Ethiopian wolves have been described in Ethiopia (Marino, 2003b), over half of the remaining wolves are found in the Bale Mountains (total population estimated at <500 individuals in 2000 (Sillero-Zubiri et al., 2000)). The Bale Mountains National Park has been under increasing pressure from a rapidly growing pastoralist population and their livestock (Marino et al., 2006). Livestock densities estimates inside Ethiopian wolf core ranges (the Web valley, Morebawa and the Sanetti plateau) at 195/149/49 tropical livestock units per km² respectively illustrate the levels of threat the Bale afroalpine is subjected to (Chapter 3) (conversion factor from (Le Houérou and Hoste, 1977):1 TLU = 1.5 cattle = 11 caprines = 1.5 transport animal). High levels of livestock grazing in Bale may affect the quality of the habitat suitable for the rodent community on which the wolves depend (Sillero-Zubiri and Macdonald, 1997) through a reduction in vegetation cover resulting in an increased predation risk (Hayward et al., 1997, Germano et al., 2001, Smit et al., 2001, Schmidt et al., 2005) and/or a exploitative competition for suitable food resources (Tokeshi, 1999, Reynolds and Trost, 1980, Keesing, 2000).

5.1.2 Exclosure studies and rodent responses to the removal of grazing pressure

Exclosure studies are widely used to investigate the grazing impacts of ungulates on vegetation and animal communities by controlling ungulate access to plant resources (Firincioglu et al., 2007, Pei et al., 2008, Valone and Sauter, 2005, Kraaij and Milton, 2006, Keesing, 1998). While the interpretation of exclosure studies may be complicated by factors such as the pre-treatment condition of the vegetation, the duration for which exclosures are in place, and the environmental variability experienced over that period, they remain an important source of information concerning the impact of grazing and browsing stock. Several studies have explored the interactions between livestock and small herbivorous rodents using such exclosures (Steen et al., 2005, Grant et al., 1982, Bock et al., 1984, Heske and Campbell, 1991, Kelt and Valone, 1995, Kerley and Whitford, 2000, Valone et al., 2002, Valone and Sauter, 2005, Flowerdew and Ellwood, 2001, Weickert et al., 2001, Jones and Longland, 1999, Hayward et al., 1997, Reynolds and Trost, 1980). These studies have provided evidence for both decreases and increases in

the abundance of rodents following the removal of ungulate grazing in multiple combinations of ungulate and rodent species: red deer (*Cervus elaphus*) and wood mice (*Apodemus sylvestris*) in Dutch deciduous forest (Smit et al., 2001), sheep and field voles (*Microtus agrestis*) in a Norwegian alpine meadow (Steen et al., 2005), sheep, cattle and field voles at two Danish wet meadows (Schmidt et al., 2005), sheep, cattle and field voles in Scottish upland meadows (Evans et al., 2006), cattle and multiple rodent species in the American short grass steppe (Milchunas et al., 1998), and multiple ungulates versus multiple rodent species in African savannas (Keesing, 1998, Hagenah et al., 2009).

The purpose of this study was to establish whether afroalpine rodent populations and vegetation in BMNP responded to the removal of livestock grazing pressure. If livestock grazing affects rodent populations in Bale through competition or removal of cover leading to increased predation risk, I would hypothesise an increase in the rodent biomass (H1) following the removal of livestock grazing pressure inside livestock-proof exclosures. Furthermore, one might expect an increase in rodent body weight (H2), reproductive success (H3) and a decrease in home range size (H4). The opposite would be true if livestock positively affected rodent populations by facilitating access to forage of a suitable height or quality (McNaughton, 1976, Gordon, 1988, Karmiris and Nastis, 2007). I also investigate whether these impacts on the rodents are mediated through changes in vegetation structure and test the following additional hypotheses: By removing the livestock grazing pressure exerted on afroalpine pastures, I expect a change in vegetation species diversity and evenness (H5), a decrease in bareground cover (H6), an increase in the cover and height of *Alchemilla* spp., grass and other common plant species (H7) with a concomitant decrease in shrubs cover and height (H8).

5.2 Materials and methods

5.2.1 Study sites

Three 50x50m livestock exclosures were built in March 2008 in the Web Valley, an area of high human and livestock density (Chapters 2&3). All three exclosures are located on pastures dominated by grasses and *Alchemilla* herbs and paired with a control site (open to livestock) located between 300 and 1000m away, and of similar topography. Rodent and vegetation surveys were carried out before the construction of the exclosures on three of

the sites (baseline data), and repeated in July, November 2008, March and June 2009 (a total of 5 surveys) (Figures 5-1.&5-2).



Figure 5-1: Photographic timeline for enclosure 1 (from top to bottom, left to right): upon completion in March 2008, July 2008, November 2008, March 2009 and June 2009.



Figure 5-2: Photographic comparisons between controls (left) and exclosures (right) on site number 3 in November 2008 (top) and March 2009 (middle) and on site number 2 in June 2009 (bottom).

5.2.2 Rodent field surveys

GM rarely leave their burrows, making them a difficult species to trap. As a result, data on GM body weight, reproductive status and movement could not be collected for inclusion in tests of H2/H3 or H4. The number of GM open burrows correlates closely with minimum population size estimated from individuals surfacing and can be used as an index of GM abundance (Tallents, 2007, Sillero-Zubiri et al., 1995b). On each grid, 25 folding Sherman live-traps (H. B. Sherman Traps, Florida, USA; model LFATDG, 12”) were arranged at 10m intervals for live-trapping of LM and AB over four consecutive days on each survey occasion. Traps were set up at dawn, baited with a mixture of peanut butter and flour, checked at midday and at dusk when they were closed. Animals were given individual marks by fur clipping on their abdomen, weighed, sexed and the trap in which they were captured recorded. Reproductive condition (signs of lactation, pregnancy or hymen perforation; testes size and position) was also recorded. Only non-pregnant adult rodents were used to calculate the average weight of LM and AB within each grid. The proportion of LM and AB adult females (PFLM/PFAB) that were pregnant was also calculated. For every recapture event, I calculated the distance between the most widely separated traps where the individual was captured, also known as the observed range length (ORL) (Pelikan and Holisova, 1969), and the distance moved between recaptures (DRC). Both have been shown to provide a reliable index of home-range size in small mammals (Moorhouse et al., 2008, van der Ree and Bennett, 2003). I then estimated an average ORL and DRC for LM and for AB on each grid.

5.2.3 Modelling rodent abundance

I used Tallents (2007) equations to extrapolate minimum GM abundance (A) from the total number of open burrows (D) recorded at time C (hours after midnight):

$$A = 0.370 \times (-3.445 + 0.634 \times C - 0.025 \times C^2) \times D \quad \text{Equation 5-1}$$

The average trapping success was 17.9% (0-50%) with 310 individuals LM and AB trapped and 216 recapture events observed, giving an average recapture probability of 37.6% (0-100%) (Table 5-1).

		LM		AB		GM
		Total captures	Recaptures	Total captures	Recaptures	Density (/km ²)
Before	Control 1	2	0	2	0	508.8
	Control 2	24	10	15	2	1037.1
	Control 3	4	0	0	0	582.8
	Exclo 1	0	0	1	0	365.4
	Exclo 2	33	9	2	0	1227.9
	Exclo 3	3	0	2	0	327.4
After 4 months	Control 1	34	23	8	3	390.6
	Control 2	32	12	0	0	822.1
	Control 3	0	0	0	0	210.8
	Exclo 1	0	0	0	0	203.5
	Exclo 2	41	19	0	0	349.7
	Exclo 3	12	4	1	0	272.9
After 7 months	Control 1	0	0	0	0	0
	Control 2	6	1	1	0	1119.3
	Control 3	0	0	0	0	274
	Exclo 1	0	0	1	0	54.6
	Exclo 2	19	2	1	0	61.4
	Exclo 3	9	3	1	0	491.2
After 11 months	Control 1	50	26	0	0	25
	Control 2	1	0	0	0	191.1
	Control 3	0	0	0	0	508.8
	Exclo 1	29	14	11	3	31.2
	Exclo 2	43	25	4	0	639.4
	Exclo 3	0	0	0	0	1058.2
After 14 months	Control 1	34	15	3	1	390.6
	Control 2	21	8	9	4	913.4
	Control 3	1	0	0	0	12.5
	Exclo 1	21	7	6	2	163.7
	Exclo 2	39	19	8	2	91.3
	Exclo 3	0	0	0	0	182.7

Table 5-1: The number of total captures (first capture and recaptures) and recaptures for LM and AB, alongside the estimated GM density across all survey grids for each trapping season.

LM and AB population sizes were estimated from minimum number known alive (MNKA). To reduce the negative bias inherent in this population estimate, a correction factor was applied based on closed capture estimates from all our survey grids (Chapter 4) with a recapture probability of at least 25% ($n = 33$) using Rcapture (Baillargeon and Rivest, 2007). A strong relationship existed between MNKA and these closed capture

estimates ($p < 0.001$, $r^2 = 0.83$, $n = 33$); and MNKA was multiplied by 1.44 (95% CI: 1.20-1.68) to provide bias-corrected estimates for all grids.

The effective trapping area was calculated by adding a boundary strip equivalent to half the mean distance moved between successive captures (Otis et al., 1978). The mean distance moved by rodents between recaptures was 17.08 m ($n = 216$, 95% CI 6.82-27.35) making the effective trapping area for each grid 2356.13 m². Population densities for LM and AB (individuals.km⁻²) were calculated using the bias-corrected population estimates for each species and the size of the effective trapping area. Overall rodent biomass for all three species combined was calculated using the density estimate for each species and the mean body mass. Mean body masses of AB and LM were 144.85g \pm 21.27 SD ($n = 46$), and 107.89g \pm 8.28 SD ($n = 198$) respectively. Mean body mass for GM was taken from Sillero-Zubiri (1994): mean 618g \pm 190 SD ($n = 11$).

5.2.4 Vegetation field surveys

Twenty 1m² quadrats were randomly placed inside each grid and all species, with the exception of grasses, were identified. The flower structures necessary for identification of grasses were often not present, so all grasses were split into two categories only: wetland sedges and other grasses (referred to as grasses from this point on). The height of all species was estimated using a 1-5 scale (1 = 0/10 cm, 2 = 10/20 cm, 3 = 20/30 cm, 4 = 30/40 cm and 5 = >40cm). The percentage cover for all species and bareground was calculated, using the mid-point coverage for each Braun-Blanquet scale, inside each random quadrat and averaged over all the quadrats to calculate the mean percentage cover for each grid. The same approach was adopted with respect to height measurements. I then used the cover estimates to calculate Shannon diversity (H') and evenness (J) indices (Shannon, 1948). Species density was also computed.

I computed the list of the five most common species present within all six sites (controls and exclosures) and found that *Alchemilla* spp. (*A. abyssinca* and *A. rothii*) and grasses dominated the composition, followed by *Helichrysum* shrubs (*H. citrispinum* and *H. gofense*), *Salvia merjame* and *Hebenstretia dentata*. I used the species above as indicators for the changes in vegetation cover for inclusion in the models. Changes in the

vegetation structure were modelled using the height data from the three most common vegetation species group: *Alchemilla* spp., grasses and *Helichrysum* shrubs.

5.2.5 Data analysis and model selection

Proportion and percentage data were arcsine transformed before being analysed. The data were analysed in R (R Development Core Team, 2009) using generalised linear models with treatment (i.e. grazed/ungrazed), site (paired sites 1, 2 or 3) and survey (before, after 4/7/11/14 months) as fixed factors. Nested models were compared and adopted using the likelihood ratio test. P-values larger than 0.10 were judged to demonstrate non-significance, to reflect the unusually small sample size that resulted from logistical restrictions in the field. The results from the present analyses should therefore be considered with caution.

5.3 Results

5.3.1 Rodent analyses

5.3.1.1 Abundance

I did not find that the removal of livestock had a significant effect on overall rodent biomass (Table 5-2 M1: $\Delta LL = 0.12$ 1df, $p = 0.27$). However, I did observe that although overall rodent biomass declined during the drier months (November to February) in both the exclosures and control sites, the decline appeared more severe in the rodent populations on the grazed control plots (Figure 5.3).

I observed a significant positive response of LM populations to the removal of livestock, although this response was site specific (Table 5-2, M2). Although time of survey was not a significant explanatory variable, LM densities tended to be higher inside the exclosures during the drier months (Figure 5.4A & Table 5-3). The removal of livestock was found to have a significant positive effect on population densities of AB after 11 months (Table 5-2 M3 & Figure 5.4B). Populations of GM did not appear to respond significantly to the removal of livestock (Table 5-2 M4: $\Delta LL = 0.43$, 1df, $p = 0.49$), although GM density inside the exclosures was more than double that of the control sites after 11 months (Figure 5.4C & Table 5-3).

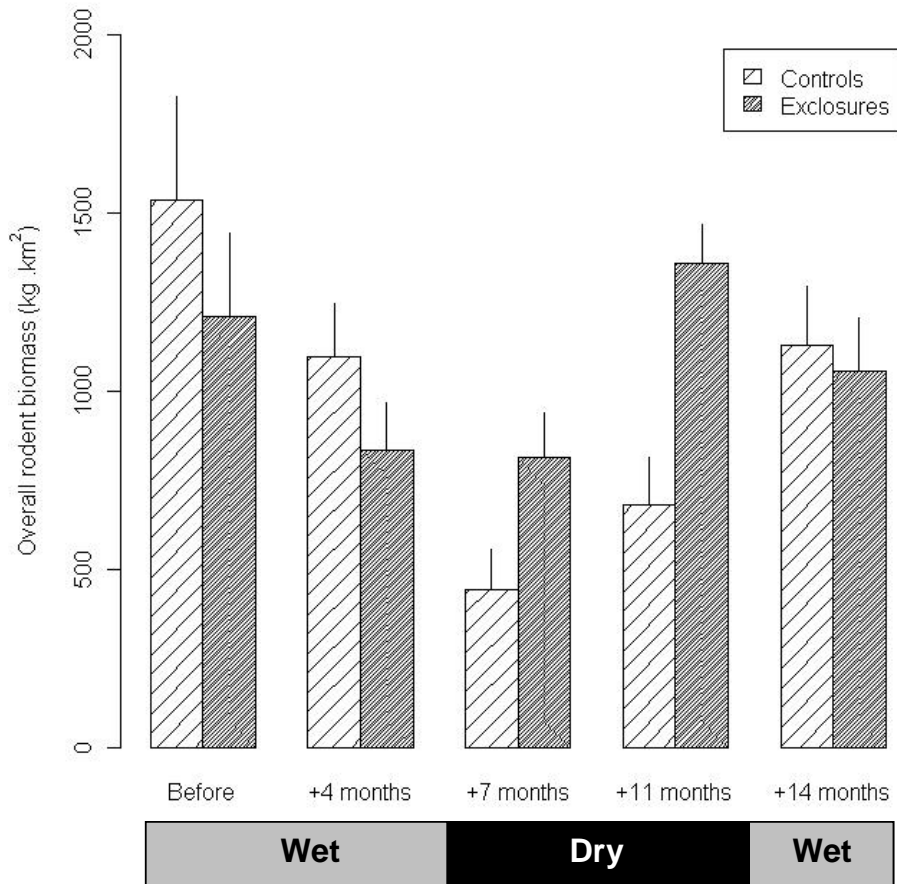


Figure 5-3: Overall rodent biomass on the control sites and exclosures before and 4 months (July 2008), 7 months (November 2008), 11 months (February 2009) and 14 months (June 2009) after the removal of livestock grazing pressure from inside the exclosures. The error bars represent one standard error, and the seasons (wet and dry) are indicated under the x axis.

5.3.1.2 Body weight, reproductive success and home range

I did not find the removal of livestock to have any impact, over the 14 months study period, on the weight of LM (Table 5-2 M5: $\Delta LL = 0.77$, 1df, $p = 0.62$) or AB adults (Table 5-2 M6: $\Delta LL = 0.89$, 1df, $p = 0.65$), or on the proportion of females LM (Table 5-2 M7: $\Delta LL = 0.59$, 1df, $p = 0.56$) and AB (Table 5-2 M8: $\Delta LL = 2.04$, 1df, $p = 0.85$) that were pregnant. Nevertheless, I observed a non-significant trend for higher reproductive successes inside the exclosures for LM and AB (Table 5-3). ORL and DRC for LM were affected by grazing treatment (Table 5-2 M9 & M11) and were around 30% shorter inside the exclosures than on the grazed control (Figure 5.5 & Table 5-3). The opposite trend was found for AB individuals, which had larger home ranges inside the exclosures (Table 5-3 M10 & M12), however this finding is based on few data points (Table 5-3) and may not be reliable.

Model	Response variable	Best model	Significant explanatory variables
M1	Overall rodent biomass	Site	Site (2): $t = 3.13, p < 0.01$
M2	Density LM	Treatment * Site	Site (3): $t = -2.31, p = 0.03$ Treatment * Site (2): $t = 2.24, p = 0.03$
M3	Density AB	Treatment * Survey	Survey (after 7 months): $t = -1.99, p = 0.06$ Survey (after 11 months): $t = -2.12, p = 0.05$ Treatment * Survey (after 11 months): $t = 2.20, p = 0.04$
M4	Density GM	Site + Survey	Site (2): $t = 3.67, p < 0.01$ Survey (after 4 months): $t = -1.75, p = 0.09$ Survey (after 14 months): $t = -2.23, p = 0.04$
M5	Weight LM	Survey	Survey (after 4 months): $t = -1.80, p = 0.09$ Survey (after 7 months): $t = -2.50, p = 0.02$ Survey (after 11 months): $t = -3.53, p < 0.01$ Survey (after 14 months): $t = -1.82, p = 0.09$
M6	Weight AB	Null	
M7	PFLM	Null	
M8	PFAB	Null	
M9	ORL LM	Treatment * Survey	Treatment * Survey (after 7 months): $t = -3.63, p = 0.02$
M10	ORL AB	Treatment	Treatment: $t = 3.34, p = 0.02$
M11	DRC LM	Treatment	Treatment: $t = -2.03, p = 0.07$
M12	DRC AB	Treatment	Treatment: $t = 2.24, p = 0.08$

Table 5-2: Summary of the models adopted for the rodent analyses inside the enclosures and control sites. All models were fitted in R and all parameters estimated in relation to the intercept for site 1 before grazing treatment (i.e. removal of livestock) was applied. Models with interactions contain the components of the interactions as main effects. A null model (Y = intercept) was fitted when no explanatory variable significantly explained part of the variation in the response variable.

Treatment	Survey	Rodent biomass (kg/km ²)		LM density (ind/km ²)	AB density (ind/km ²)	GM density (ind/km ²)	LM weight (g)	
Exclosures	Before	1207.89 (± 774.10)		6467.95 (± 5609.12)	783.99 (± 195.99)	640.25 (± 294.05)	112.20 (± 5.30)	
Exclosures	After 4 months	836.06 (± 432.36)		5901 (± 3794.23)	196.72 (± 196.72)	275.34 (± 42.21)	107.05 (± 0.08)	
Exclosures	After 7 months	813.13 (± 413.11)		4524.59 (± 2937.68)	590.16 (± 0)	386.58 (± 169.74)	102.84 (± 12.17)	
Exclosures	After 11 months	1357.06 (± 357.48)		6098.36 (± 3091.72)	2360.66 (± 1362.93)	576.28 (± 298.14)	101.16 (± 4.288)	
Exclosures	After 14 months	1055.29 (± 854.87)		6295.08 (± 3309.36)	1967.21 (± 1040.95)	145.92 (± 27.83)	107.14 (± 4.22)	
Control sites	Before	1535.51 (± 954.38)		5683.95 (± 4217.38)	3331.97 (± 2764.90)	819.78 (± 159.56)	119.03 (± 3.90)	
Control sites	After 4 months	1094.48 (± 496.59)		6048.36 (± 3412.99)	983.61 (± 983.61)	474.48 (± 181.39)	108.76 (± 3.32)	
Control sites	After 7 months	443.01 (± 361.66)		1180.33 (± 1180.33)	196.72 (± 196.72)	464.43 (± 336.83)	104.80 (± 0)	
Control sites	After 11 months	680.47 (± 434.03)		4918.03 (± 4626.09)	0 (± 0)	241.62 (± 141.92)	99 (± 1)	
Control sites	After 14 months	1129.50 (± 532.08)		6098.36 (± 2937.68)	1377.05 (± 857.49)	438.84 (± 261.20)	109.46 (± 4.03)	
Treatment	Survey	AB weight (g)	%LMPF	%ABPF	Range LM (m)	Range AB (m)	DRC LM (m)	DRC AB (m)
Exclosures	Before	135.67 (± 11.84)	78 (± 23)	100 (± 0)	100 (± 0)	NA	16.02 (± 0)	NA
Exclosures	After 4 months	160 (± 0)	21 (± 1)	NA	23.78 (± 3.09)	NA	22.51 (± 2.05)	NA
Exclosures	After 7 months	156 (± 0)	84 (± 13)	NA	9.13 (± 9.13)	NA	7.75 (± 7.75)	NA
Exclosures	After 11 months	135.67 (± 25.67)	14 (± 4)	100 (± 0)	18.51 (± 2.09)	18.46 (± 0)	17.53 (± 0.56)	18.46 (± 0)
Exclosures	After 14 months	175.42 (± 2.92)	47 (± 11)	100 (± 0)	15.95 (± 1.26)	19.26 (± 3.10)	15.48 (± 1.73)	14.97 (± 1.22)
Control sites	Before	136.35 (± 8.35)	20 (± 20)	100 (± 0)	21.2 (± 0)	10 (± 0)	18.69 (± 0)	10 (± 0)
Control sites	After 4 months	124 (± 0)	54 (± 14)	75 (± 0)	25.69 (± 3.18)	10 (± 0)	20.69 (± 0.90)	10 (± 0)
Control sites	After 7 months	NA	50 (± 0)	NA	30 (± 0)	NA	30 (± 0)	NA
Control sites	After 11 months	NA	67 (± 34)	NA	25.23 (± 0)	NA	24.59 (± 0)	NA
Control sites	After 14 months	143 (± 13)	23 (± 13)	50 (± 50)	21.16 (± 2.09)	14.14 (± 0)	19.56 (± 2.49)	14.14 (± 0)

Table 5-3: Summary of rodent variables measured in both exclosures and control sites throughout the 5 surveys (mean ± standard error).

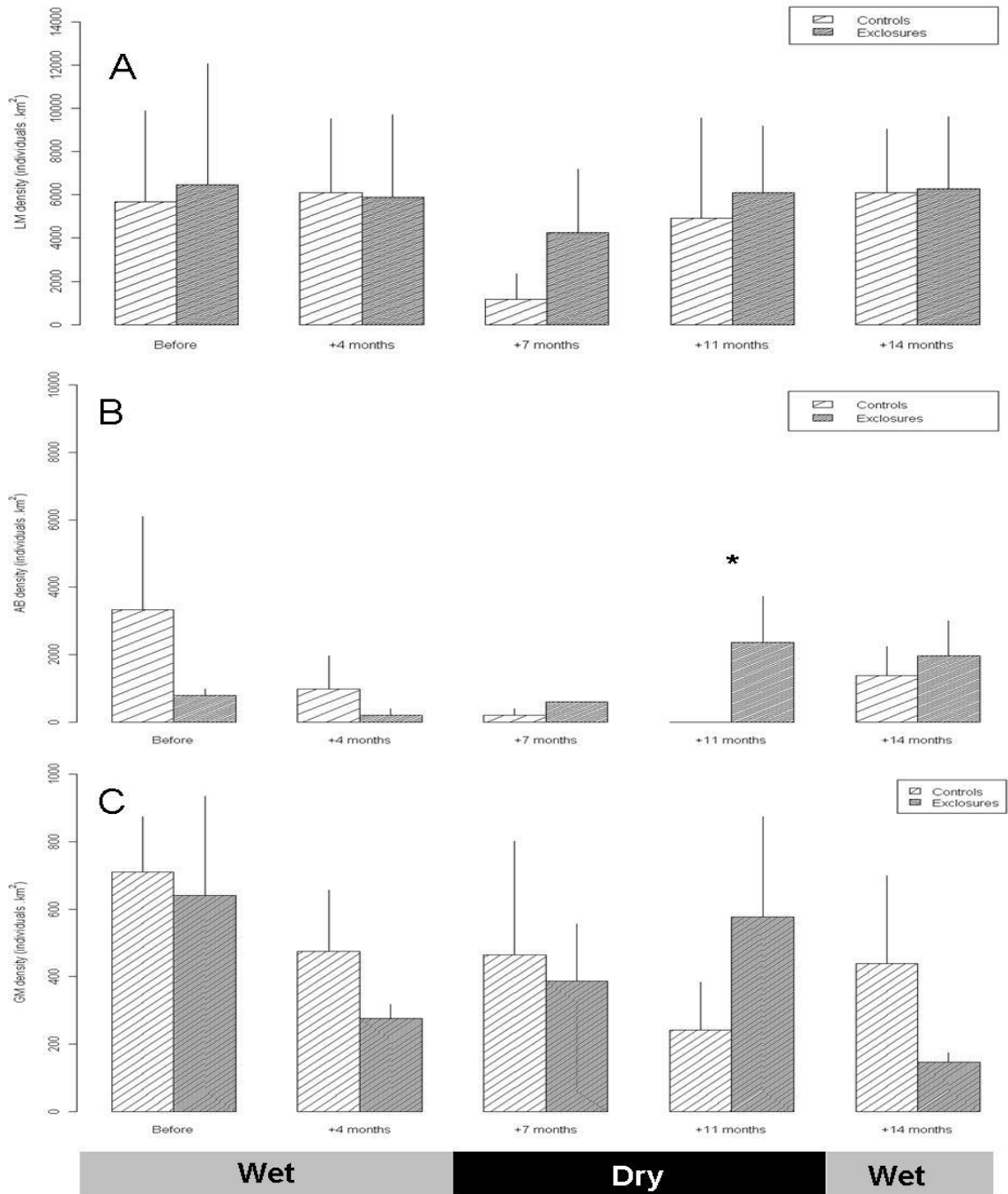


Figure 5-4: Species-specific responses of rodent populations to the removal of livestock (from top to bottom: LM, AB and GM). Densities of each species before and 4/7/11 and 14 months after the removal of livestock are plotted in both control sites and exclosures. The error bars represent one standard error, and the seasons (wet and dry) are indicated under the x axis. A significant Treatment * Survey interaction is indicated by *.

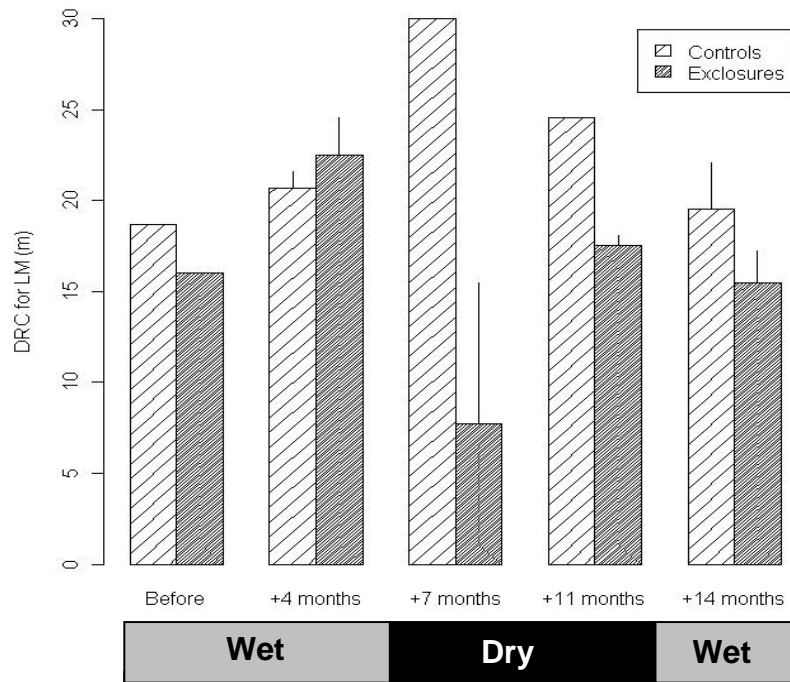


Figure 5-5: Average distance moved between recaptures (DRC) for LM is plotted for both control sites and exclosures before and 4/7/11 and 14 months after the removal of livestock. The error bars represent one standard error, and the seasons (wet and dry) are indicated under the x axis.

5.3.2 Vegetation analyses

5.3.2.1 Species richness, diversity and evenness

I found the removal of livestock to have a significant negative effect on the vegetation species density (Table 5-4 M13 & Figure 5.6A) and on Shannon's diversity (Table 5-4 M14 & Figure 5.6B). I did not detect an effect of livestock removal on species evenness (Table 5-4 M15: $\Delta LL = 0.06$, 1df, $p = 0.19$).

5.3.2.2 Vegetation cover & height

I found that the removal of livestock led to a significant decrease in bareground cover (Table 5-4 M16 & Figure 5.6C) and a significant increase in the cover of *Alchemilla* spp. (Table 5-4 M17 & Figure 5.6D), although both effects were survey specific. The cover of grass spp. was not affected by the removal of livestock (Table 5-4 M18: $\Delta LL = 0.12$, 1df, $p = 0.27$).

Model	Response variable	Best model	Significant explanatory variables
M13	Species richness	Treatment + Survey	Treatment: $t = -1.90$, $p = 0.07$ Survey (after 4 months): $t = -2.74$, $p = 0.01$
M14	Species diversity	Treatment * Survey	Survey (after 4 months): $t = 2.31$, $p = 0.03$ Survey (after 7 months): $t = 4.70$, $p < 0.01$ Survey (after 11 months): $t = 2.17$, $p = 0.04$ Survey (after 14 months): $t = 3.81$, $p < 0.01$ Treatment * Survey (after 14 months): $t = -2.27$, $p = 0.03$
M15	Species evenness	Survey	Survey (after 7 months): $t = 3.16$, $p < 0.01$ Survey (after 11 months): $t = 2.05$, $p = 0.05$ Survey (after 14 months): $t = 2.39$, $p = 0.02$
M16	% bareground cover	Treatment * Survey	Survey (after 4 months): $t = 2.95$, $p < 0.01$ Survey (after 11 months): $t = 2.49$, $p = 0.02$ Survey (after 14 months): $t = 2.65$, $p = 0.02$ Treatment * Survey (after 4 months): $t = -1.79$, $p = 0.09$
M17	% <i>Alchemilla</i> cover	Treatment * Survey + Site	Site (3): $t = -4.33$, $p < 0.01$ Treatment: $t = -2.12$, $p = 0.05$ Survey (after 4 months): $t = -4.15$, $p < 0.01$ Survey (after 7 months): $t = -2.26$, $p = 0.04$ Survey (after 11 months): $t = -2.68$, $p = 0.02$ Survey (after 14 months): $t = -2.65$, $p = 0.02$ Treatment * Survey (after 4 months): $t = 2.03$, $p = 0.06$ Treatment * Survey (after 7 months): $t = 2.24$, $p = 0.04$
M18	% grass cover	Site	Site (2): $t = 2.48$, $p = 0.02$ Site (3): $t = 7.03$, $p < 0.01$

Table 5-4: Summary of the models adopted for the vegetation analyses inside the exclosures and control sites. Models with interactions contain the components of the interactions as main effects. All models were fitted in R and all parameters estimated in relation to the intercept for site 1 before grazing treatment (i.e. removal of livestock) was applied. Continues...

Model	Response variable	Best model	Significant explanatory variables
M19	% <i>S. merjame</i> cover	Treatment * Survey + Site	Survey (after 7 months): t = 4.46, p<0.01 Survey (after 14 months): t = 2.20, p = 0.04 Site (2): t = -7.80, p<0.01 Site (3): t = -9.14, p<0.01 Treatment * Survey (after 7 months): t = -3.15, p<0.01
M20	% <i>H.dentata</i> cover	Treatment * Survey + Site	Survey (after 7 months): t = 2.15, p = 0.05 Site (2): t = -2.76, p = 0.01 Site (3): t = -2.78, p = 0.01 Treatment * Survey (after 7 months): t = -2.24, p = 0.04
M21	% shrub cover	Treatment * Site	Survey (after 7 months): t = 4.46, p<0.01 Survey (after 14 months): t = 2.20, p = 0.04 Site (2): t = -7.80, p<0.01 Site (3): t = -9.14, p<0.01 Treatment * Survey (after 7 months): t = -3.15, p<0.01
M22	Height <i>Alchemilla</i>	Treatment * Survey	Treatment * Survey (after 7 months) : t = 2.98, p < 0.01
M23	Height grass	Treatment * Survey + Site	Site (3): t = 2.23, p = 0.04 Treatment * Survey (after 7 months): t = 2.93, p < 0.04
M24	Height shrubs	Site	Site (3) : t = 2.33, p = 0.04

Table 6-3 (continued.)

I found the cover of *S. merjame* (Table 5-4 M19 & Figure 5.6E) and *H. dentata* (Table 5-4 M20 & Figure 5.6F) to be significantly lower inside the exclosures than on the control sites (Table 5-5), although the effects were once again survey specific. The removal of livestock had a positive impact on the height of *Alchemilla* spp. (Table 5-4 M22 & Figure 5.7B) and grass spp. (Table 5-4 M22 & Figure 5.7C) after the first full wet season. The removal of livestock also resulted in a site-specific reduction in the cover (Table 5-4 M21 & Figure 5.7A) but not the height (Table 5-4 M21: $\Delta LL = 0.74$, 1df, p = 0.74) of *Helichrysum* shrubs inside the exclosures.

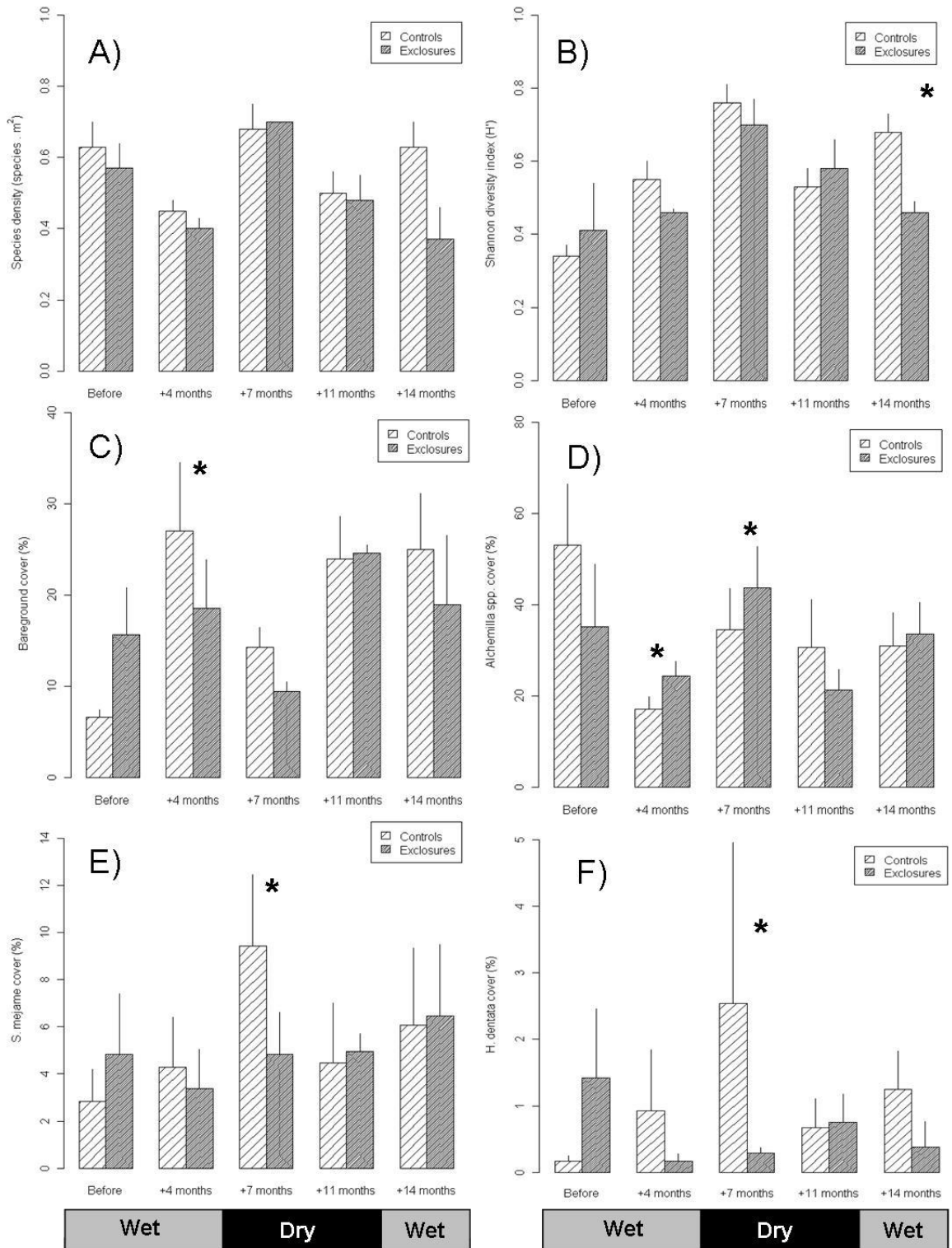


Figure 5-6 : Vegetation responses to the removal of livestock plotted for both control sites and exclosures before and 4/7/11 and 14 months after the removal of livestock: A) species density, B) Shannon diversity index, C) bareground cover, D) *Alchemilla* spp. cover, E) *S. mejame* cover and F) *H. dentata* cover. Significant Treatment * Survey interactions are indicated by *. The error bars represent one standard error, and the seasons (wet and dry) are indicated under the x axis.

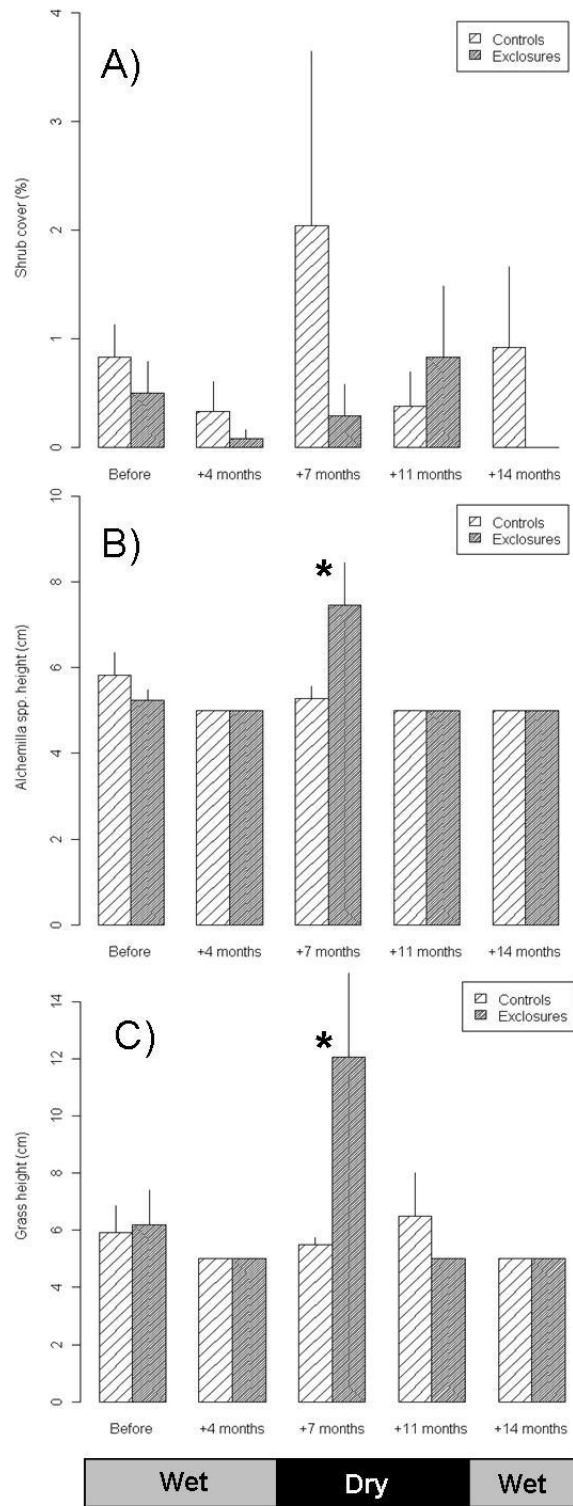


Figure 5-7: Vegetation responses to the removal of livestock plotted for both control sites and exclosures before and 4/7/11 and 14 months after the removal of livestock: A) shrub cover, B) *Alchemilla* spp. height, C) grass height. Significant Treatment * Survey interactions are indicated by *. The error bars represent one standard error, and the seasons (wet and dry) are indicated under the x axis.

Treatment	Survey	Richness (sp/m ²)	Diversity (H')	Evenness (J)	Bareground (%)	<i>Alchemilla</i> spp. (%)	Grass spp. (%)
Exclosures	Before	0.57 (±0.07)	0.41 (±0.13)	0.51 (±0.13)	15.67 (±5.14)	35.08 (±13.84)	20.50 (±10.51)
Exclosures	After 4 months	0.40 (±0.03)	0.46 (±0.01)	0.53 (±0.01)	18.54 (±5.30)	24.25 (±3.28)	24.58 (±13.15)
Exclosures	After 7 months	0.70 (±0)	0.70 (±0.07)	0.62 (±0.06)	9.42 (±1.02)	43.75 (±8.94)	33.67 (±7.07)
Exclosures	After 11 months	0.48 (±0.07)	0.58 (±0.08)	0.60 (±0.07)	24.58 (±0.87)	21.21 (±4.49)	29.08 (±7.04)
Exclosures	After 14 months	0.37 (±0.09)	0.46 (±0.03)	0.57 (±0.07)	18.92 (±7.60)	33.46 (±7)	28.17 (±6.63)
Control sites	Before	0.63 (±0.07)	0.34 (±0.03)	0.41 (±0.01)	6.58 (±0.79)	53 (±13.54)	26.33 (±9.74)
Control sites	After 4 months	0.45 (±0.03)	0.55 (±0.05)	0.58 (±0.07)	27 (±7.52)	17.13 (±2.69)	13.29 (±5.45)
Control sites	After 7 months	0.68 (±0.07)	0.76 (±0.05)	0.68 (±0.03)	14.25 (±2.17)	34.50 (±9)	28.29 (±9.11)
Control sites	After 11 months	0.50 (±0.06)	0.53 (±0.05)	0.24 (±0.05)	23.96 (±4.69)	30.54 (±10.65)	33.21 (±12.93)
Control sites	After 14 months	0.63 (±0.07)	0.68 (±0.05)	0.63 (±0.05)	25 (±6.13)	31 (±7.13)	28.13 (±14.69)
Treatment	Survey	Shrub (%)	<i>S.mejame</i> (%)	<i>H.dentata</i> (%)	<i>Alchemilla</i> height (cm)	Grass height (cm)	Shrub height (cm)
Exclosures	Before	0.50 (±0.29)	4.83 (±2.59)	1.42 (±1.04)	5.24 (±0.24)	6.21 (±1.21)	5 (±0)
Exclosures	After 4 months	0.08 (±0.08)	3.38 (±1.65)	0.17 (±0.11)	5 (±0)	5 (±0)	20 (±0)
Exclosures	After 7 months	0.29 (±0.29)	4.83 (±1.80)	0.29 (±0.08)	7.47 (±0.97)	12.08 (±3.44)	7.14 (±0)
Exclosures	After 11 months	0.83 (±0.65)	4.96 (±2.89)	0.75 (±0.43)	5 (±0)	5 (±0)	5 (±0)
Exclosures	After 14 months	0 (±0)	6.46 (±3.03)	0.38 (±0.38)	5 (±0)	5 (±0)	NA
Control sites	Before	0.83 (±0.30)	2.83 (±1.36)	0.17 (±0.08)	5.83 (±0.53)	5.93 (±0.93)	5 (±0)
Control sites	After 4 months	0.33 (±0.27)	4.29 (±2.13)	0.92 (±0.92)	5 (±0)	5 (±0)	13.75 (±8.75)
Control sites	After 7 months	2.04 (±1.61)	9.42 (±3.05)	2.54 (±2.42)	5.28 (±0.28)	5.50 (±0.25)	15.84 (±5.46)
Control sites	After 11 months	0.38 (±0.31)	4.46 (±2.56)	0.67 (±0.44)	5 (±0)	6.50 (±1.50)	8.75 (±3.75)
Control sites	After 14 months	0.92 (±0.74)	6.08 (±3.25)	1.25 (±0.57)	5 (±0)	5 (±0)	6.94 (±1.94)

Table 5-5: Summary of vegetation variables measured in both exclosures and control sites throughout the 5 surveys (mean ± standard error).

5.4 Discussion

The data collected over the first 14 months of this experiment indicates that rodent populations can respond to the removal of livestock, particularly during the dry season, although this response may be species-specific (Bakker et al., 2009, Jones and Longland, 1999, Blaum et al., 2007, Jones et al., 2003, Hagenah et al., 2009). I did not find that the removal of livestock had a significant effect on overall rodent biomass (H1 rejected). Although populations of LM and AB can respond positively to the removal of livestock, I found their responses to be highly site-specific or survey-specific. GM populations did not significantly respond to the removal of livestock, which may explain why I did not detect a significant difference in overall rodent biomass as GM, being by far the heaviest species, constitute the bulk of the rodent biomass. I also observed that, although overall rodent biomass declined during the drier months (November to February) in both the exclosures and control sites, the decline appeared more severe in the rodent populations trapped on the grazed control plots. This may indicate that competition for food and/or increased predation risk were heightened during the dry season when resources were scarce and vegetation cover greatly reduced, and that livestock grazing during that critical period may have exacerbated the effects of difficult environmental conditions. As a result of their design, the exclosures have excluded the main predator of these rodent species, the Ethiopian wolf, in addition to livestock, so that the increase in rodent abundance may be the result of the combination of both factors. However, raptors, another main predator for those diurnal rodents, had aerial access to the exclosures and were therefore unlikely to have been affected by the fences. While it is difficult to quantify the degree to which the partial release from predators may have contributed to an increase in rodent populations inside the exclosures, I judge unlikely that this experimental side-effect was substantial.

Smaller home ranges and higher reproductive success for LM inside the exclosures may be an indication that resources were more limited (or of lesser quality) on grazed sites, although this did not result in individuals being heavier inside the exclosures. Interestingly, I found the opposite trend for AB individuals which had larger home ranges inside the exclosures. This may be an indication that livestock could cause an increase in the quantity or quality of resources available to some species (Keesing, 2000) and that differences among rodent species in their responses to grazing may be mediated by interactions between the direct effects of grazing on habitat quality and species-specific habitat requirements (Bakker et al., 2009, Jones and Longland, 1999, Blaum et al., 2007, Jones et al., 2003). AB populations may preferentially respond to trampling and soil compaction by livestock,

migrating to ungrazed sites although larger home ranges may need to be maintained under these conditions. Trampling is known to affect the habitat quality for rodents by reducing the soil suitability for building and maintaining burrow systems (Torre et al., 2007). Heavy grazing pressures are known to increase surface run-off and soil loss, reduce the infiltrability of the soil on other Ethiopian rangelands, and results in vegetation changes (Taddese et al., 2002b, Tefera et al., 2007a, Mwendera and Saleem, 1997). The existence of such mechanisms should be tested in the BMNP afroalpine in the light that, over the long-term, livestock-induced soil compaction and exploitative competition may both be important factors in the local decline and extinction of rodent populations.

While previous studies have reported that the response of vegetation and rodent populations to the removal of livestock can be habitat-specific (Eccard et al., 2000), I provide some evidence of the heterogeneous (i.e. site-specific) nature of this response within a particular habitat type (Rosenstock, 1995) through a significant Treatment * Site interaction for LM. Such an interaction may be the result of unmeasured differences in livestock utilisation, soils or other site characteristics. Rodent populations are known to exhibit large-magnitude, geographically synchronous fluctuations, including temporary local extinctions (Brown and Zeng, 1989). The lack of grazing impact on some sites could reflect the small size and isolation of ungrazed patches which may not have provided big enough suitable habitats to detect significant differences in overall rodent use (Brown, 1987).

Looking at the concomitant changes in vegetation composition and structure, I found some evidence that the impacts of livestock on rodent densities are concurrent with changes in the vegetation. I found a higher species richness and diversity in the grazed control sites compared to inside the exclosures (H5 supported), accompanied by a reduced cover of *S. mejame* and *H. dentata* inside the exclosures after 7 months of livestock exclusion. Both findings are consistent with other studies in which exclosures harboured more abundant species than open plots which had more rare and occasional species (Oba et al., 2001), and highlight the role livestock can play, especially in nutrient-rich systems (Proulx and Mazumder, 1998), in favouring the creation of niches for colonising species (Olf and Ritchie, 1998, Veen et al., 2008). I detected a significant decrease in bareground cover only after 4 months of livestock removal (H6 partially supported) although a similar trend was observed after 7 months and after 14 months. Bareground cover at the end of the first dry season (after 11 months) was similar in both exclosures and control sites, and tended to be lower inside the exclosures during the wetter months. This may suggest that vegetation had enhanced capacities to respond to rainfall availability under ungrazed conditions. I also found

that, after one full wet season (after 7 months), the removal of livestock had a positive impact on the height of *Alchemilla* spp. and grass (H7 partially supported). It is however unclear whether grazing rodents are responsible for the decline in vegetation height between month 7 and month 11 (corresponding to the length of the dry season). I also found that shrub cover was higher on the grazed sites than inside the exclosures (H8 supported). While the recovery of grasses may be relatively modest, it may still be ecologically significant in protecting the rodents from predators, particularly raptors, for example (Valone and Sauter, 2005, Jones et al., 2003, Birney et al., 1976, Peles and Barrett, 1996).

The key conservation implications of this study relate to the endemic nature and patchy distribution of the rodent populations as well as the indirect impact livestock grazing has on their predators which are themselves rare and/or threatened. Excluding livestock grazing on parts of Bale's *Alchemilla*/grass pastures, especially during the drier months, could benefit rodent populations, as this study shows that some species do respond to livestock removal after only a few months. However, the site-specific nature of rodent and vegetation response to the removal of grazing illustrates the necessity to consider management options at the landscape level such as the impact assessment of grazing treatment may not produce significant differences at a smaller habitat-scale (Alzerreca et al., 1998, Stohlgren et al., 1999, Kelt and Valone, 1995). The increase in rodent density, although species-specific, could be beneficial to Ethiopian wolves and raptors by providing increased prey resources especially during the drier months when Ethiopian wolves raise their pups (Sillero-Zubiri and Macdonald, 1997). The ban on livestock grazing would also result in taller vegetation, especially during the wet season, which may reduce the predation success of both wolves and raptors and therefore limit the predators' population growth, and/or render the relationship non-linear, despite increasing rodent biomass. While sociological and epidemiological factors are likely to affect Ethiopian wolf population growth at high density (Tallents, 2007), a livestock ban remains likely to result in a substantial increase in wolf carrying capacity in Web and improve the long-term conservation prospect for that particular population of wolves and of this endemic and endangered species as a whole.

6 Limits to exploitation: Modelling the impact of livestock grazing on Ethiopian wolves and their prey in the Bale Mountains, Ethiopia.

6.1 Introduction

African rangelands illustrate vividly the challenge of balancing biodiversity conservation with sustainable development. They support around 230 million cattle, 246 million sheep and 175 million goats (FAO, 2007b) as well as very large wild herbivore populations, yet are mostly located in arid and semi-arid systems, with low and erratic rainfall and harsh environmental conditions. There are significant associations between human population density and biodiversity hotspots in Africa (Balmford et al., 2001, Sachs et al., 2009), inside which conflicts over natural resources are frequent (Stewart, 2002), and often centred on contested access to land resulting in clashes between wildlife conservation interests and rural livelihoods (Peluso, 1993). Competition for grazing and water is increasing, and conflicts between wildlife managers and livestock owners are growing as pastoralists are increasingly settling in the vicinity of, or inside, protected areas. The main factors driving this transformation in land-use patterns are increasing human demographic pressure, consequent expansion of cultivation, and a reduction in rangeland resources, through privatisation for commercial agriculture and ranching (Macdonald et al., 2006, Macdonald and Sillero-Zubiri, 2004).

Acting on these concerns, conservation policy has sought to protect as extensive a set of areas as possible. The past three decades have seen a 500% increase in land designated as protected areas for nature conservation (IUCN, 2003). In Ethiopia alone, there are today 101 nationally designated protected areas, the most important of which is the Bale Mountains National Park (BMNP) (06°41'N, 39°03'E and 07°18'N, 40°00'E). The Bale mountains represent the largest area of afroalpine habitat over 3000m in Africa (Yalden, 1983), and form part of Conservation International's Eastern afroalpine hotspot (Brooks et al., 2004), harbouring a diverse array of endemic and range-restricted species, including the largest remaining populations of Ethiopian wolves (*Canis simensis*). The Ethiopian wolf is the rarest canid in the world, with a total remaining population of less than 500 individuals, limited to seven isolated ranges across the Ethiopian highlands (Marino, 2003b). Ethiopian wolf core ranges in BMNP are located in the Web valley, Morebawa and on the Sanetti plateau. Ethiopian wolves are at the top of one of the most simple, yet critical, food chains in the afroalpine of BMNP (Sillero-Zubiri et al., 1995b) where wolves prey upon the diurnal fossorial rodent fauna, especially the endemic giant molerat, *Tachyoryctes macrocephalus*, and two species of murine rodents, *Arvicanthis blicki* and *Lophuromys melanonyx*. These species represent an estimated 46.6%, 26.7% and 15.5% of the wolves' diet (by volume) respectively (Sillero-Zubiri and Gottelli, 1995).

These rodents are primarily herbivorous, feeding primarily on the above ground structures of grasses and flowering plants (*Alchemilla* spp. in particular) on the afroalpine pastures (Yalden, 1988).

Ethiopian wolf populations have been affected by diseases spilling over from domestic dog populations (Sillero-Zuberi et al., 2004, Randall et al., 2006), but livestock grazing, through its impact on the wolves' rodent prey, is considered to represent a more profound long-term threat to their persistence (Nievergelt, Good & Guttinger, 1998, Ashenafi, 2001, Stephens et al., 2001). Livestock density estimates for 2007/2008 based on distance-sampling along 500km of transects throughout the three main wolf sub-ranges (Chapter 3) showed the densities of cattle and caprines (sheep and goats) in the Web valley to be c. 195 tropical livestock units (TLU).km⁻² (95% CI: 125-325 TLU.km⁻²), c. 149 TLU.km⁻² (95% CI: 69-342 TLU.km⁻²) for Morebawa and 49 TLU.km⁻² (95% CI: 13-194 TLU.km⁻²) for the Sanetti plateau in 2007-2008 (1 TLU = 1.5 cattle, 11 sheep/goats or 1.5 horse/mule/donkey (Boudet and Riviere, 1968)). It has been shown that rodent biomass significantly declines as the livestock numbers increase along a grazing gradient (Chapter 4) and that rodent populations increase in response to the experimental removal of livestock grazing from inside exclosures (Chapter 5). Such experiments have also revealed some evidence that the impact of livestock on rodent biomass is concurrent with changes in the vegetation. In particular, the removal of livestock has a positive impact on the biomass of *Alchemilla* spp. and grasses, and results in smaller home ranges and higher reproductive success for *L. melanonyx*, an indication that resources may be more limited for some rodent species on grazed sites (Chapter 5).

As human activities play an increasingly important role in affecting ecosystem processes, the ability to predict the direct and indirect effects of these impacts becomes a priority. Food webs provide insight into the trophic structure and energy flows of ecosystems, the factors affecting trophic dynamics, as well as the trophic effects of disturbances (Pauly et al., 2000, Tsehaye and Nagelkerke, 2008). Much of the large body of theoretical work on food webs is based on Lotka's and Volterra's continuous-time ecological models for n species (Lotka, 1925, Volterra, 1926). While Lotka-Volterra models can be complex enough to exhibit dynamical chaos (Gilpin, 1975), they often exhibit stable equilibria allowing food web analyses to focus on equilibrium behaviour. Perturbation experiments (Bender et al., 1984), in which one or more species densities are altered and changes in the density of other species in the communities are observed, are widely viewed as a revealing probe to elucidate interspecific interactions and anticipate

human impacts on ecosystems (Yodzis, 1996, Schmitz, 1997). Sustainability can then be evaluated in terms of a system's ability to withstand disturbances (Holling, 1973), that is the capacity of a system to absorb change while preserving its structure and dynamics. There are two common ways of measuring this property: stability and resilience. A number of sometimes contradictory meanings have been attached to both those terms. Here we will use stability as "the propensity of a system to attain an equilibrium condition" (Holling, 1986). While the concept of resilience has often been used to describe many different properties of a system, we will define resilience as the "domain over which disturbance can be experienced" while still retaining an equilibrium condition (*sensu* Holling 1973).

In the following models, we explicitly look at the potential effects of exploitative competition between livestock and rodents for primary production in the BMNP ecosystem and its possible repercussions on trophic levels higher in the food chain. The dynamic trophic models developed provides a framework for the objective examination of biomass flows and standing crops, an approach rarely adopted when considering these questions. We apply Lotka-Volterra (LV) and non-LV predator-prey models to explore the interactions between trophic levels and their response to disturbance by livestock. We then use the models to answer the three primary questions:

- What is the impact of increasing livestock numbers on the food chain's stability and resilience?
- Does this impact depend on the type of functional response that link the different trophic levels?
- Do livestock densities estimated to exist in the Web valley, Morebawa and the Sanetti plateau exceed our models' estimated resilience to disturbance thereby threatening Ethiopian wolves' persistence in part of their range in BMNP.

6.2 Materials & Methods

6.2.1 General model

We explore the dynamics of a 3-trophic level model where biomass (kg) per unit area (km^{-2}) of vegetation (X_v), rodents (X_r) and wolves (X_w) is represented by a set of ordinary differential equations:

$$\frac{dX_v}{dt} = b_v X_v - a_{vv} X_v^2 - C_r(X_v) X_r - C_L(X_v) L \quad \text{Equation 6-1}$$

$$\frac{dX_r}{dt} = -b_r X_r - a_{rr} X_r^2 + \kappa_{rv} C_r(X_v) X_r - C_w(X_r) X_w \quad \text{Equation 6-2}$$

$$\frac{dX_w}{dt} = -b_w X_w - a_{ww} X_w^2 + \kappa_{wr} C_w(X_r) X_w \quad \text{Equation 6-3}$$

The parameters b_i are the rates of change of biomass in the absence of other trophic levels ($\text{kg.km}^{-2}.\text{yr}^{-1}$) and therefore positive for vegetation, and negative for rodents and wolves. The a_{ii} terms govern the density dependence at each trophic level; L is the biomass of livestock (kg.km^{-2}) and is assumed to be imposed on the landscape and not subject directly to the trophic dynamics so is represented as a parameter; κ_{ij} is the conversion efficiency of biomass from the j^{th} level to the i^{th} .

C_i describes the functional response that relates biomass consumption per kg of consumer per year to resource availability. In this model there are 3 such functional responses: $C_r(X_v)$ – the biomass of vegetation consumed per kg of rodent as a function of the biomass of vegetation; $C_L(X_v)$ – the biomass of vegetation consumed per kg of livestock as a function of the biomass of vegetation; and $C_w(X_r)$ – the biomass of rodents consumed per kg of wolf as a function of the biomass of rodents. We investigate combinations of these functional responses, assuming them to be either type 1 (linear) or an extreme version of type 2, where per capita consumption is independent of resource availability so long as resource is available at all.

6.2.2 Parameterization

All coefficients are expressed as wet biomass unless stated otherwise. We parameterize functional responses by considering an equilibrium state of the system in which wolves (X_w^*) are present at a biomass density of 30 kg.km^{-2} (a wolf weighs $\sim 14\text{kg}$, and are often observed at densities of $2\text{-}3 \text{ km}^{-2}$, Sillero et al., 1994); rodents (X_r^*), a mixture comprising grass rats and giant mole rats, present at a biomass density of 2860 kg.km^{-2} ; and vegetation (X_v^*) at $385,000 \text{ kg.km}^{-2}$ (Asefa et al., 2003, Mwendera et al., 1997, Woldu, 1986, Yayneshet et al., 2003). Wolves are assumed to consume an

equivalent biomass of one giant mole rat (0.62 kg) per day, hence $C_w(X_r^{*'}) = (0.62/14) \times 365 = 16.16 \text{ kg.km}^{-2}.\text{yr}^{-1}$. Rodents are assumed to consume a biomass of vegetation equivalent to 20% of their own biomass, hence $C_r(X_v^{*'}) = 0.2 \times 365 = 73 \text{ kg.km}^{-2}.\text{yr}^{-1}$.

With type 1 functional responses, as assumed by classical Lotka-Volterra dynamics, $C_j(X_i) = a_{ij} X_i$, and $a_{ij} = C_j(X_i^{*'})/X_i^{*'}$, and consumption rate depends linearly on the availability of the resource. In the case of the extreme type 2 functional response, consumption is independent of resource availability and fixed at $C_j(X_i^{*'})$. In this case it is assumed individuals compensate for resource scarcity by increased effort in acquiring resources. Obviously there are limits to such compensation, but the intention here is to bracket reality - the real functional responses will likely lie somewhere between these two extremes.

The trophic efficiency parameters κ_{rv} and κ_{wr} are assumed to be 5% and 10% respectively (Grodzinski and French 1983, Colinvaux and Barnett 1979). The b_i terms are estimated assuming a doubling time for vegetation (at low densities) of 1 month, and a half-life of rodents and wolves of 1 month and 6 months respectively. The a_{ii} terms are then the only remaining unknown parameters and can then be solved assuming the system to be at equilibrium and setting the right hand-sides equal to zero.

Livestock grazing pressure is modelled as TLUs each equivalent to 250kg and requiring $2,300 \text{ kg.yr}^{-1}$ of dry vegetation biomass. Thus assuming a wet-dry conversion factor of 2.2 (Le Houerou and Hoste, 1977), $C_L(X_v^{*'}) = 2,300 \times 2.2/250 = 20.44 \text{ kg.yr}^{-1}$. We examined how the system responded to a range of grazing pressures equivalent to between 0 and 200 TLU $.\text{km}^{-2}$.

Table 6-1 provides a summary of the parameters used in the trophic models as well references for the empirical work they are based on.

Parameters	Estimates	References
a_{wv} (km ² .kg ⁻¹ .year ⁻¹)	0	
a_{vw} (km ² .kg ⁻¹ .year ⁻¹)	0	
a_{rl} (km ² .kg ⁻¹ .year ⁻¹)	0	
a_{rr} (km ² .kg ⁻¹ .year ⁻¹)	-1.7*10 ⁻⁴	a, c, e, f, g, i, j & k
a_{rv} (km ² .kg ⁻¹ .year ⁻¹)	9.5*10 ⁻⁶	a, c, e, f, j & k
a_{vr} (km ² .kg ⁻¹ .year ⁻¹)	-1.9*10 ⁻⁴	a, e, f, j & k
a_{ww} (km ² .kg ⁻¹ .year ⁻¹)	-7.5*10 ⁻³	b, g & h
a_{wr} (km ² .kg ⁻¹ .year ⁻¹)	5.6*10 ⁻⁴	a & g
a_{vl} (km ² .kg ⁻¹ .year ⁻¹)	-5.3*10 ⁻⁵	a, d, e, j & k
a_{vv} (km ² .kg ⁻¹ .year ⁻¹)	-1.9*10 ⁻⁵	a, e, g, j & k
a_{rw} (km ² .kg ⁻¹ .year ⁻¹)	-5.6*10 ⁻³	g
b_v (kg.km ² .year ⁻¹)	7.82	a, e, j & k
b_r (kg.km ² .year ⁻¹)	-3.00	i
b_w (kg.km ² .year ⁻¹)	-1.39	h

Table 6-1: Summary of trophic model parameters: point estimates for the instantaneous growth rates (b_i) and per capita species effects (a_{ij}) as used in the trophic models. Empirical work and data on which parameter estimates are based are referenced as follow: a) (Asefa et al., 2003); b) (Colinvaux and Barnett, 1979); c) (Grodzifliski and French, 1983); d) (Le Hou rou and Hoste, 1977); e) (Mwendera et al., 1997); f) (Rubal et al., 1995); g) (Sillero-Zubiri, 1994); h) (Sillero-Zubiri and Macdonald, 1997); i) Chapters 4 & 5; j) (Woldu, 1986); k)(Yayneshet et al., 2003)

6.2.3 Model analysis

We set out to examine how grazing pressure changes the biomass of vegetation, rodents and wolves at equilibrium. Of particular interest was the grazing pressure (L_{max}) at which wolf biomass could no longer be sustained. We also examined the stability of this equilibrium point.

Model 1 (M1) assumed that all functional responses were type 1, and under these assumptions the model (in the absence of grazing) takes the simple Lotka-Volterra form. The equilibrium points (\mathbf{X}^*) can be recovered by inversion of the interaction matrix \mathbf{A} (containing the a_{ij} elements) and multiplication by the vector \mathbf{b} (containing the b_i elements): $\mathbf{X}^* = \mathbf{A}^{-1}\mathbf{b}$. We also evaluated the local stability of these equilibrium points (conditional on their feasibility: $X_i^* > 0$ for all i) by examining the dominant eigenvalue of the appropriately formulated Jacobian matrix (\mathbf{J}) evaluated at \mathbf{X}^* .

We examined 4 models variants:

- M2: Similar to M1 except that the impact of livestock grazing on vegetation was modelled according to a type 2 response.
- M3: Similar to M2 except that the impact of rodent grazing on vegetation was also modelled according to a type 2 response.
- M4: Similar to M2 except that the impact of wolf predation on rodents was modelled according to a type 2 response.
- M5: All functional responses were type 2.

With the introduction of alternative non-type 1 functional responses the model loses its Lotka-Volterra form and the equilibrium is most easily evaluated computationally.

Sensitivity and elasticity analyses were performed on the parameters about which there was the greatest uncertainty: b_w , b_r , b_v and X_v^* .

6.3 Results

Equilibrium biomasses of the different trophic levels responded differently to increased disturbance by livestock depending on the type of functional responses (Figure 6-1). Equilibrium biomass declines steadily with increasing grazing pressure, but more quickly when rodents maintained a type 2 response to vegetation (models M3 and M5, Figure 6-1A). If rodents and wolves exhibit a type 1 response (as in M1 and M2), both populations steadily decline as a result of increasing livestock grazing pressure on the vegetation (regardless of the type of functional response exhibited by livestock). If rodents exhibit a type 2 response (as in M3 and M5), the consumer species remain unaffected by increasing livestock grazing pressure as populations of rodents and wolves stay close to

their initial equilibrium until the vegetation biomass crashes. If wolves exhibit a type 2 trophic response (as in M4), the predators remain largely unaffected by increasing livestock grazing pressure with densities close to their initial equilibrium until the rodent population crashes (Figure 6-1B and C).

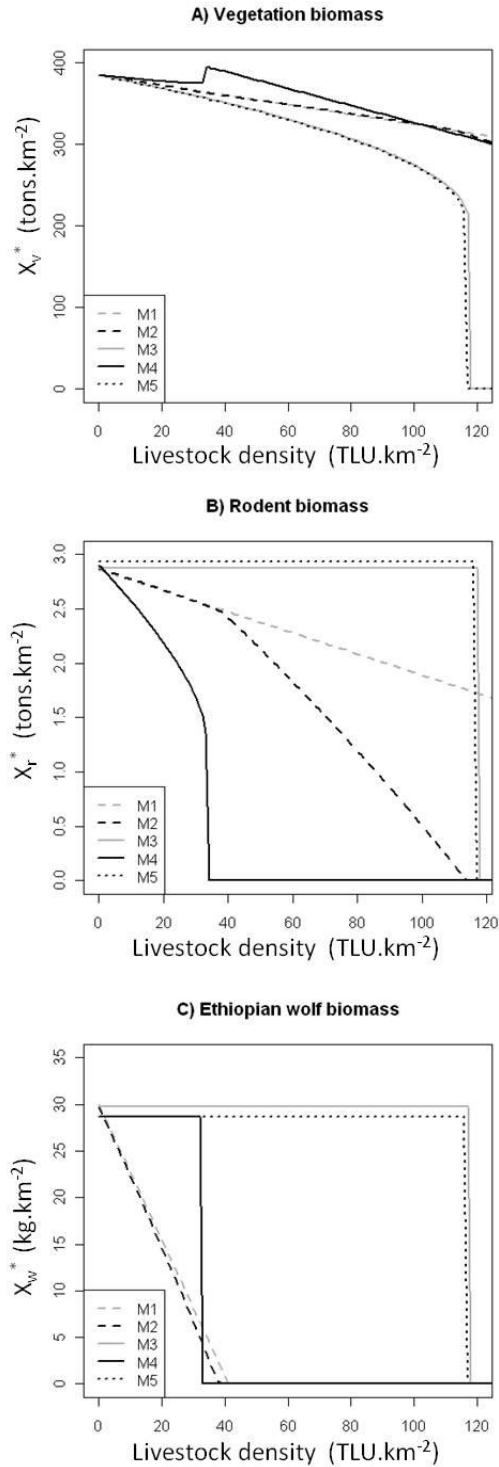


Figure 6-1: Changes in the equilibrium biomasses of vegetation (top), rodent (middle) and Ethiopian wolves (bottom) as livestock density increases under all five model scenarios.

The analyses of all five models indicated that the equilibrium was locally stable whenever it was feasible (i.e. biomass at all trophic levels > 0), but depending on the functional response linking the trophic levels, increasing livestock grazing pressure could push the system into a less locally stable state (Figure 6-2). The system's resilience, L_{max} , for the LV model (M1) is estimated at 41 TLU.km⁻² (Table 6-2). By numerically integrating the differential equations (Equations 6-1,6-2 & 6-3), we can also obtain estimates of the system's resilience, L_{max} , for the non-LV models 2-5 (Table 6-2). Maximum resilience to disturbance by livestock (117 TLU.km⁻²) was achieved under scenarios where rodents exhibited a type 2 response to vegetation availability, regardless of the wolves' functional response to rodent availability. Minimum resilience occurred when wolves exhibited a type 2 response but their prey a type 1 response to vegetation availability. The likely true functional response of the consumer species in our trophic chain lies somewhere in between those two extreme scenarios and so we expect the system's true resilience to lie between 32 and 117 TLU.km⁻². For afroalpine pastures stocked with livestock densities similar to the Web valley (195 TLU.km⁻², i.e. L_{max}), time to local extinction for Ethiopian wolf packs was estimated between < 1 year (M2, M3, M4 & M5) and 5 years (M1).

Trophic responses

Model	Livestock	Rodents	Wolves	L_{max}
M1	Type 1	Type 1	Type 1	40 TLU.km ⁻²
M2	Type 2	Type 1	Type 1	38 TLU.km ⁻²
M3	Type 2	Type 2	Type 1	117 TLU.km ⁻²
M4	Type 2	Type 1	Type 2	32 TLU.km ⁻²
M5	Type 2	Type 2	Type 2	116 TLU.km ⁻²

Table 6-2: Summary of five trophic models with the type of trophic response assumed for each consumer species. The resilience of the food chain (L_{max}) represents the maximum possible sustainable livestock density parameters before wolves are eliminated from this food chain.

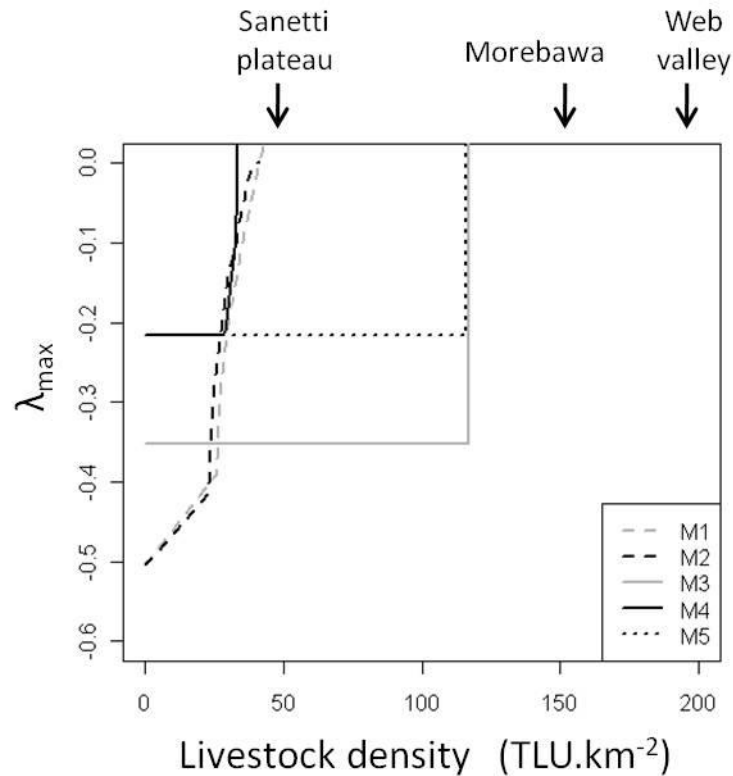


Figure 6-2: Changes in the dominant eigenvalue (λ_{max}) of the Jacobian matrix governing the equilibrium point (in which wolves are represented) for each of the five trophic models as livestock density on the afroalpine pastures increases. Models 1 and 2 both predict that the stability of the equilibrium point is steadily reduced as grazing pressure increases. Models 3 and 5 predict no change in the stability of the equilibrium point until L_{max} is reached and then the food chain suddenly collapses. Model 4 exhibits intermediate behaviour. The arrows indicate the average livestock densities in the three wolf sub-populations' ranges in 2007/2008 (from left to right): the Sanetti plateau, Morebawa and the Web valley.

Uncertainty in the estimate of the wolves' instantaneous growth rate (b_w) resulted in the biggest difference in the estimate of the system's resilience under scenario M1. If b_w is overestimated by 5%, the resulting L_{max} will be underestimated by 12%. Similarly, uncertainty in the estimate of b_r resulted in >5% difference in L_{max} while b_v and X_v^* were found to have little effect on the resilience of the system. We performed sensitivity analyses on all four parameters under both extreme scenarios M1 and M5 (Figure 6-3). In M1, an increase in the instantaneous growth rates (for b_w and b_r this means being more negative) results in an increased L_{max} , with the effect being more pronounced (contours are tighter) for b_w . However, under M5, the system's resilience is less sensitive to changes b_w and b_r , although biologically plausible food chains did not exist for some combinations of parameters (horizontal zero contour). An increase in vegetation equilibrium biomass (X_v^*)

has a positive impact on L_{max} under both M1 and M5 (tighter contours suggest even more so for the latter).

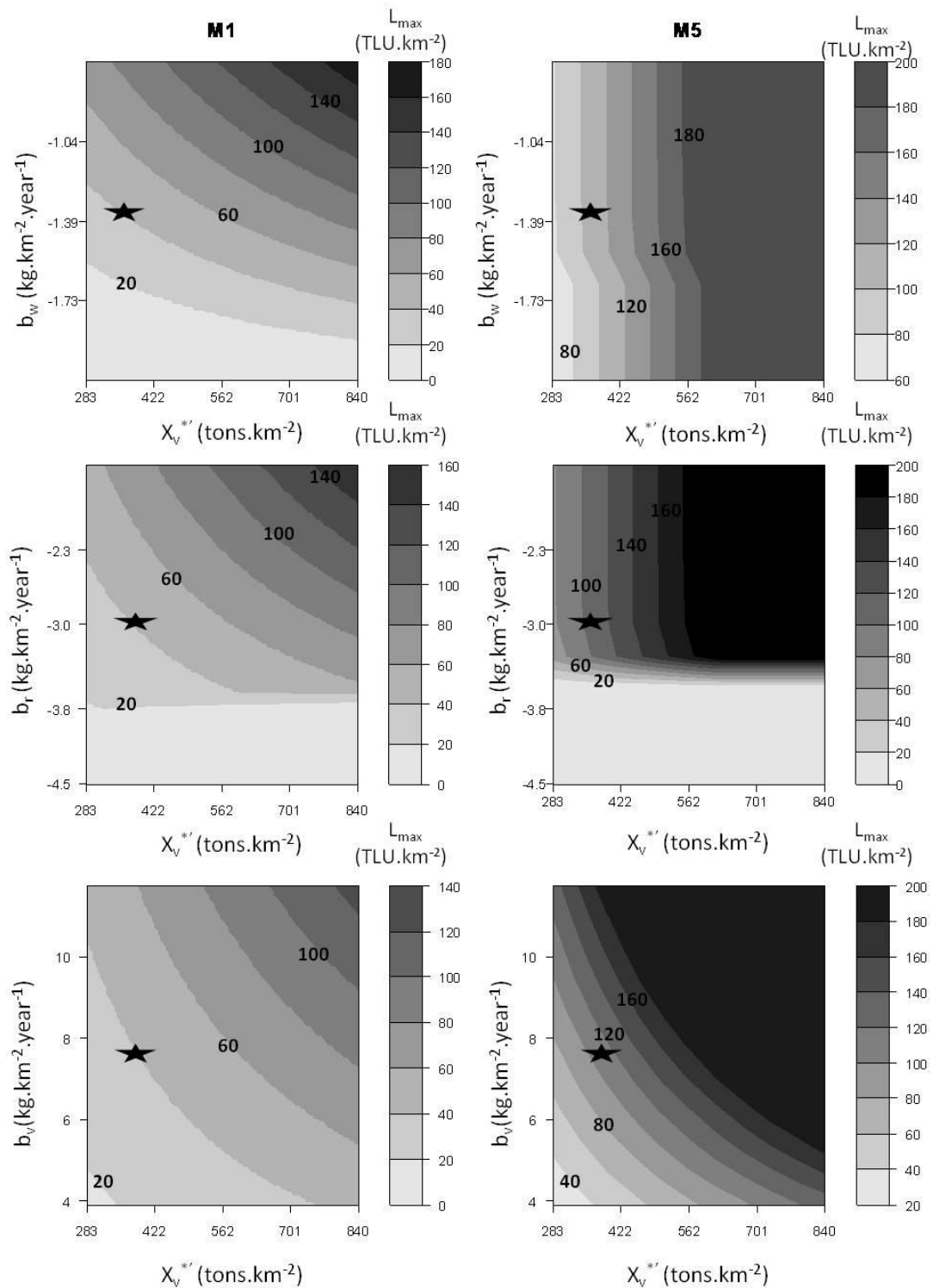


Figure 6-3: Contour plots showing the predicted L_{max} under the both extreme scenarios. M1 (left- all type 1 trophic responses) and M5 (right- all type 2 trophic responses) as a function of b_w and X_v^{*1} , b_r and X_v^{*1} and b_v and X_v^{*1} . The stars indicate parameter estimates used in the trophic models.

6.4 Discussion

6.4.1 Response of afroalpine food chain to disturbance by livestock

We have used a simplified representation of the food chain supporting the largest remaining population of Ethiopian wolves to explore the sensitivity of trophic dynamics to increased levels of grazing pressure resulting from the increased use of the rangelands in this ecosystem by domestic livestock. Depending on assumptions about the shape of the functional response governing the grazing behaviour of rodents the models indicate that the system's resilience L_{max} (the maximum density of livestock that can be consistent with the maintenance of even a single pack of wolves), lies between 32 and 117 TLU.km⁻². The Web valley and Morebawa are currently stocked at an estimated 195 and 149 TLU.km⁻² respectively, and therefore lie outside of the models projected sustainable range. The intensity of grazing pressure is illustrated by the fact that the model estimates the ratio of primary productivity consumed by livestock relative to that consumed by rodents to be between 4.8 and 5.9 for the Web valley for the current stocking rate. The model outputs suggest that both systems, in their current state, may already be unstable while the Sanetti plateau (49 TLU.km⁻²), currently lie within our resilience "envelope" for the system. The results of the sensitivity analyses suggest that, under the M1 scenario, both the Web valley and Morebawa would still be overstocked for $X_v^* = 840,000 \text{ kg.km}^{-2}$, the maximum Ethiopian afroalpine vegetation biomass density empirically recorded (Woldu, 1986). However, under the M5 scenario, current livestock densities could be sustainable in both areas for $X_v^* \geq 617,000 \text{ kg.km}^{-2}$.

Estimates of the maximum sustainable livestock stocking rates for all three ranges can also be calculated using a simple model developed by Le Houerou and Hoste's (1977) linking primary productivity to rainfall data in these areas (Vial, 2010). Le Houérou and Hoste's (1977) model predicts a sustainable livestock density of 44, 43 and 34 TLU.km⁻² for the Web valley, Morebawa and the Sanetti plateau respectively, estimates that fall within our resilience "envelope" for the system .

6.4.2 Methodological considerations: model and assumptions

The estimate of L_{max} is based on the assumption that the primary productivity across all three wolf ranges are equal. However, the Sanetti plateau is a less productive system as shrubs constitute the main vegetation type on the plateau (Miehe and Miehe, 1993) but an estimate for vegetation carrying capacity in afroalpine shrublands could not be estimated with any confidence. It is therefore very likely that L_{max} , for Sanetti is lower than the one predicted by this trophic model, in which case Sanetti's afroalpine system may be closer to an unsustainable condition than currently anticipated.

Little is known about the basic biology and ecology of the components of the afroalpine trophic chain modelled here, making it difficult to estimate accurately the per-capita species effects and their instantaneous growth rates for the different trophic levels. The results of the sensitivity analyses suggest that more accurate estimates of the afroalpine vegetation (b_v), rodent (b_r) and wolf (b_w) instantaneous growth rates and of the afroalpine vegetation equilibrium biomass (X_v^*) for the three wolf ranges in BMNP should be a priority.

Knowledge of functional responses governing trophic interactions is critically important to applied aspects of predator-prey biology. While this knowledge is not available for the species making up the trophic chain described above, the literature can be used to provide some guidance. Specialist predators, such as the Ethiopian wolf, tend to exhibit a type 2 functional response with a curve rising rapidly as prey density increases (Andersson and Erlinge, 1977), even when these predators are solitary hunters, as for example the Eurasian lynx (*Lynx lynx*) (Nilsen et al., 2009). However, all three major types of functional responses have been observed in herbivorous small mammals (sometimes within the same species (Klinger and Rejmánek, 2009)): from a linear intake rate (type 1) in brown lemmings (*Lemmus sibericus*) (Batzli et al., 1981); to a type 2 functional response in white-footed mice (*Peromyscus leucopus* L.) preying on moth pupae and a type 3 in the same species preying on sunflower seeds (Elkinton et al., 2004). Since the three main rodent prey species were clumped into one rodent trophic "class" in order to simplify the superficial description of the food chain dynamics, this model only allows us to look at the response of the trophic "class" rather than the response of individual species to changes in resource availability. If the rodent class mostly specialises on a few plant species or specific plant parts, it may be best described by a type 2 functional response. However, if the rodent class is more generalist and can switch to an

alternative prey type if it is more abundant (such as invertebrates for the more insectivorous species such as *L. melanonyx*), then the functional response adopted may take a concave form over some range of resource availability (type 3).

Vegetation was also modelled as one trophic “class” as this exercise did not seek to model the shift in species composition and/or diversity that is usually associated with livestock grazing (Diaz et al., 2007, Milchunas and Lauenroth, 1993). However, herbivores’ carrying capacity is not solely dependent on vegetation biomass but also on vegetation type and condition, based on foliage cover and botanical composition, as well as the nutritive value of the pasture (Squires and Bennet, 2004).

Similarly, the predictions of the model are based on the assumption that Ethiopian wolves’ diet is fixed and consists exclusively of rodents. However, predators, and especially canids, are known to display functional responses to variation in prey availability (Fedriani et al., 2001, Farias and Kittlein, 2008, Eide et al., 2004). Such differentiation can be enhanced when human-induced changes in land use increase spatial heterogeneity in prey availability (Pia et al., 2003). In Bale, the contribution of different species of prey to the diet of the Ethiopian wolf correlates with abundance of prey (Sillero-Zubiri and Gottelli, 1995). Circumstantial evidence also suggests that wolves may predate more frequently on livestock, or become crepuscular or nocturnal when human interference is severe in densely populated areas (Marino, 2003a). As a result, we are likely to underestimate X_w^* by assuming that Ethiopian wolves’ diet has no plasticity. It is therefore possible that by changing their diets in response to diminishing rodent densities, Ethiopian wolves may be more resilient to an increase in livestock density than currently shown by this model.

The absence of long-term baseline monitoring of rodent densities and vegetation condition precludes any assessment of changes in the state of this ecosystem since the advent of the high grazing pressures recorded on parts of the Ethiopian wolf range in BMNP. The ability of these populations to recover from disease, and the rapidity of their recovery, is limited by the formation of breeding units, and subsequent recruitment of young to the population (Marino et al., 2006), itself largely determined by prey abundance (Tallents, 2007). Historically, the Web valley has supported the highest wolf densities in the BMNP and wolves there have until recently recovered from periodic rabies outbreaks suggesting that past conditions have supported positive wolf population growth rates. However, the models suggest that the long-term persistence of wolves there (and in

Morebawa) may not be compatible with current grazing pressures with estimated times to local extinction between < 1 year (M2, M3, M4 & M5) and 5 years (M1).

This projection is evidently at odds with the continuing presence of wolves in the Web valley and Morebawa, and there are two possible explanations for this. The first is that the models structure or parameters are simply wrong. We have parameterized these models the best we can given the available data, and we have conducted a range of sensitivity analyses to explore the consequences of our uncertainty, but the model is a only a first step. Given the absence of more detailed information, analyzing a simple model is a useful prerequisite to the inclusion of greater complexity and it remains possible that a more detailed treatment of primary production, seasonality, space, and the taxonomic grouping of plant and rodent species might lead to different conclusions. The second is that the system is in transition and moving towards the state that the models predict given the heavy grazing pressure. Long-term transients are an anticipated property of some types of ecological system (Hastings, 2004), but all the models analyzed here predict a time to extinction of less than 5 years, with models that assume type 1 functional responses taking longer than those that assume type 2. We are, however, cautious in placing too much confidence in these transients which may very well be sensitive to assumptions about seasonality and the lack of an explicitly spatial dimension.

6.4.3 Management implications

Households in Bale are reliant on the environment, particularly on access to commonly-owned grazing areas and rivers, to support the health and reproduction of their domestic livestock (Flintan et al., 2008). Traditional land use practices by pastoralists can be less detrimental to the environment and more sustainable than other types of land use such as agriculture or illegal resource harvesting (Boyd et al., 1999, Perkin, 1995), provided that the economic return derived from livestock production remain profitable to those societies (CDC/FZS, 1997) and that pastures are correctly managed to avoid irreversible shifts in vegetation and the fall in productivity that ensue (van de Koppel et al., 1997). The models suggest that monitoring of the species at the top of afroalpine food chains may not always be informative of the ecological changes happening at lower trophic levels. We show, in this example, that if consumer species exhibit type 2 functional responses, their populations may be maintained close to unperturbed equilibrium levels for a long time even when vegetation biomass has been greatly reduced as a result of grazing disturbance by livestock. Such dynamics makes it difficult to predict population crashes

and/or local extinction of Ethiopian wolves. While the monitoring of this predator species of great conservation interest remains important for early detection of disease outbreaks for example, we would recommend setting up a regular monitoring system of the afroalpine vegetation and its productivity in order to be able to foresee dramatic shifts in the stability of this trophic chain.

Despite its methodological simplicity, the trophic model produces output which allows us to assess the areas of BMNP that are likely to be currently overgrazed and those that will be particularly sensitive to future increases in livestock numbers. This approach provides a first step in evaluating the seriousness of likely conflict between resident pastoralist communities and the ecological processes taking place in the Bale Mountains.

7 Predicting livestock habitat use in the afroalpine

7.1 Introduction

7.1.1 *The relevance of livestock habitat use patterns*

Livestock grazing has major impacts on native biodiversity and ecosystem functioning throughout the world (De Vries et al., 2007, Diaz et al., 2007, Milchunas and Lauenroth, 1993). Consequently, understanding the spatial and temporal dynamics of landscape use by livestock is critical for multi-species rangeland management (Coughenour, 1991, Senft et al., 1987). For example, interspecific interactions between wild and domestic ungulates have been shown to influence the spatial behaviour of the former, particularly when domestic animals outnumber their wild counterpart (Baldi et al., 2001). The displacement of wild herbivores by livestock may result from competition for food, especially at times when such resources are limited (Shrestha and Wegge, 2008b, Voeten and Prins, 1999), or the active avoidance of disease/parasites transmission (Fankhauser et al., 2008). Cattle have been shown to displace elk (*Cervus elaphus*) and reduce vegetative cover essential for fawning habitat for mule deer (*Odocoileus hemionus*) in North American meadows (Loft et al., 1991, Wallace and Krausman, 1987); and compete with bharal (*Pseudois nayaur*) for forage in the Himalayas (Shrestha and Wegge, 2008b). Smaller stock, such as sheep and goats, also have the capacity to displace wild herbivores, such as the endangered Tibetan argali (*Ovis ammon hodgsoni*), into less productive habitat (Namgail et al., 2007).

Livestock may also modify habitat suitability for a suite of smaller species such as rodents (Schmidt et al., 2005), invertebrates (Kruess and Tschardtke, 2002), birds (Coppedge et al., 2008), reptiles (Castellano and Valone, 2006) and fish (Bayley and Li, 2008). As such, mapping habitat use by livestock and understanding the drivers behind their distribution should be part of conservation planning when domestic animals pose a threat to rare or endangered species (Johnson et al., 2004). Although the collection of extensive datasets is time-consuming and the specialised analyses required to produce such maps rapidly become complex, this knowledge can ultimately serve as a powerful tool in the design and placement of ecological reserves, in mitigating development, directing remediation efforts and planning further research (Flather et al., 1998). Even in areas where livestock does not pose a threat to native wildlife, uneven grazing and trampling by livestock onto pastures may still be a key factor underlying land deterioration (Hiernaux, 1998, Hiernaux et al., 1999) and an understanding of livestock distribution may contribute to evaluating the sustainability of grazing systems.

Resource use patterns are a consequence of the influence of selection on survival and reproduction which determines fitness in various habitats (Southwood, 1977). In many environments, forage, water, minerals, or resting places are not uniformly dispersed and physiological constraints may demand that herbivores centre their activities in the vicinity of important resources (Stuth, 1991). As a result, general relationships have been observed between habitat characteristics and patterns of grazing use (see (Bailey and Putman, 1981) for review). Permanent surface water is usually naturally restricted on many rangelands and can provide a limit to the density of herbivores that can be sustained in a particular area (James et al., 1999). Indeed, distance to water is recognised as one of the most important predictors of livestock distribution patterns (Adler and Hall, 2005, Andrew, 1988, Fernandez-Gimenez and Allen-Diaz, 2001, Gonnet et al., 2003, Nash et al., 1999), followed by the distribution of salt/mineral sources (Martin and Ward, 1973). Other abiotic factors such as degree of slope (Ganskopp and Vavra, 1987) or the presence of fences or natural barriers (e.g.: rocky surfaces, steep terrain, dense woody vegetation) (Holechek et al., 1998) both affect pastures' accessibility to livestock. The need of livestock to maintain their body temperature within a thermal neutral zone strongly influences their distribution. Microsite characteristics, such as the presence of shade and/or wind, affect where animals rest and can affect where they graze (Lynch et al., 1992). Grazing animals spend more time in patches and plant communities that are higher in forage quality and quantity (Bailey et al., 1996, Senft et al., 1985). Riparian zones often receive heavy use because they provide water, shade, thermal cover, and a productive source of high-quality forage. Animal factors, such as species and breed of animal (Herbel et al., 1967, Lynch et al., 1992), and knowledge of the area (Bailey, 2005) also play an important role in deciding where to graze.

The wide availability of geographic information systems (GIS) facilitates the study of selection of multiple habitat variables by animals (Brock and Owensby, 2000, Kawamura et al., 2005, Rutter et al., 1997). When linked to the multitude of recent statistical developments in the modelling of habitat selection (for example (Calenge et al., 2005, Freitas et al., 2008, Gillies et al., 2006)), GIS offers a user-friendly visual framework with which to understand both species-habitat associations and derive habitat suitability maps. For example, resource selection functions (RSF) are statistical models that offer a quantitative characterisation of resource use (Boyce and McDonald, 1999, Manly et al., 2002). RSF can accommodate virtually any type of resource being selected, including both categorical and continuous variables, and can be interfaced with GIS to facilitate rapid

analysis and use of remote sensing data (Boyce and McDonald, 1999, Erickson et al., 1998).

RSF have been employed to provide guidelines for conservation, for example examining the avoidance of human activity by individual wolves (*Canis lupus*) (Hebblewhite and Merrill, 2008) or determining important habitats for the mountain caribou (*Rangifer tarandus*) in which forest harvesting and human access should be managed (Johnson et al., 2004). Few attempts have been made to derive habitat selection models for livestock within African ecosystems (see (Coppock et al., 1986, Fritz et al., 1996) for example) and even fewer attempts have been made to assess their utility to real-world policy-makers. Sitters and colleagues (Sitters et al., 2009) provide an example of how spatial distribution data for wild grazers and cattle in Kenya can be used to inform rangeland management. The study showed spatial partitioning by livestock and wildlife in the use of permanent and seasonal water bodies, but not in their forage resources. They conclude that pastoralist decisions play an important role in the interactions between livestock and wildlife in African savannas and that herd mobility is a key component in supporting sustainable use of resources for both wildlife and livestock.

7.1.2 The afroalpine and rodents of the Bale Mountains

The Bale Mountains lie between 06°41'N, 39°03'E and 07°18'N, 40°00'E, in the southern highlands of Ethiopia. They represent the largest area of afroalpine habitat over 3000m in Africa (Yalden, 1983), and form part of Conservation International's Eastern afroalpine hotspot (Brooks et al., 2004), harbouring a diverse array of endemic and range-restricted species. The giant molerat (*Tachyoryctes macrocephalus*), Blick's grass rat (*Arvicanthis blicki*) and the brush-furred mouse (*Lophuromys melanonyx*) are endemics restricted to the southern highlands of Ethiopia (Yalden, 1988). These fossorial diurnal rodents are of great ecological importance as the dominant wild herbivores within the afroalpine ecosystem (Sillero-Zubiri et al., 1995a). They are important components of the diet of a diverse guild of diurnal raptors which inhabit the Bale massif (Clouet et al., 2000). However, these rodents have been most closely studied as the main prey of the endangered Ethiopian wolf (*Canis simensis*). Giant molerats also have an important secondary role in the afroalpine as ecosystem engineers (Tallents, 2007, Yalden, 1985).

The Bale Mountains National Park (BMNP) was established in 1969 to protect the endemic mountain nyala (*Tragelaphus buxtoni*) and Ethiopian wolf and c. 2,200 km² of

montane habitats upon which they depend (Hillman, 1986). Although, six isolated populations of Ethiopian wolves have been described in Ethiopia (Marino, 2003b), over half of the remaining wolves are found in the Bale Mountains (Sillero-Zubiri et al., 2000). BMNP has been under increasing pressure from a rapidly growing pastoralist population and their livestock (Marino et al., 2006). Livestock densities estimates inside Ethiopian wolf core ranges (the Web valley, Morebawa and the Sanetti plateau) at 195/149/49 tropical livestock units per km² respectively illustrate the levels of threat the Bale afroalpine is subjected to (Chapter 3). High levels of livestock grazing in Bale has been demonstrated to negatively impact on the rodent populations on which the wolves depend (Chapter 5), possibly through a reduction in vegetation cover resulting in an increased predation risk (Hayward et al., 1997, Germano et al., 2001, Smit et al., 2001, Schmidt et al., 2005) and/or a exploitative competition for suitable food resources (Tokeshi, 1999, Reynolds and Trost, 1980, Keesing, 2000).

For this chapter, I build on Lucy Tallent's work, who used species distribution models and GIS to develop finely-detailed and extensive maps of giant molerat, Blick's grass rat and the brush-furred mouse densities in BMNP afroalpine (Tallents, 2007). In order to highlight "ecologically sensitive" areas of both high rodent biomass and high relative probability of livestock use, I develop RSFs for cattle and sheep/goats (caprines) inside the three main Ethiopian wolf sub-ranges in Bale: the Web valley, Morebawa and Sanetti plateau. These models will also allow us to create livestock habitat suitability maps for each range as well as help park managers to gain a better understanding of the major drivers behind the heterogeneous use of the landscape by livestock.

7.2 Methods

7.2.1 Assessing habitat use and availability

Livestock habitat use was assessed through focal follows of individual livestock (cattle and caprines) that took place between February 2007 and June 2009. Observers would leave the camp in the morning in opposite directions at 7.30 am (time when livestock are let out of their overnight pens or *bomas*) and would walk for 20 minutes before selecting a focal animal in the first herd they encountered. Focal animals were followed throughout the day until the herd was taken back to the village. Observers recorded the focal individual's location with a hand-held GPS unit every 20 minutes. Over two years, data on 863 cattle and 600 shoat sightings were collected in the Web valley,

Morebawa and Sanetti. This dataset was supplemented by unpublished livestock data collected by Lucy Tallents during her PhD in Bale (2002-2007). Tallents had collected 293 cattle and 132 shoat sightings throughout the Web valley and Sanetti plateau with UTM locations of individuals and herd size. Livestock sightings were classified by species (cattle or caprines) and season (dry or wet) for Web and Morebawa but only by season for Sanetti as the number of sightings for each individual species was <100.

Our study design involves contrasting a sample of resource units where the species is known to occur (data above) with a random sample of “available” resource units (where the species was not observed but could have been present) drawn without replacement within the domain of the area of study (Pearce and Boyce, 2006). The whole of the Web valley and Morebawa were defined as available habitat, while available habitat was restricted to the Eastern side of the Sanetti plateau, since the area sampled was much smaller than the whole area covered by the plateau. A stated assumption in the application of RSFs is that availability of resources does not spatially vary (Manly et al., 2002). As a result, a RSF estimated in one area (small part of Sanetti) cannot generally be applied to another area (in our case, the whole of the Sanetti plateau) unless the relationship between selection coefficients and availability is modelled explicitly (Boyce and McDonald, 1999), which I was not able to do. One thousand random points were generated inside each available habitat in ArcGIS (Environmental Systems Research Institute Inc., 2004) and used to define the characteristics of available habitat.

7.2.2 Extracting habitat characteristics

Seven abiotic and biotic habitat traits, $x_1 \cdots x_7$, were used to build the RSF: altitude, slope, vegetation type, rodent biomass, distance to the nearest river, distance to the nearest village and distance to the nearest *hora* (mineral spring with high levels of sodium, potassium, calcium, manganese and zinc). Euclidian distances to rivers, villages and *horas* (in Web only) were computed from distance surface GIS layers (resolution 28.5m) and altitude, slope and rodent biomass were extracted from available GIS layers for every livestock location and random points generated for all three study areas. All values for continuous variables were transformed by first subtracting the variable mean and dividing the result by the standard deviation of that particular variable. Such transformation, termed centering, prevents high intercorrelations among independent variables.

I used Tallent's (2007) classification of the afroalpine vegetation to determine the vegetation types of used and available habitats (Figure 7.1). The number of vegetation classes was reduced by:

1. merging habitat types with < 10 livestock sightings (<5 for Sanetti due to smaller dataset) into a "Minor" category.
2. using generalised linear models to examine whether the use of all vegetation types differed from the reference vegetation type (largest in terms of area) (Table 7-1). Vegetation types not statistically different from the reference type were merged with the latter.

New vegetation maps were produced based on this reduced classification: 4 distinctive vegetation types in the Web valley, 7 distinctive types in Morebawa and 2 in Sanetti (Table 7-1). Vegetation type attributes were extracted for all livestock sightings and random points.

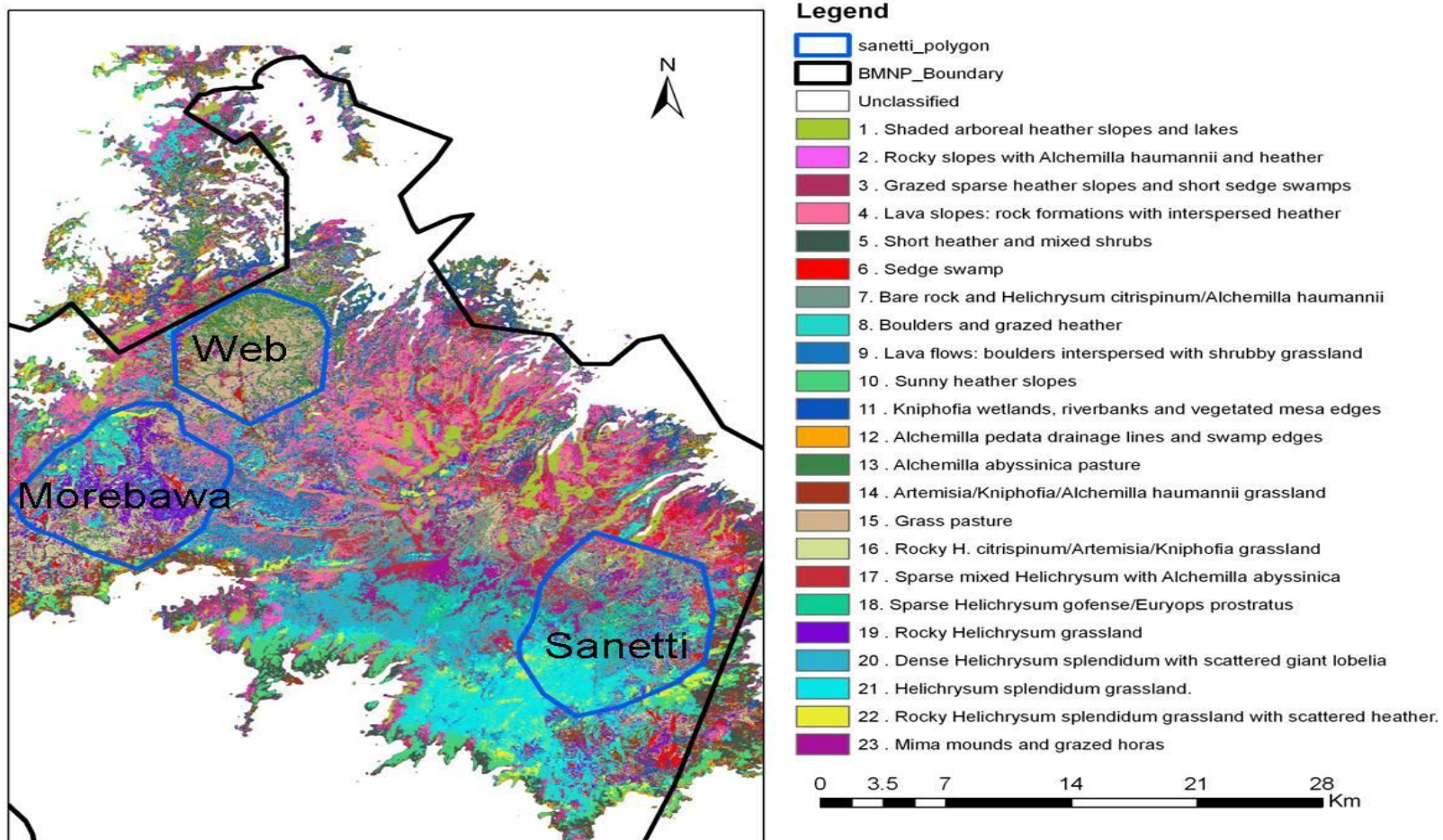


Figure 7-1: Afroalpine vegetation classification in the Bale Mountains with polygons of the study areas: Web valley, Morebawa and Sanetti plateau (adapted from Tallents 2007).

Study area	New vegetation classification	Corresponding vegetation classes from Tallent's classification
Web valley	V	15 [*] , 1,4,7,8,9,11,12,13,16,17 & 19
	P	6
	R	14
	Minor	2,3,5,18,20 & 23
Morebawa	T	19 [*] , 3,10,11,13,15,18 & 21
	B	2
	P	6
	F	7
	R	14
	S	16
	Minor	1,4,5,8,9,12,17,20,22 & 23
Sanetti	N	21 [*] , 1,2,3,4,5,6,7,9,10,11,12,13,14,15,16, 17,18,19,20,21,22 & 23
	L	8

Table 7-1: Simplified vegetation classification used to produce the RSFs. * denotes the reference vegetation class in each study area.

7.2.3 RSF analysis & model validation

A RSF consists of a number of coefficients (β_k) that quantify selection for or avoidance of k environmental features (\mathbf{x}). Here I use logistic regressions for all five datasets (2 areas * 2 species + 1 area with cattle and caprines combined) to estimate functions that discriminate between two distributions of habitat covariates, one set with locations where the species is present, $f_{y=1} \mathbf{x}$, and another set associated with random (available) locations, $f_{y=0} \mathbf{x}$ (Keating and Cherry, 2004, Pearce and Boyce, 2006). The relative likelihood of a given species being present at a location with covariates \mathbf{x} , given that it is sampled becomes:

$$\log \left(\frac{f_{y=1}(\mathbf{x})}{f_{y=0}(\mathbf{x})} \right) = \beta_0 + \beta_1 x_1 + \dots + \beta_k x_k + \left(\frac{\pi_1}{\pi_2} \right) \quad \text{Equation 7-1}$$

Where π_1 represents the probability of a sampled observation (from the joint distribution of presence and available sites) being a presence record and π_2 of it being an available

record. The sampling constant, $\left(\frac{\pi_1}{\pi_2}\right)$, can be combined with the intercept, β_0 . Because I have no information on the sampling proportions, the RSF yields a relative likelihood of livestock occurrence (continuous and not constrained below 1), rather than a true probability, by dropping the intercept term.

I first included season (wet or dry) into the model and looked for interactions with the habitat variables. Since no significant interactions were found in the five datasets (i.e. no season-related effect on selection), I removed season as an explanatory variable in the regression models since, as a categorical variable, its effect would only modify the intercept (β_0) which is dropped out of the final RSF. I had unequal numbers of sightings for each individual ($\approx 30\%$ individuals only sighted once, the remaining producing between 2-8 sightings), producing samples that were not completely independent from each other. Random effects can accommodate non-independence within groups and be used to control for unbalanced designs (Gillies et al., 2006, Bennington and Thayne, 1994). However, it was decided not to include “Individual ID” as a random effect in the final RSF models for several reasons:

1. The maximum number of sightings per individual (8) is very low compared to the number of non-independent locations obtained from a GPS collar for example. I acknowledge that not all the samples are independent but recognise that scale of the issue is relatively minor.
2. 30% of individuals were only sighted once, making the estimation of a random intercept for single data points meaningless for a significant proportion of the dataset.
3. Generalised linear mixed models (GLMM) run with “Individual ID” as a random effect often failed to converge.
4. When they did converge, GLMM outputs were very similar to the corresponding generalised linear models run without the addition of a random effect.

I estimated the coefficients $\beta_1 \dots \beta_k$ in Equation 7-1, allowing for quadratic terms, and used it to create two grazing likelihood maps (one for each species) for each study area. I grouped all RSF predicted values into ten synthetic bins representing a low (1) to

high (10) strength of selection. I based bin size on histogram-equalized stretches (quantiles) that base bin levels on frequency of occurrence (Lillesand and Kiefer, 1994).

The AIC provided evidence of the most parsimonious model for each dataset but did not permit the evaluation of discriminatory performance. I used k -fold validation to evaluate the predictive success of the most parsimonious RSF model (Boyce et al., 2002). I randomly divided the livestock locations into five equal sets based approximately on Huberty's (Huberty, 1994) rule-of-thumb for the model training-to-testing ratio (only three sets for Sanetti due to smaller size of dataset). RSF models were constructed based on 80% (66% for Sanetti) of the data (training set), withholding 20% (33% for Sanetti) for evaluation (test set) for each iteration. For each withheld test set, RSF values were calculated from the model constructed with the training set. Then, one can plot the frequency of observations of RSF scores, adjusted for area, within that particular RSF-score category. A Spearman-rank correlation (R_s) between area-adjusted frequency of test livestock locations within individual bins and the bin rank was calculated for each cross-validated model. Area-adjusted frequencies are the frequency of cross-validated use locations with a bin adjusted (divided) by the area of that range of RSF scores available across the landscape. Adjusted frequencies should be highly correlated with the RSF scores if the model is a good one, i.e. indicating that the RSF model was indeed predicting the relative probability of occurrence of the organisms on the landscape. This process was repeated five times (three for Sanetti) using each 20% as a test set. A Spearman-rank correlation for mean frequency values by bins ($\overline{R_s}$) was also calculated from the full dataset.

7.3 Results

7.3.1 RSF model for the Web valley

7.3.1.1 Cattle

Four of the seven habitat variables tested indicated strong selection by cattle grazing in the Web valley (Table 7-2 & Figure 7.2). Cattle preferred pastures of lower altitudes ($t = -11.30$, $p < 0.01$) and belonging to vegetation class V ($t = 1.99$, $p = 0.05$), thereby selecting for grass and *Alchemilla* pastures, wetlands, river banks and drainage lines. The likelihood of cattle use decreased as the distance to villages increases ($t = -7.62$, $p < 0.01$), while the significant non-linear effect of the distance to the nearest *hora* ($t = -$

12.42, $p < 0.01$) indicated that likelihood of cattle use was highest at an intermediate distance of around 3 km from the mineral spring (Figure 7.3).

7.3.1.2 Caprines

Three of the seven habitat variables tested indicated strong selection by caprines grazing in the Web valley (Table 7-2 & Figure 7.2). Caprines also preferred pastures of lower altitudes ($t = -4.36$, $p < 0.01$). The significant non-linear effects of the distance to the nearest river ($t = -2.27$, $p = 0.02$) and the nearest village ($t = -5.122$, $p < 0.01$) indicated that likelihood of shoat use was highest at the intermediate distances of around 300m from rivers and 800m from villages (Figure 7.3).

Dataset	Best RSF model	\overline{R}_s
Web Cattle	Altitude + Veg_type + Dist_village + Dist_hora + (Dist_hora) ²	0.99
Web Caprines	Altitude + Dist_water + Dist_village + (Dist_water) ² + (Dist_village) ²	0.97
Morebawa Cattle	Altitude + Veg_type + Dist_water + Dist_village + Slope + Rodent + (Dist_water) ² + (Dist_village) ² + (Rodent) ²	0.98
Morebawa Caprines	Altitude + Dist_water + Dist_village + Rodent + (Dist_water) ² + (Dist_village) ²	0.98
Sanetti	Altitude + Dist_village + Slope + Rodent + (Altitude) ² + (Dist_village) ² + (Rodent) ²	0.70

Table 7-2 : Summary of the best RSF models for each of the five datasets and the corresponding average Spearman Rank correlation coefficient (\overline{R}_s) after k -cross model validation.

7.3.1.3 Model validations

Both models were successfully validated using the k -cross validation method (Figure 7.5). The average Spearman-rank correlation by bins for cattle ($\overline{R}_s = 0.99$, $p < 0.01$) and caprines ($\overline{R}_s = 0.97$, $p < 0.01$) indicate that both models predicted use locations well.

7.3.2 RSF model for Morebawa

7.3.2.1 Cattle

All six of the habitat variables tested indicated strong selection by cattle grazing in Morebawa (Table 7-2 & Figure 7.6). Cattle preferred pastures of lower altitudes ($t = -14.33$, $p < 0.01$) and grazing on more gentle slopes ($t = -3.56$, $p < 0.01$). Cattle strongly selected against vegetation class “F” ($t = -2.89$, $p < 0.01$), vegetation class “Minor” ($t = -2.49$, $p = 0.01$), vegetation class “R” ($t = -3.13$, $p < 0.01$), and vegetation class “S” ($t = -2.16$, $p = 0.03$), thereby selecting against mima mounds, *H. citrispinum/H.splendidum* shrublands, *Artemisia/Kniphofia/A. haumanii* grasslands, heather and swamp edges. The likelihood of cattle use decreased as the distance to villages increased ($t = -3.59$, $p < 0.01$). The significant non-linear effects of the distance to the nearest river ($t = -3.47$, $p < 0.01$) and rodent biomass ($t = -2.95$, $p < 0.01$) indicated that likelihood of cattle use was highest between 500/700m from rivers and in areas supporting 7/8kg of rodents per hectare (Figure 7.4).

7.3.2.2 Caprines

Four of the six habitat variables tested indicated strong selection by caprines grazing in Morebawa (Table 7-2 & Figure 7.6). Caprines preferred pastures of lower altitudes ($t = -6.88$, $p < 0.01$) and I also found rodent biomass to be a good predictor of habitat use ($t = 3.97$, $p < 0.01$). The significant non-linear effects of the distance to the nearest river ($t = -2.96$, $p < 0.01$) and the distance to the nearest village ($t = 3.95$, $p < 0.01$) indicated that likelihood of goat use was highest between 500/700m from rivers and within 100m from villages, although the likelihood increases slightly after 3.5 km (Fig 7.4).

7.3.2.3 Model validations

Both models were successfully validated using the k -cross validation method (Figure 7.5). The average Spearman-rank correlation by bins for cattle ($\overline{R}_s = 0.98$, $p < 0.01$) and caprines ($\overline{R}_s = 0.98$, $p < 0.01$) indicate that both models predicted use locations well.

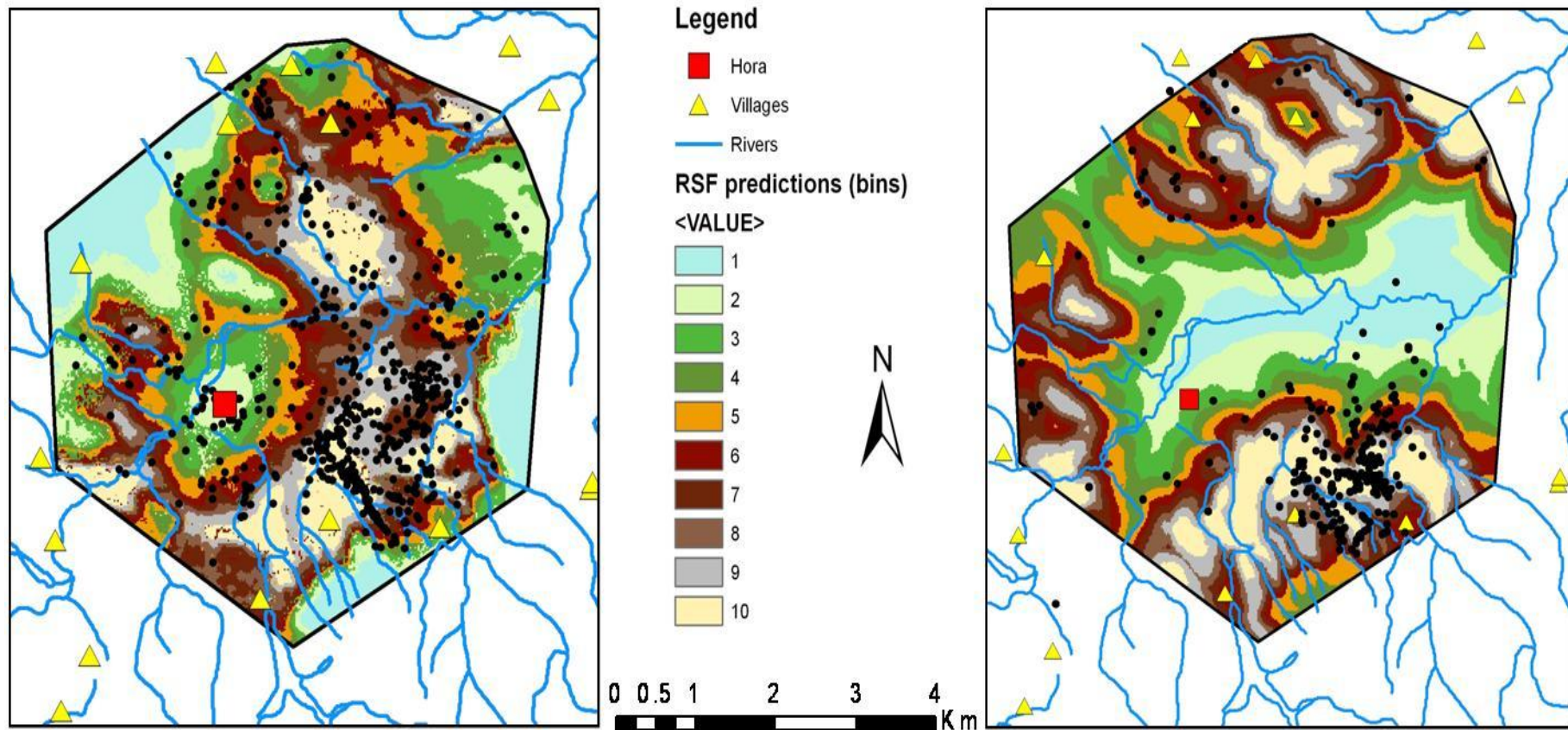


Figure 7-2: Predicted likelihood of land use by cattle (left) and caprines (right) in the Web valley. The RSF predictions are shown as bins from the lowest likelihood in bin 1 (pale blue) to the highest likelihood in bin 10 (pale yellow). The black circles represent the livestock sightings of each species within the area.

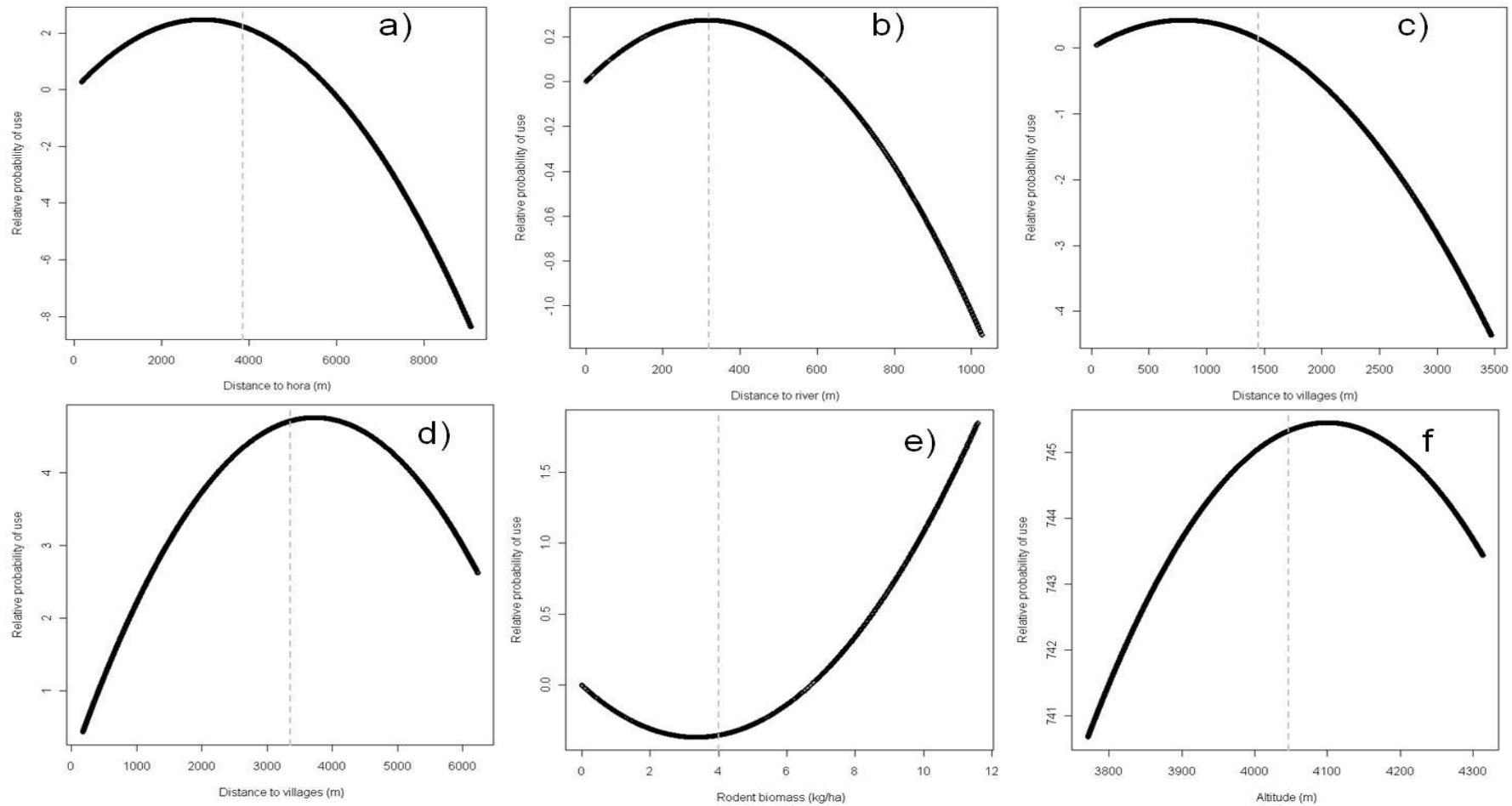


Figure 7-3: Quadratic relationships between the relative probability of use by livestock and explanatory variables: a) distance to hora (Web cattle); b&c) distance to water and distance to villages (Web caprines);d,e&f) distance to villages, rodent biomass and altitude (Sanetti).

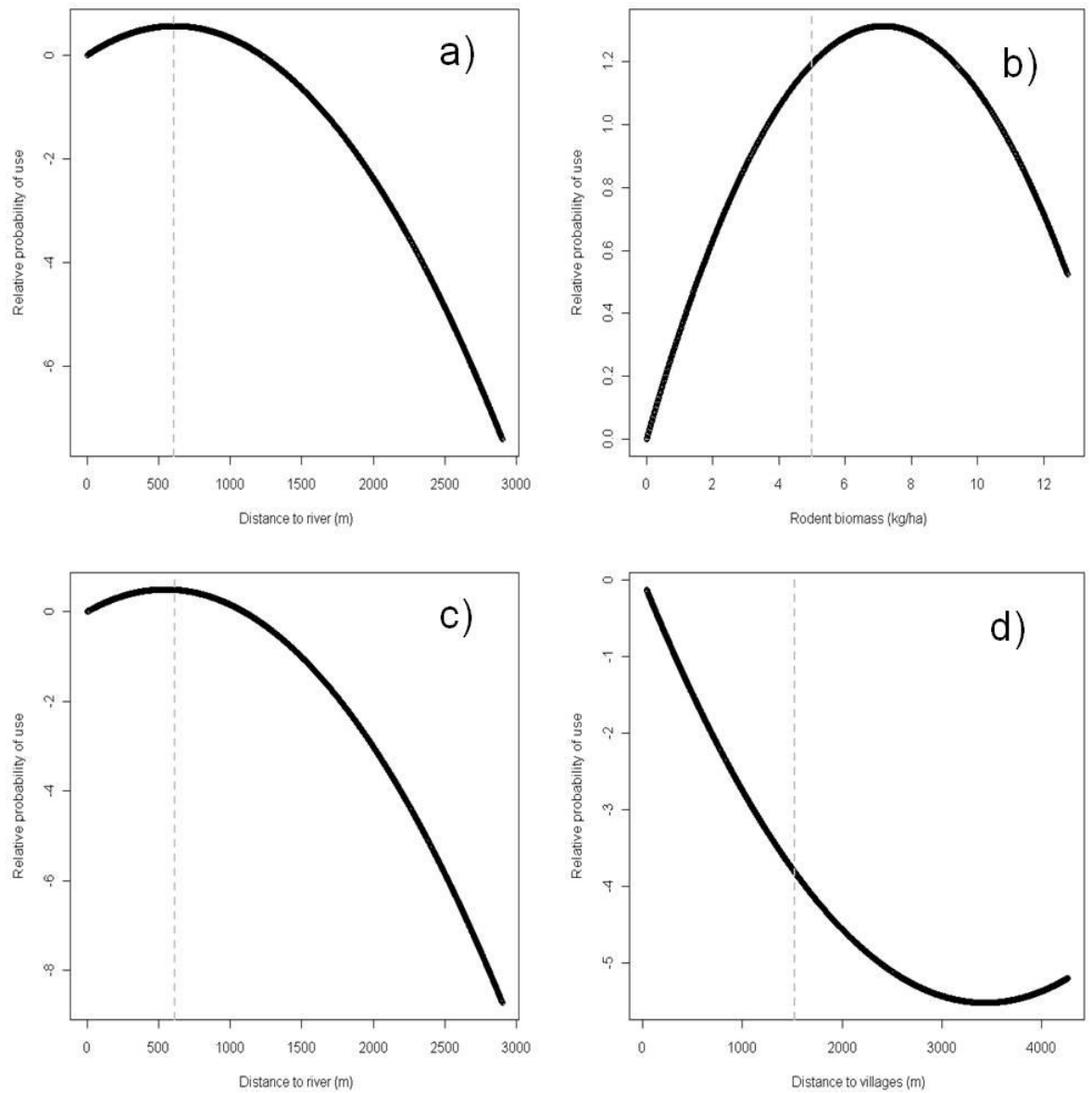


Figure 7-4: More quadratic relationships between the relative probability of use by livestock and explanatory variables: a&b) distance to water and rodent biomass (Morebawa cattle); c&d) distance to water and distance to villages (Morebawa caprines).

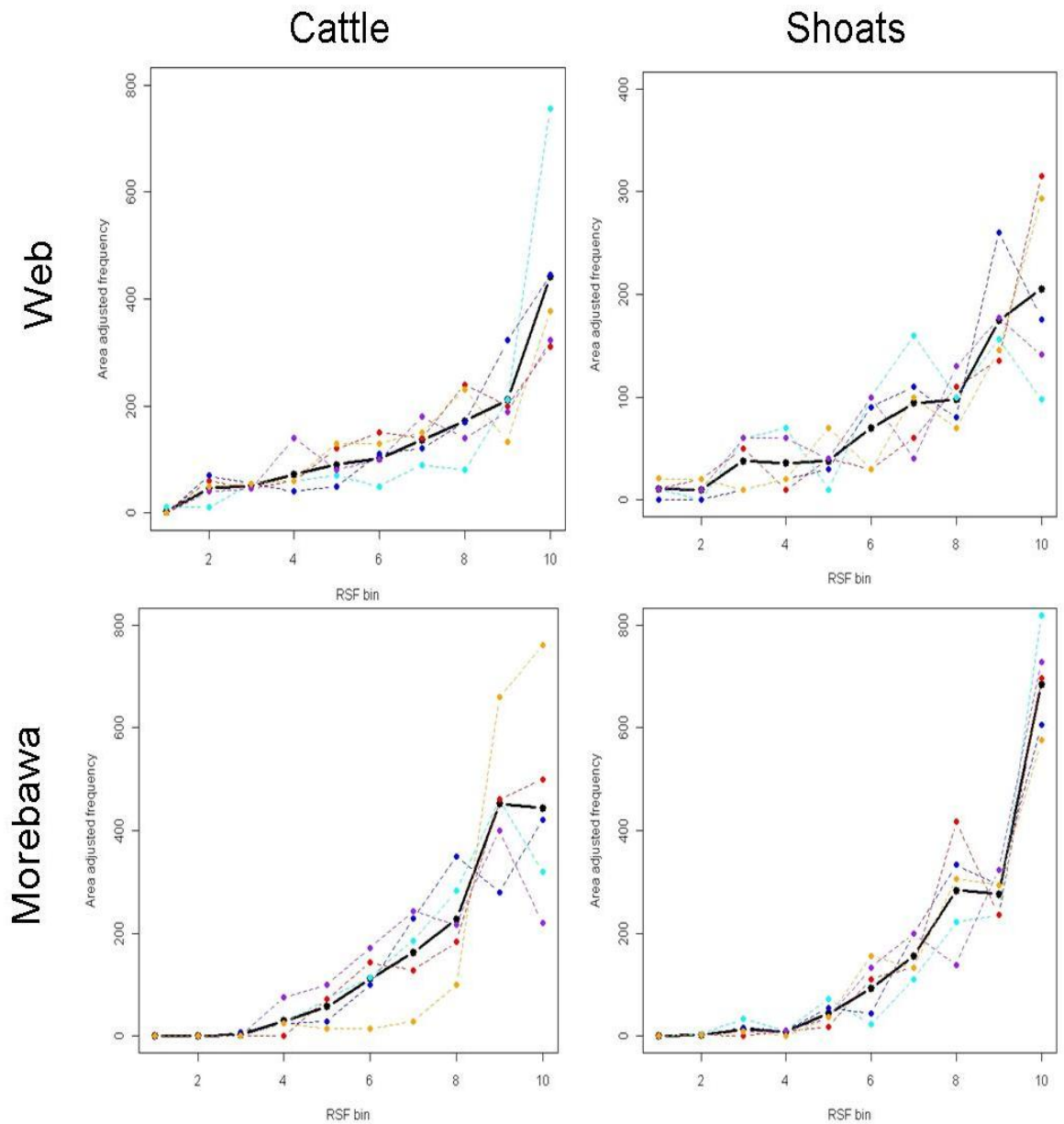


Figure 7-5: Area-adjusted frequency of binned cross-validated use locations for cattle (left) and caprines (right) in the Web valley (top) and Morebawa (bottom). Frequency values for individual cross-validation sets ($n = 5$) are depicted using unique colours, while mean frequency values by bin are depicted in black.

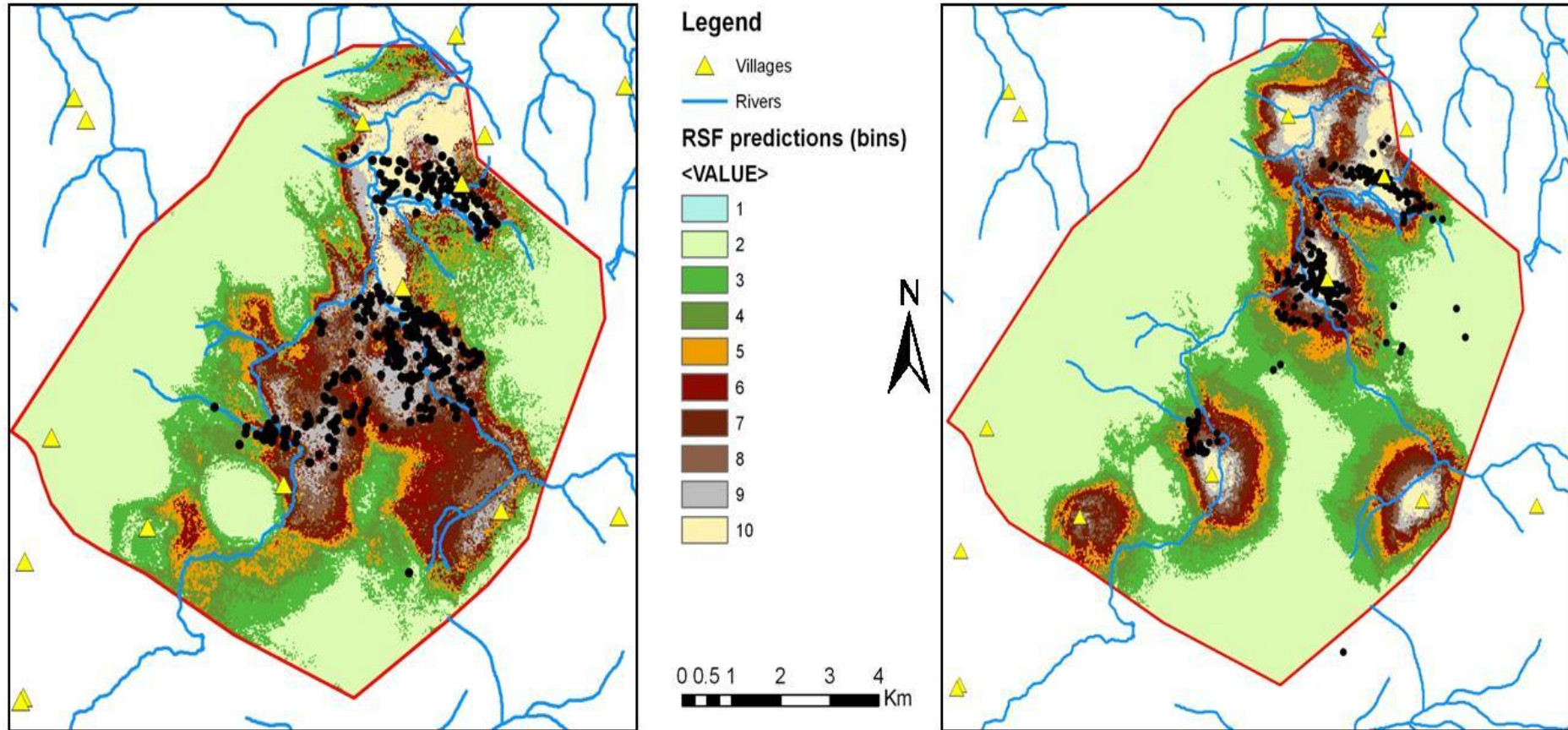


Figure 7-6: Predicted likelihood of land use by cattle (left) and caprines (right) in Morebawa. The RSF predictions are shown as bins from the lowest likelihood in bin 1 (pale blue) to the highest likelihood in bin 10 (pale yellow). The black circles represent the livestock sightings of each species within the area.

7.3.3 RSF model for Sanetti

Four of the six habitat variables tested indicated strong selection by livestock grazing in Sanetti (Table 7-2 & Figure 7.6). Livestock preferred grazing on more gentle slopes ($t = -2.34$, $p = 0.02$). The significant non-linear effects of altitude ($t = -2.33$, $p = 0.02$), the distance to the nearest village ($t = -3.75$, $p < 0.01$) and rodent biomass ($t = 3.26$, $p < 0.01$) indicated that likelihood of livestock use was highest around 4100m above sea level, and in pastures located around 4km from villages (Figure 7.3). The relationship between rodent biomass and likelihood of use by livestock is harder to interpret but indicates that the likelihood is lowest in pastures harbouring rodent biomasses around 4 $\text{kg}\cdot\text{ha}^{-1}$ (Figure 7.3).

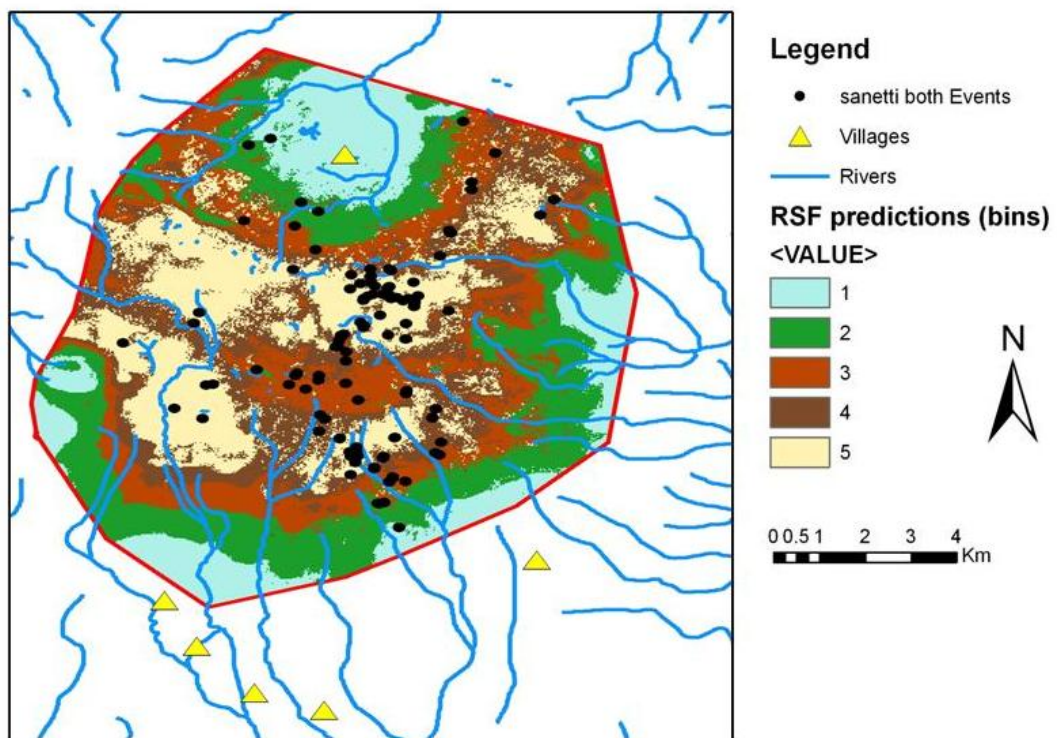


Figure 7-7: Predicted likelihood of land use by livestock in Eastern Sanetti. The RSF predictions are shown as bins from the lowest likelihood in bin 1 (pale blue) to the highest likelihood in bin 5 (pale yellow). The black circles represent the livestock sightings for both species within the area.

7.3.3.1 Model validation

The model was not successfully validated using the k -cross validation method (Figure 7.7). The average Spearman-rank correlation by bins for livestock ($\overline{R_s} = 0.70$, $p =$

0.12) indicates that the model did not predict cross-validated use locations well, most likely as a result of the very small sample size of the dataset for this area.

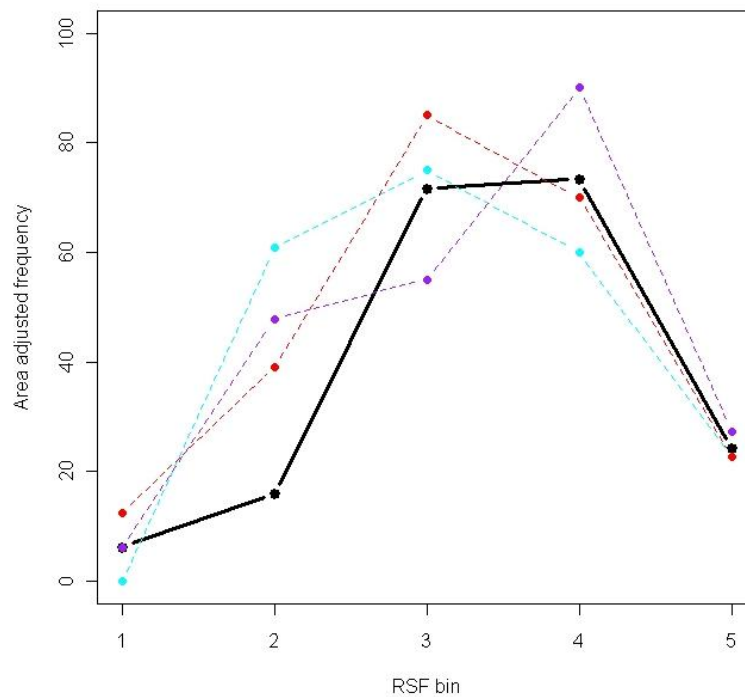


Figure 7-8 : Area-adjusted frequency of binned cross-validated use locations for livestock in Sanetti. Frequency values for individual cross-validation sets ($n = 3$) are depicted using unique colours, while mean frequency values by bin are depicted in black.

7.4 Discussion

7.4.1 Major drivers behind livestock heterogeneous use of the afroalpine

I will only discuss the drivers observed behind livestock habitat use in the Web valley and Morebawa since RSF model for Sanetti could not be validated. The limited dataset of livestock sightings for Sanetti is suspected to be the main reason behind the failure of the k -cross validation procedure and I would advocate the need to collect more data points throughout the entire plateau before attempting to produce again valid RSF for cattle and caprines for that particular area .

Distance to the nearest source of water (river or *hora*) appears to be one of the major drivers behind both cattle and shoat use of the afroalpine pastures. Many studies have observed that the physiological dependence of livestock on water results in their

activity being concentrated in the vicinity of long-lasting water, and usually dissipating rapidly with increasing distance from it (Pringle and Landsberg, 2004, Fensham and Fairfax, 2008), although it has been observed that cattle generally travel further from water than caprines (Coughenour, 1991). Interestingly, the relationship between use and the distance to water is a non-linear one. I found that the likelihood of use peaked at a distance between 300m and 700m away from the rivers (for caprines in Web and cattle/caprines in Morebawa) and 3km away from the *hora* (for cattle in Web). This observed pattern may be the result of herders actively leading cattle away from the *hora* after the herd has spent time drinking in the mineral spring (perhaps in an attempt to preserve the habitat surrounding the springs) or of cattle travelling further to graze as the grass in the immediate vicinity of the *hora* or rivers may be overgrazed. The results from the RSF reinforce the livestock use patterns I described in Chapter 3. Many studies have used the distance to the nearest source of water (Adler and Hall, 2005, Andrew, 1988, Blanco et al., 2008, Fernandez-Gimenez and Allen-Diaz, 2001, Gebremeskel and Pieterse, 2006, Gonnet et al., 2003, Nash et al., 1999, Solomon et al., 2006) to assess the impact of grazing on rangeland structure. These studies not only often assume that the probability of livestock use of an area decreases as the distance from the nearest source of water increases, but also assume that this grazing gradient operates on a very small spatial scale (sometimes less than 50m away from water). In Chapter 3, I observed with the livestock dung counts a “reverse” grazing gradient, in which the number of dung observed increased as the observer moves away from water, suggesting that livestock use of an area increased as they moved away from water. I also found that this “reverse” grazing gradient operates on a very large spatial scale with an increase of +5.8 dung pile.km⁻² per 1m from a water source (equivalent to +9 dung pile/grid per 1000m).

I also found that the likelihood of habitat use decreased in a linear fashion for cattle as the distance from the villages increased, and in a non-linear fashion for caprines for which the relative probability of use peaked at 800m and 100m from villages for Web and Morebawa respectively. Other studies have used the distance gradient from a livestock camp/village to assess the impact of grazing on rangeland structure (Hoshino et al., 2009, Sasaki et al., 2008). The results in Chapter 3 suggested that in Bale, the distance from the nearest village is not a significant predictor of livestock use of an area as revealed by livestock dung counts in the survey grids, and the RSF output predict that this is indeed the case for caprines, but not cattle.

Grazing activity has been shown to often focus on more productive, often lower-lying landscapes (Coughenour 1991). Our data demonstrate that both cattle and caprines are preferentially found on lower-altitude pastures throughout their afroalpine grazing range in Bale. It is interesting to note that some watering points which rely on surface runoff, will often be located on lower-lying grounds, possibly exacerbating the impacts of livestock on these areas (Pringle and Landsberg, 2004).

Only cattle seemed to strongly select for/against particular vegetation types throughout their grazing range in Web and Morebawa. (Senft et al., 1985). Cattle's activities in Web mainly focused on the most extensive vegetation types (grass and *Alchemilla* pastures) and on riparian plant communities and wetlands, possibly attracted to their vicinity by a source of permanent water. Cattle in Morebawa selected against low-productive vegetation types such as heather, bareground and shrub-dominated grasslands. Ungulates are known to allocate their foraging time between different habitats in proportion to their supply in several required nutrients such as protein levels (Ben-Shahar and Coe, 1992), or concentrations of sodium, phosphorus and magnesium (Seagle and McNaughton, 1992, McNaughton, 1988). For example, Belovsky (Belovsky, 1978) showed that moose (*Alces alces*) need to include in their diet aquatic plants to satisfy the requirements for sodium, while terrestrial plants were more advantageous with respect to energy intake. Similar nutrient requirements for cattle could explain the pattern of habitat selection observed here.

7.4.2 Management implications and future research

7.4.2.1 Highlighting possible ecologically sensitive areas

If selection is consistent with fitness, I should find more animals in better-quality habitats and therefore expect areas with a greater habitat use likelihood to harbour more livestock, although limited data suggests that the relationship between animal density and habitat selection may sometimes be constrained (Hobbs and Hanley, 1990, Johnson and Seip, 2008, Mitchell et al., 2005, Nielsen et al., 2005). Such prediction is worrying as the RSFs developed have highlighted a strong association between livestock use likelihood and rodent biomass in Morebawa and Sanetti for both cattle and caprines. The predicted likelihood of land use by livestock in Morebawa peaked at intermediate rodent biomass ($7/8 \text{ kg}\cdot\text{ha}^{-1}$), while in Sanetti for both cattle and caprines the use likelihood almost linearly increased with rodent biomass. The Web valley is an area of overall very high rodent biomass (Tallents, 2007), and may not present enough variation in rodent biomass for

selection by livestock to take place, especially since the livestock numbers are particularly high in the area (Chapter 3). The apparent strong association between livestock habitat use and rodent biomass is concerning as both ranges constitute low-quality habitat for Ethiopian wolves as rodent availability there is already limited, while high numbers of livestock in the optimal wolf and rodent habitat (such as the Web valley) render the threat posed by livestock to rodents (Chapter 4 & 5) and wolves (Chapter 6) ubiquitous throughout the Bale afroalpine.

The concentration of livestock around water sources such as wetlands and *horas* has serious implications for the degradation of these particular systems. Livestock tracks are a major cause of breaching (Fanning, 1994) making riparian areas particularly vulnerable to physical degradation as a result of trampling, in addition to livestock's impacts on vegetation through preferential grazing (Ash A. J. et al., 1997). As the areas around watering points become degraded as a result of intensive use by livestock, the latter travel further from water to graze, increasing the piosphere (zone of impact) so that the degraded zone around the water becomes larger (Hunt, 2001). Wetlands are one of the principal ecosystem components for the afroalpine under the Parks' ecological management programme (OARDB, 2007). The afroalpine wetlands regulate and stabilise the water flow to the arid and semi-arid areas of South-Eastern and Southern Ethiopia. The livelihoods and food security of the people in these lowland areas are highly dependent on good environmental management in the highland areas. Degradation of the rangelands surrounding the areas with permanent water will ultimately lead to increased food aid dependency in both highlands and lowlands.

7.4.2.2 Future research

The collection of data on the extent of potential threats to the afroalpine ecosystem components has been recognised as a research priority in the BMNP General Management Plan (OARDB, 2007, BMNP, 2007). The RSF models developed for livestock in this chapter contribute to providing a better understanding of the potential extent of livestock-mediated habitat degradation. However, the livestock use likelihood maps can also form the basis of future research in the park. For example, interspecific interactions between livestock and native ungulates may influence habitat use of the latter if sympatric species compete for space or food, forcing indigenous animals to use marginal habitats (Yeo et al., 1993). There are concerns that cattle may displace the endemic mountain nyala (*Tragelaphus buxtoni*) into marginal habitats in BMNP (Brown, 1969). Less than 1000

mountain nyala remain in Ethiopia, with Bale making up 95% of the total population. Displacement of this population by livestock into less suitable habitat where agriculture and settlements are expanding could seriously jeopardise the long-term future of this other endemic species. Combining our maps with GIS data on the distribution and/or the home ranges of the different nyala populations located in the Web valley may inform us whether wild and domestic ungulates show spatial or temporal partition of resources such as forage or water, and highlight areas of significant spatial overlap.

Wetlands provide many important services to the Bale region but are at the same time ecologically sensitive systems. Our results highlight the serious threat posed by the preferred use of riparian habitats and wetlands by livestock. Quantifying the effect of grazing on the hydrological system is considered a research priority by BMNP (OARDB, 2007, BMNP, 2007). Particularly, data on wetland extent and dynamics, water flow and quality as well as water retention properties of soil and vegetation and how these change when subjected to increasing livestock pressure are urgently required for the adequate management of the park's hydrological resources.

8 General discussion

Applied research should be directed at providing predictive tools for risk assessment as well as decision support for managers throughout the management process. The challenges facing grassland ecologists are considerable in striving to advise the potentially conflicting needs of agriculture and nature conservation. Growing agricultural demands and climate change will inevitably intensify the management problems and management pressures on the natural and semi-natural grasslands that remain. As seen in Ethiopia and in many nomadic pastoral areas, rangeland-based lifestyles, their associated industries and the rangeland environment are under threat. The reasons for this process include increasing human population, extreme climatic fluctuations, land-use changes and the demand from an increasingly important cash-based economy (Abule et al., 2005). As grazing pastures become scarcer and over-utilised, pastoralists are increasingly infringing on protected areas to graze their livestock on more productive rangelands.

The purpose of Bale Mountains National Park (BMNP) has been described as “to conserve the ecological and hydrological systems of the Bale mountains, including the afroalpine and montane forest habitats with their rare, diverse and endemic species while contributing to the social and economic wellbeing of the present and future generations of people locally in Ethiopia and in the wider region” (OARDB, 2007). In order to achieve this management goal the following steps need to be taken (adapted from (Yvonne, 2008)):

1. Identify threats and assess their impact on the management goal. For example, pressure from agricultural expansion, livestock overstocking, over harvesting of natural resources and settlement are high level threats that are affecting a number of ecosystem components in BMNP (OARDB, 2007).
2. Develop management objectives. These should be measurable tasks which contribute to the overall goal. For example, human settlement, cultivation and land use in BMNP planned, controlled and reduced; and ecosystem health re-established through restoration where necessary (OARDB, 2007, BMNP, 2007).
3. Particular management actions can then be developed to achieve the objectives of the management plan. For example, developing and implementing a zonation plan to secure a settlement-free conservation zones and conservation and sustainable natural resource management zones where sustainable use of natural resources will be allowed under negotiated agreements between rightful users and BMNP management (OARDB, 2007, BMNP, 2007).

4. Cost-benefit assessments of the management actions should be undertaken to determine that a net benefit (in terms of money and conservation of other services/species) of management is achieved (Kuhlman et al., 2010, Lovari et al., 2009, Suazo et al., 2009).

The afroalpine grasslands of the BMNP have been identified as one of the eight principal ecosystem components in the park's ecological management programme (alongside the hydrological system, Harena forest, Erica forest, *Hagenia*/juniper woodland, Gaysay grasslands, mountain nyalas and Ethiopian wolves). The present study on livestock grazing in Bale afroalpine grasslands directly feeds into the first two management steps identified above, i.e. assessing the impacts of livestock grazing and developing relevant management objectives.

8.1 Contributing to the understanding of afroalpine dynamics and anthropogenic threats

In Chapter 2, our analyses of the EWCP livestock time series demonstrated the persistence of a seasonal livestock production regime, similar to the traditional *godantu* system, in the Web valley. No historic data were available for Morebawa and no marked seasonality was detected in the livestock counts from Sanetti. I did not detect an overall trend in the livestock time series (1988-2007) in the Web valley, in spite of reportedly growing numbers of households there (BMNP 2007) suggesting that the area may have reached its carrying capacity in terms of livestock. In contrast, the number of livestock on the Sanetti Plateau increased over the monitoring period across all three sites, including the remote and inhospitable western section of the plateau.

Furthermore, the EWCP data also indicated that the risk of contact between Ethiopian wolves and free-roaming dogs has increased over the last two decades in wolf optimal habitats (the Web valley and central Sanetti). The greatest short-term threat to Ethiopian wolves is local decimation by diseases (mainly rabies and canine distemper) transmitted from domestic dogs (Laurenson et al., 1998), which can remove high proportions of a subpopulation within a matter of months (Randall et al., 2006) (Sillero-Zubiri et al., 1996). The ability of populations to recover from disease, and the rapidity of their recovery, is limited by the formation of breeding units, and subsequent recruitment of young to the population (Marino et al., 2006), itself largely determined by prey abundance (Tallents, 2007). Livestock grazing, through its impact on rodent populations, may thus indirectly affect the wolves' ability to bounce back from frequent disease epidemics.

In Chapter 3, I estimated, through the use of transects, the average density of livestock to be 195/149/49 tropical livestock units (TLU) per km² in the Web valley, Morebawa and Sanetti respectively. Those estimates were inevitably produced with a degree of uncertainty, as a result of experimental design, so I also report the conservative density estimates (lower 95% confidence interval) to be 125/69/13 TLU.km⁻² in the same three sites respectively, as a measure of the minimum density of livestock or “best case scenario”. I then showed the ratio of observed to maximum sustainable livestock density (calculated on the basis of mean rainfall (Le Houérou and Hoste, 1977)) to be at 4.4:1, 3.5:1 and 1.4:1 respectively (or 2.8:1, 1.6:1 and 0.4:1 under the conservative scenario). The conservative results suggest that the Web valley and Morebawa are overstocked given the rangeland predicted productivity for those areas, and that problem of overstocking is at its worst during the dry season.

Statistics compiled by the Food and Agriculture Organization of the United Nations (de Leeuw and Rey, 1995) report the major highlands of Ethiopia, Kenya, Rwanda and Burundi to be stocked at densities of 27, 66, 32, and 35 TLU.km⁻² respectively. The authors emphasise the fact that average stocking densities in Ethiopia mask large variations in space; for instance, in the South-Eastern, central and North-Western highlands, values were 87, 68 and 30 TLU.km⁻², respectively, with an overall mean of 48 TLU.km⁻² (Jahnke and Asamenew, 1983). The livestock stocking rates in East Africa tend to be higher in the highland systems than in the arid and semi-arid systems, such as the Kajiado district in Kenya, harbouring mainly Masai pastoralists and a livestock stocking rate of 32 TLU.km⁻² in the semi-arid zone and 18 TLU.km⁻² in the arid zone. Our conservative livestock density estimate of Bale afroalpine are much higher than the estimates reported for the Ethiopian highlands in the early 80's (Jahnke and Asamenew, 1983) and 90's (de Leeuw and Rey, 1995). This may reflect the rapid growth of the livestock population in Ethiopia concurrent with the population increase or may reflect the tendency of livestock censuses to underestimate the true population size as these are rarely based on direct counts but based on unreliable questionnaires or indirect information collected by government bodies. Our current conservative estimates are therefore worrying in view of the trends in livestock numbers observed in Chapter 2 in areas which appear to be already overstocked.

In Chapter 4, I described how overall rodent biomass significantly declined as the livestock index (livestock dung density) increased along a grazing gradient. However, I did not find the rodents' body condition, use of the habitat or breeding ecology and most vegetation variables measured to be affected by livestock. These particular findings led us to hypothesise that livestock may negatively affect rodents by increasing their predation risk (through removing vegetation cover) or by reducing the soil suitability for maintaining burrow systems (through trampling) rather than by competing for food resources. I could not, in the present experimental design, test these hypotheses.

In Chapter 5, I showed that Blick's grass rat (AB, *Arvicanthis blicki*) and the brush-furred mouse (LM, *Lophuromys melanonyx*) populations can respond to the experimental removal of livestock inside exclosures, although this response was species-specific and site-specific. Populations of giant molerats did not appear to significantly respond to the removal of livestock although their density inside the exclosures was more than double that of the control sites after 11 months. This particular experimental design allowed us to find some evidence that the impacts of livestock on rodent densities are concurrent with changes in the vegetation. Grazed plots harboured more rare plant species and had higher species richness and diversity compared to the exclosure sites. I observed a non-significant trend for reduced bareground inside the exclosures which may suggest that vegetation had enhanced capacities to respond to rainfall availability under ungrazed conditions. I also found that, after one wet season, the removal of livestock had a positive impact on the height of *Alchemilla* spp. and grasses, a recovery that may be ecologically significant in protecting the rodents from predators, particularly raptors. Smaller home ranges and higher reproductive success for LM inside the exclosures may be an indication that resources were more limited (or of lesser quality) on grazed sites, although I found the opposite trend for AB. This may be an indication that differences among rodent species in their responses to grazing may be mediated by interaction between the direct effects of grazing on habitat quality and species-specific habitat requirements, although the specific mechanism of this interaction (competition, increased predation and/or soil compaction) remains unclear.

The 14 months dataset from the exclosures and control sites also indicated that the impact of livestock on rodent populations were heightened during the dry season when resources were scarce and vegetation cover greatly reduced, and that livestock grazing during that critical period may have exacerbated the effects of difficult environmental conditions on rodent populations causing local population crashes. I also used the output from the dynamic trophic model developed in chapter 4 to quantify the predicted impact of livestock removal on wolf density in the Web Valley. I estimate that the removal of

livestock grazing pressure in the entire Web valley would lead to an average population increase of over 40 Ethiopian wolves corresponding to a substantial increase in the Web population.

In Chapter 6, I developed a series of simple dynamic food chain models to explore the interactions between these trophic levels and how they might be affected by livestock grazing. I also explored how predictions made about these trophic dynamics were affected by the type of functional response linking the different trophic levels. Analyses of these dynamic trophic models showed that increasing livestock density on afroalpine pastures pushed the system away from its equilibrium state. If rodent and/or wolf populations exhibit extreme type 2 responses to prey availability, they remained at densities close to equilibrium as livestock density increased, but rapidly crashed once vegetation biomass collapsed as a result of the grazing pressure. I estimated the maximum sustainable livestock density to lie between 32 and 117 TLU.km⁻², above which populations of wolves are expected to become locally extinct.

The models suggested that the pastures of the Web valley and Morebawa were likely to be incapable of maintaining wolves at current livestock densities, while the Sanetti plateau may be able to sustain only slight increases in livestock density before tipping into a trophic configuration unable to sustain wolves. This model is a first step in assessing the seriousness of conflict between pastoralists and wildlife in BMNP. The models suggested that monitoring of the afroalpine vegetation was necessary to predict changes in the wolf populations and their prey; and that areas of high conservation value already appear to be exploited unsustainably, thereby possibly affecting long-term conservation goals for the park's flagship species.

Finally, in Chapter 7, I developed and validated resource selection functions (RSF) for cattle and caprines grazing in the Web valley and Morebawa in an attempt to understand some of the drivers behind the heterogeneous use of the landscape by livestock. RSF models for Eastern Sanetti were developed but could not successfully be validated. I showed that grazing activity is focused on lower-lying pastures in the vicinity of water sources (rivers or mineral springs). Only cattle seemed to strongly select for/against particular vegetation types. I also found that the probability of habitat use is linked, in a linear fashion for cattle and non-linear fashion for caprines, to the distance from the nearest villages. The resource selection functions developed highlighted a strong association between livestock use and rodent biomass in Morebawa and Eastern Sanetti for both cattle

and caprines, suggesting that the threat posed by livestock to rodents is widely distributed throughout Bale afroalpine, not only affecting the Ethiopian wolf optimal habitat (Web valley and Central Sanetti) but also more marginal habitats in which rodent availability is already limited (Eastern Sanetti and Western Morebawa). Furthermore, the concentration of livestock around water sources such as wetlands and *horas* has serious implications for the degradation of these particular systems and the livelihoods and food security of the millions of people living in the depending lowlands.

8.2 Providing tools for the management of livestock grazing pressure.

Integrating research and practice is a fundamental challenge for conservation (Dettman and Mabry, 2008, Cabin, 2007, Nature, 2007, Turner et al., 2000). Commitments to biodiversity conservation cannot be translated into management practice unless reliable biodiversity monitoring schemes are put in place (de Bello et al., 2010). It is also of prime importance that ecologists and site managers collaborate in ensuring that sound ecological evaluations become an integral part of the design and application of management plans.

8.2.1 Developing an afroalpine monitoring system

I recommend in the first instance integrating the monitoring of biotic indicators with the monitoring of biodiversity drivers (such as environmental conditions, past and present disturbances) to track the afroalpine's response to environmental changes (de Bello et al., 2010). In line with the findings of the present study, I would strongly advocate the inclusion of vegetation productivity, and rodents (giant molerats and murine rodents) as biotic indicators and human population pressure, land cover changes, livestock grazing pressure and rainfall as biodiversity drivers. I recognise that many more exist but the above suggestions will be a useful starting point for the development of an afroalpine monitoring system.

While the EWCP datasets allows the detection of long-term trends in the encounter rate of livestock, human and domestic dogs, the datasets only cover the Web valley and Sanetti and do not enable reliable estimates of livestock densities in these areas. I would recommend the monitoring of livestock populations be extended to other areas of the afroalpine (such as Morebawa, an area of relatively high livestock density). I found distance sampling to be an effective method in estimating livestock densities within our

three study areas and I have made recommendations that have been included in the park's livestock monitoring protocol. A simpler design, such as the one used by EWCP, would be adequate for the monitoring of encounter rates should the management objective be the detection of trends in livestock numbers rather than estimating the size of the livestock population.

Data on the location of most settlements within the park as well as the number and status (seasonal/permanent) of households with them was collected by Frankfurt Zoological Society in 2007. This exercise should be repeated as frequently as logistically possible (perhaps aiming for every three to five years) and complemented by the surveillance of land cover changes around the settlements. Such information may be acquired through ground-truthing and/or use of satellite imagery whereby crops, clearings and burnt areas for example are located, plotted on a map and the scale of the anthropogenic disturbance assessed. Basic monitoring of meteorological data should also be promoted at several stations within the afroalpine and Harenna forest in the park as the amount and variability in rainfall will be a major driver behind observed changes in vegetation.

Vegetation and rodent populations make useful biotic indicators, although I recognise the need for Ethiopian wolf populations to be monitored separately as a result of chronic disease spill-over from the domestic dog populations. The monitoring of both vegetation and rodents should take place on permanent designated grids as the long-term continuity in both locations and methodology would provide a better understanding of both populations' intrinsic dynamics and cycles. Many examples of cyclic rodent populations or rodent populations prone to outbreaks have been described across many continents: voles in Northern (Erlinge et al., 1983) and Southern Europe (Lambin et al., 2006); lemmings and snowshoe hares in Northern America (Keith and Windberg, 1978, Wilson et al., 1999); leaf-eared mice in Southern America (Coates and Jaksic, 1999, Lima et al., 1999), *Mastomys* rats in Africa (Crespin et al., 2008, Leirs et al., 1996), wood mice in Asia (Bjornstad et al., 1999) and house mice in Australia (Sinclair et al., 1990). Such dynamics may be the result of temporal variation in the availability of food resources (Jensen, 1982, Andersson and Jonasson, 1986) linked to rainfall (Leirs et al., 1996) or other climatic events (Lima et al., 1999); predator-driven limit cycles (Lambin et al., 2000, Hanski et al., 1991a, Steen et al., 1990); density-dependent reproductive timing (Smith et al., 2006) or maturation (Saitoh et al., 1997); inter-specific competition (Otso et al., 2004, Hansen et al., 1999) or disease/parasites (Matthew et al., 2008). Outbreaks of *Arvicanthis* grass rats have

been reported throughout Africa (Hubbard, 1972, Poulet and Poupon, 1978) . Delany (Delany, 1986) reports that population levels of grass rats are usually low but that irregular outbreaks frequently occur. The *Arvicanthis blicki* populations in Bale, and other murid rodents, could exhibit similar dynamics. However, the lack of long-term rodent study in the afroalpine precludes the acquisition of such knowledge which could significantly alter our understanding of the trophic relationships and would help tease apart the real impact of livestock grazing and other disturbances on rodent populations from the normal “background noise” of natural population cycles.

Locating monitoring sites at particular distances from water sources (similar to the grazing gradient approach I used) can assist in the spatial interpretation of local changes as a result of varying livestock grazing pressure (Ludwig et al., 2000). The park’s new afroalpine monitoring protocol will include recommendations from Lucy Tallents (a previous rodent researcher in the park) and myself in terms of trapping locations, sample sizes, and vegetation censuses amongst others. Monitoring NDVI as another indicator of vegetation productivity through the use of freely available satellite imagery (see chapter 2) would be another simple and useful biotic indicator.

One of the often-overlooked aspects of developing a monitoring program is the provision and maintenance of central databases, in which both hard copies and electronic copies of the methodological manuals, datasheets used for data collection as well the actual monitoring data are kept and classified. Monitoring reports, copies of theses produced or scientific publications that resulted from the monitoring program could also be found in such database. It can be frustrating trying to gain access to relevant data collected by a previous researcher 20 year ago only to find that no-one has a copy of his/her Masters’ thesis or of his/her data. A surprising amount of research has been done by Ethiopian and foreign researchers in Bale over the last 25 years, but sadly, little of it is common knowledge to “new” researchers or managers highlighting the need for improvements in the effective dissemination of results to the policy community but also in the park’s ownership of the data.

One of the advantages of such databases is the ease of producing annual updates on the trends of particular threats or species. Data are often collected for several years before any attempt at analyses are made. Such an approach may result in delays in detecting methodological flaws and the development of solutions but also delays in detecting changes in population size of focus species or in levels of threats. As not all the necessary

information is usually available at the beginning of a management programme, an adaptive approach should be taken and the management objectives/goals revised throughout the management process. By responding to new (and frequently updated) information and adaptively managing the ecosystem, the management objectives may change throughout the management process, setting off a new cascade of actions, some of which may be urgently required.

8.2.2 Livestock exclosures as long-term research and management tools

The livestock exclosures built in 2008 for the purpose of this study have been donated to BMNP authorities to be used as long-term monitoring and research tools for the benefit of the park and the future researchers interested in the study of grazing impacts in Bale. The first 14 months of livestock exclusion have already produced results that can form the basis of a livestock management policy. Excluding livestock grazing on parts of Bale's *Alchemilla*/grass pastures, especially during the drier months, could benefit some rodent populations. However, the site-specific nature of rodent and vegetation response to the removal of grazing illustrates the necessity to consider such management option at the landscape level as the impact assessment of grazing treatment may not produce significant differences at a smaller habitat-scale (Alzerreca et al., 1998, Stohlgren et al., 1999, Kelt and Valone, 1995). The results may also indicate that degraded afroalpine pastures may not necessarily recover by simply removal of grazing pressure and they may, at some point in time, require active rehabilitation efforts to sustain natural processes (Curtin, 2002, Souter and Milne, 2009).

The short-term monitoring of the livestock exclosures has offered some lessons in ecosystem management. First, they highlight the need for the monitoring of crucial indicators of the system state and variability before the beginning of any management action, and the maintenance of unmanaged areas as "biological preserves" in case of negative impact and as controls for statistical testing of impact (Schtickzelle et al., 2007). Then, when management actions will affect habitat quality, species (as illustrated in our exclosure experiments by rodents) that vary in habitat requirements will not respond to the actions in the same way. When all these species are of conservation concern, trade-offs between them are inevitable and the selection of appropriate management actions will become less straightforward (Astrid et al., 2008, Suazo et al., 2009).

8.3 Recommending directions for future research

Stewart and colleagues have suggested an approach to decision-making called “evidence-based framework” (Stewart et al., 2005). The two key features of this framework are:

1. “The systematic review of evidence on effectiveness of actions in a comprehensive and objective manner, then disseminated effectively into practice and policy communities”. I briefly touched upon this point in sections 1.2.1 & 1.2.2.
2. “The objective identification of knowledge gaps and prioritisation of areas of primary, needs-led research.”

The present study has highlighted knowledge gaps in the basic ecology of some of the components of the afroalpine system. In particular, data on the following components would have helped with the interpretation of our results as well as improved our model predictions. Limited information is currently available on the diet of the commonest diurnal rodents in Bale (Yalden, 1975). The collection of additional field data would require snap-trapping individuals and carrying out stomach content analyses (see (Clausnitzer, 2003) for detailed methodology of the investigation of diet and food preferences in afroalpine rodents of Mt Elgon, Uganda). As diet is expected to change with resource availability, itself largely controlled by rain, trapping sessions should be planned in both the dry and wet seasons in order to get a more complete picture of resource selection in those rodents. These additional data would allow us to understand better the extent to which livestock-driven changes in the vegetation are likely to impact on the feeding ecology and fitness of rodent populations.

The results of the elasticity analysis carried out in Chapter 6 suggests that the trophic model would benefit greatly from more accurate estimates of the afroalpine vegetation instantaneous growth rate (productivity, b_v) and of the maximum vegetation standing crop in the afroalpine (K_v) in Bale in the absence of livestock grazing. Both variables could be measured inside the livestock exclosures by cutting, drying and weighing vegetation inside smaller fenced-off 1m^2 plots inside which rodents were excluded. One of the major logistical issues that prevented those measurements from being taken during the present study was the difficulty in providing a reliable and constant power source over several days in order to process vegetation samples in a drying oven.

Canids are known to display functional responses to variation in prey availability, especially in situations where human-induced changes in land use increase spatial heterogeneity in prey availability (Pia et al., 2003). In Bale, the contribution of different species of prey to the diet of the Ethiopian wolf correlates with abundance of prey (Sillero-Zubiri and Gottelli, 1995). Circumstantial evidence also suggests that wolves may predate more frequently on livestock, or become crepuscular or nocturnal when human interference is severe in densely populated areas (Marino, 2003a). It would therefore be very interesting to explore whether predation pressure on changes as a function of grazing pressure. It is possible that by changing their diets as a response to diminishing rodent densities, Ethiopian wolves and raptors may be more resilient to an increase in livestock density than currently shown by the trophic model (Chapter 4) for example.

Trampling and soil compaction by livestock may affect the habitat quality for the rodents by reducing the soil suitability for building and maintaining burrow systems (Torre et al., 2007) or leads to vegetation changes the impact of which may be delayed for small mammal populations (Mwendera et al., 1997). I suggest that evidence for such a mechanism be tested in afroalpine ranges in Bale in the light of the lack of conclusive evidence I have found of exploitative competition between livestock and rodents (Chapter 5). Soil compaction along with increased predation risk may both be important to explain the indirect effect of livestock grazing on the rodent population in Bale.

The refining of some methodological protocols would lead to significant improvements in the data collection so as to reduce biases and increase the precision of both direct (distance sampling) and indirect (dung counts) estimates of livestock densities (Elphick, 2008). Frequently re-enforcing observer training as well as the provision of range finders would contribute to more accurate distance estimates, while larger-scale dung production and dung decomposition experiments would reduce the standard errors associated with these estimates and perhaps ameliorate the mis-match between direct and indirect density estimates for livestock. Failing that, it may be possible to use the additional data to improve inference by quantifying and correcting for biases through the development of statistical methods retrospectively (Elphick, 2008).

Wetlands provide many important services to the Bale region but are at the same time ecologically sensitive systems. The results from Chapter 7 highlight the serious threat posed by the preferred use of wetlands by livestock. Quantifying the effect of grazing on the hydrological system is considered a research priority by BMNP (OARDB, 2007,

BMNP, 2007). Particularly, data on wetland extent and dynamics, water flow and quality as well as water retention properties of soil and vegetation and how these change when subjected to increasing livestock pressure are urgently required for the adequate management of the park's hydrological resources.

8.4 Final thoughts

Rodents in Bale are likely to be playing as important a role as ecosystem engineers as plateau zokors (*Myospalax fontanierii*) on the alpine meadows of Tibetan plateau, pocket gophers (*Geomys spp.*) and prairie dogs (*Cynomys spp.*) in Northern American ranges. They have profound impacts on the afroalpine ecosystem from consuming vegetation to physically altering the soil, and maintaining an heterogeneity which may be important to community dynamics and biodiversity. Unlike these other species, rodents in Bale are not yet considered as pests.

The high alpine grasslands of the Qinghai-Tibetan plateau have supported pastoralism of domestic yaks (*Bos grunniens*) and Tibetan sheep (*Ovis aries*) for approximately 2200 years. In recent decades, numbers of livestock have increased rapidly, the abundance of medium to large native mammals has been greatly reduced and rangeland productivity greatly decreased (Arthur et al., 2008). Botulinum C toxin has been spread over 320,000km² of these rangelands in an attempt to eradicate populations of plateau pika (*Ochotona curzoniae*), a lagomorph, and plateau zokor suspected to contribute to rangeland degradation and decreasing livestock productivity (Harris, 2010). The poisoning of these ecosystem engineers has already been shown to have an effect on the ground-nesting avian diversity of the plateau (Arthur et al., 2008), and now plateau zokors have been extirpated across much of the plateau (Zhang et al., 2003).

Pocket gophers and prairie dogs have also traditionally been viewed as competitors with cattle for rangeland resources in North America and have previously been the subject of large-scale eradication campaign. Beginning in 1915, a variety of federal agencies were responsible for implementing prairie dog eradication programs, which still continues in some states. There has been an estimated 98% decline in the prairie dog population (Miller et al., 1994). The semi-arid grasslands of the Janos region of northern Chihuahua, Mexico, support one of the largest (14,796 ha) remaining complex of black-tailed prairie dogs (*Cynomys ludovicianus*) on the continent. Intensive cattle grazing and drought have resulted in a 73% decline in the prairie dog colony complex (55,000 ha) since 1988

(Ceballos et al., 2010). The half million hectare Janos Biosphere Reserve was created in 2009 to help conserve grasslands, prairie dogs and regional biodiversity in a way that is compatible with human economic activities, especially grazing and agriculture. Cattle are used to open grasslands and allow prairie dogs to recolonise them more rapidly, while fire and rodents can help prevent bush encroachment and expand the more productive grasslands for the benefit of cattle.

It is of course too early to judge the success of the Janos Biosphere Reserve but the federal government of Mexico's attempt has to be saluted. Conservation is in essence a political process, and human-wildlife conflicts, by definition, involves people, and an understanding of stakeholder attitudes, beliefs and values, together with dialogue between the main actors, is essential in mitigating conflict (Redpath et al., 2004). Rangeland degradation is a global concern, affecting not only pastoralists who rely on healthy rangelands for their livelihoods but also others who suffer from resultant hydrological disturbances, commodity scarcity and social consequences of uprooted people. Rangeland health also affects biodiversity directly and indirectly as all native flora and fauna have adapted to the long-term evolutionary forces that have shaped these rangeland environments. It is logical to see an increasing interest in the development of livestock grazing management strategies that achieve environment sustainability and maintain long-term livestock production capacity. BMNP is not an isolated case in this respect as more and more rangeland managers, inside protected areas or not, find that they have to tackle together biodiversity conservation and development issues.

The Gobi Gurvansaikhan national park (GGNP) in Mongolia was established in 1993 and is used by over 1000 pastoralist families and over 200,000 herds of livestock. There are several nationally and globally threatened and endangered species within the park, including the Mongolian gazelle (*Procapra gutturosa*) and snow leopards (*Uncia uncia*) (Reading et al., 1999). The GGNP lost at least two wild ungulate species, the elk (*Cervus elaphus*) and Przewalski's wild horse in the twentieth century. The socio-economic problems faced by those herders are associated with Mongolia's transition to a market system started in the 1990's, coupled with the expansion of protected areas (30% of Mongolia protected by 2030, (Enebish and Myagmarsuren, 2000)). Herders now have to adapt to both the current economic system and changes in land use. Socio-economic research in the park in 2000 has identified a number of issues, including a significant increase in the number of herds and the size of herds, problems with marketing livestock products, declining stock movement and competition and conflict for grazing areas (Bedunah and Schmidt, 2004). The GGNP restricts grazing in Special Use Zones but allow

livestock grazing in large areas in an attempt to demonstrate that conservation of resources and continuation of traditional communal grazing use can go hand in hand. One of the challenges faced was allowing enough time to identify stable and cohesive community groups to take part in participatory initiatives. One participatory planning project that has so far met with some success is the Shavartai community whose members have agreed on dates for moving livestock to summer grazing grounds and on areas reserved as winter pastures, as well as agreeing not to use protected spaces as fuelwood. So far, adherence to these norms has been high and the group has perceived improvements in their economic and social status as well as in livestock and pasture conditions (Bedunah and Schmidt, 2004).

The situation in GGNP and BMNP present an opportunity to develop a collaborative resource management approach to these rangelands. This type of resource planning is challenging because users of these communal grazing lands will need large areas which will require coordination, which can only result from an intensive effort on the part of the government, including park administrators and the users. The conservation of protected areas' resources and the sustainable use of communal grazing lands will depend on the recognition of the values of each, a strengthening of the local institutions of the users and their co-operation with the government, as well as on policy and macro-economic aspects.

This understanding was made clear in the park's 2007 GMP, drafted at a time when BMNP was governed by the Oromia regional government. The Sustainable Natural Resource Management (SNRM) Programme, then adopted, provided a framework for the development and implementation of sustainable natural resource management in BMNP (OARDB, 2007, BMNP, 2007). The core framework of this programme ultimately involves setting up natural resource management agreements with community management groups in designated Conservation & SNRM Zones. No consumptive or damaging use of natural resources and no settlements will be permitted, within the Conservation Zone, which will represent just over 50% of BMNP. In the SNRM Zone, sustainable use of natural resources will be allowed under negotiated management agreements between rightful users and BMNP management.

Unfortunately, the BMNP has now, since 2009, returned under the control of the Ethiopian federal government, whose hard-line policy of excluding all local communities from the BMNP cannot be enforced on a sustainable basis. The reality is that the

population of Ethiopia is expected to triple to an estimated 170 million people by 2050 (Thorton et al., 2002). Although human population limitation, either by migration off core conservation zones, or by controlling population increase inside “buffer” zones, will have to form the basis of any long-term policy for BMNP, such process, to be successful, must be accompanied by the development of more efficient grazing management techniques (Holling, 1986), economic diversification (Holling, 2001) and providing local communities with a better access to education and health services. The predicted reduced capacity of degraded rangelands to absorb the results of unsustainable resource use, in view of climate change and demographic pressures, makes those changes necessary at an increasing pace.

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