THE EFFECTS OF ELEPHANTS AT LOW DENSITIES AND AFTER SHORT OCCUPATION TIME ON THE ECOSYSTEMS OF THE EASTERN CAPE PROVINCE, SOUTH AFRICA

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This thesis is dedicated to the memory of my Dad

MICHAEL HENRY PARKER (1952-2006)

I'll never forget all the wonderful hours we spent in the bush together!

ABSTRACT

Elephants (*Loxodonta africana*, Blumenbach) are recognised as keystone herbivores and ecosystem engineers in African ecosystems due to the noticeable impact they have on plant communities. This impact can influence other animal taxa and ecosystem processes, especially within enclosed systems. I investigated the effects of elephants in four vegetation types and the cascade effect on three associated taxa and two ecosystem processes at five sites with elephants and five paired sites without elephants in the Eastern Cape Province, South Africa, between April 2005 and July 2007. In grassland habitats, the physical structure of the vegetation was neither enhanced nor degraded in the presence of elephants. Within the locally important Thicket Biome, elephant browsing transformed relatively homogeneous stands of vegetation into more heterogeneous units. However, although seeds from thicket plant species were recorded in elephant dung, elephants did not promote the viability and germination success of these plants. In addition, elephant foraging on aloes caused declines in their populations. By contrast, the size of bushclumps was not reduced in the presence of elephants in bushclump savanna. The associated insect, bird and mammal communities appeared to benefit from elephant foraging in all vegetation types assessed, whereas vegetation patch dynamics and soil surface processes were neither enhanced nor degraded in the presence of elephants. I conclude that, at current densities, elephants do not (in most cases) negatively affect plant and animal communities or ecosystem processes in enclosed reserves. However, elephants have only been present at each site for a relatively short period and it is likely that their impact will be cumulative, increasing over time in these closed systems. Thus, future research along a continuum of elephant density and time since re-introduction is recommended.

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CHAPTER 1

GENERAL INTRODUCTION

Large mammalian herbivores (defined as those > 5kg) can influence ecosystem composition and function (Vesey-FitzGerald 1973; Cumming 1982; Tilghman 1989; Bergström 1992; McInnes *et al.* 1992; Hobbs 1996; Augustine & McNaughton 1998). Their effects can range from alteration of vegetation structure, affecting animal and plant species distribution in time and space (McInnes *et al.* 1992; Moolman & Cowling 1994; Cumming *et al.* 1997; Keesing 1998) to preventing regeneration or seedling growth of plants through feeding, trampling pressure and seed predation (Pellew 1983; Tilghman 1989; Ruess & Halter 1990; Cumming & Cumming 2003; Cairns & Moen 2004). Through selective feeding, large herbivores are also capable of decreasing the quantity of plant litter deposition, which is a major source of soil nutrients in some ecosystems (Persson *et al*. 2005). In addition, when linked to dramatic changes in climate (e.g. during a drought), the impact of large herbivores can be further exacerbated (Cairns & Moen 2004). However, it has been suggested that grazing by large herbivores can reduce the intensity of inter-specific competition between plant species within existing vegetation, allowing tree seedlings to establish (Cairns & Moen 2004). Furthermore, some large herbivores play significant roles in seed dispersal, especially species that move large distances and can transport seeds far from the parent plant (Lewis 1987; Lieberman *et al.* 1987; Cairns & Moen 2004).

In African savanna ecosystems, the proportion of herbaceous and woody plants is governed, to a large extent, by fire and large herbivores (Buechner & Dawkins 1961; Ruess & Halter 1990; Bergström 1992; Bowland & Yeaton 1997; Barnes 2001). Fire is responsible for preventing seedling growth and bush encroachment in grassland habitats when grass sward height and density are high (Buechner & Dawkins 1961; Barnes 2001). On the other hand, large herbivores are capable of inhibiting the growth of seedlings and small trees, and causing tree death (Ruess & Halter 1990; Bond & Loffell 2001; Birkett 2002). The combined effects of fire and large herbivores upon ecosystems can result in open woodlands being converted to grassland, and forest converted to open woodland (Buechner & Dawkins 1961; Pellew 1983; Barnes 2001). Such effects within confined areas (such as fenced game reserves), where the traditional migration patterns of large herbivores have been restricted, can thus artificially alter the dynamics between woody and herbaceous plants. Browsing by large herbivores on tree saplings can prevent the vertical growth of the saplings, and maintain the trees within the fire-susceptible height class (Pellew 1983; Ruess & Halter 1990; Barnes 2001). Thus, woodland regeneration and consequently available browse for consumption by large herbivores can become limited. In addition, changes in plant species distribution or even species extinctions may occur (Penzhorn *et al.* 1974; Barnes 2001; Bond & Loffell 2001).

Alteration of woodland structure and composition by large herbivores has been linked to losses of particular habitat-dependant plant and animal species, increasing the potential for overall losses in biodiversity (Cumming *et al.* 1997; Gillson & Lindsay 2003). Species diversity (number and kind of species) influences ecosystem processes by mediating energy and material fluxes and potentially altering the abiotic conditions (Chapin *et al.* 2000). Species diversity also enhances the resilience and resistance of ecosystems to environmental change (Chapin *et al.* 2000; McCann 2000). However, empirical data from the Kruger National Park in South Africa suggests otherwise (Kennedy *et al*. 2003). The authors demonstrated that both species-rich and species-poor grasslands were able to regain pre-drought standing crop once normal rainfall resumed, demonstrating the resilience of African savanna ecosystems (Kennedy *et al.* 2003).

It has long been argued by ecologists that once large herbivores exceed some sort of carrying capacity for their habitat that they should be removed to prevent losses in biodiversity, and thus restore the ecological balance of the ecosystem (Gillson & Lindsay 2003). Such a paradigm was central to the ecological thinking that dominated much of the applied research during the twentieth century (Van Aarde *et al.* 2006). According to this view, savannas are regarded as stable ecosystems that function at, or close to, equilibrium determined by abiotic factors (Peel *et al.* 1999; Gillson & Lindsay 2003). Under this view, it is assumed that vegetation reaches a climax , whereby it provides a stable resource for the herbivores of the ecosystem (Peel *et al.* 1999). The herbivore communities would continue to persist and increase until the ecological carrying capacity was reached, at which point herbivore populations would become self-regulating through density-dependant processes (e.g. competition for food), their reproduction would be limited and they would be forced to disperse to other areas of available habitat (Gillson & Lindsay 2003). However, it is now accepted that ecosystems and their fundamental components (species, populations and communities) are rarely at equilibrium and interact in a dynamic manner, especially semi-arid landscapes in Africa (Peel *et al.* 1999; Gillson & Lindsay 2003; Owen-Smith *et al.* 2006; Van Aarde *et al.* 2006). The concept of a carrying capacity was first developed for commercial livestock husbandry (economic carrying capacity), in order to maximise the productivity of individual animals for financial gain (Fritz & Duncan 1994; Peel *et al.* 1999; Gillson & Lindsay 2003). Thus, extrapolating the concept of carrying capacity to biodiversity conservation is extremely problematic, especially when one considers the contrasting goals of commercial farming and biodiversity conservation (Gillson & Lindsay 2003). In addition, the management of ecosystems on a carrying capacity basis implicitly assumes that vegetation condition remains constant (i.e. at equilibrium) and does not take into account the inherent variability of the system (Peel *et al.* 1999; Gillson & Lindsay 2003; Owen-Smith *et al*. 2006). Consequently, under this view the impact of large herbivores on the environment is often perceived as being negative.

Significant habitat modification by large herbivores is frequently viewed as undesirable in terms of the seemingly long term, irreversible effects on ecosystem stability and diversity (Gillson & Lindsay 2003; Western & Maitumo 2004). However, scientific evidence is at most equivocal. Evidence of wholesale losses in biodiversity and dramatic (negative) effects on ecosystem functioning due to the impact of large herbivores are difficult to find. For example, an increase in elephant (*Loxodonta africana*, Blumenbach) and other large herbivore numbers in the Chobe National Park, Botswana resulted in the replacement of large proportions of the riverine vegetation along the Chobe River with grassland and removal of almost all of the tall trees in the adjacent vegetation types, which were replaced by shrubs (Skarpe *et al.* 2004). This dramatic modification of the vegetation, which recent research suggests is what the environment would have looked like prior to ivory hunting and the rinderpest (Skarpe *et al*. 2004), created and enhanced small-scale variation, which was reflected in the species composition of the small mammal community (Skarpe *et al.* 2004). Even the pioneering work of Cumming *et al.* (1997) who tested the effects of elephants on woodland diversity cannot be regarded as unequivocal. Despite demonstrating that the species richness of woodland birds and ants were significantly lower in impacted sites, there was no difference between the species richness of woody plants, bats or mantids in impacted and non-impacted sites. Herremans (1995) also found that elephant modified habitats in Botswana supported a wider range of bird species than un-modified habitats. The concept that disturbance and change (by large herbivores) within an ecosystem builds rather than erodes diversity, by generating spatial and temporal heterogeneity, is embodied within the non-equilibrium paradigm. In addition, overgrazing (disturbance) by large herbivores will continue to be either inconsequential or beneficial as long as only small areas are affected (Owen-Smith *et al.* 2006). However, one of the reasons for the equivocal data with regards to the influence of large herbivores on biodiversity is that previous studies have lacked experimental manipulation coupled with long-term data collection. In a manipulative experiment in Kenya, Goheen *et al*. (2004) demonstrated that rodent and homopteran densities were lower in the presence of large herbivores (elephants and giraffe, *Giraffa camelopardalis*, L.). However, the reduced densities of these smaller herbivores (rodents and insects) resulted in the increased survival of *Acacia drepanolobium*, Sjostedt, seedlings, despite the presence of the large herbivores (Goheen *et al*. 2004). This example highlights the potential for facilitation by large herbivores (see below).

The "intermediate disturbance hypothesis" proposes that diversity will be highest at intermediate levels of disturbance within an ecosystem (Miller 1982). Without any disturbance in an ecosystem there is a tendency towards a loss in biodiversity because dominant species out-compete others (Gillson & Lindsay 2003). Conversely, too much disturbance can also result in a loss of diversity, as only a few extremely tolerant species are able to survive (Miller 1982). At intermediate levels of disturbance, competitive exclusion can reduce the abundance of a dominant species, by increasing a limiting resource (e.g. space), or by increasing the patchiness/heterogeneity of an area (Gillson & Lindsay 2003). Such disturbances influence both plant and animal communities. In general terms, disturbance effects on animal communities are much less dramatic than those on plant communities, especially at small spatial scales (Cramer & Willig 2005). In addition, relatively small disturbances are only likely to affect those attributes of diversity of an animal community that are sensitive to the relative abundance of species and not species richness (Richardson-Kageler 2004; Cramer & Willig 2005). For example, Cramer & Willig (2005) demonstrated that “blowouts” formed by wind, consisting of open sand and very little vegetation, within a dense shrub-dominated vegetation matrix in North America, affected the species abundance of the rodent community, but not the presence or absence of individual species. By contrast, it has been shown through modeling that severe disturbances, which reduce vegetation cover below a threshold level, result in the focusing of herbivore grazing on the remaining patches (Van de Koppel *et al.* 2002). This may eventually lead to the collapse of the vegetation on a large scale (Van de Koppel *et al.* 2002). For a spatially heterogeneous disturbance (such as tree removal by elephants), reduced plant cover in an area could result in increased water availability for remaining vegetated patches, and increased localised plant growth (production). Thus, the spatial interaction between the lateral exchanges of water acts as a negative feedback to decrease plant cover. The response of the vegetation to changes in cover is thus dynamic. If water redistributes quickly and herbivore density responds weakly to changes in within-patch production, then the effect of the improved water availability is greater than the increased grazing (on the remaining patches) and the ecosystem compensates for the disturbance (Van de Koppel *et al*. 2002). However, if the herbivores redistribute quickly in response to localised changes in plant production (patchiness), then the effects of the increased grazing may be greater than the improved water availability for the plants, resulting in reduced cover and decreased production, which will cause the collapse of the vegetation on a large scale (Van de Koppel *et al.* 2002). The potential for vegetation degradation is highest when the fine-scale (square metres) movements of herbivores are un-restricted, but large-scale (square kilometres) movements are restricted e.g. enclosed systems such as fenced game reserves (Van de Koppel *et al.* 2002).

It is clear that ecosystems are in a constant state of flux, not equilibrium, and that certain levels of disturbance are crucial in promoting biodiversity within these ecosystems. However, animal and plant communities respond differently to varying levels of disturbance depending on the scale and frequency of the event (Miller 1982). Importantly, large herbivore impact (disturbance) in enclosed areas, where large-scale movement is restricted, may have cumulative effects on ecosystem functioning.

Some species are capable of imposing stronger effects on ecosystem processes compared to others, thereby directly affecting the processes and the rates at which they occur (Chapin *et al.* 2000). Often referred to as functional or keystone species, these species play a disproportionately large role in ecosystem functioning. Some keystone species are also classified as ecosystem engineers. Jones *et al.* (1997) defined ecosystem engineers as "… organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. Physical ecosystem engineering by organisms is the modification, maintenance, or creation of habitats. The ecological effects of engineering on other species occur because the physical state changes directly or indirectly control resources used by these species.” Ecosystem engineers can have both positive and negative effects on species richness and abundance on a local level, depending on the types of changes and their magnitude, the resources that are affected, the number of species dependent on these resources, and the adequacy of these resources to support persistence in the new habitat (Jones *et al.* 1997). However, on a large scale the negative effects of an ecosystem engineer are probably ameliorated by the creation of a mosaic of engineered and non-engineered habitats that are more likely to promote species richness (Jones *et al.* 1997) much in the same way as the habitat heterogeneity and “intermediate disturbance” hypotheses predict. Linked to the concept of ecosystem engineering and keystone species is the notion of facilitation (Bruno *et al.* 2003). Bruno *et al.* (2003) contend that facilitative (or positive) interactions between organisms benefit at least one of the participants and harm neither. Such positive interactions can occur when one organism makes the local environment more favourable for another either directly or indirectly (Bruno *et al.* 2003). In the past, many keystone species have been considered to be “competitive dominants”, capable of excluding other primary space holders and decreasing diversity within an ecosystem. However, by providing habitat for numerous small species, their net effect may in fact be positive (Bruno *et al.* 2003). Similar to the effects of disturbance, it is important to consider the spatial scale of the interaction when incorporating facilitation into ecological thinking and research (Bruno *et al.* 2003).

Elephants are recognized as a keystone species in African savanna ecosystems, due to the profound influences they impose upon community structure and ecological processes (Ruess & Halter 1990; Cumming *et al.* 1997; Cowling & Kerley 2002). Elephants also occur in herds, and usually at relatively high densities. In addition, elephants constitute one of the largest proportions of herbivore biomass in many African savanna ecosystems (Van de Koppel & Prins 1998). Thus, elephants, in addition to being keystone species, are also prime examples of ecosystem engineers (Jones *et al.* 1997).

In order to understand the impacts that elephants may have on ecosystems and ecosystem processes, it is necessary to understand the feeding strategy that they employ (O'Connor *et al.* 2007). Being the largest living land mammal (4-6 tons), elephants have relatively low basal metabolic rates, but high absolute energy requirements (Owen-Smith 1992; O'Connor *et al.*2007). Thus, elephants require large amounts of forage (~150kg fresh weight for females and ~300kg for males) in order to satisfy their daily metabolic requirements (Owen-Smith 1992; O'Connor *et al.* 2007). They achieve this by increasing intake rate, spending the majority of the day foraging and increasing digestive throughput (Owen-Smith 1992). Theory predicts that large herbivores, like the elephants, will be generalist feeders, maximising input at the expense of including high-quality forage in their diet (Bell 1971; Jarman 1974; Illius & Gordon 1992). Since high-quality forage is patchily distributed in the environment, selective feeding is energetically prohibitive for elephants. Thus, they tend to forage on large amounts of low quality forage that is available in higher quantities (Bell 1971; Illius & Gordon 1992; O'Connor *et al.* 2007). However, when high quality forage is available in greater quantities (e.g. large numbers of fruiting trees) elephants will seek it out (Owen-Smith 1992). The need to maximise forage intake is further exacerbated in elephants as they have short (~14hr) gut retention times as a consequence of hindgut fermentation, and inefficient recycling of gut microflora (Owen-Smith 1992; O'Connor *et al.* 2007). Despite this seemingly "inefficient" foraging strategy, hindgut fermentation does allow elephants to survive on potentially lower quality diets than ruminants (Janis 1976), which becomes important during resource-limiting periods such as droughts. Elephants will prefer to consume foods from which the greatest amount of digestible protein (e.g. green, broad-leafed grasses and forbs) can be acquired in the shortest possible time (O'Connor *et al.* 2007). They will also consume a relatively wide variety of browse (woody) plants, fruits, bark and tubers (Cowling & Kerley 2002). However, the ingestion rates of these components are slower due to the increased time required for harvesting and chewing (O'Connor *et al.* 2007).

Consistent with the theory presented above, the ratio of various food components in the diet of elephants is dependent on availability and season. Grass and forbs are usually selected during the wetter periods, while browse becomes more important in the dry season when less green grass is available (Field & Ross 1976; O'Connor *et al.* 2007). Grass is generally the most available food source in African savannas (Fritz & Duncan 1994). Thus, it is not surprising that it constitutes one of the largest proportions of elephant diet in Africa (Field & Ross 1976; Viljoen 1989; Tchamba & Seme 1993; Paley & Kerley 1998). Between 37 and 89% of all foraging observations on elephants at the Addo Elephant National Park of South Africa consisted of grass (Paley & Kerley 1998; E. Knott unpublished data). Elephants generally forage below 2m (Guy 1976) using their trunks to break down tree branches or curling it around tufts of grass and pulling them out by their roots. Once grass has been uprooted it is often beaten against a leg or on the ground before it is brought up to the mouth (Skinner & Smithers 1990). However, the trunk is not always used for feeding. At times, elephants may browse directly off trees or shrubs of suitable height by positioning themselves adjacent to the tree or shrub and biting off portions of protruding branches with their large molar teeth (Roux 2006). This foraging technique results in the outer edges of browsed branches taking on a characteristic "toothbrush" or splayed appearance (Roux 2006). Elephants are extremely wasteful feeders, often discarding a large amount of the plant material that they remove from plants. In the Addo Elephant National Park this is estimated to be in the region of 67% (Cowling & Kerley 2002). In addition to being wasteful, elephants can be destructive in their feeding and social habits. They routinely push over mature trees in order to access roots, succulent new shoots in the canopy or merely for social display (Guy 1976; Skinner & Smithers 1990). In some parts of Africa this behaviour has resulted in the number of mature tree being reduced by up to 45% (Thomson 1975; Field & Ross 1976). The breaking of tree branches to access fresh leaves or fruit is also common (Field & Ross 1976; Skinner & Smithers 1990; Kabigumila 1993). This feeding activity can reduce the available biomass and cover of woody species as well as decrease the abundance of some plant species (Cowling & Kerley 2002). The bark of some trees, particularly from the genus *Acacia*, is favoured by elephants (Field & Ross 1976; Skinner & Smithers 1990). They access the bark by loosening it with their tusks and then stripping it off with their trunks. This behaviour is known to permanently scar trees as well as cause tree death (Thomson 1975; Field & Ross 1976). Elephants are water dependant and require about 160 litres per day (Skinner & Smithers 1990). Consequently, the majority of their foraging (and thus damage) is within riparian valleys, drainage lines or routes to and from sources of water (Anderson & Walker 1974). This is supported by recent research in the Eastern Cape Province, South Africa, which indicates that elephant herds spend the majority of their time within 600m from permanent water (usually a river), but that they range more widely during the summer (wet season) when ephemeral pans contain water (Roux 2006). Furthermore, the influence of body size and digestive physiology on the feeding strategy of elephants predicts that impact on woody plant species will be lowest during periods of high rainfall, as more green grass will be available and consumed for extended periods (O'Connor *et al.* 2007). By contrast, impact on woody species will be highest during periods of low rainfall when elephants are forced to consume more woody material (O'Connor *et al.* 2007).

All seven of southern Africa's major vegetation biomes are represented in the Eastern Cape Province of South Africa (Low & Rebelo 1996). Of these seven, the Thicket Biome is one of the best represented (17%) in the province (Lubke *et al.* 1986; Low & Rebelo 1996). The Thicket Biome comprises five main vegetation types: dune thicket; mesic succulent thicket; spekboom succulent thicket; valley thicket and xeric succulent thicket with valley thicket being the most common (9% of the province) of the five vegetation types (Low & Rebelo 1996). In general, the vegetation found in the Thicket Biome is low (2-3m), dense, often spinescent, succulent, evergreen and not fire-prone (Lubke *et al.* 1986; Hoffman 1989; Moolman & Cowling 1994). Many of the plant species found in the Thicket Biome are endemic to the region (Lubke *et al.* 1986), which is further reflected in the fact that the Thicket Biome is a major centre of endemism for several succulent and geophytic plant species (Moolman & Cowling 1994). In addition, the Thicket Biome contains the highest number of threatened plant species in the Eastern Cape Province (Lubke *et al.* 1986). However, much of the area covered by thicket is not conserved (Lubke *et al.* 1986; La Cock 1992; Low & Rebelo 1996). Furthermore, the high quality of the forage has meant that much of the vegetation is threatened by intensive goat (*Capra hircus*, L.) or ostrich (*Struthio camelus*, L.) farming outside protected areas (Low & Rebelo 1996). It has been shown that extensive goat production on thicket vegetation is deleterious to the high productivity of the vegetation type due to the inherently slow growth rates of the plants which are unable to cope with the intensive "bottom-up" browsing by livestock (Moolman & Cowling 1994). However, thicket vegetation also appears to be adversely affected by the "top-down" browsing effects of indigenous herbivores like elephants, at least at high densities, as such browsing reduces the cover and species richness of certain endemic succulents and geophytes (Moolman & Cowling 1994). Thus, it is clear that the Thicket Biome is an important component of and conservation priority for the Eastern Cape Province. It is also apparent that it is susceptible to the browsing of both large herbivores like elephants and small herbivores like goats.

The pattern of land use in the Eastern Cape Province continues to change rapidly from agriculture and livestock farming to wildlife ranching and eco-tourism. This change in land use has promoted the re-introduction and conservation of species that were once locally extinct e.g. cheetah *Acinonyx jubabtus* Schreber, wild dog *Lycaon pictus* Temminck, and elephant. In addition, a preliminary survey suggests that the establishment of eco-tourism destinations in the Eastern Cape Province has increased the area under conservation in the Province substantially and benefited the conservation of biodiversity (Sims-Castley *et al*. 2004). However, in many instances, relatively small areas (from 10km^2) have been fenced and utilized as wildlife ranches or eco-tourism destinations. Even on these relatively small properties, elephants have been re-introduced in order to attract tourists. Therefore a conflict exists. Although wildlife ranches and eco-tourism destinations may contribute towards the conservation of the thicket vegetation and the overall biodiversity of the region by releasing the land from past agricultural practices, the re-introduction of elephants to these enclosed areas could counteract the positive effects they have on conservation. Enclosed wildlife ranches, thus, provide an ideal experimental opportunity to test the effects of re-introducing a large, generalist herbivore to a region where it has been absent for almost 100 years.

1.1 RESEARCH HYPOTHESES

As discussed above, elephants are known to significantly alter the vegetation structure of the ecosystems they inhabit (Moolman & Cowling 1994; Cumming *et al*. 1997; Kerley & Landman 2006). These changes to the vegetation structure can result in cascading effects throughout the ecosystem, influencing both the plant and animal communities (Cumming *et al.* 1997; Skarpe *et al.* 2004). However, elephants have only been present at each site for a relatively short (< 13 years) period and are at low densities (< 0.5 elephants/km^2). Thus, the main aims of this study are firstly, to address the effects of elephants in two vegetation types of the Eastern Cape Province (the locally important thicket and an example of the more ubiquitous savanna), and secondly, to investigate how these changes may affect other selected taxa (birds, insects and mammals) or ecosystem processes. Birds were selected as an appropriate taxon, as bird community variables such as species diversity and composition are known to accurately reflect major habitat changes (Taylor 2007). The rationale behind the selection of insects and mammals as appropriate taxa are described in the relevant experimental chapters. Collection of these data will provide an initial assessment of the effects of elephants within closed systems and will form a baseline for future studies along a continuum of elephant density and time of occupation. The five broad null hypotheses for my study were:

1. The presence of elephants will not affect the cover, species richness and diversity of grassland habitats or the associated bird communities and physical ecosystem processes.
2. Elephants will not alter the structure and composition of the locally important thicket vegetation, and this will not affect associated bird community structure or soil-surface functionality.
3. Elephant foraging on highly favoured species will not influence their abundance and this will not affect bird and insect communities.
4. In bushclump savanna habitats, elephants will not reduce the size of bushclumps to access preferred mature trees, and this will not affect mammal and bird communities.
5. Elephants do not promote the dispersal and germination of certain plant species in the Thicket Biome of the Eastern Cape Province.

1.2 MOTIVATION

The role that elephants play in the structuring of vegetation communities has been extensively investigated throughout Africa. However, only the elephants residing in the Addo Elephant National Park have been reliably studied in the Eastern Cape Province (Kerley & Landman 2006). The park was created to protect the last remaining elephants of the region in 1931, and did not include any natural water sources such as riparian valleys, which are known to be important for elephant foraging (Anderson & Walker 1974). Consequently, artificial water points were created within the park, mainly for game viewing purposes. Thus, any impacts on the vegetation could merely be an artefact and not a true reflection of the region as a whole. In addition, the cascading positive or negative impact of elephants on diversity and ecosystem processes has been poorly studied and the results are equivocal (Field 1971; Henshaw 1972; Lamprey *et al.* 1974; Ruggiero & Fay 1994; Herremans 1995; Cumming *et al.* 1997; Musgrave & Compton 1997; Fenton *et al.* 1998; Keesing 1998; Skarpe *et al.* 2004; Botes *et al.* 2006; Makhabu *et al.* 2006; Bonnington *et al.* 2007). Two of these studies reported negative elephant effects on plants and mammals (Field 1971; Henshaw 1972), while two others reported positive effects on plants and insects (Lamprey *et al.* 1974; Bonnington *et al.* 2007). The remaining nine reported both positive and negative effects. Furthermore, a review of 96 peer-reviewed publications (covering a 46 year period) assessing the impacts of elephants revealed that 66% (63) did not include adequate controls to isolate the influence of elephants on vegetation or any other ecosystem component (Appendix IV). This can be attributed to the preponderance of previous research in large systems where the incorporation of effective exclusion controls was either not possible or impractical. This study aims to address fundamental questions regarding elephant impact in a region with truly unique vegetation as well as provide further insight into the effects that elephants may have in savanna ecosystems, which dominate most of Africa.

1.3 SCOPE

This study seeks to determine the role played by elephants re-introduced to enclosed reserves in a region known for its unique botanical diversity. The investigation focused on the influence elephants have on plant communities, in terms of impact on growth forms, species abundance, species frequency, species diversity, seed dispersal and physical ecosystem processes in two vegetation types, and the cascading effects this has on selected taxa and processes. Neither the effects of enclosed reserves on re-introduced elephant populations nor elephant diet has been investigated.

CHAPTER 2

GENERAL DESCRIPTION OF STUDY SITES AND METHODOLOGY

2.1 LOCATION

The major part of the study was conducted at five sites with elephants (*Loxodonta africana*, Blumenbach)(treatment), and five paired sites without elephants (control) located adjacent to each treatment site, near Grahamstown in the Eastern Cape Province of South Africa (Figure 2.1). An additional site (and paired control) was used for some of the work discussed in *Chapter 3*. The Addo Elephant National Park (hereafter referred to as Addo; 33°44'S, 25°79'E) is approximately 94km West of Grahamstown and was used as the additional site for *Chapter 3*. Amakhala Game Reserve (Amakhala; 33°31'S, 26°06'E) is situated 48km southwest of Grahamstown. Kariega Game Reserve (Kariega; 33^{o}35'S, 26^{o}37'E) lies 45km South of Grahamstown in the Kariega River Valley. Kwandwe Private Game Reserve (Kwandwe; 33^{o}09'S, 26^{o}37'E) is situated approximately 27km northeast of Grahamstown in the Great Fish River Valley. Pumba Private Game Reserve (Pumba; 33°25'S, 26°21'E) is 18km southwest of Grahamstown and Shamwari Private Game Reserve (Shamwari; 33^{o}20'S, 26^{o}01'E) is 60km southwest of Grahamstown.

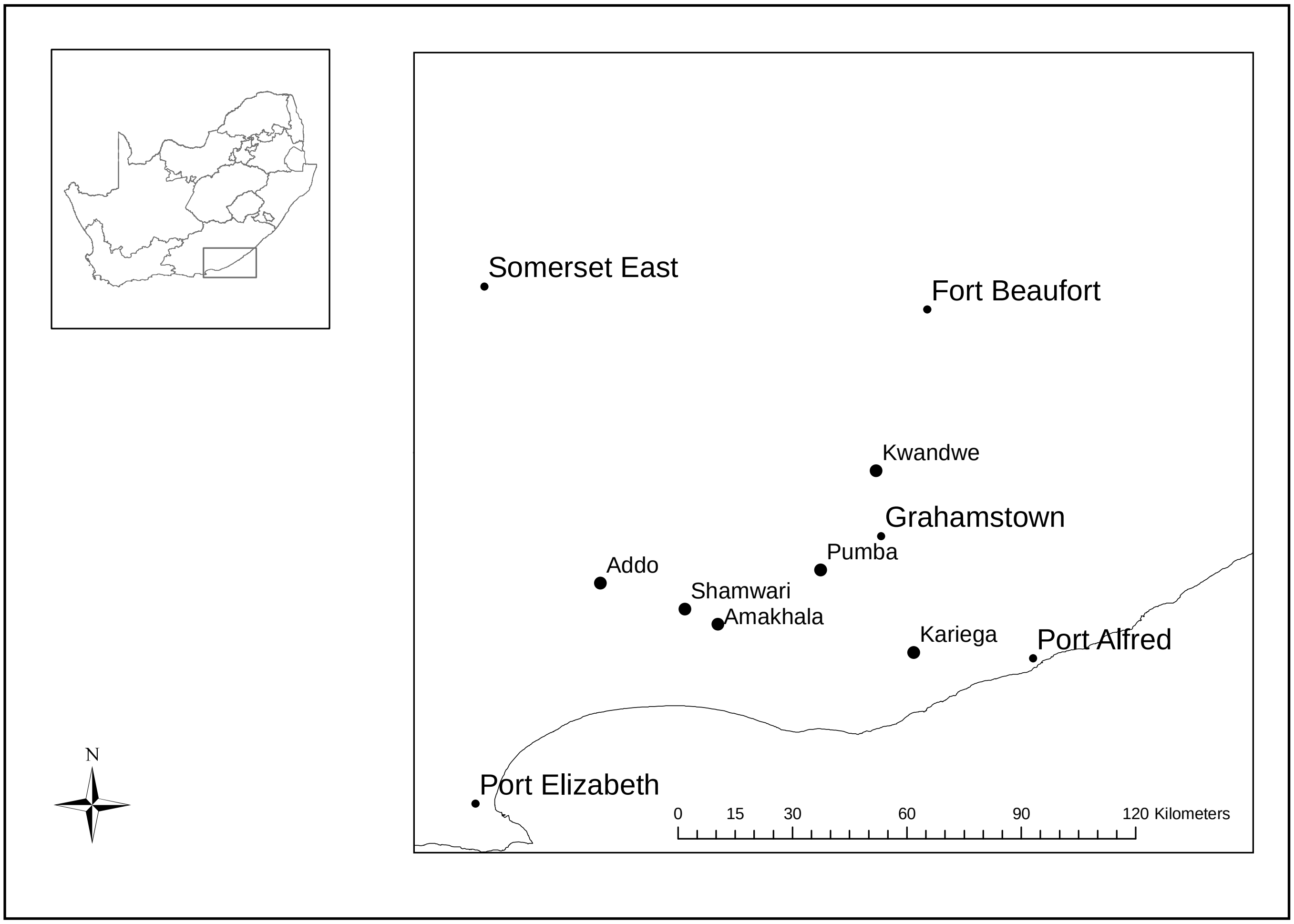

Figure 2.1: The position of the six study sites in relation to the larger centres of the Eastern Cape Province, South Africa.

2.2 CLIMATE

Due to differences in the nature of the climatic data for each site, the climatic data, supplied by the South African Weather Service, for Grahamstown were used as a convenient point of reference for the general climatic conditions of the region. However, specific details of the climate at each site are given under the site descriptions. Grahamstown has a semi-arid climate with rainfall in all seasons (Stone *et al*. 1998).

2.2.1 Rainfall

Frontal systems are responsible for the majority of precipitation in Grahamstown and rainfall is not as seasonal as it is for other parts of southern Africa (Ogutu & Owen-Smith 2003). However, there are usually 15 days of thunderstorms a year, occurring most frequently during the summer months (Stone *et al.* 1998). The mean annual precipitation for the ten-year period (January 1997- June 2007) was 519 ± 97mm, which was lower than the mean annual precipitation (595 ± 158mm) for the study period (2005-2007). The Eastern Cape Province is a transition zone of climate types (Stone *et al.* 1998). Rainfall can be expected all year round in Grahamstown with approximately 82 days of rain a year (Figure 2.2; Stone *et al.* 1998). However, distinct bimodal peaks during March-April and November-December are evident (Figure 2.2). During the study period (2005-2007), although August received unusually high rainfall, the pattern of monthly rainfall was similar to the ten-year average monthly rainfall (Figure 2.2).

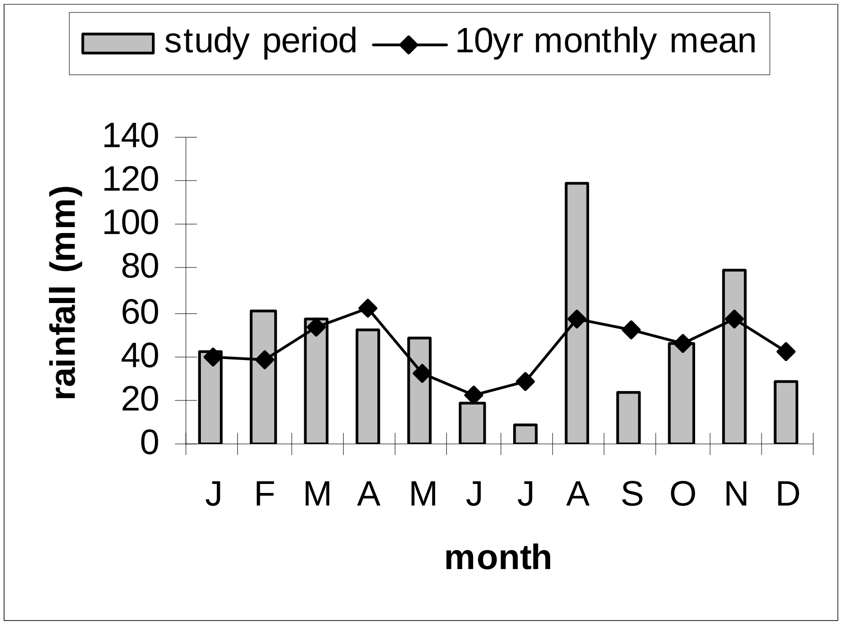

Figure 2.2: The mean monthly rainfall during the study period (2005-2007) in relation to the ten-year monthly mean for the period 1997-2007.

2.2.2 Temperature

The mean monthly maximum and minimum temperatures in Grahamstown for the period 1997-2007 reflect a temperate climate (Figure 2.3). The winter months (June-August) are the coldest, while December, January and February are the hottest (Figure 2.3). The mean monthly temperatures during the study period (2005-2007) were similar to the ten-year monthly means (Figures 2.3 and 2.4). In Grahamstown, temperatures range between 40^{o}C on the hottest day and –5^{o}C on the coldest night. On average, the temperature will exceed 35^{o}C on 5-10 days a year. Widespread frost (temperatures below 0^{o}C) is only experienced five days a year, usually between 1 July and 1 August (Stone *et al.* 1998).

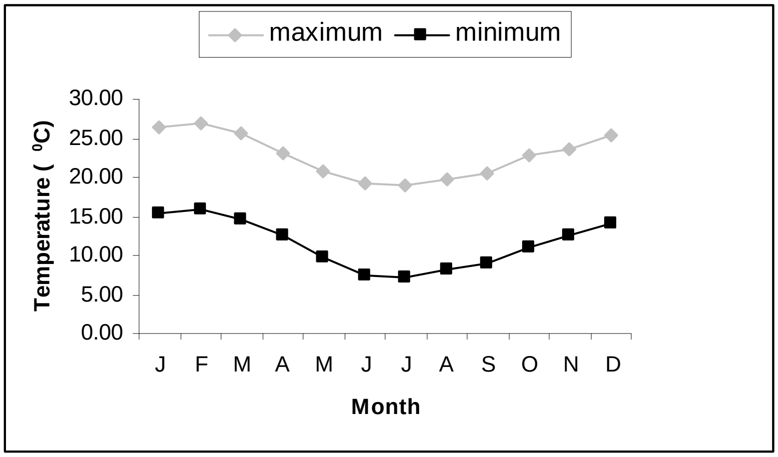

Figure 2.3: The mean monthly maximum and minimum temperatures in Grahamstown for the ten-year period 1997-2007.

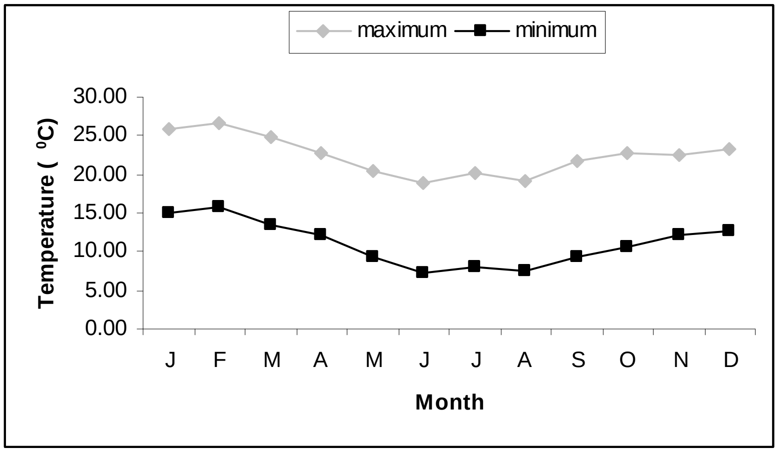

Figure 2.4: The mean monthly maximum and minimum temperatures for Grahamstown during the study period 2005-2007.

2.3 VEGETATION

The major vegetation types of all study sites are described in this section. The details of localised differences (mostly naming) to these broad vegetation types are provided under the site descriptions.

Overall, six of South Africa's seven Biomes were represented on the six treatment and six control sites used in this study, namely: Forest, Fynbos, Grassland, Nama Karoo, Savanna and Thicket (Low & Rebelo 1996). Within these biomes a further 12 vegetation types were identified across the treatment and control sites; Afromontane Forest (*Forest*), Grassy/Mountain Fynbos (*Fynbos*), Coastal Grassland (*Grassland*), Eastern Mixed Nama Karoo (*Nama Karoo*), Eastern Thorn Bushveld (*Savanna*), Mesic Succulent Thicket (*Thicket*), Spekboom Succulent Thicket (*Thicket*), Xeric Succulent Thicket (*Thicket*), Valley Thicket (*Thicket*), Bontveld (*Savanna/Thicket*), Drainage line Thicket (*Thicket*) and Old/Disused Lands (*Grassland*)(Low & Rebelo 1996; O'Brien 2000; Bissett 2004).

The Afromontane Forest is generally restricted to deep valleys where moisture is high (Low & Rebelo 1996). It is characterised by numerous tall (30-40m) trees. Species such as *Podocarpus* spp., *Apodytes dimidiata*, Mey, *Halleria lucida*, L., and *Calodendrum capense*, Thunb., are prevalent, while *Gymnosporia buxifolia,* Szyszyl., *Scutia myrtina*, Kurz, and *Rhoicissus tridentata*, Wild & Drumm., dominate the shrub layer (Low & Rebelo 1996).

The Grassy/Mountain Fynbos is only found along quartzite ridges and on soils derived from sandstone and is not a very widespread vegetation type (Low & Rebelo 1996; O'Brien 2000). Characteristic species of this vegetation type are *Leucadendron* *salignum,* Bergius, *Passerina corymbosa,* Thoday, *Aspalathus chortophila*, Eckl. & Zeyh., and *Metalasia muricata*, L. (O'Brien 2000).

Coastal Grassland is dominated by grasses such as *Themeda triandra*, Forssk., and *Eragrostis capensis*, Thunb. (Low & Rebelo 1996). Herbaceous plants and shrubs (e.g. *Rhus* spp., and *Passerina rigida*, Wikstr.) are also abundant within this vegetation type (Low & Rebelo 1996).

The Eastern Mixed Nama Karoo is a mixture of grasses and shrubs, such as *T. triandra,* Forssk., *Aristida* spp., *Pentzia incana*, Thunb., and *Eriocephalus ericoides*, L. (Low & Rebelo 1996). This vegetation type is dependent on seasonal rainfall (Low & Rebelo 1996).

Eastern Thorn Bushveld is a highly variable vegetation type in the Eastern Cape Province (Low & Rebelo 1996). In general, it takes the form of Bushclump Savanna, which consists of characteristically rounded clusters of dense, woody vegetation surrounded by a matrix of grass, forbs, small shrubs and bare soil. Several *Rhus* spp., *Pappea capensis*, Eckl. & Zeyh., *Cussonia spicata,* Thunb., *Sideroxylon inerme*, L., and *Schotia afra*, Thunb. are typically interspersed with grass such as *T. triandra*, Forssk. (Low & Rebelo 1996). *Acacia karroo,* Hayne, can also invade this vegetation type to form dense stands (O'Brien 2000).

Mesic Succulent Thicket is characterised by a high proportion of succulent shrubs, trees and lianas as well as some sclerophyllous trees and shrubs, generally lower than 3 m (Low & Rebelo 1996). Indicator species include *Aloe ferox,* Miller, *Portulacaria afra,* Jacq., *Maytenus capitata*, Szyszyl., and *Grewia robusta*, Burch. (Low & Rebelo 1996). This thicket type is distributed patchily on the slopes of hills.

Spekboom Succulent Thicket is generally found in the drier parts of the province, occurring on steep mountain slopes (Low & Rebelo 1996). Spekboom, *P. afra*, dominates this vegetation type, often forming pure stands. *Crassula ovata,* Miller, *P. capensis, G. robusta, Aloe* spp. and *S. afra* are other important species (Low & Rebelo 1996).

Xeric Succulent Thicket is invasive in savanna and grassland vegetation in the absence of browsers such as black rhino (*Diceros bicornis*, L.) and kudu (*Tragelaphus strepsiceros*, Pallas) (Low & Rebelo 1996). Indicator species include *G. robusta, Brachylaena ilicifolia,* Lam., *P. afra, M. capitata* and *Rhigozum obovatum,* Burch. (Low & Rebelo 1996).

Valley Thicket is a very dense thicket of evergreen woody shrubs and trees found on the slopes of most hills (Low & Rebelo 1996). *Cassine aethiopica,* Thunb., *Euphorbia triangularis,* Desf., *E. tetragonal*, Haw., and *Plumbago auriculata*, Lam., are indicator species of this vegetation type (Low & Rebelo 1996).

Several *Rhus* spp. and *A. karroo* grow along the drainage lines of the study sites and dominate the Drainage Line Thicket (Bissett 2004). Other important woody species in this vegetation type include *Azima tetracantha*, Lam., and *Lycium* spp.

Bontveld is restricted to flat and moderately sloped calcrete soils (O’Brien 2000). The vegetation consists of bushclumps interspersed with grass and/or Karoo shrubs. The bushclumps in the Bontveld are typically composed of several *Rhus* spp., *Canthium inerme,* Kuntze, *Zanthoxylem capense*, Thunb., *S. myrtina* and *Grewia occidentalis,* L. (O’Brien 2000).

The Old Lands are found on previously cultivated fields, usually along alluvial plains (Bissett 2004). *Cynodon dactylon,* L., *Panicum stapfianum,* Fourc., *Eragrostis* *curvula*, Schrad., and *Pennisetum clandestinum*, Hochst., dominate these areas, often as separate monocultures in the absence of trees or shrubs (Bissett 2004).

2.4 ADDO ELEPHANT NATIONAL PARK

2.4.1 Site description and history

At present, many sections of Addo are not connected, but collectively form part of the Greater Addo Elephant National Park (Kerley *et al.* 2002). The park was originally established in 1931 to protect the last 11 elephants of the Eastern Cape Province (Kerley *et al.* 2002). Three distinct management zones can be delineated: 1) areas where elephants have been present for long periods and persist at high density; 2) areas where elephants have only been present for a relatively short period and are at comparatively low density; and 3) areas where elephants are absent. All three zones are currently used for conservation. The average rainfall for the park is ~620mm per annum (Addo weather station).

The Main Camp section forms part of the original elephant enclosure that was erected in 1954 (Kerley *et al.* 2002) and is 12 500Ha in size (Figure 2.5). The elephant population (now 374) and the available area have increased since the fence was erected, albeit at disparate rates (Kerley *et al.* 2002). The current elephant density within this section is 3.0 elephants/km^2 (Kerley *et al.* 2002). There are no natural water sources, and the elephant population is sustained by several artificially pumped waterholes. The Main Camp section was used as the treatment site for Addo. Sixty-three elephants were translocated to the 13 000Ha Nyati section, which is North of the main elephant enclosure, in 2000 (Figure 2.5). At present, the elephant density at Nyati is 0.6

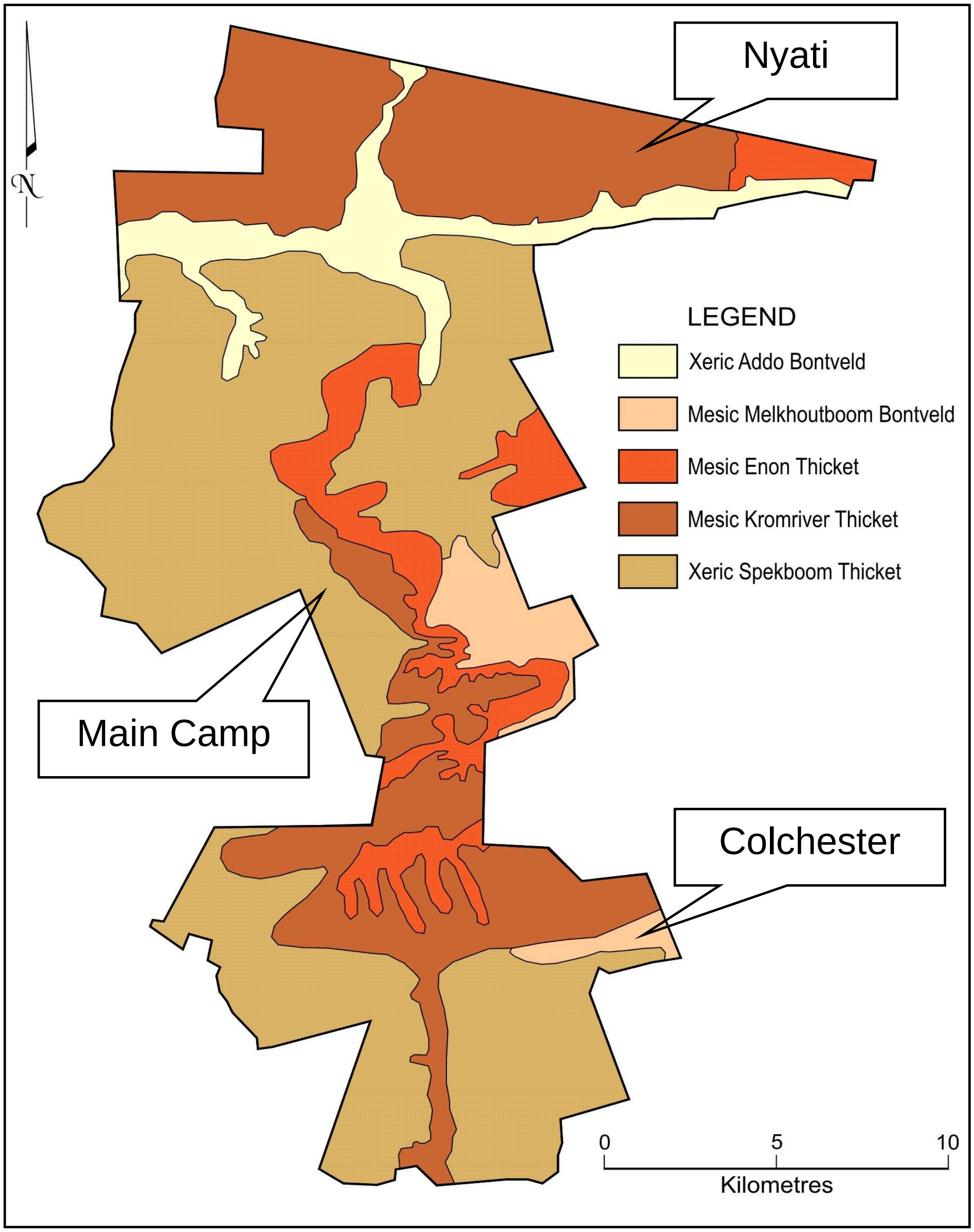

Figure 2.5: The Addo Elephant National Park depicting the five major vegetation types represented on the park. See text for the details of each vegetation type.

elephants/km^2. The Colchester section (South of the main elephant enclosure; Figure 2.5) does not have elephants present, but it is expected that elephants from Main Camp will have access to this 12 500Ha section in 2008. This section was used as the paired control site for Addo.

Before the park was proclaimed (including all new land acquisitions), small stock farming was the predominant land-use. Crops, such as peanuts, sunflowers, chicory and maize were also grown in places. The areas that were ploughed up for crops have been lying fallow since they were acquired and are now in various successional stages. Other mammalian herbivores present include: black rhino, buffalo (*Syncerus caffer*, Sparrman), red hartebeest (*Alcephalus buselaphus*, Pallas), kudu, eland (*Tragelaphus oryx*, Pallas), zebra (*Equus burchelli*, Gray), warthog (*Phacochoerus africanus*, Pallas), Cape grysbok (*Raphiceros melanotis*, Thunberg), bushpig (*Potamochoerus porcus*, L.), common duiker (*Sylvicapra grimmia*, L.), steenbok (*Raphicerus campestris*, Thunberg) and bushbuck (*Tragelaphus scriptus*, Pallas).

2.4.2 Vegetation

The vegetation of Addo comprises Xeric Addo Bontveld (*Bontveld*), Mesic Melkhoutboom Bontveld (*Bontveld*), Mesic Enon Thicket (*Mesic Succulent Thicket*), Mesic Kromriver Thicket (*Mesic Succulent Thicket*) and Xeric Spekboom Thicket (*Spekboom Succulent Thicket*)(Figure 2.5). Xeric Succulent Thicket dominates the park, with the Bontveld restricted mainly to the central ridges (Figure 2.5).

2.4.3 Topography and geology

Addo ranges in altitude from 100m in the Colchester (southern) section to 400m on the ridges in the North. The majority of the park is covered by undulating low hills, with the extreme northern section of the park being dominated by more incised valleys.

The dominant geological formations of the reserve include Uitenhage Group clay, sandy-clay loams, sandstone; and quartzitic and shale substrata (Low & Rebelo 1996).

2.5 AMAKHALA GAME RESERVE

2.5.1 Site description and history

Amakhala is 5500Ha in size and is situated South of Shamwari, with the N2 national road separating the two reserves. The major water source is the semi-perennial Bushmans River, which flows through the reserve for ~22km (Figure 2.6). Several small dams and pans are the other important water sources on the reserve. Amakhala, like Shamwari, is situated in the spring dominant rainfall strip of the province and receives approximately 550mm of rainfall per annum (Low & Rebelo 1996; Stone *et al.* 1998). Bimodal rainfall is experienced during the autumn and spring months (O'Brien 2000). The temperatures experienced at Amakhala are similar to Grahamstown. Frost can occur on cold winter nights especially in the low-lying areas.

Amakhala was formed in 1999 after several stock farmers joined portions of their land together. The alluvial plains of the Bushmans River were also used for growing crops in places, but these areas have been lying fallow since the reserve's inception. Elephants (10) were re-introduced to the reserve in 2003 from the Phinda Resource Reserve, KwaZulu-Natal. The current population stands at 13 individuals (3 bulls, and 10

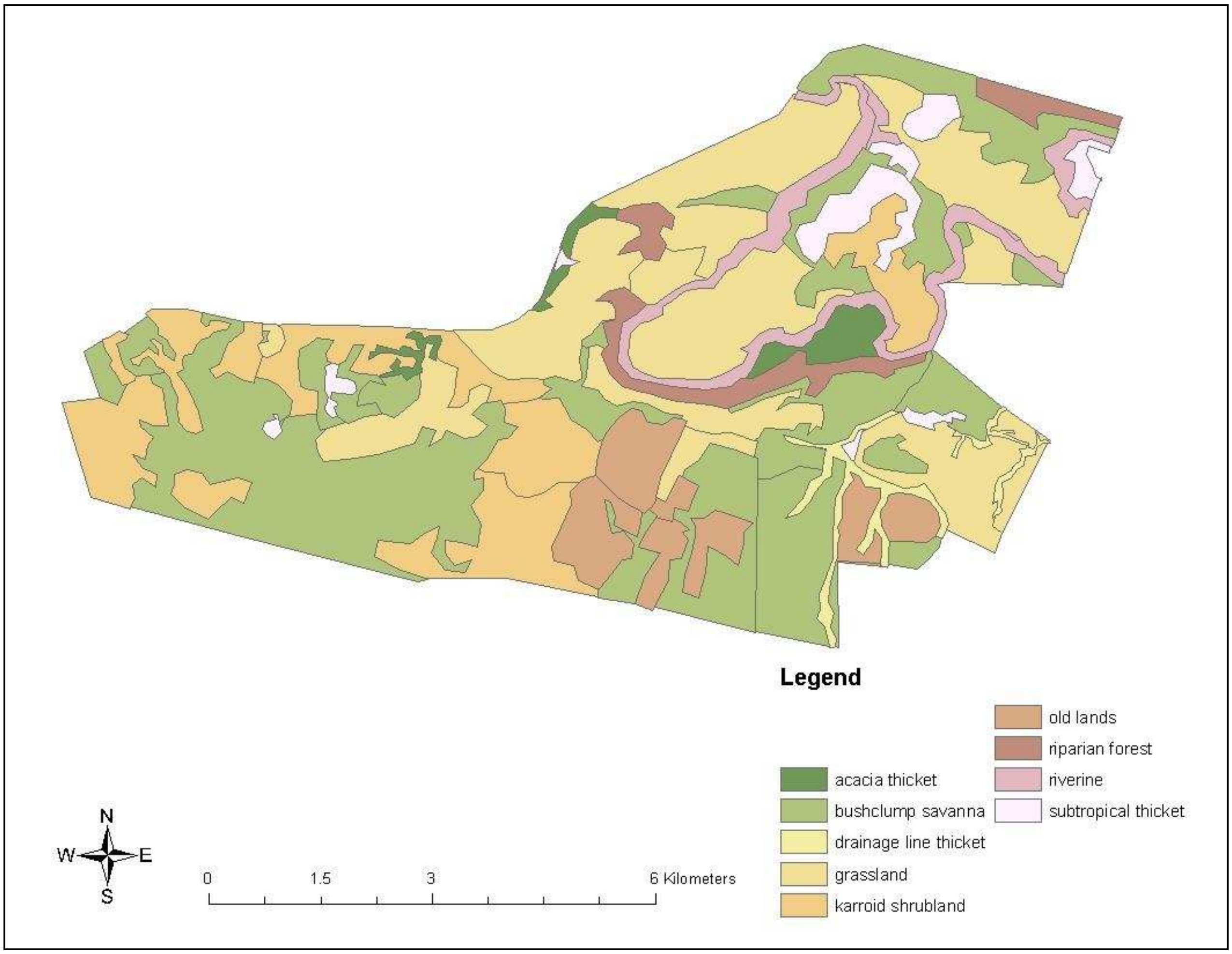

Figure 2.6: The Amakhala Game Reserve depicting the nine major vegetation types represented on the reserve.

cows and calves) at a density of 0.2 elephants/km^2. Other mammalian herbivores present include: white rhino (*Ceratotherium simum*, Burchell), giraffe (*Giraffa camelopardalis*, L.), gemsbok (*Oryx gazella*, L.), buffalo, red hartebeest, black wildebeest (*Connochaetes gnou*, Zimmerman), kudu, eland, zebra, waterbuck (*Kobus ellipsiprymmus*, Ogilby), springbok (*Antidorcas marsupialis*, Zimmerman), impala (*Aepyceros melampus*, Lichtenstein), blesbok (*Damaliscus pygargus phillipsi*, Pallas), warthog, Cape grysbok, bushpig, common duiker, steenbok and bushbuck.

Brentwood Farm, located to the North of Amakhala (33^{o}48'S, 26^{o}14'E), was used as its paired control. The climate and vegetation are similar although it is used as a dairy farm. The “Old” lands present on the farm are the only exception in terms of the vegetation as they are mainly cultivated grass pastures for the cattle. *Cynodon dactylon* and *P. clandestinum* dominate these pastures. Low numbers of indigenous ungulates such as kudu, duiker, Cape grysbok, bushpig, warthog and bushbuck are present.

2.5.2 Vegetation

Nine major vegetation types are recognised on Amakhala; Acacia Thicket, Bushclump Savanna (*Eastern Thorn Bushveld*), Drainage line Thicket, Grassland (*Coastal Grassland*), Karroid Shrubland (*Eastern Mixed Nama Karoo*), Old lands, Riparian Forest (*Afromontane Forest*), Riverine (*Drainage line Thicket*) and Subtropical Thicket (*Mesic Succulent Thicket*) (Figure 2.6). The major part of the reserve is composed of relatively open vegetation in the form of Bushclump Savanna, Karroid Shrubland and Grassland (Figure 2.6). Comparatively, there is much less Succulent Thicket vegetation at Amakhala (Figure 2.6) than the other reserves.

2.5.3 Topography and geology

Amakhala ranges in altitude from 100m in the South to 400m in the North and the topography consists of gently undulating hills.

The dominant geological formations in the reserve are Uitenhage Group clay, Beaufort Group sandstones. Four main substrata are available for the plants, namely: shale, sandstone, mudstone and calcrete. In addition, deeper alluvial soils are found on the lower lying lands (Low & Rebelo 1996).

2.6 KARIEGA GAME RESERVE

2.6.1 Site description and history

The regional road (R343) divides Kariega in two (Figure 2.7). The perennial Kariega River flowing through the eastern section (1900Ha) for 11km and is the major water source apart from several small dams. The western part of the reserve (3000Ha) borders the Bushmans River in the West. Kariega falls within the spring-dominated rainfall strip of the province but has a pronounced bimodal rainfall pattern (Stone *et al.* 1998) receiving the highest rainfall of the six sites (~ 700mm) per annum (Low & Robelo 1996). The increased precipitation at Kariega can also be attributed to coastal fog, which occurs when moist air from the sea moves over a cold land surface (Stone *et al.* 1998). The reserve's proximity to the coast also means that the weather is influenced by the land/sea breezes, which occur in the late afternoon/evening due to the differential heating and cooling of the land and sea (Stone *et al.* 1998). Effectively, these breezes decrease day-time temperatures and increase night-time temperatures resulting in a more moderate

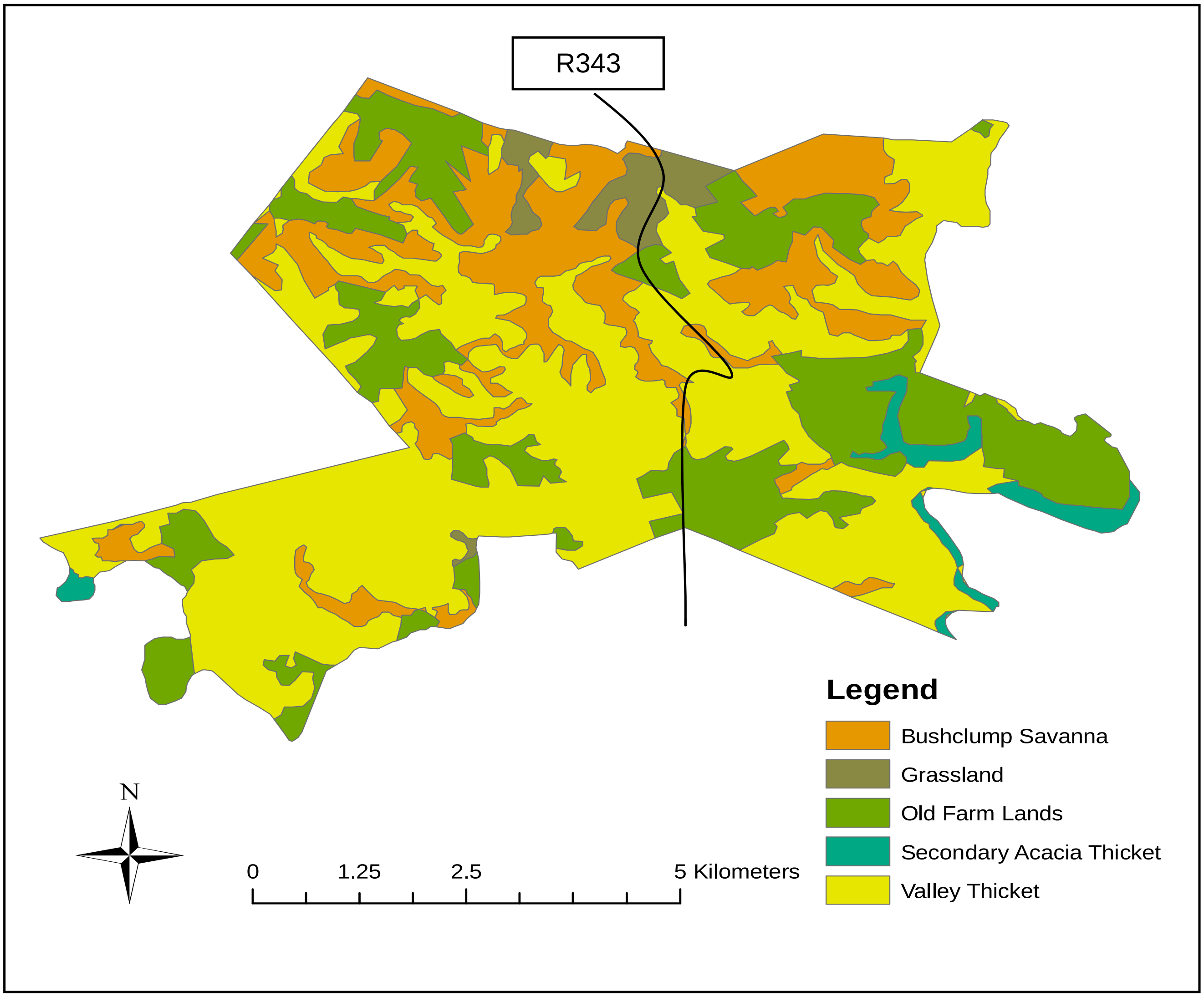

Figure 2.7: The Kariega Game Reserve depicting the five major vegetation types represented on the reserve.

climate and reducing frost, which can cause dramatic leaf-loss on some tree species (Stone *et al.* 1998; Parker *et al.* 2003).

Before the eastern section of the reserve was formed in 1990, the land was used predominantly for small stock farming with some crops grown on the flood plain of the Kariega River. The areas that were ploughed up for crop planting near the river have been lying fallow since the reserve was formed and are now in various successional stages. The western section of the reserve was acquired in 2003 and was used for similar farming practices as the eastern section prior to its incorporation. Eleven elephants were re-introduced to the western section of the reserve in 2004 from the Sabi Sands Wildtuin, adjacent to the Kruger National Park. The current elephant population is 15 individuals (six bulls, seven cows and two calves) at a density of 0.5 elephants/km^2. Other mammalian herbivores present include: white rhino, giraffe, gemsbok, buffalo, red hartebeest, black wildebeest, blue wildebeest (*Connochaetes taurinus*, Burchell), kudu, eland, zebra, waterbuck, springbok, impala, blesbok, warthog, Cape grysbok, bushpig, common duiker, steenbok and bushbuck.

The eastern section of Kariega was used as its paired control site.

2.6.2 Vegetation

The vegetation of Kariega is comprised of Valley Thicket, Bushclump Savanna, Secondary Acacia Thicket (*Eastern Thorn Bushveld*), Grassland and Old Farmlands (Figure 2.7). The northern regions, as well as a few ridges in the South, are dominated by Bushclump Savanna (Figure 2.7). The Old Farmland is found on the flood plains of the Kariega and Bushmans rivers as well as some of the ridges in the North (Figure 2.7).

2.6.3 Topography and geology

Kariega ranges in altitude from 23m at the base of the Kariega River valley to 262m on the ridges in the North. The northern half of the reserve is situated on a plateau above the Kariega River valley. The southern half of the reserve is dominated by undulating hills and incised valleys (Figure 2.7).

The dominant geological formations of the reserve include Beaufort Group shale, mudstone, solonetic soils and sandstone; and Cape Supergroup sandy clays and lithosols (Low & Rebelo 1996).

2.7 KWANDWE PRIVATE GAME RESERVE

2.7.1 Site description and history

Kwandwe is ~21 000Ha in size and the perennial Great Fish River flows through the reserve for 25km. Two large man-made dams and several smaller dams also provide important sources of water. Kwandwe straddles both the spring and autumn-dominant rainfall regions of the province. Consequently, distinct bimodal rainfall is experienced (Stone *et al.* 1998). However, rainfall at Kwandwe is only approximately 400mm per annum (Low & Robelo 1996). Kwandwe is situated on the leeward side of an extension of the *Kaprivierberge* and thus receives less rainfall than Grahamstown. The reserve experiences hot summers (temperatures often exceeding 35^{o}C) and cold (below 5^{o}C) winters with widespread frost due to radiational cooling on clear winter nights (Stone *et al.* 1998). The high temperatures promote thunderstorm development during the summer months (Stone *et al.* 1998).

Several farms that were previously utilised for ostrich (*Struthio camelus*, L.) and small stock farming were purchased to form Kwandwe in 2000. Twenty-one elephants were re-introduced to Kwandwe in 2001 from the Kruger National Park and Madikwe Private Game Reserve, and since then, the population has grown to 24 (three bulls, six cows and 15 sub-adults and calves) at a density of 0.1 elephants/km^2. Other mammalian herbivores present include: black rhino, white rhino, giraffe, gemsbok, buffalo, red hartebeest, black wildebeest, kudu, eland, zebra, waterbuck, springbok, impala, blesbok, warthog, nyala (*Tragelaphus angasii*, Gray), bushpig, common duiker, mountain reedbuck (*Redunca fulvorufula*, Afzelius), Cape grysbok, grey rhebuck (*Pelea capreolus*, Forster), steenbok and bushbuck.

The Great Fish River Reserve (33°07'S; 26°38'E), situated East of and adjacent to Kwandwe, was used as the paired control site for Kwandwe. No elephants are present on this 45 000Ha reserve. However, it does support ~100 black rhino. Other mammalian herbivores present include: buffalo, red hartebeest, kudu, eland, springbok, warthog, nyala, bushpig, common duiker, Cape grysbok, steenbok and bushbuck. The climate and vegetation of the Great Fish River Reserve are similar to Kwandwe.

2.7.2 Vegetation

The vegetation of Kwandwe can be divided into 11 major vegetation types, namely: Portulacaria Thicket, Short Euphorbia Thicket, Tall Euphorbia Thicket, Euphorbia-Portulacaria Mosaic, (all divisions of *Xeric Succulent Thicket*), Dry Forest (*Afromontane Forest*), Drainage line Thicket, Bushclump Karroid Thicket, Bushclump Savanna, Riverine (all three *Eastern Thorn Bushveld*), Karroid Shrubland (*Eastern Mixed Nama Karoo*), and Old lands (Figure 2.8). The Dry Forest at Kwandwe consists of evergreen

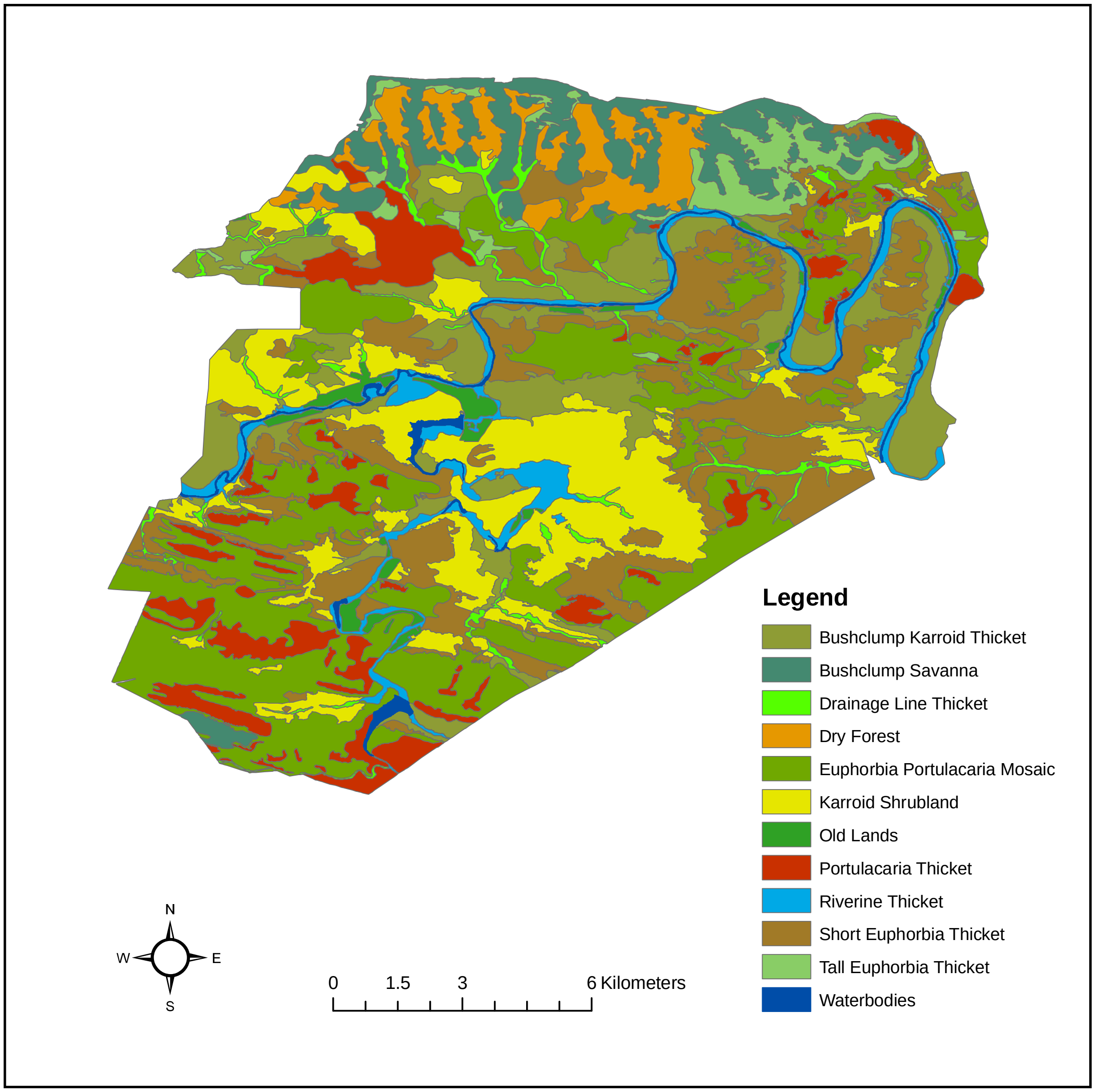

Figure 2.8: The Kwandwe Private Game Reserve depicting the 11 major vegetation types represented on the reserve.

trees found in the deep valleys of the North (Figure 2.8). *Cassine aethiopica*, *E. triangularis, E. tetragona, Harpephyllum caffrum*, Bernh., and *Schotia latifolia*, Jacq., are indicator species of this vegetation type on the reserve (Low & Rebelo 1996). Euphorbia-Portulacaria Mosaic (a form of *Xeric Succulent Thicket*) constitutes approximately 4300Ha of the reserve (Bissett 2004), while Bushclump Karroid Thicket (more open vegetation) is found on the sandy/clay slopes bordering the alluvial plains of the Great Fish River (Figure 2.8; Bissett 2004).

2.7.3 Topography and geology

Kwandwe ranges in altitude from 580m in the Northeast on the *Fish River Rand,* to 283m in the Great Fish River valley. The reserve is dominated by steep valleys and gorges in the South and northeast and undulating hills in the central portion.

The dominant geological formations include Ecca Group shales producing deep lime-rich, sandy loam soil, Cape Supergroup sandy clays and lithosols, Dwyka and Ecca Formations and deep solonetic soles from Beaufort group dolerites (Low & Robelo 1996).

2.8 PUMBA PRIVATE GAME RESERVE

2.8.1 Site description and history

Pumba is 6000Ha in size and is situated 18km southwest of Grahamstown on the N2 national road. The major water sources are two large dams in the centre of the reserve (Figure 2.9). Pumba's proximity to Grahamstown means that it experiences a very similar climate, receiving approximately 520mm of rainfall per annum (Low & Rebelo 1996; Stone *et al.* 1998). Bimodal rainfall is experienced during the autumn and spring months

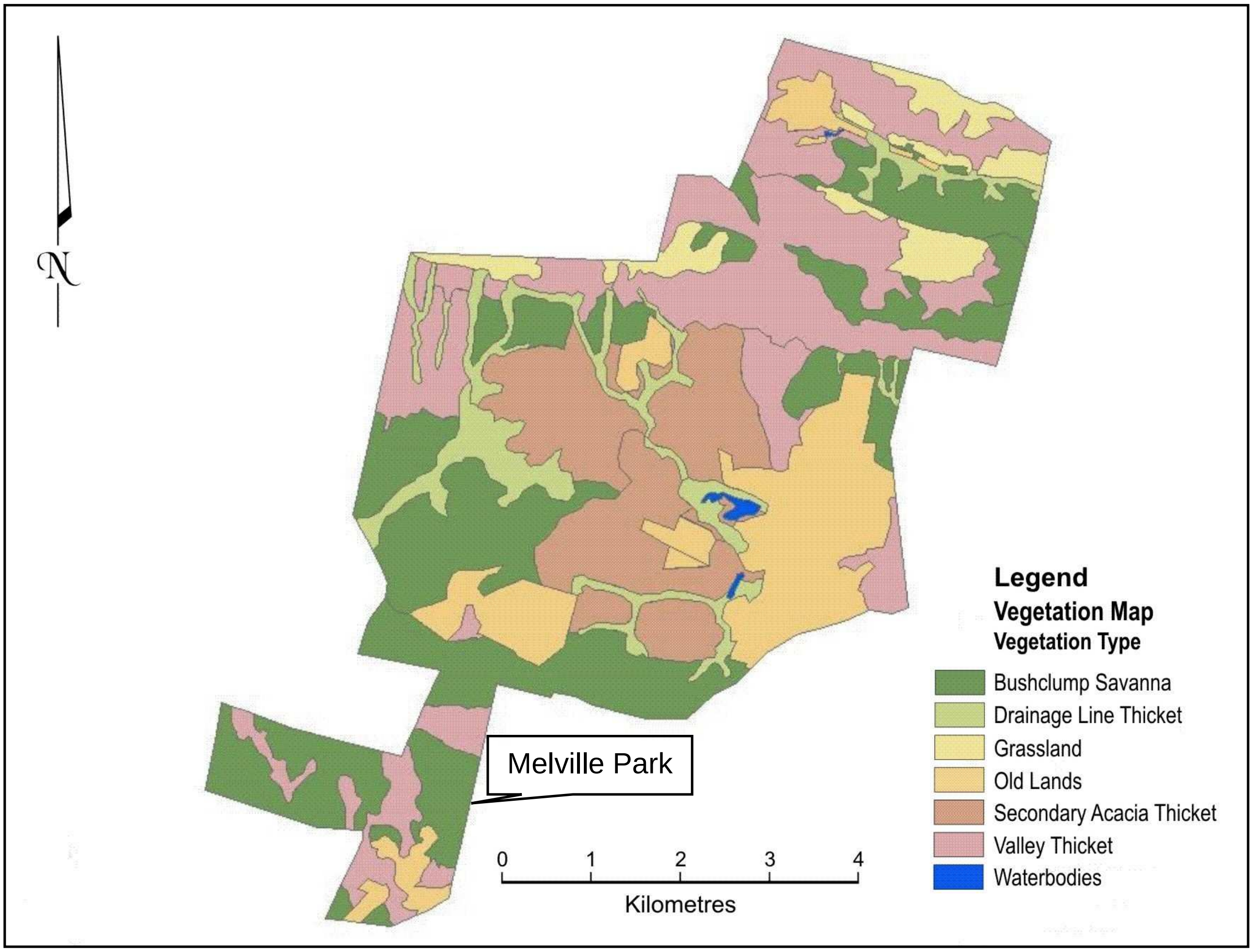

Figure 2.9: The Pumba Private Game Reserve depicting the six major vegetation types represented on the reserve.

(Figure 2.1). The temperatures experienced at Pumba are similar to Grahamstown. Frost can occur on cold winter nights especially in the low-lying areas.

Pumba was formed in 2004 after several farms, previously used for small stock farming were purchased. Several crops were grown in places around the major waterbodies, but this was on a relatively small scale. The fields have been lying fallow since the reserve's inception. Eight elephants from Kapama Game Reserve, North-West Province, were re-introduced to the reserve in 2004. The current population stands at 13 individuals (10 bulls and 3 cows) at a density of 0.2 elephants/km^2. Other mammalian herbivores present include: white rhino, giraffe, gemsbok, buffalo, red hartebeest, black wildebeest, blue wildebeest, kudu, eland, zebra, waterbuck, springbok, impala, blesbok, warthog, bushpig, common duiker, steenbok and bushbuck.

The southern section of the reserve (known as Melville Park) is separated from the rest of the reserve by the Alicedale district road (Figure 2.9). As the elephants do not have access to this section, it was used as Pumba's paired control site. This section had the same suite of other herbivores present as the northern section.

2.8.2 Vegetation

The vegetation at Pumba can be divided into six main categories; Bushclump Savanna, Secondary Acacia Thicket (*Eastern Thorn Bushveld*), Drainage line Thicket, Grassland, Old Lands and Valley Thicket (Figure 2.9). Bushclump Savanna dominates the southern section of the reserve and the plateau in the North (Figure 2.9). Grasslands are only found adjacent to patches of Bushclump Savanna in the North of the reserve (Figure 2.9). The Old Lands are disturbed habitats that were cleared to create grazing for stock or lands that were used to cultivate crops. This vegetation type is prevalent in the East of the reserve, around old homesteads and near the major waterbodies (Figure 2.9).

2.8.3 Topography and geology

Pumba ranges in altitude from 300m in the South to 800m on the plateau in the North. The major part of the reserve is covered by low, undulating hills.

The dominant geological formations of the reserve include Beaufort Group mudstone and sandstone, Cape supergroup and Dwyka and Ecca formations (Low & Rebelo 1996). Substrata include sandy-clay loams, sandstone and shale (Low & Rebelo 1996).

2.9 SHAMWARI PRIVATE GAME RESERVE

2.9.1 Site description and history

Shamwari is approximately 20 000Ha in size and lies between Alicedale in the North and the N2 national road in the South. The major water source is the semi-perennial Bushmans River, which flows through the reserve for 27.6km. Numerous small dams and pans, dotted throughout the reserve are the other important water sources. Shamwari is situated in the spring dominant rainfall strip of the province and receives approximately 550mm of rainfall per annum (Low & Robelo 1996; Stone *et al.* 1998). However, bimodal rainfall is experienced during the autumn and spring months (O'Brien 2000). Shamwari experiences temperatures similar to Grahamstown. Frost can occur on cold winter nights especially in the low-lying areas.

Shamwari was formed in 1992 after several farms previously used for small stock and beef farming were purchased. Many areas that had natural vegetation removed when the area was used for farming were incorporated into the reserve. These areas have been lying fallow since the reserve's inception (some longer) and are in various successional stages. Thirty-one elephants, all originally from the Kruger National Park, were re-introduced in 1992. The current population stands at 54 individuals (23 bulls, 19 cows and 12 sub-adults and calves) at a density of 0.3 elephants/km^2. Other mammalian herbivores present include: black rhino, white rhino, giraffe, gemsbok, buffalo, red hartebeest, black wildebeest, kudu, eland, zebra, waterbuck, springbok, impala, blesbok, warthog, bushpig, common duiker, mountain reedbuck, Cape grysbok, steenbok and bushbuck.

The Shamwari Breeding Centre (33°49'S; 26°02'E), to the East of the main reserve was used as the paired control for Shamwari. The Centre is 2349Ha in size and supports small populations of buffalo, zebra and several other ungulates, including kudu, nyala, common duiker and eland. The climate and vegetation are similar to that of Shamwari.

2.9.2 Vegetation

Shamwari can be divided into thirteen vegetation types (O'Brien, 2000). These are Afromontane Forest, Subtropical Thicket (*Mesic Succulent Thicket*), Bontveld, Bushclump Savanna (*Eastern Thorn Bushveld*), Grassy and Calcrete Fynbos, Karoo Scrub (*Eastern Mixed Nama Karoo*), Riverine Bush (*Drainage line Thicket*), Montane and Open Grassland (*Coastal Grassland*), Primary Acacia Thicket, Secondary Acacia Thicket (*Eastern Thorn Bushveld*) and Cleared and Cultivated Land (*Old Lands*)(Figure 2.10). The Subtropical Thicket accounts for 44.2% of the total area of the reserve (Figure

2.10). When combined the Primary and Secondary Acacia thickets account for 7.4% of the total area of the reserve (Figure 2.10).

2.9.3 Topography and geology

Shamwari ranges in altitude from 196m in the South to 628m in the North. The topography ranges from gently undulating hills in the South to deep valleys and gorges in the North.

The dominant geological formations in the reserve are Bokkeveld Series shale, Witteberg quartzites, Karoo sandstone and Sundays River Formations. The quartzite ridges traverse the central and northern parts of the reserve, while the southern part of the reserve is dominated by the Sundays River Formation resulting in shallow soils underlain by calcrete. Four main substrata are available for the plants, namely: shale, sandstone, quartzite and calcrete. In addition, deeper alluvial soils are found on the lower lying lands (O’Brien 2000).

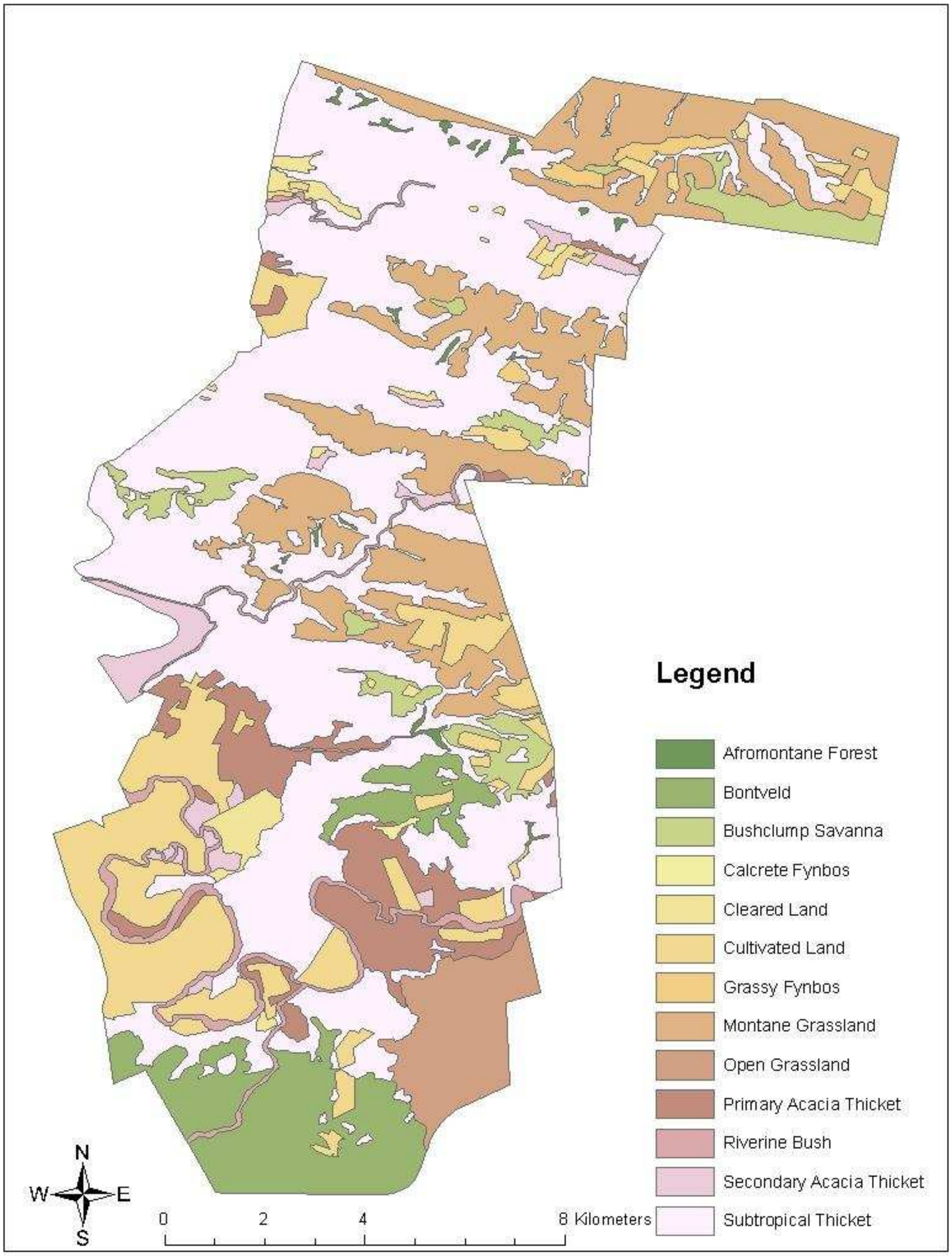

Figure 2.10: The Shamwari Private Game Reserve depicting the thirteen major vegetation types represented on the reserve, after O'Brien (2000).

2.10 GENERAL METHODOLOGY

The overall experimental design of the study is described in this section. The bird sampling protocol is also described in order to avoid unnecessary repetition of method descriptions in the experimental chapters.

2.10.1 Experimental design

In order to account for the large amount of inherent temporal and spatial variability in natural populations, when assessing potential impacts (such as those of elephants) the most robust and powerful design is a modified Before-After, Control-Impact (BACI) protocol (Underwood 1994; Stewart-Oaten & Bence 2001; Queiroz *et al.* 2006). The procedure requires the collection of replicated population data “before” an impact and then the further collection of replicated population data “after” the impact from the putatively impacted site with multiple controls (Underwood 1994; Stewart-Oaten & Bence 2001; Queiroz *et al.* 2006). As highlighted by Glasby (1997), in most assessments of environmental impact, data can usually only reliably be collected “after” an impact event. Glasby (1997) goes on to describe the use of an asymmetrical study design and analysis for such data. However, the process of analysis is iterative and relies on strong assumptions that are difficult to clarify (Glasby 1997; Stewart-Oaten & Bence 2001). In addition, the test itself is not very powerful (Glasby 1997; Stewart-Oaten & Bence 2001). Thus, a modified BACI design should have ideally been employed in my study. However, obtaining “before” data was not possible, and the sampling of multiple control sites per treatment site, as suggested by Underwood (1994) and Glasby (1997), was not logistically possible. Consequently, a stratified sampling design was used (Cohen & Holliday 2001). This approach has been employed in numerous studies that have assessed the impacts of elephants in Africa (Hatton & Smart 1984; Cumming *et al.* 1997; Fenton *et al.* 1998; Musgrave & Compton 1998; Botes *et al.* 2006; Guldemond & Van Aarde 2007; Bonnington *et al.* 2007). The strata in the design were based on different vegetation types (thicket, grassland, aloe stands and bushclump savanna). Between three and five sampling stations were selected at the treatment and control sites for each vegetation type and sampled haphazardly with either transects or quadrats. The number of transects/quadrats varied for each vegetation type (stratum), and was usually dictated by species accumulation curves (Colwell 2005). The sampling of birds, insects, mammals and ecosystem processes followed the same procedure. Five treatment sites (with elephants) were used where elephants had been present for a short period prior to the study (range: 1 – 13 years) and were at similar (low) densities (between 0.1 – 0.5 elephants/km^2). Addo was the only site that did not conform to these criteria (see above and *Chapter 3*). I considered the absence of elephants on game reserves or commercial farmland adjacent to areas with elephants as regional controls for the study. The five paired control sites were selected based on their proximity to each treatment site so as to mirror all other conditions (i.e. vegetation, rainfall, geology, aspect, past land-use, history of fire and the presence of other ungulates/herbivory) as closely as possible and to account for the range of inherent spatial and temporal variability across control sites (Table 2.1). Although as much care as possible was taken to reduce potentially confounding factors (e.g. past land-use, herbivory, fire etc.) it was recognised that it would be impossible to completely control for their effects. However, the data analysis was at a regional scale using mean values for most variables at treatment and control sites and testing for differences using paired t-tests (Cohen & Holliday 2001). When data were not normally distributed, data were transformed or an equivalent non-parametric test (usually a Wilcoxon matched-pairs test) was used (Zar 1974; Cohen & Holliday 2001). This type of analysis was deemed to be highly desirable for my study (in light of the potentially confounding factors) as the data collected from treatment sites would almost certainly be associated with (or correlated to) the data collected from the control sites (Zar 1974). By pairing the data from each treatment and control site, the over-riding effects of location and any other potentially confounding factors would (as far as possible) be factored out of the analysis (Zar 1974). In addition, the use of paired t-tests (or a non-parametric equivalent) significantly reduces the possibility of committing a Type II error (Zar 1974). Furthermore, the data analysis approach adopted in my study is almost identical to the published work of Cumming *et al.* (1997). Although this approach is likely to be conservative (i.e. the magnitude of an “elephant” effect may be too small relative to the overall variance across all sites), studies regarding the impact of elephants have become highly personalised and politicised in recent years. Thus, a conservative approach to the data analysis ensures a more objective assessment of elephant impact. It was recognised that the local distribution and abundance of plants (the main stratum in all analyses) at each site was likely to be strongly influenced by abiotic factors such as rainfall and soil. However, these effects were ameliorated by utilising controls in proximity to treatment sites.

Table 2.1: The past and present land-use of each treatment and control site and the number of years (up to 2005) each site has been under its current land-use. Farm = agriculture ([1]livestock; [2]crops); Reserve = conservation.

	Treatment			**Control**		
Location	**Past**	**Present**	**Years**	**Past**	**Present**	**Years**
Addo	Farm[1, 2]	Reserve	74	Farm[1, 2]	Reserve	2
Amakhala	Farm[1]	Reserve	6	Farm[1]	Farm	-
Kariega	Farm[1, 2]	Reserve	2	Farm[1, 2]	Reserve	15
Kwandwe	Farm[1]	Reserve	5	Farm[1]	Reserve	32
Pumba	Farm[1,2]	Reserve	1	Farm[1, 2]	Reserve	7
Shamwari	Farm[1]	Reserve	13	Farm[1]	Reserve	10

2.10.2 Bird sampling

The point transect method was employed in my study (Naidoo 2004; Buckland 2006; Toms *et al*. 2006; Taylor 2007). This method was chosen ahead of other methods, such as line transects, as it is capable of detecting more species and is more time efficient (Bibby *et al.* 2000; Taylor 2007). In addition, point transects are more practical for dense habitats (such as thicket vegetation in this study) compared to other methods (Taylor 2007). Survey points were located haphazardly within the relevant vegetation type at each treatment ($n = 5$) and control site ($n = 5$), being at least 150m apart to ensure independence of observations (Naidoo 2004; Toms *et al.* 2006). As far as possible, bird survey points were located within the vegetation sampling stations for each treatment and control site. Sampling at each survey point occurred over a 5-minute period with an initial 1-minute wait to reduce disturbance and allow birds to resume normal behaviour (Buckland 2006; Toms *et al*. 2006). With the exception of raptors, water birds (e.g. ducks, geese and storks) and aerial foragers (swifts and swallows) all bird species (seen and heard) within a 60m radius during the 5-minute period were recorded (Naidoo 2004; Buckland 2006; Taylor 2007). Raptors and aerial foragers were excluded as they are often silent and are usually only observed whilst in flight (Naidoo 2004; Taylor 2007). This combination makes detection difficult and does not allow an accurate distance to be recorded during point transects (Naidoo 2004; Taylor 2007). Water birds have specific habitat requirements, which are not necessarily dictated by the surrounding vegetation. Consequently, water birds were excluded so as not to artificially inflate estimates (Bibby *et al.* 2000; Taylor 2007). The Cape Weaver (*Ploceus capensis*, L.), Spectacled Weaver (*P. ocularis*, Smith), Village Weaver (*P. cucullatus*, Müller) and Southern masked Weaver (*P. velatus*, Vieillot) were treated as one morpho-species (Weaver) due to the difficulty in distinguishing between the females whilst in a flock (Taylor 2007). Sampling took place from 20 minutes before sunrise to 4 hours thereafter and was always conducted by the same observer (DMP). No surveys were conducted on days when it was raining or windy as such conditions are known to reduce bird activity and/or detection (Brotons *et al.* 2005; Butler *et al.* 2005). Data collected included locality of point transect (GPS position), time spent surveying (minutes), species, group size and distance (m) from point-to-bird. Distances to a point vertically below the bird were measured (using a Nikon Laser 800S rangefinder) and not the bird itself to ensure that measurements of distance were accurate (Buckland 2006). Birds detected aurally were placed in intervals of 10m from the observer (Taylor 2007). Where possible, distances to the approximate position of a bird detected aurally were also measured to improve accuracy (Buckland 2006). Species accumulation curves were constructed for each treatment and control site to determine adequate sampling effort using the Mao Tau method (Colwell 2005). Adequate sampling effort was defined as the point where the rate of species accumulation over five sampling intervals fell below 0.10 (Taylor 2007). The sample sizes for each site are summarised in Appendix I. For each vegetation type assessed, the data analysis was at the regional level and the sampling unit was the individual treatment or control site. For each treatment and control site the total number of species, Shannon Wiener index of diversity (H’) and species richness were calculated using EstimateS (Colwell 2005). The programme DISTANCE 4.1 was used to calculate relative densities across treatment and control sites (Thomas *et al.* 2004) To provide reliable estimates of density, the software requires a minimum of 60 individual observations per sample. In order to satisfy this requirement, all observations from point transects completed within each treatment and control site were combined. Several methods of probability density function (half normal, uniform and hazard-rate with cosine or polynomial adjustment terms) were applied to the data (Buckland 2006; Taylor 2007) and selected based on the best-fit detection model using Akaike Information Criteria. Once the model was selected, the density of individual birds per hectare for each treatment and control site was obtained. From these data the relative abundance of individual bird species was calculated using the species-specific contribution (frequency of occurrence) to the total group (Appendix II). Bird species at treatment and control sites were then assigned to one of six feeding and five nesting categories based on Maclean (1993) and the mean relative abundance of birds in each category calculated. Feeding categories included birds that forage mainly in trees or bush (arboreal), those that forage on the ground, those that make use of an open perch and swoop to the ground, those that glean insects from foliage, those that utilise an open perch and hawk insects, and those that forage both in trees and on the ground (arboreal and ground) (Maclean 1993). Nesting categories included birds that nest in holes above the ground, those that nest in any enclosed chambers above the ground, those that construct bowls made from a loose arrangement of twigs above the ground, those that nest on the ground and those that construct small cup nests above the ground (Maclean 1993). The family, common and scientific names (including authorities) of all bird species recorded during the course of the study are provided in Appendix III.

CHAPTER 3

THE POTENTIAL EFFECTS OF ELEPHANTS ON ECOSYSTEM FUNCTIONING AND ASSOCIATED BIRD COMMUNITIES IN GRASSLAND HABITATS

3.1 INTRODUCTION

In grassland landscapes, large herbivores are known to reduce the cover and biomass of plants (Rambo & Faeth 1999; McEvoy *et al.* 2006; Olofsson 2006; Johnson & Cushman 2007). However, some grass species have the ability to rapidly invest resources into secondary tiller growth following defoliation (Tomlinson & O'Connor 2005). Despite such phenological adaptations, the removal of aboveground biomass can increase the presence of bare ground in grasslands (Dorrough *et al.* 2004; McEvoy *et al.* 2006). This, in turn, can have a cascading influence on other ecosystem components such as soil chemistry (Britton *et al.* 2005; Carline *et al.* 2005). For example, Britton *et al.* (2005) demonstrated that high levels of cattle grazing significantly reduced the levels of Carbon, Nitrogen and Phosphorous in the soil.

Semi-arid landscapes (rangelands in particular) exhibit a high degree of spatial organisation, with different kinds of vegetation patches (e.g. grass and shrub patches) dispersed and nested across the landscape (Aguiar & Sala 1999; Ludwig *et al.* 2003; Tongway & Hindley 2004). In general terms, vegetation within these environments is organised in a two-phase mosaic with patches of high plant cover interspersed in a low-cover matrix (Aguiar & Sala 1999). In most African ecosystems, these dense patches of vegetation are usually arranged in the form of bands or stripes orientated perpendicular to the slope and separated by bare soil or sparse vegetation (Aguiar & Sala 1999). This two-phased organisation means that the rates of several important ecosystem processes are affected (Aguiar & Sala 1999). For example, water dynamics are different in the two areas (Aguiar & Sala 1999; Ludwig *et al.* 2003). Inter-patch zones act as catchment areas for water to be spatially transferred over the landscape (Aguiar & Sala 1999; Ludwig *et al.* 2003), whereas vegetation patches act as sinks and capture the transported water (Aguiar & Sala 1999; Ludwig *et al.* 2003). Water moves across the inter-patch areas because of the gentle slope and the low infiltration rates of the area. By contrast, the vegetation patches function as storage reserves to reduce water velocity and increase infiltration (Aguiar & Sala 1999; Ludwig *et al.* 2003). Empirical research has shown that disturbance (e.g. grazing) is the main driver of patch dynamics (e.g. size, shape and longevity) in a number of different ecosystems (Aguiar & Sala 1999; Naděžda & Tomáš 2001; Ludwig *et al.* 2003; Jäkäläniemi *et al.* 2005). Thus, the assessment of the spatial distribution (or patchiness) within a semi-arid landscape is important in providing insight into how scarce resources (e.g. water and nutrients) are captured and stored for plants to use in the maintenance of their populations and for the functionality of the landscape as a whole (Ludwig *et al.* 2003).

Evidence of significant habitat modification by elephants (*Loxodonta africana*, Blumenbach) is widespread throughout Africa (see *Chapter 1*). In addition, between 37 and 89% of all foraging observations on elephants can be of grass (Paley & Kerley 1998; E. Knott unpublished data). However, very little research has been conducted on the effects of such an important herbivore on the composition and overall functionality of grasslands. To my knowledge, evaluations of the influence of elephants on landscape patchiness *per se* and landscape functioning are restricted to one published article and unpublished data (see Kerley & Landman 2006 for review). Significantly, previous work on other large herbivores has clearly demonstrated that grazing has a cascading influence on other ecosystem components and processes (Britton *et al.* 2005; Carline *et al.* 2005). In addition, grassland habitats provide important nesting habitat and sources of food for birds (Atkinson *et al.* 2005; Butler *et al.* 2005; West & Messmer 2006). Certainly, granivorous bird species are less common in grasslands of the Eastern Cape Province when food resources are reduced (Craig *et al.* 2005).

Thus, if elephants are grassland engineers affecting functioning then the presence of elephants in grasslands would increase the proportion of bare earth and that this would alter patch dynamics and the associated bird fauna. The specific aims of this part of the study were to: 1) Quantify the grass species composition and percentage cover of vegetation and bare earth in areas with and without elephants; 2) Investigate the functional status of these landscapes (patch dynamics) using observable landscape organisation attributes (see below) in relation to elephant presence; and 3) Determine the extent to which any changes in the bird fauna might be associated with changes in grassland structure.

3.2 MATERIALS AND METHODS

The field sampling of grasslands took place between December 2005 and January 2006. For logistical reasons, bird sampling was completed between March and April 2006 at the same sites.

3.2.1 Vegetation sampling

Five sampling stations were sampled at each treatment (*n* = 5) and control site (*n* = 5). Sampling stations on each treatment and control site were selected by using digitized vegetation maps of each area and choosing sites that they were located in grassland (*Chapter 2*; Low & Rebelo 1996). To ensure independence of the data, all sampling stations were located at least 500m apart within each treatment and control site, providing as much coverage of each site as possible. Not all locations had sufficient grassland areas to incorporate all five sampling stations (see *Chapter 2*). In these situations the remaining sampling stations (max. two in all cases) were located in either Karroid shrubland or old lands (*Chapter 2*). Although not grassland habitats *per se* these vegetation types are used by elephants in the same way (i.e. time spent feeding) as “natural” grasslands (D. Parker pers. obs.) and despite differences in species composition, will function in the same way as “natural” grasslands (Ludwig *et al*. 2003; Tongway & Hindley 2004). Thus, these areas were considered suitable for sampling. At each sampling station a variable number of haphazardly located 1m^2 quadrats were used to sample the vegetation. The placement of quadrats involved selecting a point on the horizon, walking ten paces and throwing the quadrat. The point at which the quadrat landed was then sampled and used as the starting point for the next quadrat, following the same point on the horizon (Bond & Loffell 2001). In each quadrat the identity of all grass species, height of the vegetation (m), percentage vegetative cover, and percentage bare earth were recorded (Butler *et al*. 2005; Smet & Ward 2005). Grass species were only recorded if they were rooted within the quadrat. Maximum grass height was measured once in each quarter of each quadrat. Percentage vegetative cover and percentage bare earth were rated subjectively by the same observer (DMP) as a proportion of the entire quadrat e.g. if vegetation made up 85% of the quadrat then bare earth could only occupy a maximum of 15%. Adequate sampling effort was determined for each treatment and control site by throwing quadrats at the first sampling station of the control site and constructing a species accumulation curve using the Mao Tau method in EstimateS (Colwell 2005). Adequate sampling effort was defined as the point where the rate of plant species accumulation over five sampling intervals (quadrats) fell below 0.10 new species (Taylor 2007). Accordingly, I surveyed 25 quadrats per sampling station at Amakhala treatment and 25 quadrats per sampling station at Amakhala control, 29 at Kariega sampling stations (treatment and control), 37 at Kwandwe sampling stations (treatment and control), 47 at Pumba sampling stations (treatment and control) and 50 at Shamwari sampling stations (treatment and control). These data were used to determine the mean height (m), percentage vegetative and bare earth cover and grass species frequency of occurrence for treatment and control sites. Frequency of occurrence was based purely on the presence/absence of individual grass species at each sampling station. Thus, if a grass species was recorded at all five sampling stations it had a frequency of occurrence of 100% for that site.

3.2.2 Ecosystem Function Sampling

The landscape functioning analysis (LFA) described by Tongway & Hindley (2004) and Ludwig *et al.* (2003) was used. This method was preferred over other possible techniques due to its ability to make use of simple visible indicators (e.g. percentage vegetative cover) to assess the biogeochemical functioning of rangelands (Tongway & Hindley 2004). Two transects of approximately 50m each were completed at each treatment and control site (Tongway & Hindley 2004). Two transects were considered as an adequate sampling effort, as a preliminary assessment indicating that there was little change in the standard error of the measured variables (see below) when including data from additional transects (Tongway & Hindley 2004). Both transects were chosen at random within two sampling stations at each treatment and control site (Tongway & Hindley 2004). The two areas used for the transects were selected by numbering the sampling stations at each site (1-5) and generating two random numbers within this range using Microsoft Excel. Transects were at least 500m apart at each site to ensure independence of the data and were at least 500m away from permanent water. Each transect was located at the upslope of the local watershed, in the area of maximum slope (along the gradient), and a 50m measuring tape was laid taut on the ground (Tongway & Hindley 2004). Patches of perennial plant growth (defined as grass and shrub patches) inter-patches (defined as bare soil) were identified along each transect. Inter-patches were zones where resources, such as water are freely transported downslope. The cover length (m) and maximum width (cm) of all patches were recorded. For inter-patches, only the distance (m) between plant patches was measured (Tongway & Hindley 2004). The measurement of the size and number of patches is important in rangeland dynamics as patches tend to accumulate resources by slowing or restricting the flow of water, topsoil and organic matter across the landscape (Aguiar & Sala 1999; Tongway & Hindley 2004). Each transect included at least five replicates of each patch/inter-patch type (Tongway & Hindley 2004). From these data the number of patches per 10m, average patch width (cm), total patch area (m^2), patch area index (total patch area/transect length x 10) and proportion (%) of each patch type (Tongway & Hindley 2004) were calculated for each treatment and control site. All landscapes are organised as a series of patches and inter-patches (Aguiar & Sala 1999). However, as vegetation becomes more dense there comes a point when litter and soil are no longer mobilised and transported by flowing water (Tongway & Hindley 2004). In such situations, a patch is recognised as a sward of functionally linked individual plants (Tongway & Hindley 2004). Swards are typically greater than 10m wide and show very little evidence of soil or litter transport between or around plant butts (Tongway & Hindley 2004). Consequently, the maximum width of all transects was 10m.

A soil surface assessment (SSA) was also conducted along each transect (Tongway & Hindley 2004). In order to do so, a series of “query” zones within each patch and inter-patch were identified using the transect log i.e. one “query” zone per patch/inter-patch along the transect. “Query” zones were usually 1m in length, except where patch/inter-patch length was insufficient, and were sited symmetrically within the patch/inter-patch to avoid edge effects (Tongway & Hindley 2004). In each “query” zone the rainsplash protection (scale = 1-4), perennial vegetation cover (scale = 1-4), amount/origin and decomposition of litter (scale = 1-10), cryptogram (algae, fungi, lichen and moss) cover (scale = 0-4), crust brokenness (scale = 0-4), soil erosion type and severity, deposited materials (scale = 1-4), soil surface roughness (scale = 1-5), surface nature (scale = 1-5), slake test (scale = 0-4) and texture (4 classes) were visually assessed by the same observer, DMP (Tongway & Hindley 2004). These data were then used to calculate soil stability, infiltration and nutrient cycling status using pre-existing equations (Tongway & Hindley 2004). Stability was defined as the ability of the soil to withstand erosive forces and re-form after disturbance. Infiltration was defined as the way in which the soil partitions rainwater into soil water for plants to use, and nutrient cycling as how efficiently organic matter is cycled back into the soil (Tongway & Hindley 2004).

For this aspect of the chapter, data collected from Addo and its paired control site (Colchester) were incorporated. Only SSA data were collected, as it was part of a small National Parks-approved project. It was not possible to include Addo as an additional study site for any other aspect of my study.

3.2.3 Bird Sampling

The bird sampling procedures are fully described in *Chapter 2* (p.48). There were insufficient observations at the individual site level to calculate relative species abundances for each site. Thus, only the overall relative abundance data for birds at treatments and controls is presented (Appendix II).

3.2.4 Data Analysis

The shared species, unique species, Morista-Horn index, overall species richness and diversity (Shannon Wiener H’) statistics were all calculated using EstimateS (Colwell 2005). Differences between the mean height, percentage vegetative cover and percentage bare earth at treatment and control sites were tested using paired t-tests (Statistica, Statsoft, version 7.0). Differences in the species richness and diversity of grass and bird species were tested in the same way. Chi-Square tests were used to test for differences in the overall species composition of grasses and birds at treatment and control sites (Cohen & Holliday 2001). In both cases, the control values were used as the expected values. The differences between treatment and control sites for the various landscape function indicators and soil-surface indices were tested using a series of non-parametric Wilcoxon matched-pair, signed-rank tests (Statistica, Statsoft, version 7.0). A two-way ANOVA after arcsine transformation was used to test for differences between the proportion of patch types (grass, shrub and bare soil) at treatment and control sites (Statistica, Statsoft, version 7.0). The categorical predictors in this analysis were “treatment” (with or without elephants) and “patch type” (e.g. grass). A Tukey post-hoc test was performed to ascertain the source of the variation (Statistica, Statsoft, version 7.0).

3.3 RESULTS

The height of vegetation measured in quadrats at treatment sites was marginally higher than the height of vegetation at control sites (Figure 3.1A). However, this difference was not significant ($P = 0.48$, $t_{24} = 0.716$). Similarly, the percentage vegetative cover at treatment sites was higher than controls (Figure 3.1B), while the proportion of bare earth at treatment and control sites followed the opposite trend (Figure 3.1C). In neither case were the differences significant (P = 0.41, t_{24} = 0.832 and P = 0.41, t_{24} = -0.835 respectively).

The species richness of grasses was higher at treatment sites compared to controls, but this difference was not significant (Figure 3.2A; P = 0.09, t_4 = 2.269). Likewise, the Shannon-Wiener diversity index was higher at treatment sites than controls and the difference was not significant (Figure 3.2B; P = 0.16, t_4 = 1.701). Twenty-six grass species were identified across treatment and control sites, and 19 species were shared between the two sites. Both treatments and controls had a similar number (4 and 3 respectively) of unique species (Table 3.1). *Alloteropsis semialata*,Hitch., *Aristida diffusa,* Trin., *Eragrostis curvula*, Schrad., and *Panicum ecklonii*, Nees, were only found at treatment sites while *Eragrostis capensis,* Thunb., *Lolium perenne*, L., and *Pentachistis curvifolia*, Schrad., were only found at control sites (Table 3.1). All four unique species at the treatment sites are tufted-perennial grasses and considered climax grasses that offer excellent protection against wind and sun (Oudtshoorn 2002). In addition, these grasses do not generally occur in highly disturbed areas (Oudtshoorn 2002). By contrast, at control sites only *P. curvifolia* is considered a climax (and tufted-perennial) grass species. *Eragrostis capensis* is a sub-climax grass that offers less protection than a climax species and *L. perenne* is classed as a pioneer species that affords even less protection and grows in highly disturbed areas (Oudtshoorn 2002). Despite these differences, there was no significant difference between the frequency of occurrence of different grass species at treatment and control sites (Table 3.1; P = 0.10, χ^2 = 1.636, df = 19) and grass species composition was similar at treatments and controls (Table 3.1; Morista-Horn Similarity Index = 0.844).

At the landscape organisation level within grasslands, although treatment sites had slightly more patches per 10m than controls, this was not significant (Table 3.2; $P = 0.29$, $Z = 1.059$). The median patch width was more than five times greater at control sites compared to treatments, but this relationship was also not significant (Table 3.2; $P = 0.15$, $Z = 1.423$). Similarly, total patch area was higher at control sites but there was no significant difference between the treatments and controls (Table 3.2; $P = 0.25$, $Z = 1.156$). The patch area index, which integrates patch area, transect length and transect width, was similar at both treatments and controls (Table 3.2; $P = 0.53$, $Z = 0.628$).

Treatment (with or without elephants) did not have a significant effect on the proportion of different patch types (grass, shrub and bare soil) per transect (Figure 3.3; $P = 0.86$, $F_{1, 66} = 0.033$). By contrast, the overall proportion of the three patch types was significantly different ($P < 0.001$, $F_{2, 66} = 74.011$). Transects at treatments and controls consisted of significantly more grass patches than any other patch type (Figure 3.3; $P < 0.001$, $F_{2, 66} = 74.011$). There was no significant interactive effect between treatment and patch type ($P = 0.64$, $F_{2, 66} = 0.456$).

Like the results for the overall organisation of grasslands, the indices of stability, infiltration and nutrient cycling were very similar between treatment and control sites (Table 3.3). Values for the three indices were very slightly higher at the controls, but there was no significant difference between treatments and controls overall (Table 3.3; $P = 0.37$, $Z = 0.901$, stability; $P = 0.16$, $Z = 1.399$, infiltration; $P = 0.07$, $Z = 1.813$, nutrient cycling).

The species richness and diversity of birds within grasslands at the treatment and control sites followed an almost identical trend to the grasses. The species richness and diversity of birds was higher at treatment sites compared to controls, but these differences were not significant (Figure 3.4A & B; $P > 0.30$, $t_4 = 1.191$ and 0.774 respectively). In contrast to the grasses, treatment and control sites only shared nine bird species (Morista-Horn Similarity Index = 0.545) out of a total of 24 (Appendix II). Treatment sites had more (13) unique species compared to the controls (2; Appendix II). African Hoopoe, Cape Glossy Starling, Cape Sparrow, Cape Wagtail, Common Fiscal, Crowned Lapwing, Greater Double-collared Sunbird, Karoo Prinia, Karoo Scrub-Robin, Red-backed Shrike, Rufous-eared Warbler, Rufous-naped Lark and Tawny-flanked Prinia were only recorded at treatment sites. By comparison, Cape Bunting and Dark-capped Bulbul were the only species that were recorded exclusively at controls (Appendix II). Despite these differences, there was no significant difference in the overall species composition of birds at treatment and control sites ($P = 0.99$, $\chi^2 = 2.894$, df = 12).

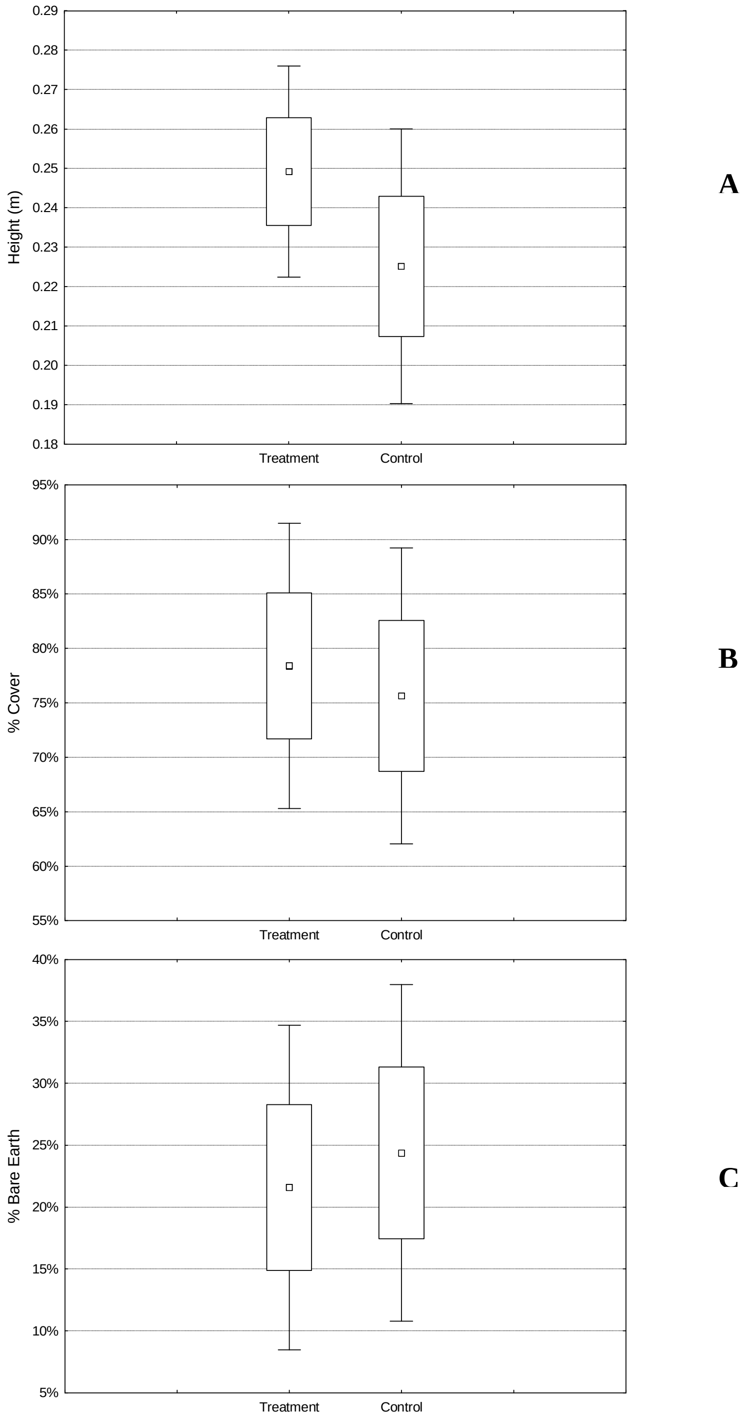

Figure 3.1: The height (m) of vegetation (**A**), percentage vegetative cover (**B**) and percentage bare earth (**C**) measured in grassland quadrats at treatment and control sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

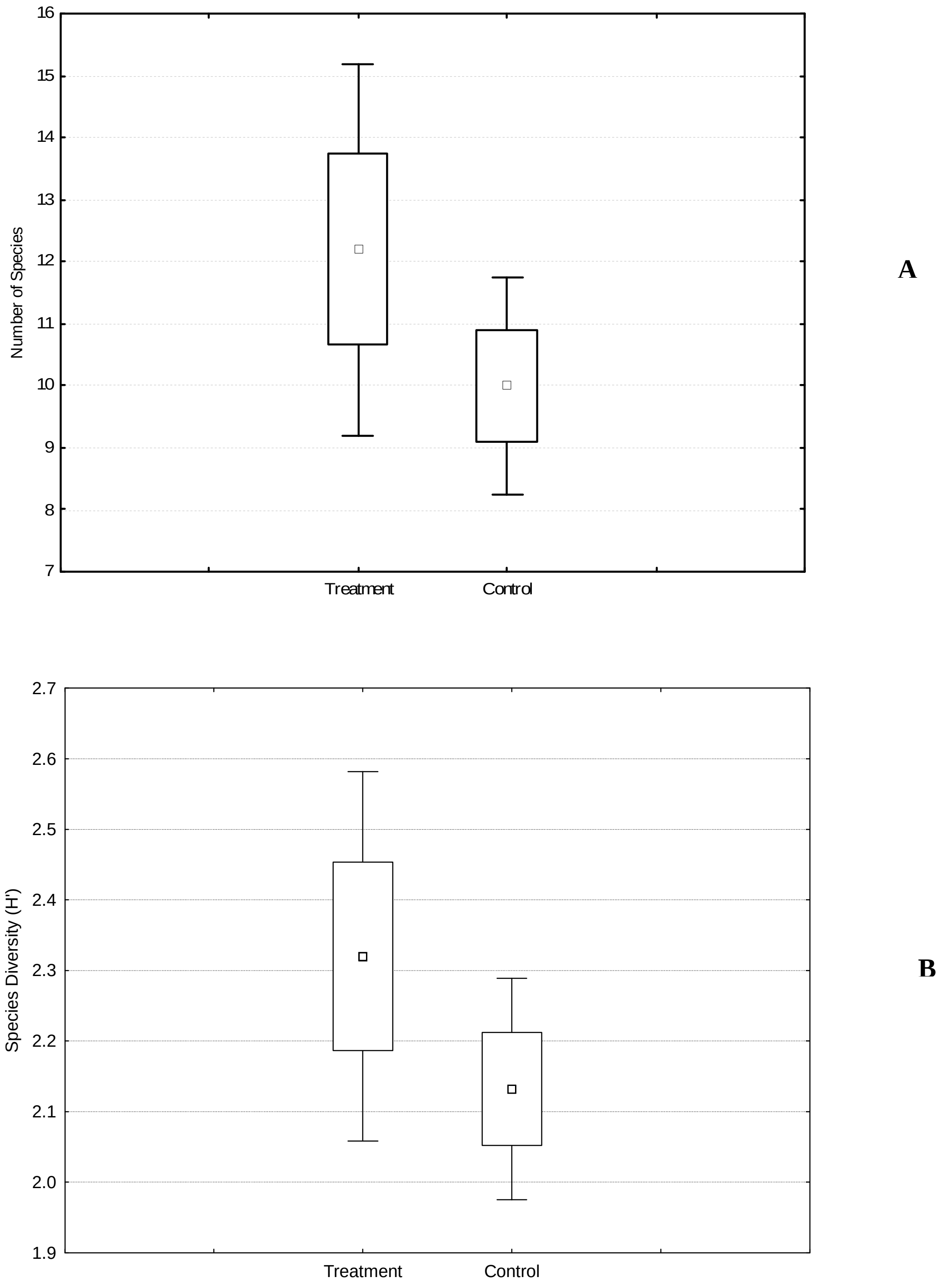

Figure 3.2: The number of species (**A**) and Shannon-Wiener diversity (H')(**B**) of grasses identified in grasslands at treatment and control sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

Table 3.1: The mean frequency of occurrence of the grass species sampled at treatment and control sites. SD = Standard Deviation. Morista-Horn Similarity Index for treatments and controls = 0.844.

Grass species	Treatment	SD	Control	SD
Alloteropsis semialata	4%	8.94%	0%	0%
Aristida congesta	36%	29.66%	24%	16.73%
Aristida diffusa	4%	8.94%	0%	0%
Bromus catharticus	12%	17.89%	4%	8.94%
Chloris gayana	20%	24.49%	16%	21.91%
Cymbopogon plurinodus	4%	8.94%	4%	8.94%
Cynodon dactylon	84%	26.08%	88%	17.89%
Ehrharta calycina	28%	33.47%	12%	17.89%
Eragrostis capensis	0%	0%	16%	26.08%
Eragrostis curvula	24%	32.86%	0%	0%
Eragrostis obtusa	28%	38.99%	28%	22.80%
Eragrostis superba	8%	17.89%	12%	26.83%
Lolium perenne	0%	0%	4%	8.94%
Melinis repens	12%	10.95%	8%	10.95%
Panicum ecklonii	4%	8.94%	0%	0%
Panicum maximum	56%	32.86%	64%	29.66%
Paspalum dilatatum	16%	26.08%	4%	8.94%
Pennisetum clandestinum	24%	21.91%	8%	10.95%
Pentachistis curvifolia	0%	0%	16%	35.78%
Setaria sphacelata	44%	32.86%	24%	21.91%
Sporobolus africanus	40%	24.49%	36%	49.80%
Sporobolus fimbriatus	44%	26.08%	52%	30.33%
Sporobolus ioclados	4%	8.94%	4%	8.94%
Sporobolus nitens	8%	17.89%	4%	8.94%
Themeda triandra	40%	31.62%	44%	32.86%
Tragus betonicus	8%	17.89%	16%	35.78%

Table 3.2: Landscape function indicators (median values) observed for grass and shrub patches at treatment and control sites. Lower and upper quartiles are indicated in brackets. There was no significant ($P > 0.05$) difference between treatment and control sites for any of the indicators (see text for details).

	Number of patches/10m	**Patch width (cm)**	**Patch area (m^2)**	**Patch area index**
Treatment (*n* = 12)	6.60 (*3.40 / 18.75*)	99.80 (*45.20 / 500.0*)	134.60 (*10.70 / 232.0*)	0.88 (*0.13 / 0.95*)
Control (*n* = 12)	4.15 (*2.30 / 5.35*)	518.05 (*285.30 / 500.0*)	202.60 (*22.40 / 341.55*)	0.89 (*0.58 / 0.95*)

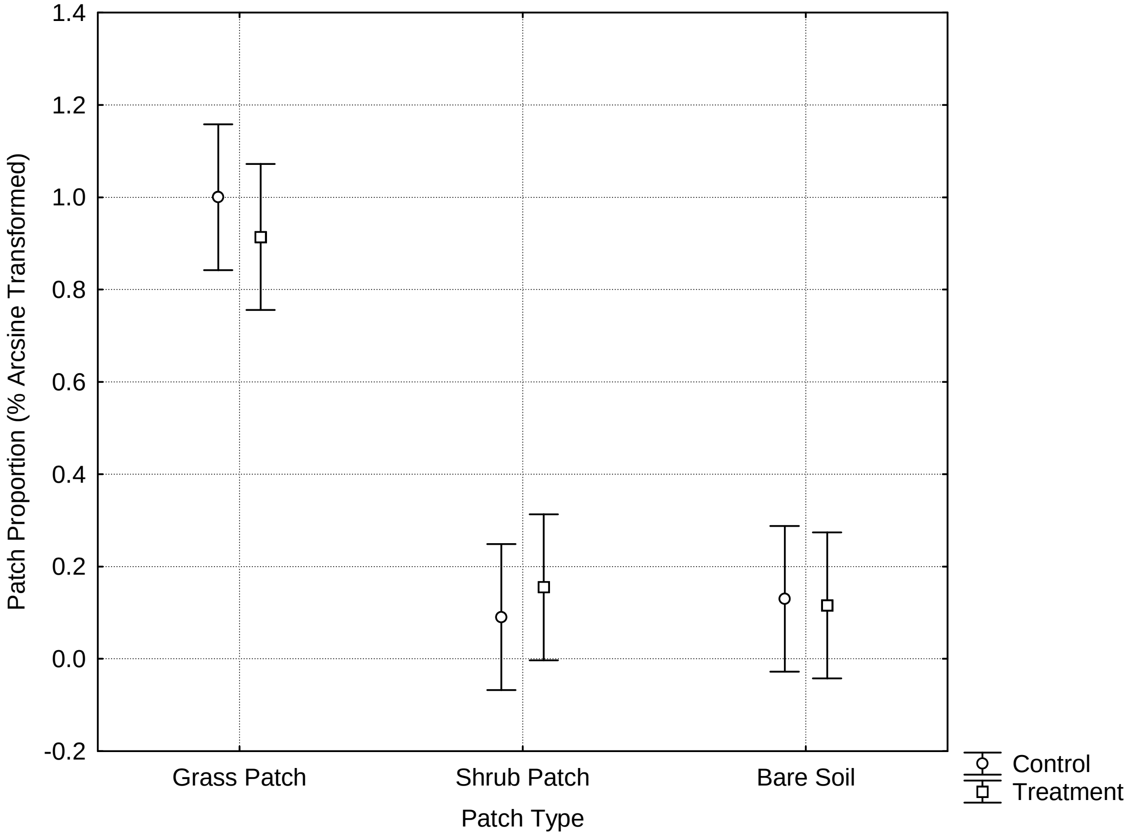

Figure 3.3: The proportion of each patch type (grass, shrub and bare soil) at treatment and control sites. Values are arcsine-transformed percentages and error bars denote 95% confidence levels. Statistical results are described in the text.

Table 3.3: Soil-surface indices (median values) calculated for the treatment and control sites. Lower and upper quartiles are indicated in brackets. There was no significant ($P > 0.05$) difference between treatment and control sites for any of the indices (see text for details).

	Stability	**Infiltration**	**Nutrient Cycling**
Treatment (*n* = 36)	62.58 (*49.81 / 72.43*)	29.79 (*24.44 / 36.78*)	18.0 (*11.83 / 23.16*)
Control (*n* = 36)	67.58 (*23.67 / 79.52*)	34.32 (*12.43 / 41.75*)	18.76 (*12.18 / 28.59*)

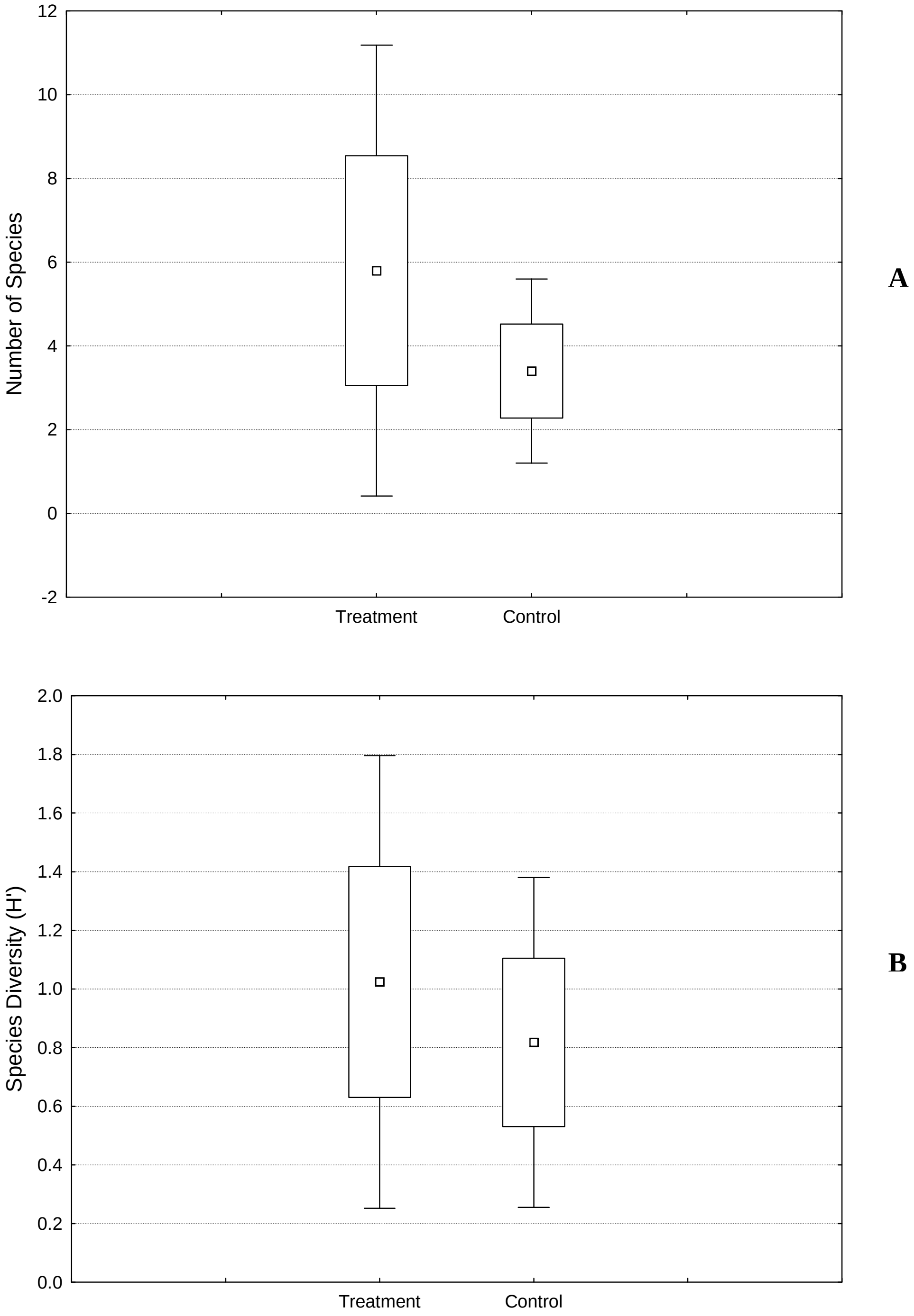

Figure 3.4: The number of species (**A**) and Shannon-Wiener diversity (H')(**B**) of birds identified in grasslands at treatment and control sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

3.4 DISCUSSION

Several authors have demonstrated that grazing by large herbivores reduces plant cover and increases the proportion of bare earth in grassland habitats (Novellie *et al.* 1991; Johnson & Cushman 2007; McEvoy *et al.* 2006; Olofsson 2006). However, in all cases the response of the respective plant communities was to increase species richness and diversity (Johnson & Cushman 2007; McEvoy *et al.* 2006; Olofsson 2006). McEvoy *et al.* (2006) suggest that such initially counterintuitive findings are driven by two mechanisms. Firstly, that the presence of herbivores promotes nutrient cycling and heterogeneity through the addition of dung and by trampling (McEvoy *et al.* 2006). Secondly, that by grazing, herbivores create greater patch heterogeneity at a relatively local (quadrat) level (McEvoy *et al.* 2006). Although species richness and diversity may be similar across the entire landscape, ungrazed areas may be dominated by a single species whereas disturbed or grazed areas have altered microhabitats that promote the growth and establishment of a different suite of species (McEvoy *et al.* 2006).

The results from my study may add further empirical support to these proposals. When the levels of grazing by large herbivores (as the main defoliation agents) in grasslands remain low, the formation of bare patches can promote seedling establishment of light-demanding species by removing competing vegetation and litter cover (McEvoy *et al.* 2006). Conversely, over-grazing is likely to increase the levels of soil compaction through trampling resulting in increased denitrification and anaerobic conditions, reducing seedling establishment (Britton *et al.* 2005; McEvoy *et al.* 2006). Although not statistically significant, I recorded more individual species and a marginally greater diversity of grasses at treatment sites compared to the controls, supporting the previous studies that have reported an increase in diversity with large herbivores present (McEvoy *et al.* 2006). Grasses have evolved under grazing conditions and it is likely that the balance of grass species in grazed habitats will shift in favour of species that are tolerant to sustained grazing (Tomlinson & O'Connor 2005; McEvoy *et al.* 2006). Tomlinson & O'Connor (2005) illustrated that such compositional shifts occur in South African grasslands for two common bunchgrasses (*Themeda triandra*, Forssk., and *Eragrostis curvula*) when defoliated experimentally. Under conditions where defoliation was more common, *T. triandra* dominated *E. curvula* as the former had greater tiller (ramet) recruitment (Tomlinson & O'Connor 2005). In my study, *E. curvula* was more common at treatment sampling stations than *T. triandra,* which was found at an equal number of sampling stations at both treatment and control sites, suggesting that the current levels of grazing are lower at treatment sites than controls. This contention is supported by presence of unique species with differing successional strategies at treatment and control sites. Those species that were unique to controls are most commonly associated with disturbed (e.g. heavily grazed) areas or are pioneer species (Oudtshoorn 2002). Novellie *et al.* (1991) reported similar results for the Addo Elephant National Park, South Africa, where *Eragrostis obtusa*, Munro, a species symptomatic of over-grazing, was more prevalent in plots where elephants were present compared to plots in a botanical reserve.

While it is tempting to suggest that, at current densities, elephants may enhance the physical plant attributes and species composition of grasslands in the Eastern Cape Province, elephants have only been present at each study site for a relatively short period and it is likely that their influence on grasslands will increase over time. In addition, it was not possible over the course of this study to erect elaborate exclosures at each site to control for the effects of other herbivores.

Furthermore, it was not possible (despite replication) to completely isolate the effects of other factors such as land-use history and bush clearing practices prior to each site being used for conservation. Thus, the current data must be interpreted within the correct context and with care, avoiding gross generalities regarding the effects of elephants in grasslands. At current densities, my results suggest that elephants neither enhance nor degrade grassland habitats through their foraging.

At the landscape scale, Palmer *et al.* (2001) showed that there was significantly more bare earth between relatively small patches of vegetation within communal rangeland (with grazing) and commercial farming in the Eastern Cape Province, South Africa. The authors argue that resource control within communal rangeland is highly variable due to the increased proportion of bare soil that act as “run-off” zones for water and organic material (Palmer *et al.* 2001). In addition, the authors suggest that communal rangelands, possessing the high degree of observed patchiness, are fragile ecosystems that will lose functionality due to erosion and water loss (Palmer *et al.* 2001). However, in semi-arid African grasslands, overall patch size does not appear to be as important as the mere presence of patches in the functioning of the landscapes (Aguiar & Sala 1999). Patches within these landscapes tend to be richer in resources compared to adjacent inter-patches, which might increase the overall production of the system (Aguiar & Sala 1999; Tongway & Hindley 2004). My results indicated similar levels of patchiness (number/10m) between treatments and controls. In addition, although patch size (width and area) was lower at treatments than controls it was highly variable. Importantly, my estimates for patch size and frequency are greater than any other previous estimates (Jäkäläniemi *et al.* 2005; mean = 1.9, size = 2.7m^2). The more sinks (or patches) present within a landscape, the greater the likelihood that water and nutrients will be incorporated into the system

(Aguiar & Sala 1999). Thus, it appears that grasslands at both treatment and control sites are functioning as similarly productive, heterogeneous systems (Aguiar & Sala 1999). This is reinforced by the results obtained for the soil-surface indices. Despite the incorporation of Addo as an additional site (with unusually high elephant density), there was no significant difference between treatments and controls for the indices of stability, infiltration and nutrient cycling. In addition, these values are within the range obtained for fully functioning Australian rangelands (Tongway & Hindley 2004). Thus, landscape functioning within the grasslands of the Eastern Cape Province does not currently appear to be negatively affected by the presence of elephants.

Martin & Possingham (2005) demonstrated that grazing by large herbivores alters the vertical and horizontal structure and composition of the vegetation in grasslands. In addition, under severe grazing pressure the grass sward can become homogeneous (Martin & Possingham 2005). When this occurs, the abundance of certain granivorous bird species can decline (Martin & Possingham 2005). In my study, I found that the composition of bird species was similar at treatments and controls. Treatments had more unique species and a marginally higher diversity and richness compared to the controls. Butler *et al.* (2005) reported similar results for birds utilising cereal fields in England. In their study, there was no significant difference between treatment (short cereal stubble) and control (higher cereal stubble) plots for bird abundance (Butler *et al.* 2005). In addition, treatment sites (shorter cereal stubble) had more unique species present than the controls (Butler *et al.* 2005). The authors contend that birds had lower energetic costs within shorter vegetation than in plots where the vegetation was higher, as it was more difficult to move through the denser vegetation, especially when it was wet (Butler *et al.* 2005).

Moreover, the level of visual obstruction offered by the shorter vegetation would have been lower in the treatment plots. Thus, bird species that rely on the early detection of predators to flee to an area of safety (i.e. most granivorous birds that feed in grasslands) would perceive treatment plots as having a lower predation risk and utilise them more intensively (Butler *et al.* 2005). Another potential factor that must be considered when interpreting bird abundance and diversity in particular habitats is the presence of alternative habitat types adjacent to the one in question (Mangnall & Crowe 2003; Naidoo 2004; Brotons *et al.* 2005). For example, the presence of a species rich habitat, neighbouring (~500m) the grassland being studied will inflate estimates in the grassland due to the high mobility of birds (Naidoo 2004; Brotons *et al.* 2005). I propose that the mosaic of habitats and land-use types surrounding the treatment sites in my study has ultimately enhanced the overall species richness and diversity of birds in grassland habitats, and, for the reasons outlined previously, is not an elephant foraging effect *per se*.

I have shown that there is no clear relationship between the presence of elephants and the physical structure of grasslands and how scarce resources (e.g. water and nutrients) are captured and stored for plants to use within enclosed reserves. There was no significant difference in the avifauna between treatment and control sites and bird species composition appears to be influenced by adjacent habitat and land-use types. In terms of the initial hypothesis, I do not believe that there is sufficient unequivocal data at present to adequately accept or reject the hypothesis. Consequently, continued long-term research, using exclosure-based experiments is desperately required in this field of elephant research. However, the comparison must be at a regional scale in order to accommodate the heterogeneous mosaic of land-use types across the Eastern Cape Province.

CHAPTER 4

ELEPHANT BROWSING IN THE THICKET BIOME AND THE CASCADING EFFECTS ON BIRD COMMUNITIES AND SOIL PROCESSES

4.1 INTRODUCTION

In an evolutionary context, all thicket vegetation types within the Thicket Biome (See *Chapter 1*) begin as a series of small clumps of woody plants, most commonly from the spike-thorn family, Celastraceae (Vlok & Euston-Brown 2002). When environmental conditions are favourable (e.g. low herbivore density), these clumps increase in size and number and ultimately link together to displace the original matrix vegetation (Vlok & Euston-Brown 2002). The displacement of the surrounding matrix vegetation results in the formation of the dense and spinescent thicket described in *Chapter 1* & *2*. However, the process of thicket formation is bi-directional and can be driven forwards ("thicket building") or backwards ("thicket depletion") depending on the occurrence and magnitude of disturbance in the form of fire and herbivory, the main drivers of thicket vegetation (Vlok & Euston-Brown 2002; Kerley *et al.* 2006). Consequently, there is often a high degree of patchiness within thicket vegetation types, which promotes increased plant diversity (Lubke *et al.* 1986; Moolman & Cowling 1994; Vlok & Euston-Brown 2002). A conservative estimate of 1558 plant species within the Thicket Biome has been proposed (Vlok & Euston-Brown 2002). However, as Vlok & Euston-Brown (2002) concede, with less rigid selection criteria this number can easily increase to 3000 species. The plant species that predominate within thicket are mostly of subtropical origin (Tongoland-Pondoland Flora; Lubke *et al.* 1986) and thus do not occur where frost is frequently experienced or where the mean winter temperature is less than 0.9^0C (Vlok &

Euston-Brown 2002). In addition, thicket generally only occurs where there is an equal amount of summer and winter rainfall (Vlok & Euston-Brown 2002). When more than 50% of the annual rainfall occurs in either summer or winter, thicket vegetation becomes highly fragmented and displaced by alternative vegetation types such as Fynbos in some of the western parts of the Eastern Cape Province (Vlok & Euston-Brown 2002). However, extensive stands of thicket vegetation are not restricted to or by any particular soil type (Vlok & Euston-Brown 2002).

Bird species diversity is affected by habitat structure and complexity (MacArthur & MacArthur 1961; Martin & Possingham 2005) and habitat heterogeneity and scale (Mangnall & Crowe 2003; Naidoo 2004; Brotons *et al.* 2005). Generally, habitats that have a more complex architecture (such as extensive stands of thicket vegetation) support a greater diversity of birds than structurally simple habitats (such as savanna) because they provide more resources and potentially more segregation at the microhabitat/niche level (MacArthur & MacArthur 1961; Martin & Possingham 2005). MacArthur & MacArthur (1961) found that bird species diversity in North and South America was positively correlated to foliage height. Similarly, Martin & Possingham (2005) demonstrated that the species diversity of birds in Australia declined as herbivore grazing (vegetation height reduction) intensified. In addition, habitat heterogeneity and scale are also important determinants of bird diversity (Mangnall & Crowe 2003; Naidoo 2004; Brotons *et al.* 2005). Birds are highly mobile and estimates of diversity can be increased by the presence of neighbouring (~500m) habitats (Naidoo 2004; Brotons *et al.* 2005). In addition, increased heterogeneity (patchiness) also provides an increased number of niches for birds to utilise and thereby promotes diversity (MacArthur & MacArthur 1961).

Major habitat alteration not only influences bird diversity but can also cause declines in overall biodiversity, reduced seed output in plants, lower plant recruitment, decreased soil infiltration rates, greater soil erosion and shrub encroachment (Ludwig *et al.* 2003; Eldridge & Freudenberger 2005). In Australian woodlands, Eldridge & Freudenberger (2005) demonstrated that soil infiltration rates were seven times lower in landscapes where woody plants had been removed. In an African situation, Kerley *et al.* (1999), measuring microtopography and soil nutrients in the Addo Elephant National Park, South Africa, found that there were more patches of bare earth in the browsed thicket vegetation compared to protected thicket in an adjacent botanical reserve resulting in decreased soil nutrients within the park.

Elephants (*Loxodonta africana*, Blumenbach) are known to significantly alter the structure of vegetation through their browsing habits (*Chapter 1*; Moolman & Cowling 1994; Cumming *et al*. 1997). Significantly, in the Thicket Biome, elephants at high densities can reduce the available biomass and cover of woody species as well as decrease the abundance of some plant species (Cowling & Kerley 2002). This is particularly relevant when it is considered that herbivory is one of the most important factors influencing the distribution of the Thicket Biome in the Eastern Cape Province (Vlok & Euston-Brown 2002). Thus, I hypothesise that in the presence of elephants at low densities, relatively homogeneous stands of structurally complex thicket vegetation will be transformed to structurally simpler, heterogeneous (patchy) habitats, and that this will positively influence the associated bird communities but that soil processes will be similar. The specific aims of this part of the study were to: 1) Compare the community composition of thicket vegetation within enclosed reserves; 2) Assess the extent of elephant damage; and 3) Determine the degree to which damage to thicket vegetation caused by elephants affects the associated bird fauna and soil processes.

4.2 MATERIALS AND METHODS

The field sampling of thicket vegetation took place between October and December 2006. For logistical reasons, bird sampling was completed between June and September 2006 at the same sites.

4.2.1 Vegetation sampling

Three sampling stations were sampled at each treatment (*n* = 5) and paired control site (*n* = 5). Sampling stations on each treatment and control site were selected by using digitized vegetation maps of each area and ensuring that they were all located in Subtropical Thicket (Low & Rebelo 1996) and far enough apart (all at least > 500m) to ensure independence of the data. A sampling effort of three sampling stations per treatment and control site was considered adequate given the practical difficulties of sampling within this vegetation type and a preliminary plant species accumulation assessment at each site, using the MaoTau method (Colwell 2005). This revealed that the 95% confidence intervals for the second and third transects overlapped at all sites. At each sampling station the vegetation was characterised using the point-centred-quarter (PCQ) method (Cottam & Curtis, 1956) with modifications as suggested by Dahdouh-Guebas & Koedam (2006). This technique was chosen over other potential methods as it provides the least variable results for distance measures and provides more data on each tree species per sampling point than other methods (Cottam & Curtis 1956). In addition, with a sample size (points per transect) of 28 or more, the method has a standard error of < 10%, which is considered satisfactory for biological studies (Cottam & Curtis 1956). PCQ methods are also the most practical in terms of the costs associated with labour, time and equipment (Rutherford 1979; R. Lubke pers. comm.). Thus, at each sampling station, a transect of 28 points (separated by 10m intervals) was conducted in a predetermined cardinal direction. All transects were completed on North facing slopes of similar gradient at each treatment and control site. At each individual point, a cross was laid down, to represent four quarters and the nearest individual plant (> 1.3 m in height) in each quarter identified (Guy 1976; Jachmann & Bell 1985; Dahdouh-Guebas & Koedam 2006). This height was chosen as the cut-off for sampling as it is similar to the preferred foraging height of elephants (Guy 1976; Jachmann & Bell 1985) and improves the accuracy of the basal area estimates calculated by the modified PCQ method (Dahdouh-Guebas & Koedam 2006). Plants >5m from the sampling point were excluded from the analysis to ensure that no one plant was considered more than once (Dahdouh-Guebas & Koedam 2006). The distance (m) from the sampling point to the centre of the plant was measured using a tape measure; the height (m) measured using a calibrated pole, and the stem girth (cm) at 1.3m above ground level, measured using a tape measure. For multi-stemmed plants, the stem girth of the central stem(s) was recorded instead of the nearest stem (Dahdouh-Guebas & Koedam 2006). In addition, a damage rating (0-7 scale) and the type of damage (elephant or other) for each plant were recorded (Anderson & Walker 1974; Walker 1976; Conybeare 1991). Damage was defined as a loss of vegetative biomass or as mortality (Anderson & Walker 1974; Conybeare 1991). The categories of damage were: 0 = no damage; 1 = 1-10% loss; 2 = 11-25% loss; 3 = 26-50% loss; 4 = 51-75% loss; 5 = 76-90% loss; 6 = 91-99% loss; 7 = 100% loss or dead individual (Walker 1976; Conybeare 1991). In order to arrive at a particular rank, a series of value judgements were made for each plant sampled i.e. is it more or less than half? Is it less than a quarter? etc. Damage was classed as either being due to elephants or some other factor. Elephant damage was relatively easy to identify, and included uprooted trees, evidence of bark stripping and characteristically browsed branches (see *Chapter 1*). Other damage included any visible signs of browsing by other ungulates, frost damage, insect damage or disease (Anderson & Walker 1974; Conybeare 1991). From these data the % damage to plants, stem density (trees/m^2), basal area (m^2/0.1 Ha) and average height (m) were calculated for treatment and control sites (Dahdouh-Guebas & Koedam 2006). In addition, an importance value for each species was calculated (Dahdouh-Guebas & Koedam 2006). The importance value was calculated for each species at treatment and control sites by adding the density (trees/m^2), dominance (basal area per species/total basal area, expressed as a percentage) and frequency (number of trees of a species/total number of trees, expressed as a percentage) estimates for each species (See Dahdouh-Guebas & Koedam 2006).

In addition to the above, an assessment of vegetation complexity (canopy cover) was also made. Using a modified checkerboard method, as described by MacArthur & MacArthur (1961), vegetation complexity was assessed at 1.5m above the ground and 25m along each transect. The method involved recording the proportion (%) of the checkerboard (90cm x 60cm and consisting of 10cm x 10cm red and white blocks) obscured by vegetation 10m away from the central point. Open vegetation had a lower percentage of the checkerboard obscured, while more complex vegetation had a higher percentage of the checkerboard obscured. The procedure was conducted four times, once in each cardinal direction, at each sampling station. The mean complexity (%) for treatment and control sites was calculated using these data.

4.2.2 Bird sampling

See the bird sampling section described in *Chapter 2* (p.48).

4.2.3 Soil Sampling

A slightly modified version of the soil surface assessment (SSA) described in *Chapter 3* (p. 55) was used for this component. Along each transect, five 1m “query” zones were haphazardly sampled. The location of each “query” zone was predetermined in that one “query” zone was sampled every five points (roughly 50m) along the vegetation sampling transect, except for the fifth “query” zone which was located at point 28.

4.2.4 Data Analysis

The shared species, unique species, Morista-Horn index, overall species richness and diversity (Shannon Wiener H’) statistics were all calculated using EstimateS (Colwell 2005). Differences between the mean height, plant density, basal area, complexity, percentage damage and soil-surface indices at treatment and control sites were all tested using paired t-tests (Statistica, Statsoft, version 7.0). Significant variation in the species richness, diversity and relative abundance (importance values for plants) of plant and bird species was tested in the same way. Chi-Square tests were used to test for differences in the overall species composition of plants and birds at treatment and control sites (Cohen & Holliday 2001). In both cases, the control values were used as the expected values. Differences between the relative abundance of birds in each feeding and nesting category at treatment and control sites were tested using two-way ANOVAs (Statistica, Statsoft, version 7.0). The categorical predictors in these analyses were “treatment” and “category” (either feeding or nesting). A Tukey post-hoc test was performed to ascertain the source of the variation in each test (Statistica, Statsoft, version 7.0).

4.3 RESULTS

Although control sites had slightly higher plant densities compared to the treatments (Figure 4.1), there was no significant difference between treatments and controls (Figure 4.1; $P = 0.43$, $t_{14} = -0.816$). The basal area occupied by thicket plants followed a similar trend, with plants at control sites covering a greater area per 0.1Ha (Figure 4.2) however this difference was not significant (Figure 4.2; $P = 0.07$, $t_{14} = -1.941$). In addition, the mean height (Figure 4.3A) and complexity (Figure 4.3B) of thicket vegetation were similar at treatment and control sites, albeit marginally higher at control sites in both cases (Figure 4.3A & B; $P > 0.23$, $t_{14} = -1.143$ & -1.266 respectively).

At a community level, the plant species composition of thicket vegetation was similar at treatment and control sites (Figure 4.4A & B). The species richness and diversity of thicket vegetation were slightly higher at the treatment sites (Figure 4.4A & B; $P > 0.23$, $t_{14} = 0.914$ & $t_4 = 1.388$ respectively). These results are reinforced at a species level, with 36 plant species shared between the treatment and control sites (Table 4.1; Morista-Horn Similarity Index = 0.913). However, the importance values of the individual thicket species were significantly different between treatment and control sites (Table 4.1; $P < 0.001$, $\chi^2 = 224.632$, df = 53). Treatment sites had more unique species (10) than controls (3; Table 4.1). In addition, *Aloe africana,* Miller, *Cassine aethiopica*, Thunb., *Crassula ovata*, Miller, and *Euclea undulata*, Thunb., were all substantially more important at the treatment sites compared to the controls (Table 4.1). However, *Azima tetracantha,* Lam., *Euphorbia triangularis,* Desf., *Grewia robusta,* Burch., *Gymnosporia polyacantha*, Szyszyl., and *Schotia afra*, Thunb., were by contrast substantially more important at control sites than treatments (Table 4.1).

Damage (or percentage biomass removal) to thicket vegetation was low and not significantly different at both treatment and control sites (Figure 4.5A; $P = 0.55$, $t_4 = -0.651$). In addition, damage caused exclusively by elephants to thicket species was lower at treatment sites than the damage caused by other herbivores and natural causes (Figure 4.5B; $P = 0.47$, $t_4 = -0.793$).

The community variables for the birds that utilised thicket vegetation followed a trend analogous to the plants (Figure 4.6). Bird species richness was higher at treatment sites compared to controls, but this difference was not significant (Figure 4.6A; $P = 0.22$, $t_4 = 1.455$). Similarly, species diversity and the relative abundance of all birds were higher at treatment sites than controls but these differences were not significant (Figure 4.6B & C; $P = 0.12$, $t_4 = 1.963$ and $P = 0.16$, $t_4 = 1.702$ respectively).

At an individual species level, treatments and controls shared 33 bird species and the species composition was similar (Morista-Horn index = 0.776). However, treatments had more (11) unique species present compared to the controls (8; Appendix II). Despite this, the relative abundance of individual bird species in thicket vegetation was not significantly different between treatments and controls (Appendix II; $P = 1.00$; $\chi^2 = 3.244$; df = 48). Treatment did not have a significant effect on the relative abundance of birds in six feeding categories (Figure 4.7; $P = 0.92$, $F_{1, 73} = 0.010$). However, significantly more birds were arboreal feeders compared to those that foraged on the ground (Figure 4.7; $P = 0.04$, $F_{5, 73} = 2.472$). There was no significant interactive effect between the two categorical predictors (treatment and feeding strategy) ($P = 0.91$; $F_{5, 73} = 0.306$). Similarly, the relative abundance of birds utilising five different nesting strategies was comparable between treatment and control sites (Figure 4.8; $P = 0.77$, $F_{1, 75} = 0.089$), but significantly more birds were chamber nesters than any other nesting strategy except bowl nesters (Figure 4.8; $P < 0.01$, $F_{4, 75} = 4.875$). There was no significant interactive effect between these two factors ($P = 1.00$; $F_{4, 75} = 0.050$).

The soil-surface assessment completed within thicket vegetation at treatment and control sites indicated that the indices of stability, infiltration and nutrient cycling were extremely similar (Figure 4.9). There was no significant difference between treatments and controls (Figure 4.9; $P = 0.54$, $t_{14} = -0.624$, stability; $P = 0.87$, $t_{14} = -0.173$, infiltration; $P = 0.99$, $t_{14} = 0.018$, nutrient cycling).

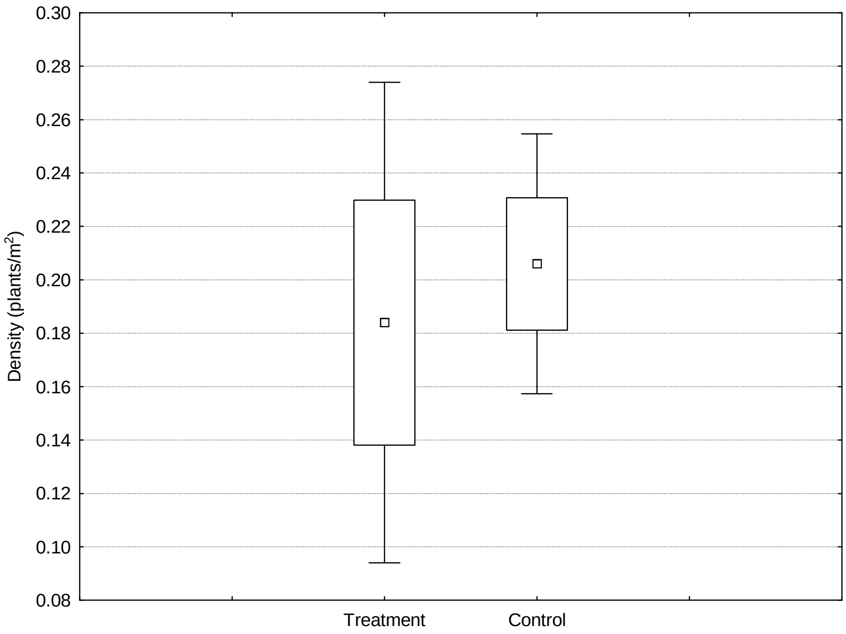

Figure 4.1: The density (plants/m^2) of thicket vegetation at treatment (*n* = 15) and control (*n* = 15) sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

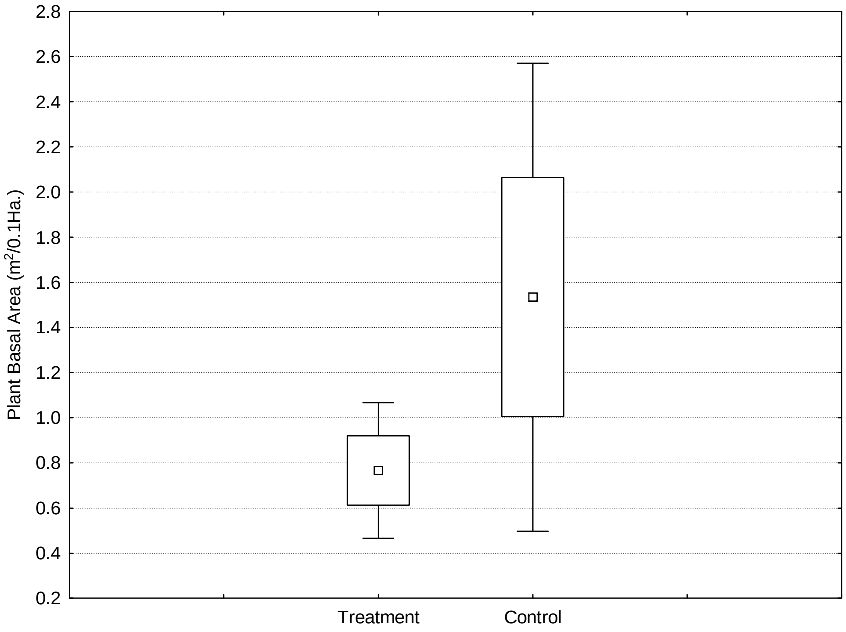

Figure 4.2: The basal area covered by thicket plants (m^2/0.1 Ha.) at treatment (*n* = 15) and control (*n* = 15) sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

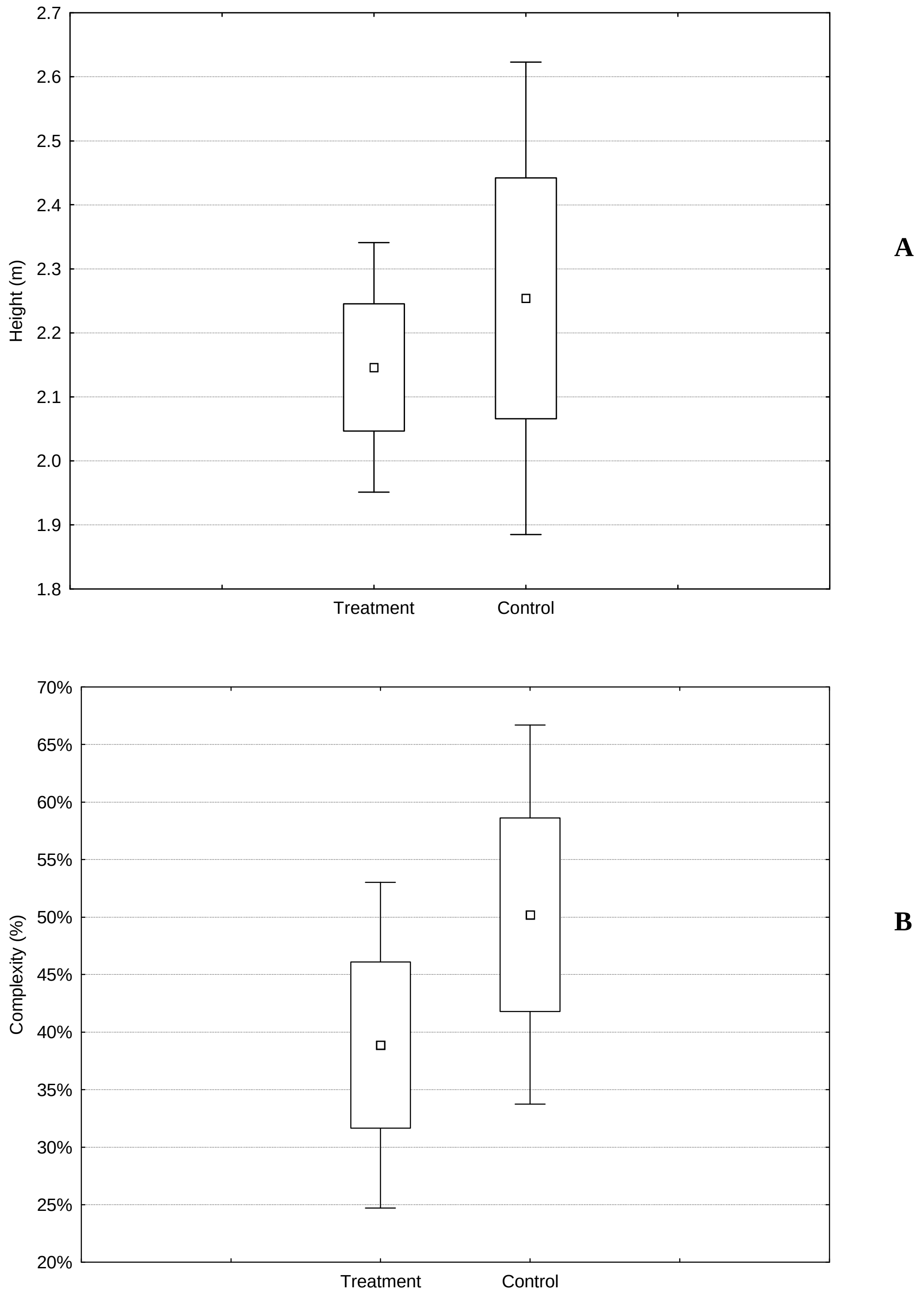

Figure 4.3: The height **(A)** and complexity **(B)** of thicket vegetation at treatment (*n* = 15) and control (*n* = 15) sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

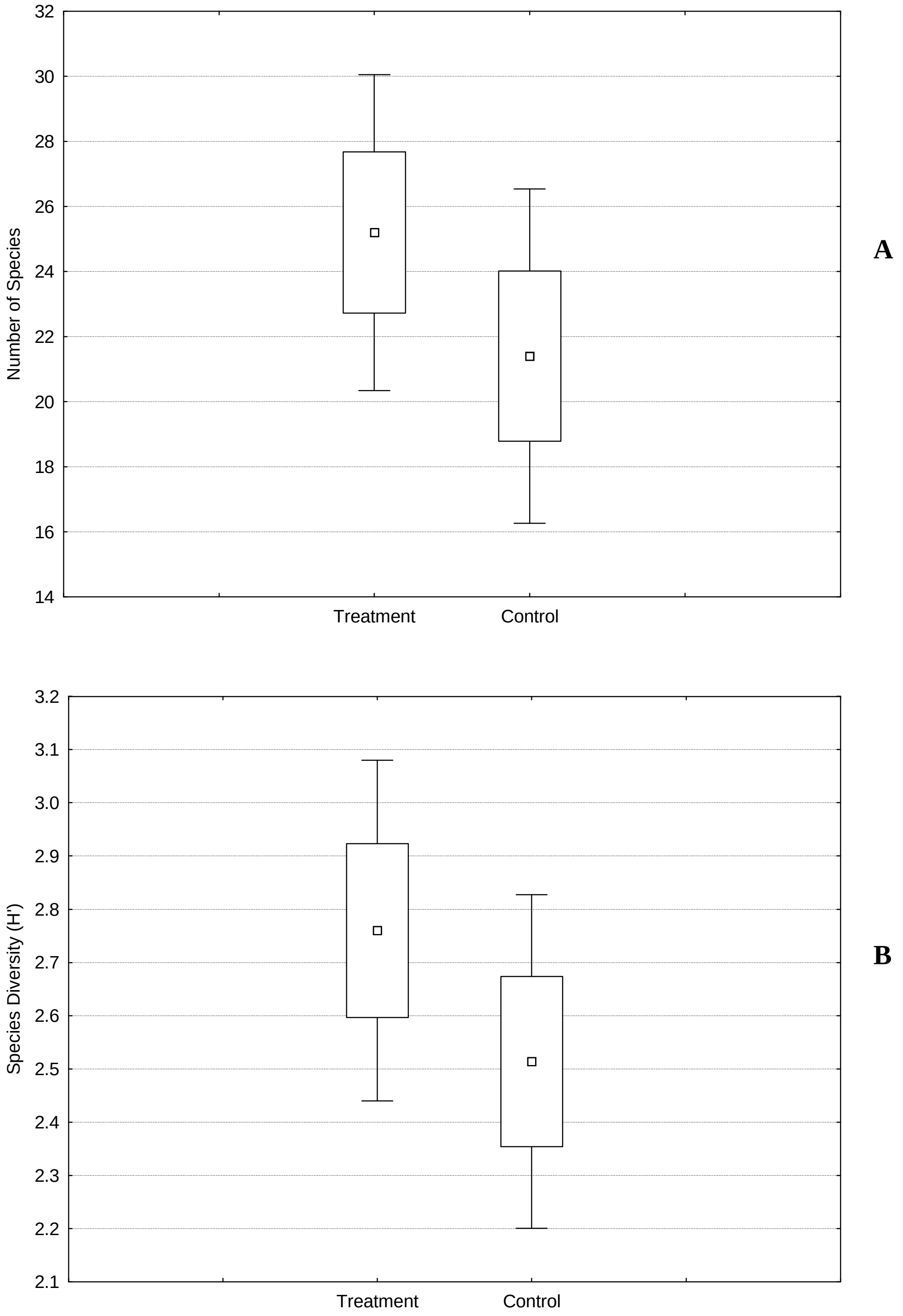

Figure 4.4: The species richness **(A)** and diversity **(B)** of thicket vegetation sampled at treatment (*n* = 15) and control (*n* = 15) sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

Table 4.1: The mean importance values for thicket plant species across treatment and control sites. SD = standard deviations.

Family	**Species**	**Treatment**	**SD**	**Control**	**SD**
Mimosaceae	*Acacia karroo*	6.73	15.37	4.70	9.90
Liliaceae	*Aloe africana*	10.19	32.32	1.45	3.42
Liliaceae	*Aloe bainsii*	0.00	0.00	0.51	1.99
Liliaceae	*Aloe ferox*	15.12	33.81	19.62	32.81
Salvadoraceae	*Azima tetracantha*	8.45	10.08	16.49	13.07
Asteraceae	*Brachylaena ilicifolia*	1.31	2.45	8.87	16.21
Buddlejaceae	*Buddleja saligna*	5.20	14.43	1.51	5.86
Rubiaceae	*Canthium inerme*	0.70	2.81	0.00	0.00
Capparaceae	*Capparis sepiaria*	6.03	9.99	4.65	5.56
Apocynaceae	*Carissa bispinosa*	2.28	4.49	1.81	3.65
Celastraceae	*Cassine aethiopica*	11.81	16.87	3.46	4.04
Rubiaceae	*Coddia rudis*	2.16	4.74	0.47	1.28
Crassulaceae	*Crassula ovata*	7.25	19.42	0.00	0.00
Crassulaceae	*Crassula* sp.	0.62	1.07	0.00	0.00
Araliaceae	*Cussonia spicata*	1.65	3.55	1.93	5.21
Ebenaceae	*Diospyros lycioides*	2.17	4.94	1.45	3.03
Ebenaceae	*Diospyros* sp.	0.15	0.59	0.00	0.00
Boraginaceae	*Ehretia rigida*	6.31	6.65	5.54	9.10
Ebenaceae	*Euclea natalensis*	0.29	1.14	0.00	0.00
Ebenaceae	*Euclea undulata*	41.85	29.92	32.64	23.46
Euphorbiaceae	*Euphorbia bothae*	0.16	0.62	0.00	0.00
Euphorbiaceae	*Euphorbia tetragona*	0.00	0.00	0.57	2.19
Euphorbiaceae	*Euphorbia triangularis*	2.53	6.67	10.23	32.08
Tiliaceae	*Grewia occidentalis*	1.55	2.43	1.61	4.01
Tiliaceae	*Grewia robusta*	2.63	5.06	9.85	14.99
Celastraceae	*Gymnosporia buxifolia*	1.43	2.37	3.15	5.76
Celastraceae	*Gymnosporia polyacantha*	6.54	10.90	11.97	18.23
Sapindaceae	*Hippobromus paucifloris*	0.15	0.59	0.21	0.80
Solanaceae	*Lycium* sp.	0.53	1.12	1.45	2.27
Celastraceae	*Maytenus capitata*	5.60	8.80	6.56	13.11
Loganiaceae	*Nuxia congesta*	0.00	0.00	0.14	0.54
Oleaceae	*Olea europea*	1.21	2.30	0.78	2.02
Cactaceae	*Opuntia ficus-indica*	7.99	19.43	10.69	16.55
Anacardiaceae	*Ozoroa mucronata*	2.51	4.81	1.20	2.30
Sapindaceae	*Pappea capensis*	12.33	19.83	10.13	15.80
Euphorbiaceae	*Phylanthus verrucosa*	4.07	9.59	0.45	0.94
Plumbaginaceae	*Plumbago auriculata*	2.49	3.79	1.31	3.25

Family	**Species**	**Treatment**	**SD**	**Control**	**SD**
Polygalaceae	*Polygala myrtifolia*	0.77	2.97	0.00	0.00
Portulacaceae	*Portulacaria afra*	49.45	56.55	47.51	53.94
Ptaeroxylaceae	*Ptaeroxylon obliquum*	4.02	13.69	0.88	2.38
Celastraceae	*Putterlickia pyracantha*	3.98	6.79	0.75	2.04
Rhizophoraceae	*Rhigozum obovatum*	5.73	12.96	7.53	18.37
Anacardiaceae	*Rhus crenata*	6.61	9.32	5.81	7.80
Anacardiaceae	*Rhus longispina*	7.50	11.53	2.75	3.16
Anacardiaceae	*Rhus pallens*	3.19	6.49	3.65	8.12
Anacardiaceae	*Rhus* sp.	0.55	1.15	0.00	0.00
Caesalpinioideae	*Schotia afra*	16.55	16.10	34.51	27.25
Caesalpinioideae	*Schotia latifolia*	2.65	7.08	0.27	1.06
Flacourtiaceae	*Scolopia zeyheri*	1.57	3.37	0.65	1.49
Rhamnaceae	*Scutia myrtina*	6.48	10.45	10.99	16.81
Asteraceae	*Senecio odontophyllus*	0.51	1.99	0.00	0.00
Sapotaceae	*Sideroxylon inerme*	3.21	7.66	6.32	10.58
Asteraceae	*Tarchonanthus camphoratus*	2.37	6.35	0.00	0.00
Rutaceae	*Zanthoxylem capense*	0.68	2.63	0.13	0.52

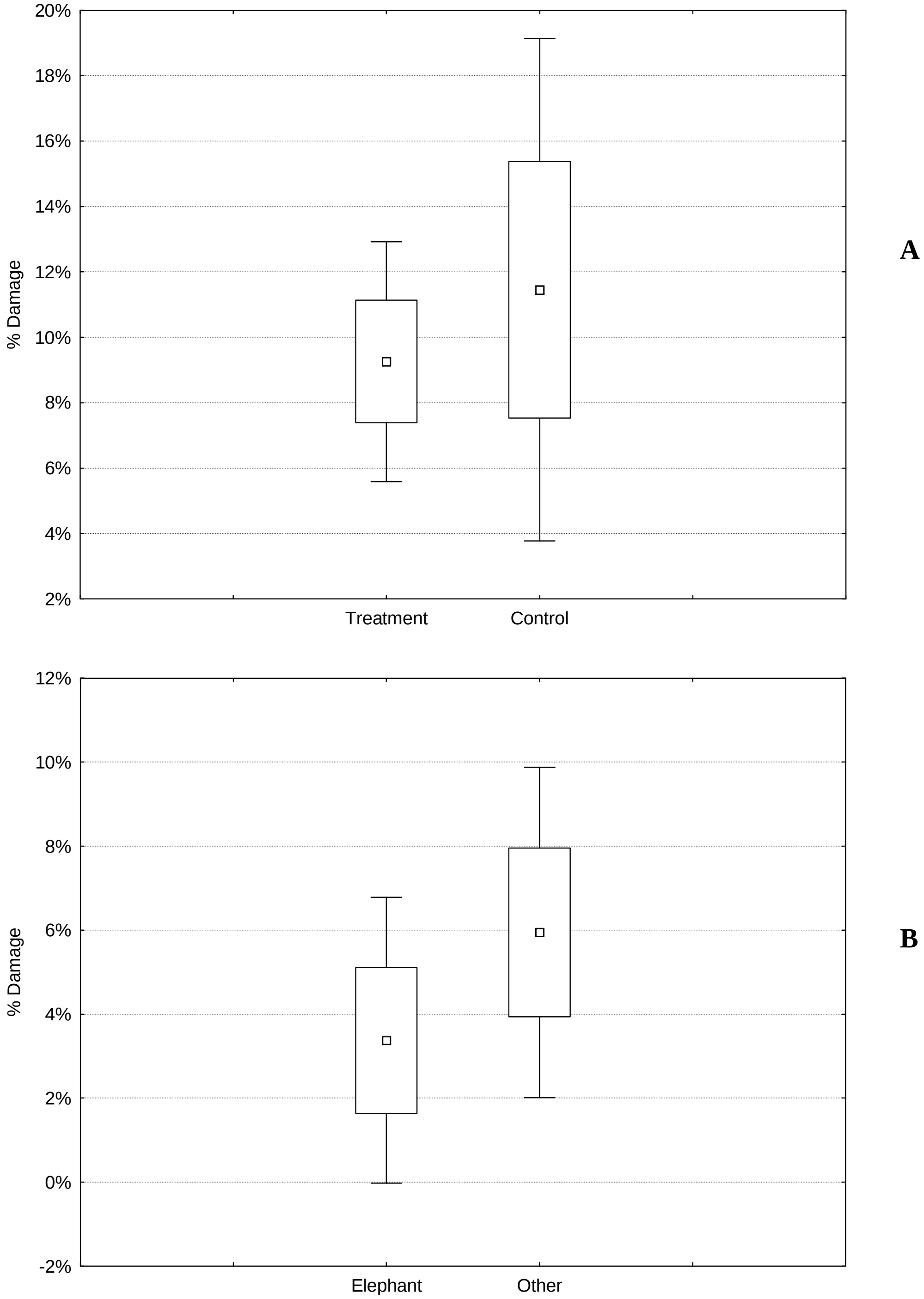

Figure 4.5: The overall percentage damage (biomass removed) to thicket vegetation at treatment and control sites **(A)** and the percentage damage caused by elephants and other factors for treatment sites only **(B)**. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

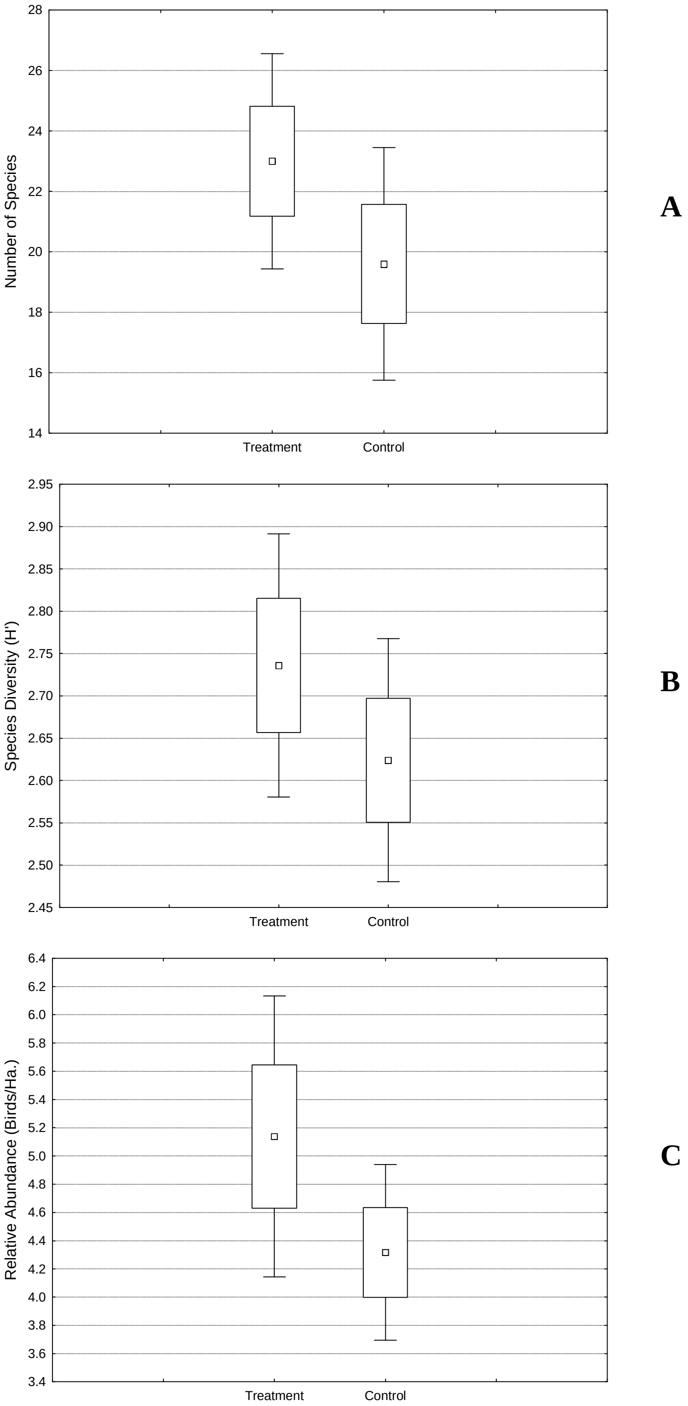

Figure 4.6: The Species richness (**A**), Shannon-Wiener diversity (H') (**B**) and density estimates of birds per hectare (**C**) in thicket vegetation at treatment and control sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

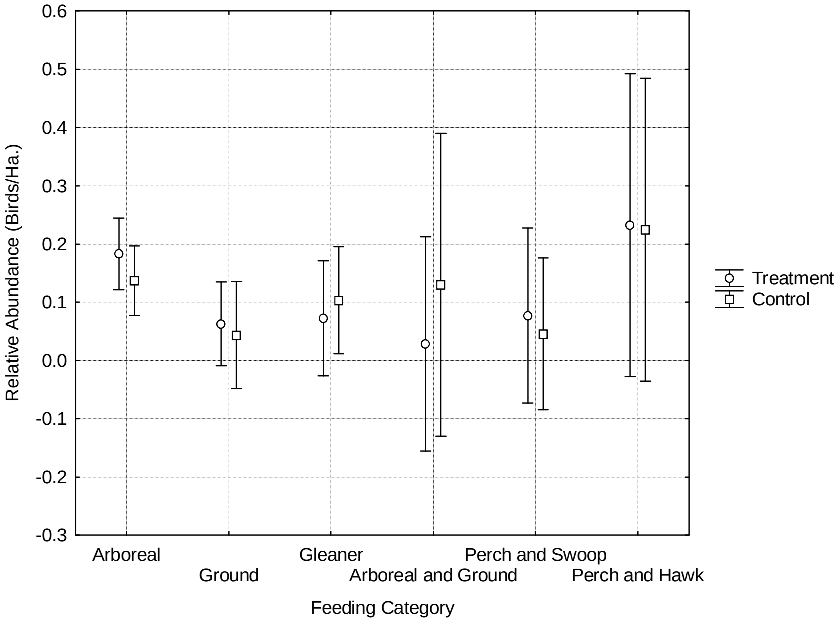

Figure 4.7: The relative abundance of birds per hectare at treatment and control sites falling into one of six feeding categories (Maclean 1993).

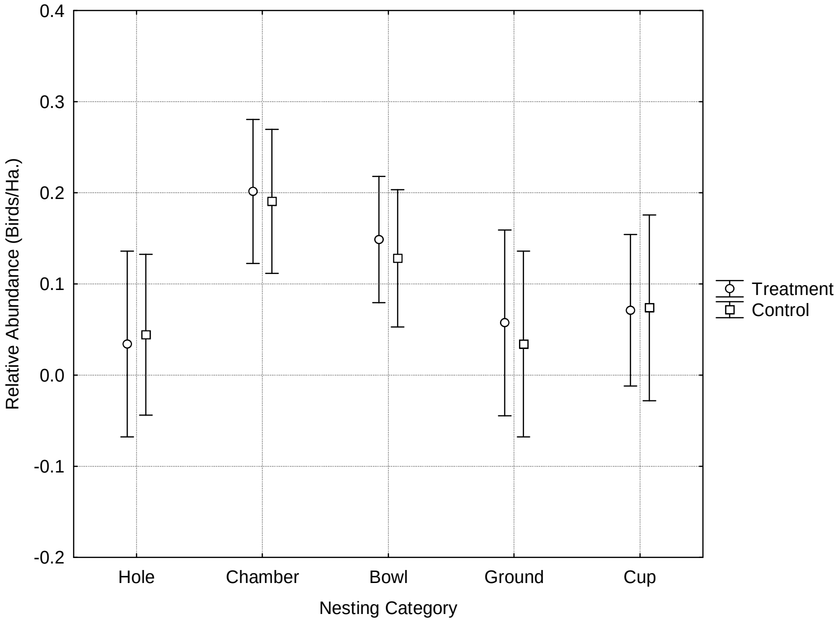

Figure 4.8: The relative abundance of birds per hectare at treatment and control sites falling into one of five nesting categories (Maclean 1993).

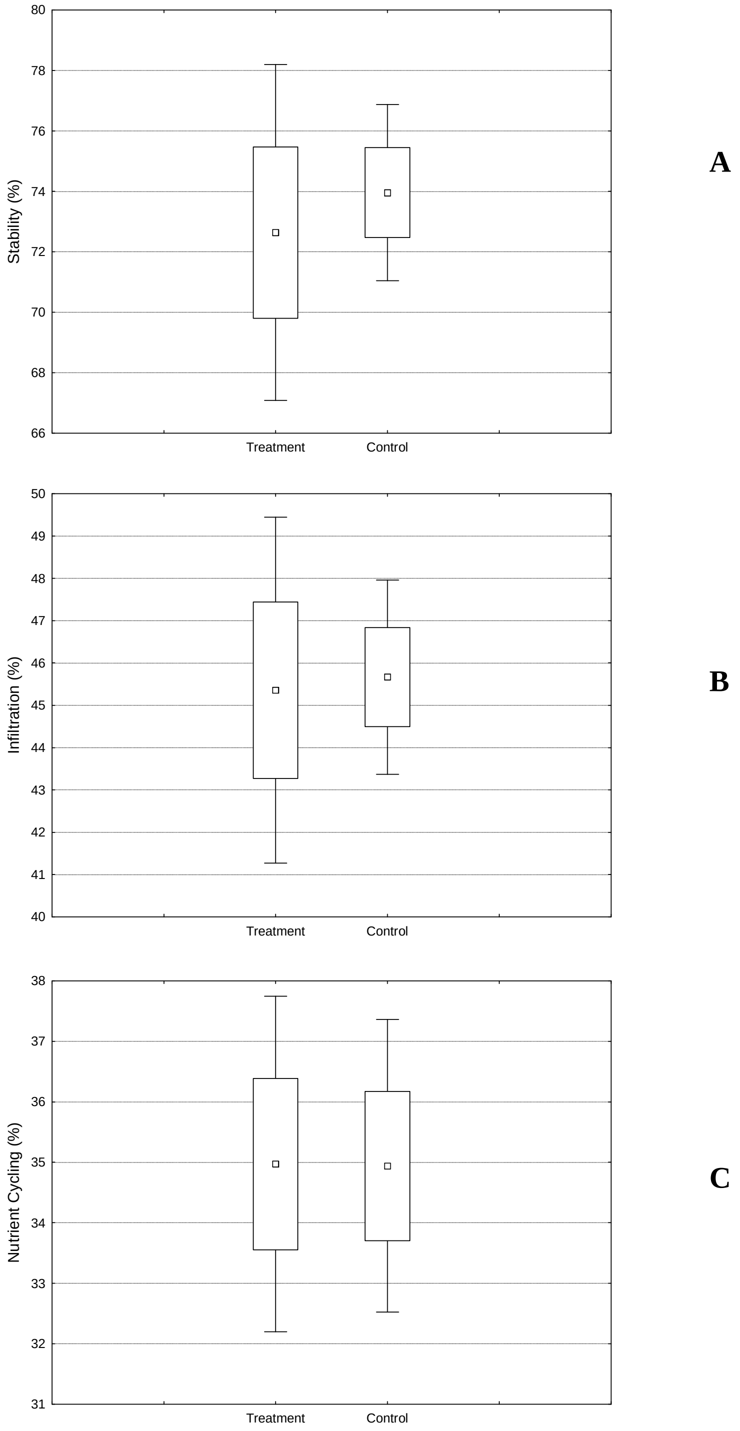

Figure 4.9: Indices of stability **(A)**, infiltration **(B)** and nutrient cycling **(C)** calculated for the treatment and control sites. Lower and upper quartiles are indicated in brackets. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

4.4 DISCUSSION

Although there were no significant differences between treatment and control sites in my study, there were similar trends for several factors. Vegetation at treatment sites was less dense, covered less basal area, was generally shorter and was less complex compared to control sites. In terms of habitat structure and complexity, examples of dramatic alteration to woody plant populations, reportedly caused by elephants, abound in the scientific literature and have been discussed in *Chapters 1* & *8*. In addition, these examples are widespread and cover broad spatial and temporal scales on the African continent (Van Wyk & Fairall 1969; Croze 1974; Penzhorn *et al.*1974; Guy 1981; Barnes 1985; Stuart-Hill 1992; Lock 1993; Barnes *et al.*1994; Cumming *et al.*1997; Trollope *et al.*1998; Skarpe *et al.* 2004). Since this material has been discussed elsewhere, in this chapter only those studies that incorporated adequate spatial and temporal controls are discussed (Penzhorn *et al.*1974; Stuart-Hill 1992; Cumming *et al.*1997; Trollope *et al.*1998; Skarpe *et al.* 2004). All of these authors reported substantially (sometimes significantly) lower tree cover, density or biomass, as described in my study, along with an associated increase in shrub cover, at sites with elephants compared to those where elephants were absent. Importantly, those studies conducted within the Addo Elephant National Park of South Africa found that elephant exposed plots had 45% less woody biomass than control plots (Penzhorn *et al.* 1974), and that canopy cover was significantly lower in the presence of elephants (Stuart-Hill 1992). In addition, overall woody plant density was higher where elephants were absent compared to plots sampled within the national park (Stuart-Hill 1992). The results from the Addo Elephant National Park are more dramatic than those from the present study and it is likely that this reflects the longer exposure (over 50 years) to elephants (also at a high density) that has been experienced at Addo and the provision of artificial water points, which seems to concentrate the effects of elephants (Penzhorn *et al.* 1974; Stuart-Hill 1992).

At a community level my results indicated that the species composition of treatment and control sites were similar. However, the importance values of thicket plants were significantly different between treatment and control sites, with some species being more important at treatments than controls and *vice versa*. Guldemond & Van Aarde (2007) reported analogous results when assessing the impact of elephants on plant communities in Maputaland, South Africa. Although there were statistically significant differences between habitats inside and outside of areas with elephants, some plant species were either abundant or rare in the park (with elephants present) compared with sites outside and *vice versa* (Guldemond & Van Aarde 2007). In addition, Richardson-Kageler (2004) assessed changes to plant communities that had been exposed to herbivores (including elephants) for 10 years using fence-line contrasts in Zimbabwe, and demonstrated that the total species richness and the number of species with different functional attributes (e.g. seed dispersal mechanisms) were similar across seven fence-line contrasts. However, Smart *et al.* (1985) demonstrated that the long-term (14 years) exclusion of elephants and other large herbivores in Uganda enhanced the species diversity of woodlands. Moreover, Moolman & Cowling (1994) assessing the influence of elephants on endemic thicket plants in the Addo Elephant National Park showed that the total number of endemic thicket species was consistently lower within the park compared to a botanical reserve that had excluded elephants and all other large herbivores for a period of approximately 38 years. It has been suggested that plant species compositional patterns (losses or gains) are not as sensitive to disturbance (such as browsing) as are the relative abundances of the same species in the short (< 10 years) term

(Richardson-Kageler 2004). The findings of Smart *et al.* (1985) and Moolman & Cowling (1994) support this suggestion. However, in both of these publications elephant-induced changes were compared to a “total” control where all large herbivores were excluded (Smart *et al.* 1985; Moolman & Cowling 1994), which represents an unnatural situation in terms of the evolution of plant diversity (Cowling & Kerley 2002). Thus, I suggest that more elaborate exclusion/inclusion studies, like those employed by Goheen *et al.* (2007), are required in the Thicket Biome to disentangle the role of elephants in structuring the functional components (richness and diversity) of the plant community. Notwithstanding the above, my findings suggest that at current densities, elephants either 1) do not disrupt the compositional make-up of thicket vegetation (Guldemond & Van Aarde 2007), 2) that thicket vegetation is resilient to browsing by elephants (Stuart-Hill 1992; Guldemond & Van Aarde 2007) or 3) that the treatment sites have not been exposed to elephants for long enough. My results for elephant damage to thicket vegetation corroborate the latter proposal. Biomass removal attributed exclusively to elephants was lower than damage caused by any other factor at treatment sites. However, elephants have only been present at each study site for a relatively short period and it is likely that their influence on thicket species will increase over time.

Similar to the plant community variables discussed above, the literature that exists for elephant impact on bird communities is divided, reporting both positive and negative elephant effects (Herremans 1995; Cumming *et al.*1997). These studies demonstrated that specialist bird species (i.e. those with specific habitat requirements) were negatively influenced by elephant browsing and a reduction in tree cover (see *Chapter 5*; Herremans 1995; Cumming *et al.* 1997). However, in both cases the species richness of other generalist bird species was either higher or remained the same when comparing elephant-impacted sites to intact sites (Herremans 1995; Cumming *et al.* 1997). My results show that bird species richness, diversity and abundance were not negatively affected by elephant presence and/or browsing in thicket vegetation. In fact, thicket bird communities had higher species richness, diversity and abundance in the presence of elephants than the controls. In addition, the relative abundance of birds with specific food and nesting requirements was not significantly different between treatment and control sites. Such equivocal results highlight the need for caution when interpreting these data in the context of elephant impact. Changes in plant availability (through disturbance) and how this affects animal populations do not always follow simple logistic models and may include time lags before the effect becomes evident (*Chapter 5*; Gillson & Lindsay 2003). This may be particularly true within the enclosed reserves of the Eastern Cape Province where elephants have only recently been reintroduced. In addition, scale and the presence of species rich habitats, neighbouring (~500m) the thicket, must be considered. Due to the high mobility of birds, estimates of species richness and diversity can be inflated if there is a mosaic of habitat/land-use types at the scale of several km^2 (Naidoo 2004; Brotons *et al.* 2005). The latter is relevant in my study as the treatment and control sites will be part of the same mosaic of different land-uses (at the km^2 scale) and this is likely to be a partial explanation for the observed similarity in the avifauna. At present elephant densities and the associated damage to thicket vegetation, the bird community is not negatively affected.

There was no significant difference between treatments and controls for the indices of soil stability, infiltration and nutrient cycling. In fact, values obtained for each index at treatment and control sites were extremely similar. Palmer *et al.* (2001) reported similar trends when comparing commercial and communal rangelands in the

Eastern Cape Province. They demonstrated significant differences in landscape organisation between the two land-use practices but no difference between soil-surface indicators, despite significant differences in soil nutrients from soil samples (Palmer *et al.* 2001). The authors contend that because their method was initially designed for arid/semi-arid rangelands in Australia, it may not be sensitive enough in an African context (Palmer *et al.* 2001). However, the method used by Palmer *et al.* (2001) has subsequently been refined and modified for African conditions (Palmer *et al.* 2001; Tongway & Hindley 2004) and was used in my assessment. It is thus likely that the stands of thicket vegetation at both treatment and control sites are equally rich in resources. In addition, treatment and control sites may have enhanced soil properties compared to other vegetation types, which might increase the overall production of the ecosystems in the Eastern Cape Province (Aguiar & Sala 1999; Tongway & Hindley 2004). However, preliminary work by Kerley *et al.* (1999) inserts an important caveat. The authors demonstrated that significantly less organic carbon, nitrogen and cations were available in patches of thicket vegetation at the Addo Elephant National Park compared to sites without elephants (Kerley *et al.*1999). Again, this suggests that although at current densities elephants do not negatively influence the soil-surface properties of thicket vegetation it is likely that their impact on soil processes will increase over time.

I have shown that at current elephant densities and after a short period of exposure (< 13 years), there is little evidence of damage to thicket vegetation caused by elephants. In addition, stands of thicket vegetation show what may be the first signs of a transformation from relatively homogeneous and structurally complex vegetation to habitats that are simpler but more heterogeneous (patchy) at enclosed reserves. There was no significant difference in the plant community or that of the avifauna between treatment and control sites but in both cases, the treatment sites had higher species richness, diversity and more unique species than the control sites. In addition, soil processes were similar at treatment and control sites. Thus, the initial hypothesis is accepted. Nevertheless, I recommend continued monitoring on this aspect of elephant ecology to establish if these trends continue over an extended time-period.

CHAPTER 5

THE INFLUENCE OF ELEPHANTS ON ALOES AND THEIR ASSOCIATED INSECT AND BIRD COMMUNITIES

5.1 INTRODUCTION

Two aloe species (*Aloe ferox*, Miller and *A. africana*, Miller) are indicator species within the Thicket Biome of the Eastern Cape Province, South Africa (Low & Rebelo 1996). These aloes are succulents with a single, woody stem, crowned with a dense rosette of long, thick and fleshy leaves that have small, sharp spines on the margins (Coates-Palgrave 2000). The inflorescence consists of a candelabrum of tubular orange/red flowers (*A. ferox*) or a single tapering yellow and red flower (*A. africana*)(Coates-Palgrave 2000). *Aloe ferox* flowers between May and October each year, while *A. africana* flowers from July to August (Coates-Palgrave 2000). The dry inflorescences of these plants are used by at least two species of carpenter bees (Anthophoridae) for the excavation of nest cavities (Gess 1981). One of these bees, *Xylocopa sicheli*, Vachal, makes cavities and nests exclusively in the dry inflorescences of *A. ferox* (Gess 1981). In addition, natural populations within the genus *Xylocopa* are known to have low fecundity due to high rates of mortality of prereproductive adults (Watmough 1983). A further nine other hymenopteran species from four families (Sphecidae, Anthophoridae, Megachilidae, Chrysididae) have been known either to modify a pre-existing cavity within an aloe inflorescence for nesting or utilise the cavity created by the initial nester (without modification) once it has been vacated (Gess 1981).

The winter flowering of aloes means that their nectar provides an important food source for specialist nectarivorous birds such as Sunbirds (Nectariniidae)

(Symes *et al.* 2007). In addition, a suite of other bird species from numerous families has also been recorded occasionally feeding on aloe nectar (Johnson *et al.* 2006; Symes *et al.* 2007). In a study conducted on the birds utilising *Aloe marlothii*, Berger, as a food source in the Gauteng Province of South Africa, Symes *et al*. (2007) recorded 42 bird species from 19 families making use of the flowers. In the Eastern Cape Province approximately 19 bird species have been recorded either feeding on or being associated with aloe inflorescences (Skead 1997; A.Craig pers. comm.).

Although elephants (*Loxodonta africana*, Blumenbach) are regarded as generalist herbivores, it has been demonstrated that they are capable of imposing a greater impact on certain preferred plant species, especially in enclosed areas (Barnes 1980; Midgley & Joubert 1991; Moolman & Cowling 1994; Steyn & Stalmans 2001; Cowling & Kerley 2002). This can either lead to alterations in the population structure of these plants or, in some cases, localised extinctions (Barnes 1980: Cowling & Kerley 2002). In South Africa, aloes are highly preferred by elephants and elephants, either break off the crown or push the whole plant over to access the succulent apical meristem (Steyn & Stalmans 2001; Cowling & Kerley 2002). However, the cascading impact that this may have upon the specialised insect and bird fauna that rely upon aloes as a resource has not been documented.

Given the above, it was hypothesised that elephant foraging would cause an increase in aloe mortality. However, since elephants have only been present at each site for a relatively short period the associated insect and bird fauna would be similar in areas with and without elephants. The specific aims of this part of the study were to: 1) Quantify the damage caused to aloe plants within enclosed reserves; and 2) Determine the extent to which damage to aloes affects the associated insect and bird fauna. These three aims are discussed in relation to the historical occurrence of aloes and elephants in the Eastern Cape Province, South Africa.

5.2 MATERIALS AND METHODS

The field sampling of aloes took place between May and June 2005, with the collected inflorescences processed at the same time. For logistical reasons, bird sampling was completed between June and August 2006 at the same sites.

5.2.1 Aloe sampling

Five sampling stations were located at each treatment (*n* = 5) and control site (*n* = 5). Sampling stations were located at least 250m apart and never in the same stand of aloes at treatment and control sites. At each sampling station a wandering transect following a pre-determined cardinal direction (Bond & Loffell 2001), was used to sample the first 20 aloe plants (*A. ferox* and *A. africana*) encountered. This provided a sample size of 100 individual aloes per treatment and control site and an effective sample size of 1000 for the region. It was assumed that the influence of elephants was approximately equal on the two aloe species (Cowling & Kerley 2002; D. Parker pers. obs.). Each aloe sampled was rated subjectively as either being living or dead. Living aloes were defined as any plant with green leaves and that was not uprooted or had its stem broken. An aloe was defined as being dead if it was uprooted, had a broken stem, had its crown (head) broken off or any combination of the above (Steyn & Stalmans 2001). For each plant, the presence/absence of a dry inflorescence from the previous fruiting season and height (m) were recorded.

The density of living aloes was measured using a modified Point-Centred Quarter Method (Dahdouh-Guebas & Koedam 2006). At least five points per sampling station were sampled along a straight line transect in a predetermined cardinal direction at each site. This provided a total of 28-30 sample points per treatment and control site, which is considered acceptable for biological studies (Cottam & Curtis 1956). The density of living aloes was then calculated using the input spreadsheets detailed in Dahdouh-Guebas & Koedam (2006) for each treatment and control site.

5.2.2 Insect sampling

If a dry flower inflorescence was present it was inspected for the presence/absence of insect tunnelling activity (almost perfectly circular entrance holes in the pithy stem). Those inflorescences that exhibited insect tunnelling activity were returned to the laboratory, frozen for storage and later carefully dissected to expose the cavity and any insects that may have been present. All insects found were identified to at least genus level at the Albany Museum in Grahamstown. The occupant of an empty cavity was also identified at the Albany Museum; based on diagnostic characteristics such as colour, cell partitions, plugs, and any identifiable provisions remaining in the cavity. The availability of potential nest sites (presence/absence of inflorescences), species richness, species abundance, number of unique species and Morista-Horn similarity and Simpson’s diversity indices were calculated for each treatment and paired control site (Colwell 2005).

5.2.3 Bird sampling

See the bird sampling section described in *Chapter 2* (p.48).

5.2.4 Data analysis

The shared species, unique species, Morista-Horn similarity index, overall species richness and diversity (Simpson’s and Shannon Wiener H’) statistics were all calculated using EstimateS (Colwell 2005). Differences between the proportion of dead aloes at treatment and control sites were tested using a two-way ANOVA after arcsine transformation (Statistica, Statsoft, version 7.0). The categorical predictors in this analysis were “treatment” (with or without elephants) and “location” (individual site e.g. Amakhala). A Tukey post-hoc test was performed to ascertain the source of the variation (Statistica, Statsoft, version 7.0). The differences between densities of living aloes across treatment and control sites were tested in the same way.

A one-way ANOVA, with “treatment” as a categorical predictor, was used to detect differences in the potential cause (e.g. uprooting) of aloe death. Differences between the availability of nest sites for insects were tested using a paired t-test (Statistica, Statsoft, version 7.0). The differences between the number of bored (or utilised) inflorescences at treatment and control sites were tested using a non-parametric Sign test (Statistica, Statsoft, version 7.0). The differences between the number of unique species present at treatment and control sites was tested in the same way. A series of paired t-tests (Statistica, Statsoft, version 7.0) were used to test for significant variation in the three bird community variables (species richness, diversity and relative abundance). A Chi-Square test was used to test for differences in the overall species composition of birds at treatment and control sites (Cohen & Holliday 2001). The values obtained from the controls were used as the expected values. Differences between the relative abundance of birds in each feeding and nesting category at treatment and control sites were tested using two-way ANOVAs (Statistica, Statsoft, version 7.0). The categorical predictors in these analyses were “treatment” and “category” (either feeding or nesting). A Tukey post-hoc test was performed to ascertain the source of the variation in each test (Statistica, Statsoft, version 7.0).

5.3 RESULTS

Treatment (with or without elephants) had a significant effect on the proportion of dead aloes ($P < 0.001$, $F_{2, 39} = 10.983$). However, damage to aloes was also significantly affected by geographical location ($P = 0.003$, $F_{8, 78} = 3.283$), and there was a significant interactive effect between these two factors ($P < 0.001$, $F_{8, 78} = 4.204$). The proportion of dead aloes was significantly higher at the Kwandwe and Shamwari treatment sites compared to all other sites (Figure 5.1; $P < 0.001$, $F_{8, 78} = 4.205$).

Although control sites had slightly higher aloe densities compared to the treatments (Table 5.1), the density of living aloes was not significantly influenced by the presence of elephants (Table 5.1; $P = 0.25$, $F_{1, 20} = 1.376$). By contrast, living aloe density was significantly affected by location (Table 5.1; $P = 0.002$, $F_{4, 20} = 6.471$). Kwandwe had the highest density of living aloes of all the sites, while Kariega had the lowest density of all sites (Table 5.1; $P = 0.002$, $F_{4, 20} = 6.471$). There was no significant interaction between the two categorical predictors ($P = 0.05$, $F_{4, 20} = 2.825$).

Headlessness and aloes that were uprooted and headless were the two most frequently recorded causes of aloe death at treatment sites (Figure 5.2). Uprooting was the most common cause of aloe death at control sites (Figure 5.2). There were significantly more headless aloes at treatment sites compared to the controls (Figure 5.2; $P = 0.03$, $F_{5, 44} = 2.752$), but no significant difference between any of the other causes of aloe death at treatment or control sites (Figure 5.2).

There was no significant difference between the overall availability of inflorescences at treatment and control sites (Table 5.2; $P = 0.94$, $t_4 = -0.082$). However, of the 100 aloe plants sampled at each treatment and control site, less than half of them had inflorescences present (Table 5.2). In fact, two sites (Shamwari treatment and Kwandwe treatment) had less than 10 inflorescences present (Table 5.2). The number of inflorescences that showed insect activity (i.e. visible tunnelling present) was low and was not significantly different between treatment and control sites ($P = 0.39$, $Z = 0.866$; Treatment = 12, Control = 8).

The insect species composition of bored inflorescences was relatively similar at treatment and control sites (Table 5.3; Morista-Horn Similarity Index = 0.615). Four species were shared between treatment and control sites (Table 5.3). Although treatments had more unique species (4) than controls (1; Table 5.3), this difference was not significant ($P = 0.10$, $Z = 0.00$). A *Dasyproctus* sp. was the most commonly encountered primary nester in bored inflorescences at treatment sites, while a *Crematogaster* sp. was most common at control sites (Table 5.3). The abundance of the other species at treatment sites remained low (Table 5.3). However, the diversity indices (Simpson's $H_{\text{treatment}} = 3.74$; Simpson's $H_{\text{control}} = 4.03$) indicate that both treatment and control sites had similar levels of insect diversity in aloe inflorescences.

The species richness of birds was higher at treatment sites compared to controls, but this difference was not significant (Figure 5.3A; $P = 0.29$, $t_4 = 1.218$). Similarly, overall species diversity and relative abundance were higher at treatment sites than controls but not significant (Figure 5.3B & C; $P = 0.19$, $t_4 = 1.579$ and $P = 0.44$, $t_4 = 0.855$ respectively).

Treatments and controls shared 36 bird species and the species composition was similar (Morista-Horn index = 0.809). In addition, the relative abundance of individual bird species in aloe stands was not significantly different between treatments and controls (Appendix II; $P = 1.00$; $\chi^2 = 3.671$; df = 51). However, treatments did have more (11) unique species present compared to the controls (6;

Appendix II). Treatment did not have a significant effect on the relative abundance of birds in six feeding categories (Figure 5.4; $P = 0.99$, $F_{1, 77} = 0.0002$). Results for species known to use aloe nectar and pollen were equivocal. Acacia Pied Barbets, Black-headed Orioles, Dark-capped Bulbuls, Fork-tailed Drongos, Greater Double-collared Sunbirds and Malachite Sunbirds were more abundant at treatment than control sites (Appendix II), while Black-collared Barbet, Cape White-eye, Red-faced Mousebird, Streaky-headed Seedeater, Southern Double-collared Sunbird and Weaver (Johnson *et al.* 2006; Symes *et al.* 2007; A. Craig pers. comm.) were more abundant at control sites (Appendix II). However, significantly more birds were arboreal feeders compared to those that foraged on the ground (Figure 5.4; $P = 0.03$, $F_{5, 77} = 2.635$). There was no significant interactive effect between the two categorical predictors (treatment and feeding strategy) ($P = 0.87$; $F_{5, 77} = 0.363$). Similarly, the relative abundance of birds utilising five different nesting strategies was comparable between treatment and control sites (Figure 5.5; $P = 0.74$, $F_{1, 79} = 0.110$), but significantly more birds were chamber nesters than any other nesting strategy except bowl nesters (Figure 5.5; $P < 0.001$, $F_{4, 79} = 5.746$). There was no significant interactive effect between these two factors ($P = 0.95$; $F_{4, 79} = 0.167$).

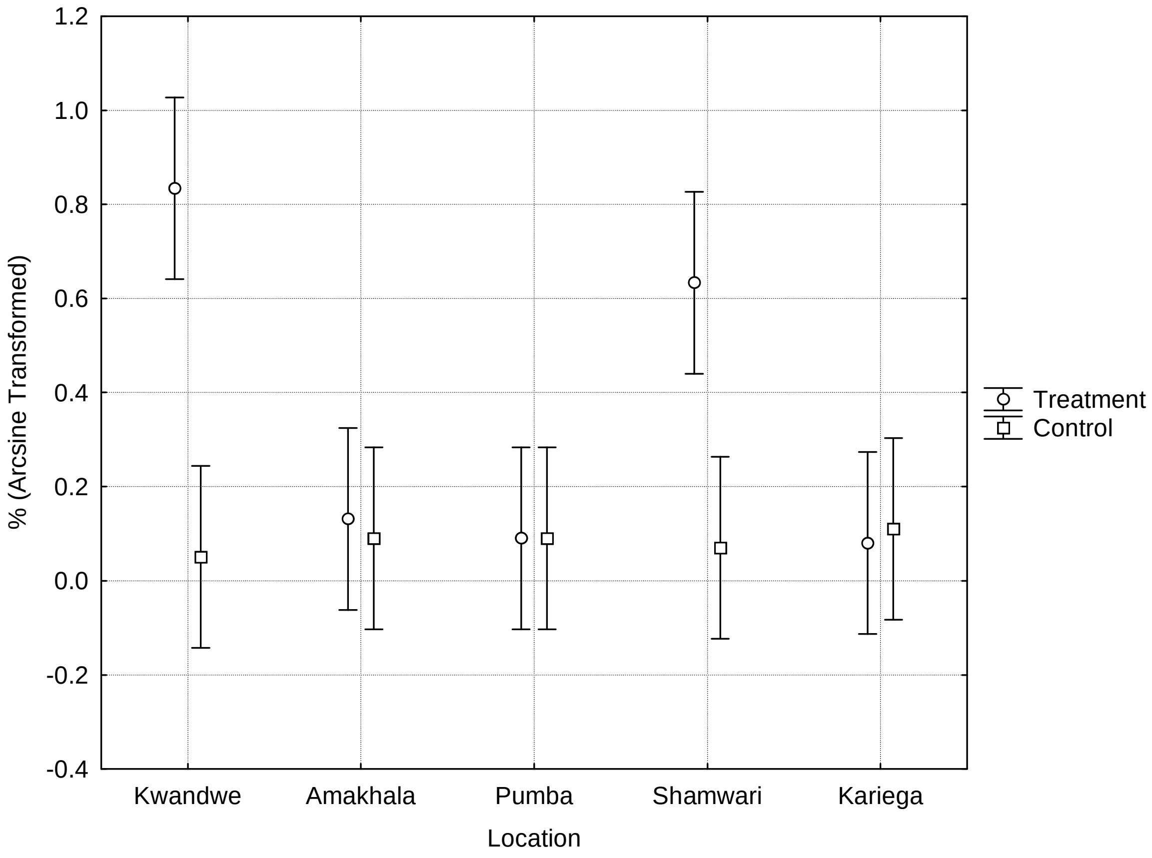

Figure 5.1: The proportion of dead aloes at treatment and control sites. Values are means ± 95 % confidence intervals. Significant results ($P < 0.05$) are described in the text.

Table 5.1: The density (km^{-2} ± SD) of living aloes present at each study site. Mean = mean density of living aloes ± SD.

Location	**Treatment**	**Control**
Amakhala	1.0 ± 0.5	3.4 ± 1.1
Kariega	2.5 ± 3.1	1.3 ± 0
Kwandwe	9.2 ± 2.5	5.8 ± 3.4
Pumba	0.7 ± 1.0	4.1 ± 3.7
Shamwari	2.5 ± 2.3	6.2 ± 1.8
Mean	**3.7 ± 1.9**	**4.2 ± 2.0**

Table 5.2: The number of inflorescences available for insects from the 100 aloes sampled at each site. The total is a mean of all sampling stations ± SD.

Site	**Treatment**	**Control**
Amakhala	35	40
Kariega	25	18
Kwandwe	9	29
Pumba	43	14
Shamwari	2	39
Mean	**22.80 ± 17.21**	**28.00 ± 11.85**

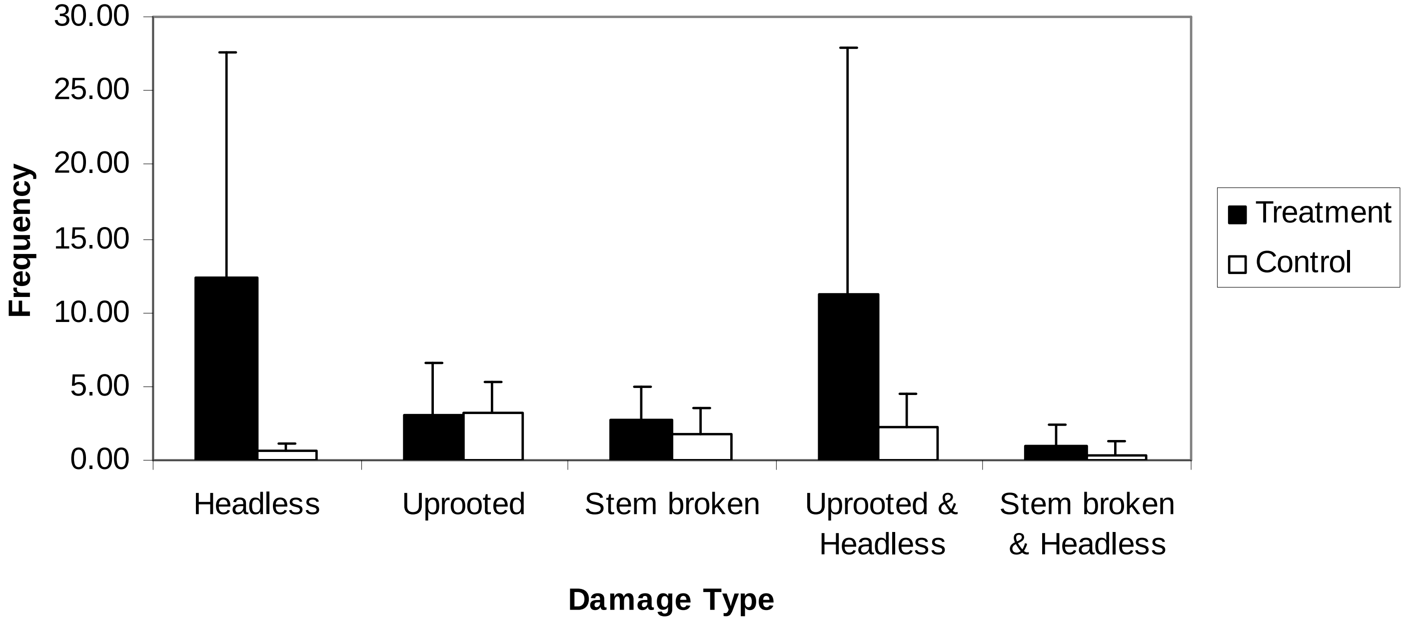

Figure 5.2: The frequency of dead aloes falling into each of five damage types at treatment and control sites. Values are means ± SD.

Table 5.3: The species composition and abundance of the insects sampled within aloe inflorescences at treatment and control sites. *P* denotes presence based on structure and composition of nesting cavity.

Family	**Species**	**Treatment Abundance**	**Control Abundance**
Anthophoridae	*Ceratina* sp.	1	-
Anthophoridae	*Xylocopa* sp	1	1
Anthophoridae	*Xylocopa sicheli*	1	2
Buthidae	*Centruroides* sp.	1	-
Formicidae	*Crematogaster* sp.	*P*	20
Megachilidae	*Megachile* sp.	-	1
Sphecidae	*Dasyproctus* sp.	6	3
Sphecidae	*Trypoxylon* sp.	1	-
	Unknown	*P*	-

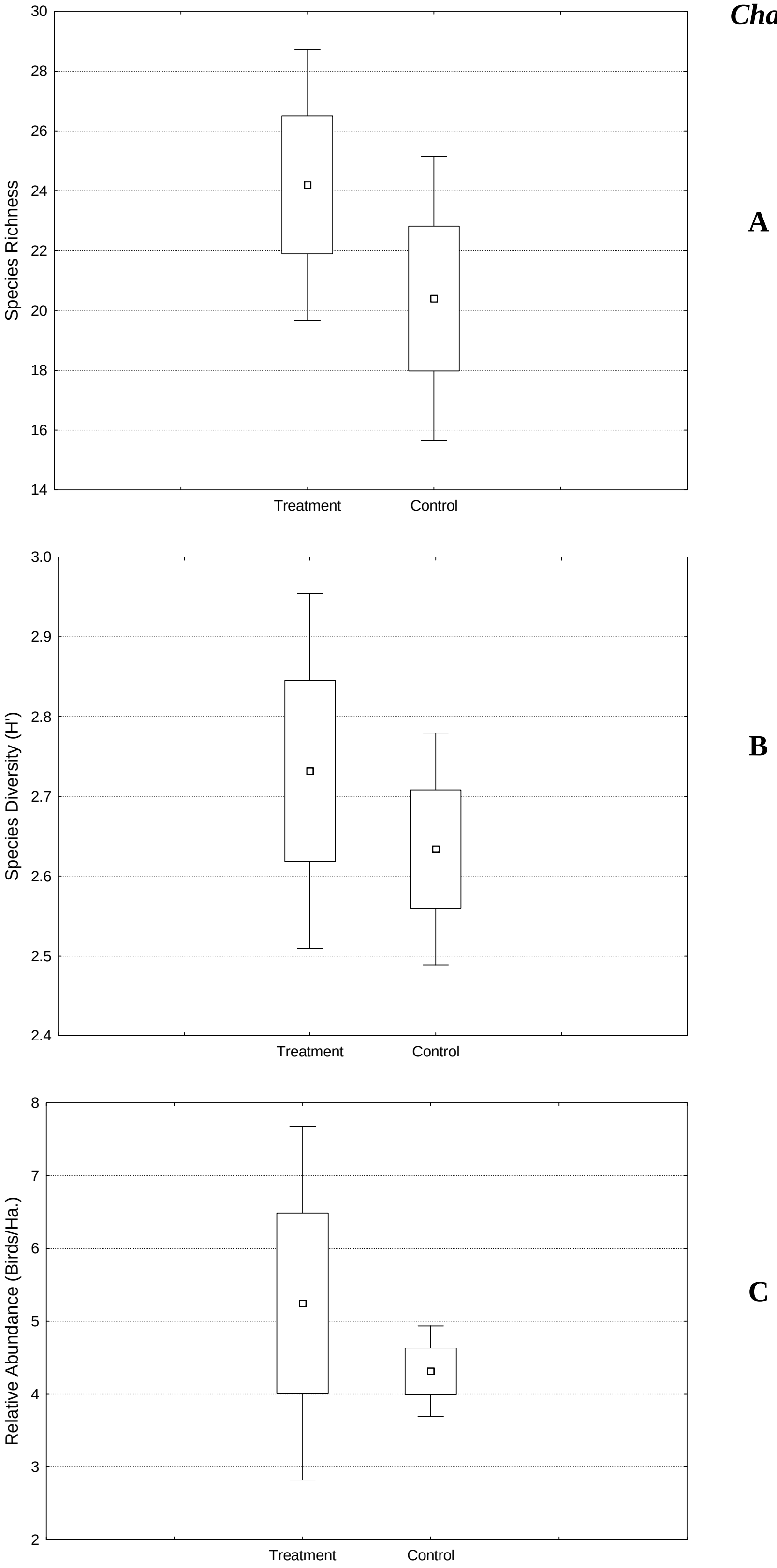

Figure 5.3: The Species richness (**A**), Shannon-Wiener diversity (H') (**B**) and density estimates of birds per hectare (**C**) in aloe stands at treatment and control sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

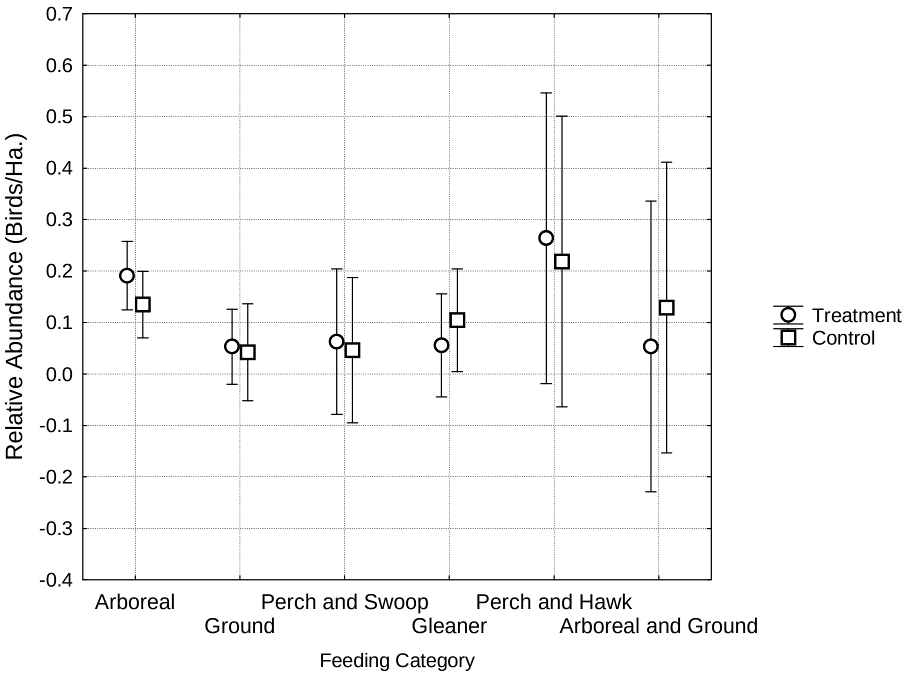

Figure 5.4: The relative abundance of birds per hectare at treatment and control sites falling into one of six feeding categories (Maclean 1993).

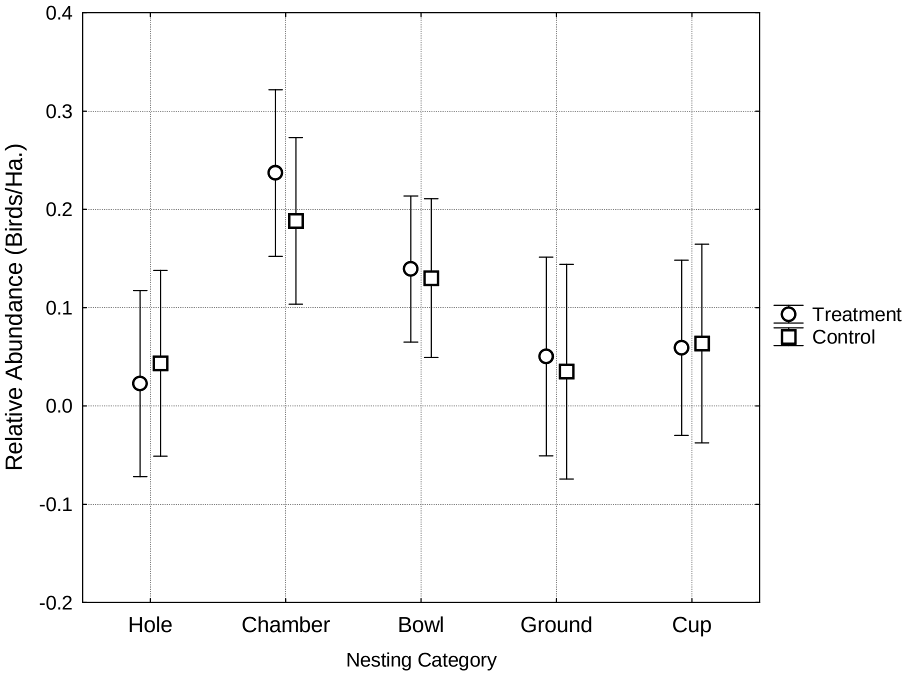

Figure 5.5: The relative abundance of birds per hectare at treatment and control sites falling into one of five nesting categories (Maclean 1993).

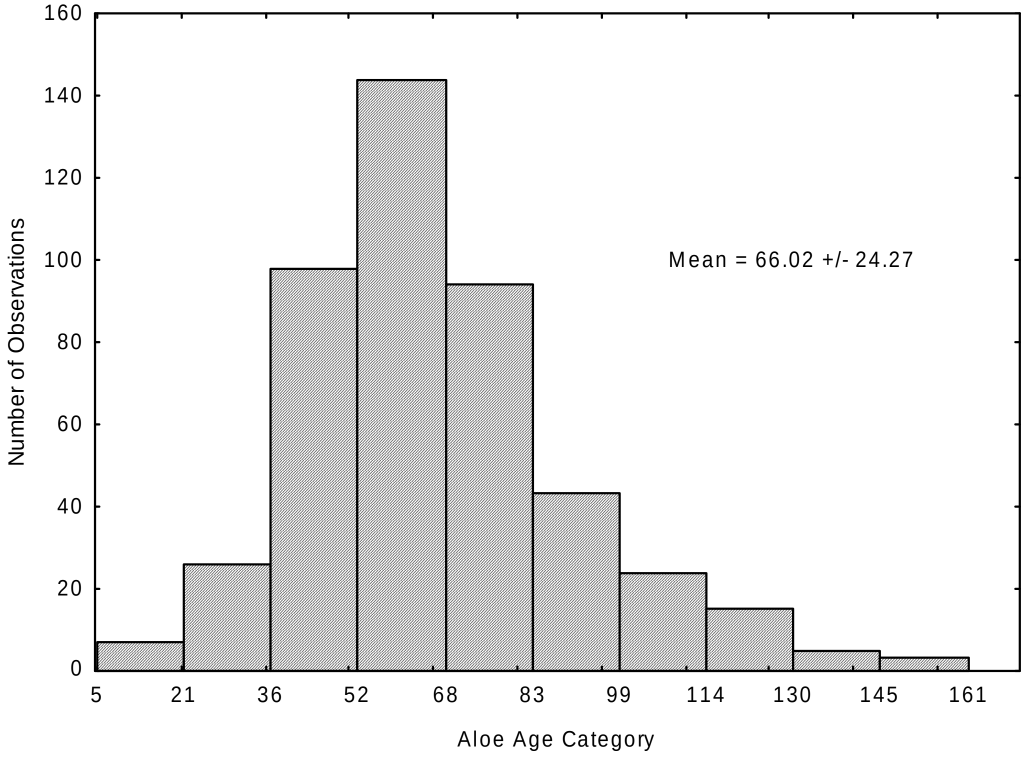

Figure 5.6: The frequency of living *Aloe ferox* individuals (n = 459) falling into one of 10 age classes at control sites.

5.4 DISCUSSION

In enclosed reserves, the utilisation of certain tree species by elephants can lead to the death of individual plants (Steyn & Stalmans 2001; Cowling & Kerley 2002). Although restricting the movement of elephants certainly compounds the influence they may have on particular species, it is not a phenomenon unique to enclosed areas. Even where the movement of elephants is relatively unrestricted, studies have shown that highly favoured tree species (e.g. baobab, *Adansonia digitata*, L., and mfuti, *Brachystegia boehmii*, Taub.) are targeted (Thomson 1975; Barnes 1980; Edkins *et al*. 2007). Elephant-induced effects on highly favoured species are further compounded by periods of low rainfall (De Beer *et al*. 2006). Studies conducted within the Addo Elephant National Park in South Africa have shown that *A. africana* was commonly recorded in control plots in the absence of elephants, but never in the treatment plots where elephants were present (Penzhorn *et al.* 1974). The results from my study support this trend with a higher proportion of dead aloes being found at the Kwandwe and Shamwari treatment sites (the two sites that have had elephants for the longest). Mortality in aloe populations (regardless of the presence of elephants) is generally high (Breebaart *et al.* 2002; Shackleton & Gambiza 2007). Aloes are not particularly robust plants due to their shallow root systems (D. Parker pers. obs.) and can be easily uprooted, especially when the soil is moist. In addition, fire can account for as much as 32% mortality in some populations (Shackleton & Gambiza 2007). However, most of the aloes sampled in my study were either headless or uprooted at treatment and control sites and headless aloes were most abundant at treatment sites. The loss of the head or rosette is a form of aloe death that is perceived to be exclusively due to elephants (D. Parker pers. obs.). Significantly, published accounts of damage to aloes by other mammals only include the loss of individual leaves and flowers (e.g. baboons, *Papio ursinus*, Kerr), uprooting (e.g. porcupine, *Hystrix africaeautralis*, Peters, and black rhino, *Diceros bicornis,* L.), browsing of leaves (e.g. kudu, *Tragelaphus strepsiceros*, Pallas, and goats, *Capra hircus*, L.) and trampling of very small individuals (e.g. cattle, *Bos taurus*, L.), not the removal of the entire head (Breebaart *et al.* 2002; Shackleton & Gambiza 2007). In the Eastern Cape Province of South Africa, leaves from aloes are routinely harvested by people for sap (Shackleton & Gambiza 2007). Thus, the presence of a single headless aloe at each of three control sites was probably due to human interference rather than some other factor, such as strong wind or large mammals.

Despite the significantly greater proportion of dead aloes at treatment sites, there was no significant effect of treatment (i.e. elephant presence) on the density of living aloes. It is plausible that elephants may not have been present for long enough in these enclosed reserves to affect the density of aloes. Data from the Addo Elephant National Park, where elephants have been enclosed for over 50 years at a high density, corroborates this contention with no living aloes present in the elephant enclosure (Penzhorn *et al.* 1974; Cowling & Kerley 2002). However, the significant effect of geographical location on living aloe density suggests that localised conditions also influence the density of aloes. Some sites may have been more favourable (e.g. Kwandwe – drier and uprooting less likely) for the growth of aloes prior to the re-introduction of elephants, while other sites (e.g. Kariega – wetter and uprooting more likely) may have been less suitable. Thus, the future influence of elephants on aloes will depend on the unique conditions of each site.

Very few studies have investigated the impact of elephants further than their effects on vegetation, despite the inherent ability of elephants to alter environments (see *Chapter 1*), particularly in enclosed reserves (Steyn & Stalmans 2001; Cowling

& Kerley 2002). Only five studies have assessed the potential impact of elephant foraging on insect communities (Cumming *et al.* 1997; Musgrave & Compton 1997; Fenton *et al.* 1998; Botes *et al.* 2006; Bonnington *et al.* 2007) and even fewer studies have attempted to quantify the influence of elephant foraging on bird communities (Herremans 1995; Cumming *et al.* 1997).

Cumming *et al.* (1997) found that significantly more ant species were present at intact sites (areas without elephants) in the Miombo woodland of Zimbabwe than those that had been impacted by elephants. In addition, cicadas were only recorded at intact sites (Cumming *et al.* 1997). However, there was no significant difference between the number of mantid species found at intact and impacted sites (Cumming *et al.* 1997). Similarly, Musgrave & Compton (1997) showed that the abundance of phytophagous insects was not affected by elephant damage to vegetation in the Addo Elephant National Park. Moreover, their data suggested a greater abundance of phytophagous insects where elephant damage was highest (Musgrave & Compton, 1997). Fenton *et al.* (1998) also reported no difference between the abundance of insects (moths and beetles) at intact versus elephant impacted sites. More recently, Botes *et al.* (2006) demonstrated that elephant-disturbed habitats in Maputaland, South Africa had significantly lower dung beetle abundance compared to intact mixed woodland. In addition, no habitat-specific species were found in the elephant-disturbed habitat (Botes *et al.* 2006). However, elephant-disturbed habitats shared more species with undisturbed habitats than did human-disturbed habitats (Botes *et al.* 2006). By contrast, sites with high elephant disturbance in Tanzania have a greater diversity of butterflies compared to sites with low elephant disturbance (Bonnington *et al.* 2007). My results indicate that the number of aloe inflorescences available to insects was low across both treatments and controls, but even lower at sites that had elephants present. Although elephants appear to be the prime cause for aloe death at treatment sites, damage to aloe inflorescences caused by baboons has been reported in the Eastern Cape Province (Shackleton & Gambiza 2007). Thus, the low availability of inflorescences for insects at treatment sites may have been reduced even further by the presence of baboons. Notwithstanding this, the insect communities utilising inflorescences were similar (in terms of similarity, diversity and abundance) at treatment and control sites. In fact, treatment sites had more unique species present than control sites, analogous to the results reported by Bonnington *et al.* (2007).

Similar to the insect studies discussed above, the literature that exists for elephant impact on bird communities is equivocal, reporting both positive and negative elephant effects (Herremans 1995; Cumming *et al.*1997). However, both of the previous studies have shown that specialist bird species (i.e. those with specific habitat requirements), are negatively influenced by elephant browsing (Herremans 1995; Cumming *et al.* 1997). Herremans (1995) sampled birds in two vegetation types that had both high and low elephant impact in northern Botswana and found that significantly fewer tree canopy specialists were present in the high elephant impact sites within riverine woodland than the low impact sites. Likewise, Cumming *et al.* (1997) demonstrated that significantly more woodland bird species were present in Miombo woodland that was intact compared to impacted sites. My results show, however, that bird species richness, diversity and abundance were not negatively affected by elephant presence and/or browsing on aloes. In fact, aloe bird communities (in terms of species richness, diversity and abundance) appear to benefit from the presence of elephants. In addition, the relative abundance of birds with specific food and nesting requirements was not significantly different between treatment and control sites. Furthermore, birds that specialise in foraging on aloe inflorescences (classed as arboreal) were more abundant at treatment sites compared to controls. Such equivocal results highlight the need for caution when interpreting these data in the context of elephant impact. Changes in plant availability (through disturbance) and how this affects animal populations do not always follow simple logistic models and may include time lags before the effect becomes evident (Gillson & Lindsay 2003). This may be particularly true within the enclosed reserves of the Eastern Cape Province where elephants have only recently been re-introduced. In addition, scale and the presence of intact aloe stands in the vicinity of (~500m) treatment sites must be considered. Due to the high mobility of birds, it is likely that the estimates of species richness and diversity at treatment sites may have been inflated if there were intact aloe stands within a several km^2 radius (Naidoo 2004; Brotons *et al.* 2005).

Using the height data collected for aloes at control sites, I estimated the ages of all living *A. ferox* individuals using a known growth rate (2.79cm/year) (Shackleton & Gambiza 2007). An overwhelming proportion (81%) of the 459 aloes were estimated to be younger than 83 years old (Figure 5.6). Interpreting the age structure of *A. ferox* populations is difficult in the absence of a full understanding of natural mortality rates. The long, right tail might simply imply that aloes over a certain age are more likely to fall over (Figure 5.6). Alternatively, it is possible that the observed age structure reflects the history of elephants in the Eastern Cape Province as the data show that at least some aloes can live for more than 150 years (Figure 5.6). The large stands of aloes currently found in the region may be derived from a cohort of seedlings that established some 100 years ago, when the elephant population was low as a result of high levels of hunting (Skead 2007; Skarpe *et al.* 2004). Thus, what is perceived to be damage may be the first step in the vegetation reverting towards a situation similar to the one before there was excessive elephant hunting *sensu* the results of Skarpe *et al.* (2004). When elephant numbers were much higher in the Eastern Cape Province (Skead 2007), aloes may have depended on local refugia (e.g. steep gorges and slopes) for persistence in the region (Breebaart *et al.* 2002; Skarpe *et al.* 2004; Edkins *et al.* 2007). However, it is important to recognise that such a single factor explanation for the observed age structure of aloes at control sites is unlikely. The previous land-use and length of time since each site reverted to conservation may have resulted a skewed aloe age-structure. For example, goats are known to browse the leaves of *A. ferox*, particularly smaller individuals, causing extensive damage (Breebaart *et al.* 2002). It is thus possible that such heavy utilisation at some control sites prior to them being used for conservation may have maintained aloe populations at control sites in a “herbivore susceptible” height class preventing the growth of large individuals.

I have shown that although elephants are an important cause of aloe mortality in the enclosed reserves of the Eastern Cape Province, they have not, at low densities, caused significant declines in living aloe density. In addition, the associated insect and bird communities were similar at sites with elephants present compared to those without elephants. Thus, the initial hypothesis is accepted. Nevertheless, I recommend continued intensive research on this aspect of elephant ecology to ascertain whether the results observed in my study persist over an extended time-period.

CHAPTER 6

THE EFFECT OF ELEPHANT FEEDING WITHIN BUSHCLUMP SAVANNA AND HOW THIS INFLUENCES ASSOCIATED BIRD AND MAMMAL COMMUNITIES

6.1 INTRODUCTION

Initially the theory of island biogeography recognised that islands contain fewer species than comparable pieces of mainland and that the number of species on islands decreased as island area decreased (MacArthur & Wilson 1963, 1967). Since its inception, the theory of island biogeography has been well supported and refined by numerous studies (Janzen 1968, 1973; Whitehead & Jones 1969; Strong 1974; Simberloff 1976; Brown & Kodric-Brown 1977; Ricklefs & Lovette 1999). In addition, it is currently one of our most powerful conceptual tools in wildlife management and conservation (Noss & Cooperrider 1994; Stiling 2002), primarily because the original theory has been modified to incorporate the concept that habitat patches may function as islands to particular groups of organisms (Brown 1978). Specifically, larger habitat “islands” have been found to exhibit higher diversity and species richness than smaller islands, consistent with the original theory (Quinn & Harrison 1988). For example, in their analysis of island biogeography in the Lesser Antilles, Ricklefs & Lovette (1999) reported the positive correlations of herpetofuana, bird, bat and butterfly diversity with habitat area. However, the biological characteristics of the target organism(s) and the geographical features of the environment can mediate the effects of habitat area on species richness (Loman & Von Schantz 1991; Ricklefs & Lovette 1999). Loman & Von Schantz (1991) demonstrated that the number of territorial farmland bird species in Sweden was highest on the smallest patches of farmland. The authors suggested that this seemingly contradictory result might be due to a combination of increased habitat quality and heightened intraspecific competition on the smaller habitat patches (Loman & Von Schantz 1991). Thus, in order to employ island biogeography effectively, as a theoretical tool in conservation, it is vital to understand the biology and abiotic requirements of target species.

Bushclumps are characteristically rounded clusters of dense, woody vegetation surrounded by a matrix of grass, forbs, small shrubs and bare soil (Fabricius *et al*. 1996). In addition, one or more mature trees are usually distributed within bushclumps (D. Parker, pers. obs.). It has been suggested that bushclumps originate (amongst other possible mechanisms) on termite mounds, which provide a concentrated source of moisture, minerals and nutrients in comparison with the surrounding environment (Fleming & Loveridge 2003). Thicket-forming plant species benefit from the conditions provided by termitaria and colonization of these mounds is thought to promote the development of thicket vegetation in predominantly grassland and shrubland habitat (*Chapter 4*; Tinley 1977). Although the exact process driving the formation of bushclumps is open to conjecture, it is reasonable to assume that the presence of islands of structurally complex vegetation will affect the species composition and abundance of birds and mammals by creating a variety of favourable microhabitats (Rosenzweig & Winakur 1969; Abramsky 1978; Bond *et al.* 1980; Kotler 1984; Abramsky *et al*. 1985; Perrin & Johnson 1999; Avenant 2000). Microhabitats can offer concentrated foraging resources for birds and mammals while at the same time reducing the risk of predation (Price 1978; Longland & Price 1991). For example, it has been demonstrated that owls have a lower capture success of rodent prey when hunting in bush habitat compared to open areas and are more cautious when hunting in complex habitats (Kotler 1984; Longland & Price 1991). This decreased hunting efficiency enhances the ability of rodents to detect and evade predators (Perrin & Johnson 1999). In addition, bushclumps may provide habitat heterogeneity at two scales for birds (*Chapter 4*; Ricklefs & Lovette 1999). The structure of the vegetation within bushclumps is more heterogeneous than the surrounding matrix vegetation, providing more resources and potentially more segregation at the microhabitat level (MacArthur & MacArthur 1961; Martin & Possingham 2005). At a greater scale, savanna habitats without (or with fewer) bushclumps will be more homogeneous and will consequently support lower bird diversity and *vice versa* (Ricklefs & Lovette 1999).

Elephants (*Loxodonta africana*, Blumenbach) routinely push over mature trees in order to access roots, fresh leaves and fruit or merely for social display (Field & Ross 1976; Guy 1976; Skinner & Smithers 1990; Kabigumila 1993). This can result in the number of mature trees being reduced by as much as 45% (*Chapter 1*; Thomson 1975; Field & Ross 1976). In addition, such feeding activity can reduce the available biomass and cover of woody species as well as decrease the abundance of some plant species (Cowling & Kerley 2002).

Given the above, it was hypothesised that elephant foraging in bushclump savanna would decrease the size of bushclumps and since elephants have only been present for a relatively short time at each site, the associated bird and mammal fauna will be similar at treatment and control sites. The specific aims of this part of the study were to: 1) Quantify the overall size of bushclumps within enclosed reserves; 2) Assess the influence of elephant foraging on woody plant species composition; and 3) Determine the extent to which changes in bushclump size and community structure affects the associated bird and mammal fauna. All three of these aims are discussed within the context of the theory of island biogeography.

6.2 MATERIALS AND METHODS

The field sampling of bushclumps and mammals took place between April and May 2007. For logistical reasons, bird sampling was completed between June and August 2006 at the same sites.

6.2.1 Bushclump sampling

Between three and five sampling stations were located at each treatment (n = 5) and control site (n = 5). Sampling stations at each site were selected by using digitized vegetation maps of each area to ensure that they were all located in bushclump savanna. Sampling stations were located at least 250m apart and never in the same stand of bushclumps at treatment and control sites. At each sampling station a wandering transect, following a pre-determined cardinal direction (Bond & Loffell 2001), was used to sample the first 10 to 17 bushclumps encountered. This provided a sample size of 50 individual bushclumps per treatment and control site and an effective sample size of 500 for the region. For each bushclump sampled, the species number and identity of all woody plant species, maximum height (m) and long and short diameters (m) of the bushclump (Anderson & Walker 1974; Walker 1976; Connybeare 1991) were recorded. From these data the volume (m^3) of each bushclump was determined using a modified equation for the volume of a sphere (Roe 1993), where it was assumed that the volume of a bushclump was approximately half of a sphere:

$$\text{Volume} = \frac{2\pi r^3}{3}$$

$$\pi = 3.1416$$

$$r = \frac{\text{(long diameter + short diameter + height)}}{5}$$

The frequency of occurrence of each plant species was calculated at a site level. Thus, the frequency of occurrence for each species was based on the number of bushclumps in which it was present at each site divided by the total number of bushclumps sampled (50) and expressed as a percentage. Mean values (± standard deviations) were then calculated for treatment and controls sites. It was recognised that given the low density of elephants at each site, some bushclumps may not have been browsed by elephants.

6.2.2 Bird sampling

The details of the bird sampling protocol are described in *Chapter 2* (p.48).

6.2.3 Mammal sampling

The utilisation of bushclumps by mammals (defined as any mammal weighing more than 100g) was assessed using a 1 x 1m quadrat within each bushclump. Every bushclump was divided into four quarters (see the Point-Centred Quarter method described in *Chapter 4*) and one quarter was haphazardly selected and sampled. In each selected quarter, the quadrat was placed on the floor of the bushclump and all small mammal droppings, tracks and sign (including burrows) within the quadrat identified (Liebenberg 1992; Stuart & Stuart 2000). Utilization based on the presence of sign rather than the capture of individuals was selected as sign includes an historic component and increases the likelihood of detecting presence. All species were identified to species level. For very small bushclumps (those < 1 x 1m in diameter), the entire bushclump was sampled. Those droppings that could not be identified in the field were returned to the laboratory and identified using the appropriate literature (Stuart & Stuart 2000). Using this technique, the presence/absence of mammals using each bushclump was recorded, and the relative frequency of occurrence (total number of species occurrences ÷ total number of bushclumps sampled x 100) of each mammal species at each site was calculated. The mammal species richness, number of unique species and Morista-Horn similarity and Shannon-Wiener diversity indices were also calculated for each treatment and control site (Colwell 2005). Due to the nature of the technique (presence/absence of sign), the occurrence of latrines did not prejudice the results.

6.2.4 Data analysis

The shared species, unique species, Morista-Horn index, overall species richness and diversity (Shannon Wiener H’) statistics were all calculated using EstimateS (Colwell 2005). Differences between the volume of bushclumps at treatment and control sites were tested using a two-way ANOVA after Log transformation (Statistica, Statsoft, version 7.0). The categorical predictors in this analysis were “treatment” (with or without elephants) and “location” (individual site e.g. Amakhala). A Tukey post-hoc test was performed to ascertain the source of the variation (Statistica, Statsoft, version 7.0). Chi-Square tests was used to test for differences in the overall species composition of plants, birds and small mammals at treatment and control sites (Cohen & Holliday 2001). The values obtained from the controls were used as the expected values in each case. Paired t-tests (Statistica, Statsoft, version 7.0) were used to test for significant variation in plant, bird and small mammal community variables (species richness, diversity and relative abundance). Differences between the relative abundance of birds in each feeding and nesting category at treatment and control sites were tested using two-way ANOVAs

(Statistica, Statsoft, version 7.0). The categorical predictors in these analyses were "treatment" and "category" (either feeding or nesting). A Tukey post-hoc test was performed to ascertain the source of the variation in each test (Statistica, Statsoft, version 7.0).

6.3 RESULTS

Treatment ($P = 0.004$, $F_{1, 490} = 8.510$) and location ($P < 0.001$, $F_{4, 490} = 25.108$) had significant effects on the volume of bushclumps and there was no significant interactive effect between these two factors ($P = 0.25$, $F_{4, 490} = 1.338$). Bushclumps were significantly larger at treatment sites compared to controls (Figure 6.1; $P = 0.004$, $F_{1, 490} = 8.510$). Kwandwe had the smallest bushclumps while the largest bushclumps were found at Kariega (Figure 6.2; $P < 0.001$, $F_{4, 490} = 25.108$). Amakhala and Shamwari had bushclumps of similar size that were significantly larger than those found at Kwandwe (Figure 6.2; $P < 0.001$, $F_{4, 490} = 25.108$). Bushclumps at Pumba were of an intermediate size, being significantly larger than bushclumps at Kwandwe, but significantly smaller than those at Kariega and Shamwari (Figure 6.2; $P < 0.001$, $F_{4, 490} = 25.108$).

The species richness of bushclump plants was higher at control sites compared to treatments, but this difference was not significant (Figure 6.3A; $P = 0.12$, $t_4 = -1.976$). Likewise, the Shannon-Wiener diversity index was marginally higher at control sites than treatments and the difference was not significant (Figure 6.3B; $P = 0.70$, $t_4 = -0.413$). Fifty-one plant species were identified across treatment and control sites with 40 species being shared between the two treatments. Both treatments and controls had similar numbers (6 and 5 respectively) of unique species (Table 6.1). *Aloe africana,* Miller, *Euphorbia bothae,* Lotsy & Goddijn, *Ptaeroxylon obliquum,* Thunb., *Pterocelastrus tricuspidatus,* Lam., *Rhus chirundensis*, Baker, and a *Rhus* sp. were only found at treatment sites while *Buddleja saligna,* Willd., *Capparis sepiaria,* L., a *Crassula* sp., *Euclea natalensis*, L., and *Harpephyllum caffrum,* Bernh., were only found at control sites (Table 6.1). However, there was no significant difference between the frequency of occurrence of different plant species at treatment and control sites (Table 6.1; $P = 1.00$, $\chi^2 = 0.876$, $df = 50$) and plant species composition was extremely similar at treatments and controls (Table 6.1; Morista-Horn Similarity Index = 0.934).

The species richness of birds was higher at treatment sites compared to controls, but this difference was not significant (Figure 6.4A; $P = 0.21$, $t_4 = 1.483$). Similarly, overall species diversity was higher at treatment sites than controls but the difference was not significant (Figure 6.4B; $P = 0.12$, $t_4 = 1.973$). By contrast, the relative abundance of birds was higher at controls compared to treatments and the difference was not significant (Figure 6.4C; $P = 0.31$, $t_4 = -1.156$). Treatments and controls shared 27 of 54 bird species and the species composition was relatively similar (Morista-Horn index = 0.667). In addition, the relative abundance of individual bird species in bushclumps was not significantly different between treatments and controls (Appendix II; $P = 1.00$; $\chi^2 = 6.0$; $df = 42$). However, treatments did have far more (20) unique species present compared to the controls (6; Appendix II). Acacia Pied Barbet, African Olive-Pigeon, Ant-eating Chat, Black-collared Barbet, Cape Longclaw, Cape Sparrow, Common Waxbill, Crowned Hornbill, Familiar Chat, Karoo Scrub-Robin, Malachite Sunbird, Olive Thrush, Red-eyed Dove, Red-fronted Tinkerbird, Rufous-breasted Wryneck, Rufous-naped Lark, Southern Grey-headed Sparrow, Southern Tchagra and Tawny-flanked Prinia were all only recorded at treatment sites (Appendix II). By contrast, Black-crowned Tchagra, Brown-hooded Kingfisher, Cardinal Woodpecker, Crowned Lapwing, Green Wood-Hoopoe and Green-backed Cameroptera were the only species to be recorded exclusively at control sites (Appendix II).

Treatment did not have a significant effect on the relative abundance of birds in six feeding categories (Figure 6.5; P = 0.21, $F_{1, 69}$ = 1.567). Similarly, the relative abundance of birds in each of the six feeding categories was similar (Figure 6.5; P = 0.48, $F_{5, 69}$ = 0.902) and there was no significant interactive effect between the two categorical predictors (treatment and feeding strategy) (P = 0.91; $F_{5, 69}$ = 0.291). Likewise, the relative abundance of birds utilising five different nesting strategies was comparable between treatment and control sites (Figure 6.6; P = 0.06, $F_{1, 71}$ = 0.3.717), and there was no difference in nesting strategy (Figure 6.6; P = 0.22, $F_{4, 71}$ = 1.453). There was no significant interactive effect between these two factors (P = 0.67; $F_{4, 71}$ = 0.595).

The mammal species composition of bushclumps was similar at treatment and control sites (Table 6.2; Morista-Horn Similarity Index = 0.947). Of the nine species recorded utilising bushclumps, eight species were shared between treatment and control sites (Table 6.2). The porcupine (*Hystrix africaeaustralis,* Peters) was only recorded at treatment sites (Table 6.2). However, the frequency of occurrence of mammal species in bushclumps was not significantly different between treatments and controls (Table 6.2; P = 1.00; χ^2 = 0.00; df = 9). The species richness of mammals was only slightly higher at treatment sites compared to controls, and this difference was not significant (Figure 6.7A; P = 0.62, t_4 = 0.535). Similarly, species diversity was only marginally higher at treatment sites and not significant (Figure 6.7B; P = 0.26, t_4 = 1.308).

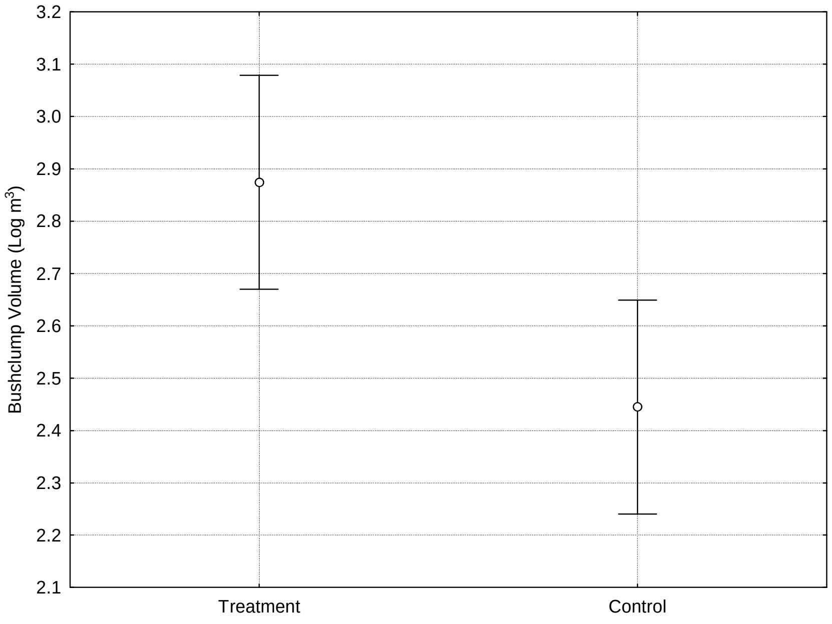

Figure 6.1: The Log volume (m^3) calculated for bushclumps at treatment and control sites. Data are means and error bars are 95% confidence intervals. Statistical results are described in the text.

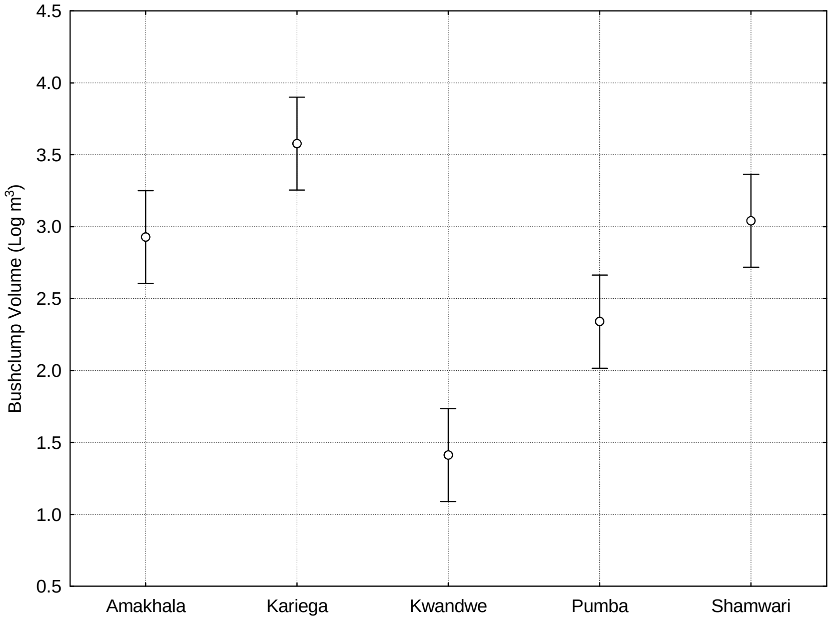

Figure 6.2: The Log volume (m^3) calculated for bushclumps at each location. Data are means and error bars are 95% confidence intervals. Statistical results are described in the text.

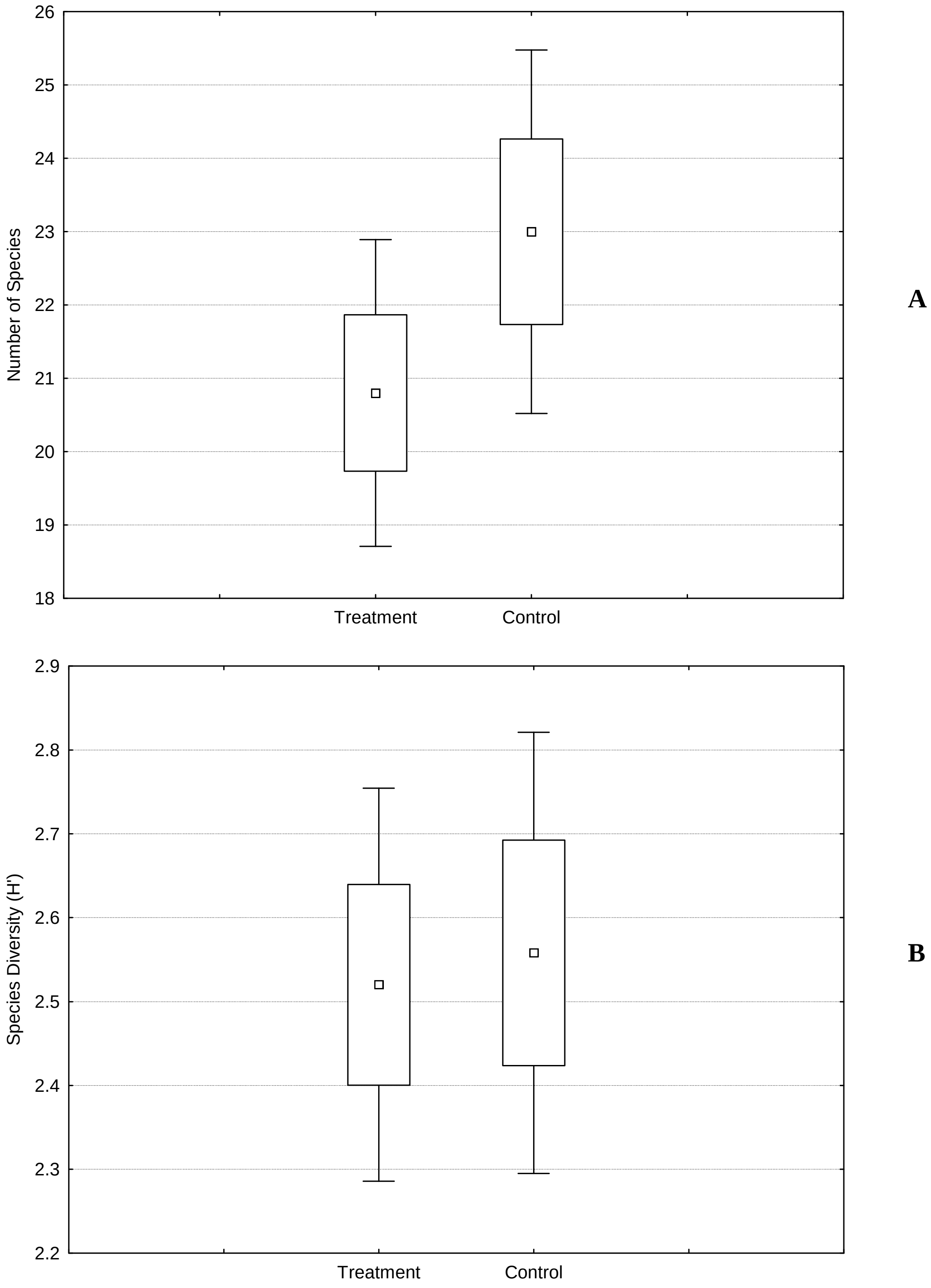

Figure 6.3: The number of species (**A**) and Shannon-Wiener diversity (H') (**B**) of plants identified in bushclump savanna at treatment and control sites. Data points are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

Table 6.1: The mean (± SD) frequency of occurrence of the plant species present in bushclumps at treatment and control sites. Morista-Horn Similarity Index for treatments and controls = 0.934.

Family	Species	Treatment	Control
Mimosaceae	*Acacia karroo*	15.6 ± 14.2%	8.0 ± 4.7%
Mimosaceae	*Acacia saligna*	1.6 ± 3.6%	0.8 ± 1.1%
Liliaceae	*Aloe africana*	2.8 ± 6.3%	0.0 ± 0.0%
Liliaceae	*Aloe ferox*	11.6 ± 16.0%	4.8 ± 4.6%
Asparagaceae	*Asparagus* sp.	22.8 ± 19.9%	27.2 ± 23.1%
Salvadoraceae	*Azima tetracantha*	21.2 ± 22.7%	12.8 ± 19.4%
Asteraceae	*Brachylaena ilicifolia*	5.6 ± 12.5%	2.4 ± 5.4%
Buddlejaceae	*Buddleja saligna*	0.0 ± 0.0%	2.0 ± 4.5%
Rubiaceae	*Burchellia bubalina*	3.6 ± 8.1%	4.8 ± 9.7%
Rubiaceae	*Canthium inerme*	4.0 ± 8.9%	5.2 ± 11.6%
Capparaceae	*Capparis sepiaria*	0.0 ± 0.0%	1.6 ± 1.7%
Apocynaceae	*Carissa bispinosa*	8.0 ± 8.7%	7.6 ± 3.3%
Celastraceae	*Cassine aethiopica*	2.8 ± 3.9%	2.4 ± 2.2%
Asteraceae	*Chrysanthemoides monilifera*	0.4 ± 0.9%	0.4 ± 0.9%
Rubiaceae	*Coddia rudis*	7.6 ± 12.2%	12.4 ± 21.7%
Crassulaceae	*Crassula* sp.	0.0 ± 0.0%	1.2 ± 2.7%
Araliaceae	*Cussonia spicata*	2.8 ± 3.4%	6.0 ± 5.5%
Ebenaceae	*Diospyros lycioides*	31.2 ± 31.5%	40.8 ± 37.4%
Boraginaceae	*Ehretia rigida*	8.4 ± 11.0%	6.4 ± 7.7%
Ebenaceae	*Euclea natalensis*	0.0 ± 0.0%	2.0 ± 2.0%
Ebenaceae	*Euclea undulata*	12.8 ± 11.8%	19.2 ± 27.3%
Euphorbiaceae	*Euphorbia bothae*	11.6 ± 25.9%	0.0 ± 0.0%
Tiliaceae	*Grewia occidentalis*	2.8 ± 4.2%	2.4 ± 4.3%
Tiliaceae	*Grewia robusta*	14.8 ± 20.7%	15.2 ± 27.8%
Celastraceae	*Gymnosporia buxifolia*	1.6 ± 3.6%	1.2 ± 1.8%
Celastraceae	*Gymnosporia polyacantha*	9.6 ± 10.0%	5.2 ± 4.8%
Anacardiaceae	*Harpephyllum caffrum*	0.0 ± 0.0%	0.4 ± 0.9%
Solanaceae	*Lycium* sp.	7.2 ± 9.0%	14.8 ± 25.6%
Celastraceae	*Maytenus capitata*	9.2 ± 14.8%	8.8 ± 11.5%
Oleaceae	*Olea europea*	2.8 ± 4.4%	6.8 ± 14.1%
Cactaceae	*Opuntia ficus-indica*	3.2 ± 3.0%	0.8 ± 1.1%
Anacardiaceae	*Ozoroa mucronata*	0.8 ± 1.8%	1.2 ± 1.8%
Sapindaceae	*Pappea capensis*	1.2 ± 1.8%	0.4 ± 0.9%

Family	Species	Treatment	Control
Plumbaginaceae	*Plumbago auriculata*	0.4 ± 0.9%	3.2 ± 3.0%
Portulacaceae	*Portulacaria afra*	1.2 ± 2.7%	3.2 ± 7.2%
Ptaeroxylaceae	*Ptaeroxylon obliquum*	1.2 ± 1.1%	0.0 ± 0.0%
Celastraceae	*Pterocelastrus tricuspidatus*	0.4 ± 0.9%	0.0 ± 0.0%
Celastraceae	*Putterlickia pyracantha*	1.6 ± 2.6%	0.8 ± 1.8%
Rhizophoraceae	*Rhigozum obovatum*	4.4 ± 9.8%	2.4 ± 5.4%
Anacardiaceae	*Rhus chirundensis*	0.4 ± 0.9%	0.0 ± 0.0%
Anacardiaceae	*Rhus crenata*	3.2 ± 4.6%	5.6 ± 4.3%
Anacardiaceae	*Rhus incisa*	4.0 ± 4.2%	6.4 ± 8.8%
Anacardiaceae	*Rhus longispina*	26.4 ± 29.6%	13.6 ± 18.2%
Anacardiaceae	*Rhus pallens*	40.8 ± 43.7%	47.2 ± 41.7%
Anacardiaceae	*Rhus* sp.	0.4 ± 0.9%	0.0 ± 0.0%
Caesalpinioideae	*Schotia afra*	6.8 ± 14.1%	7.6 ± 11.9%
Flacourtiaceae	*Scolopia zeyheri*	1.2 ± 1.8%	2.8 ± 5.2%
Rhamnaceae	*Scutia myrtina*	17.6 ± 18.9%	21.2 ± 23.1%
Sapotaceae	*Sideroxylon inerme*	9.6 ± 18.1%	13.6 ± 12.8%
Loganiaceae	*Strychnos decussata*	4.0 ± 6.9%	4.4 ± 7.0%
Rutaceae	*Zanthoxylem capense*	0.8 ± 1.8%	0.8 ± 1.8%

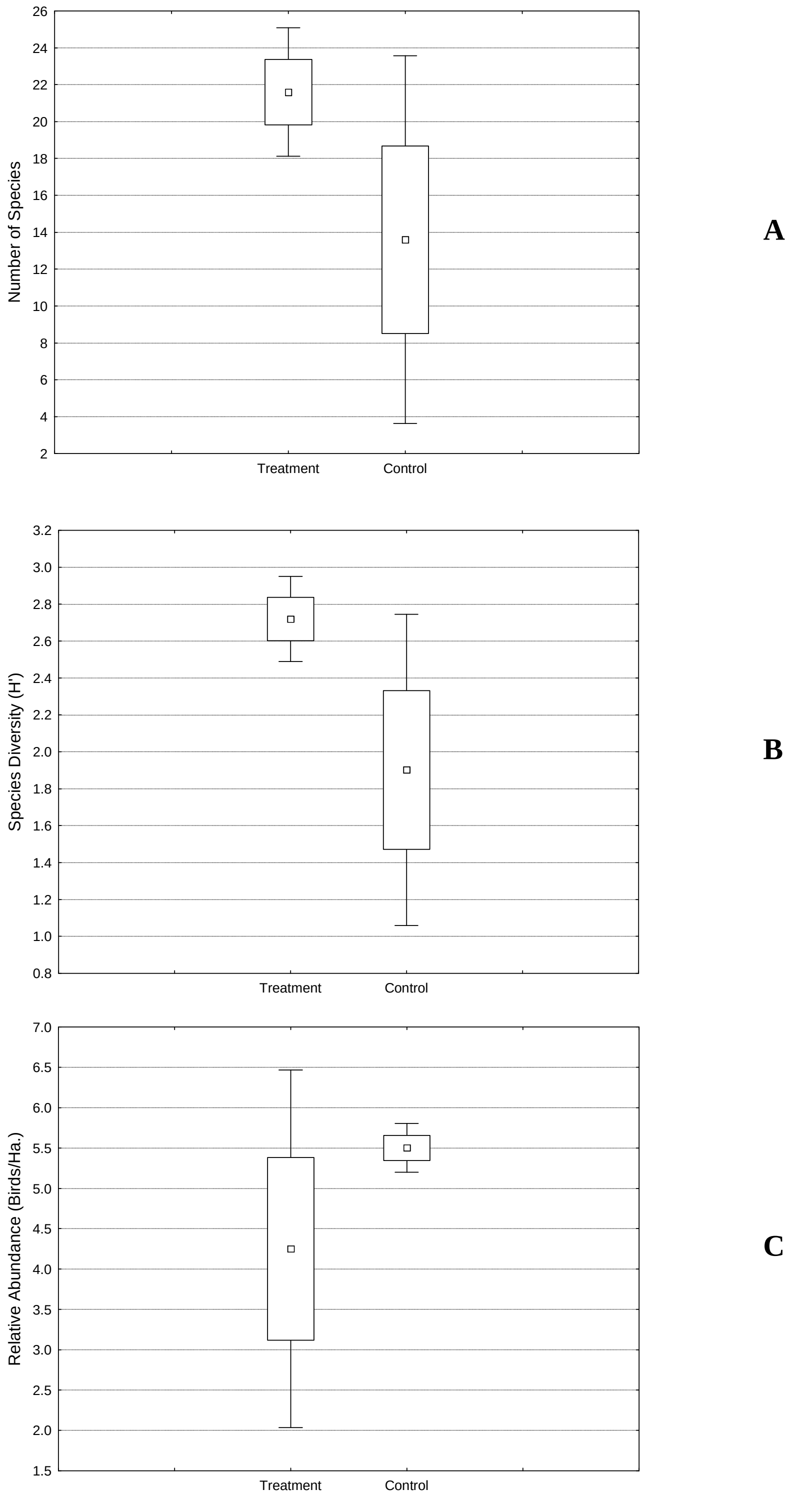

Figure 6.4: The number of species (**A**), Shannon-Wiener diversity (H') (**B**) and relative abundance (Birds/Ha.)(**C**) of birds identified in bushclump savanna at treatment and control sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

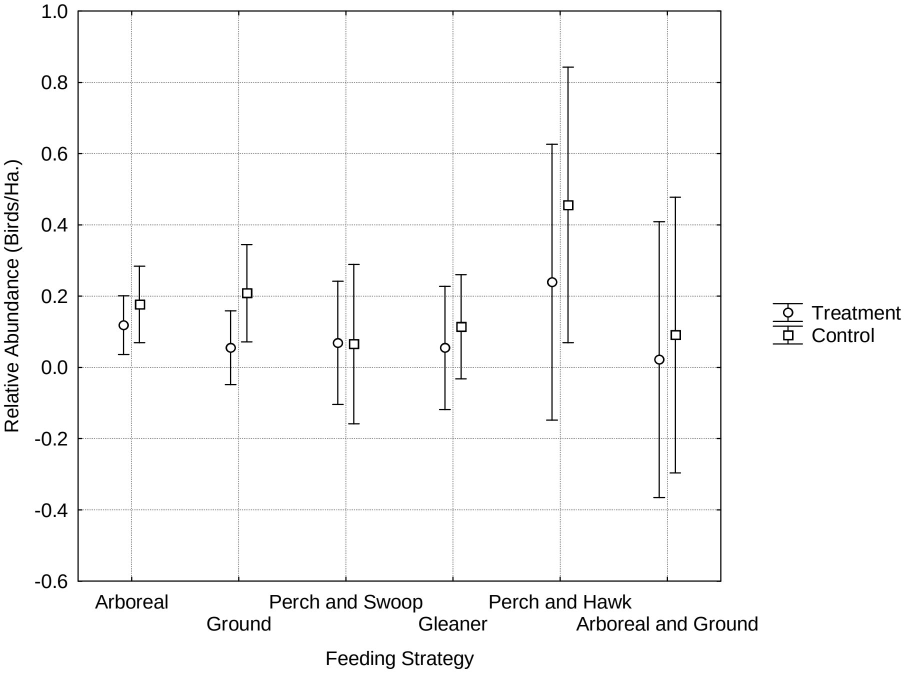

Figure 6.5: The relative abundance of birds per hectare at treatment and control sites falling into one of six feeding categories (Maclean 1993).

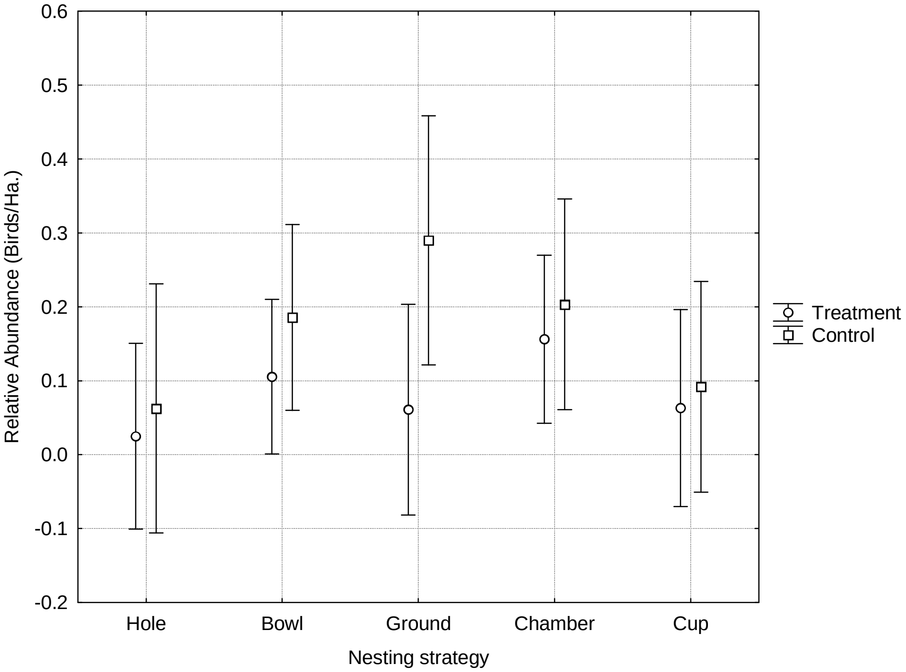

Figure 6.6: The relative abundance of birds per hectare at treatment and control sites falling into one of five nesting categories (Maclean 1993).

Table 6.2: The mean (± SD) frequency of occurrence of the mammal species present in bushclumps at treatment and control sites. Morista-Horn Similarity Index for treatments and controls = 0.947.

Order	Species	Treatment	Control
Tubulidentata	*Orycteropus afer*	1.6 ± 2.2%	0.4 ± 0.9%
Carnivora	*Otocyon megalotis*	1.2 ± 1.8%	1.6 ± 2.6%
Artiodactyla	*Sylvicapra grimmia*	1.2 ± 1.1%	3.2 ± 3.0%
Artiodactyla	*Aepyceros melampus*	0.4 ± 0.9%	2.4 ± 5.4%
Rodentia	*Hystrix africaeaustralis*	1.6 ± 2.6%	0.0 ± 0.0%
Lagomorpha	*Lepus saxatilis*	1.2 ± 1.1%	0.8 ± 1.1%
Rodentia	*Pedetes capensis*	0.8 ± 1.8%	3.2 ± 4.6%
Artiodactyla	*Raphicerus campestris*	0.8 ± 1.8%	0.4 ± 0.9%
Artiodactyla	*Phacochoerus africanus*	1.6 ± 2.2%	2.8 ± 4.2%

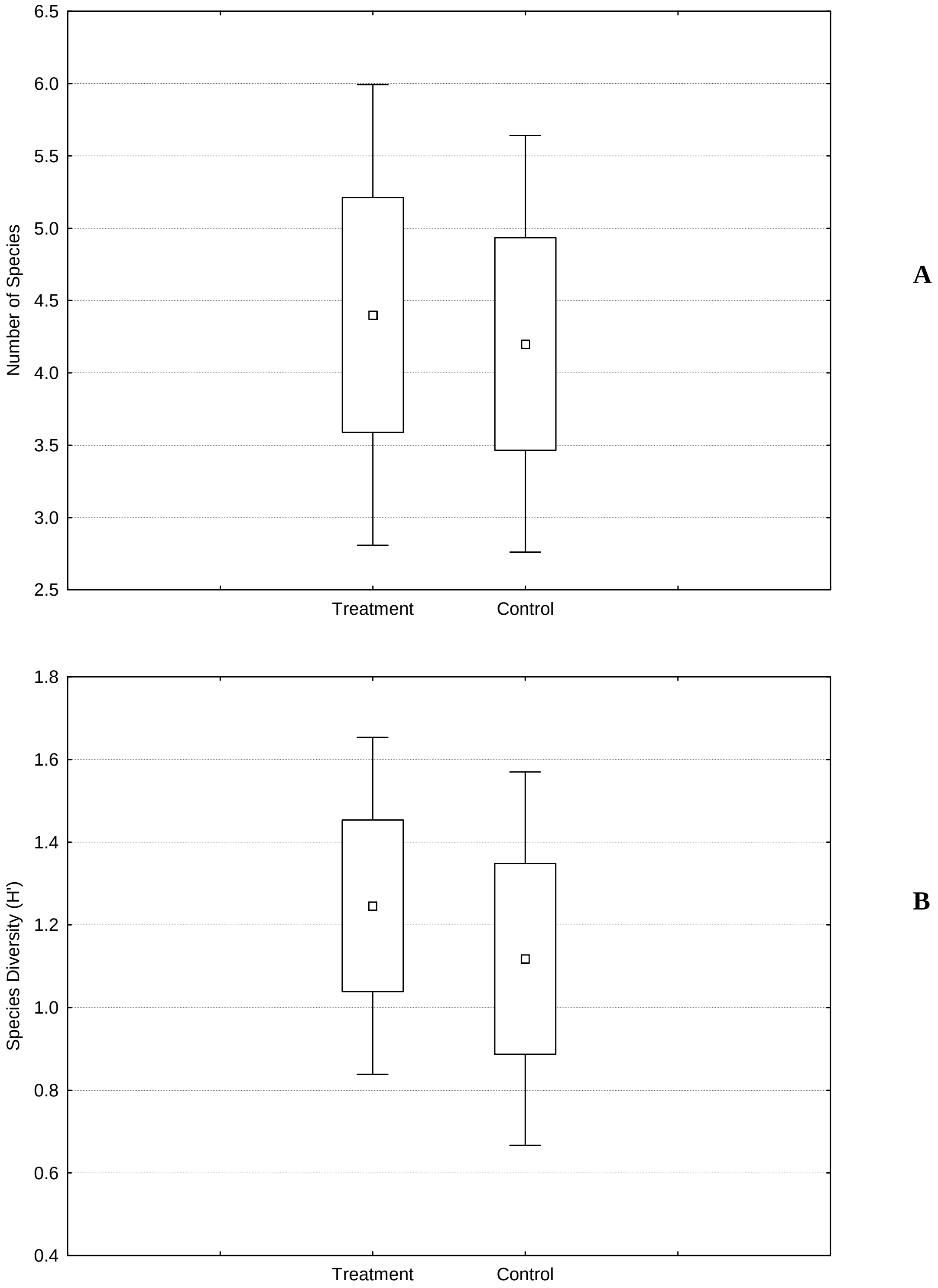

Figure 6.7: The number of species (**A**) and Shannon-Wiener diversity (H') (**B**) of mammals in bushclump savanna at treatment and control sites. Data are means, boxes are means ± SE and whiskers are means ± 1.96*SE.

6.4 DISCUSSION

Examples of dramatic reductions in mature tree populations, reportedly caused by elephants, abound in the scientific literature and have been discussed in *Chapter 1*. In addition, these examples are widespread and cover broad spatial and temporal scales on the African continent (Field 1971; Leuthold 1977; Coetzee *et al.* 1979; Eltringham 1980; Weyerhaeuser 1985; Okula & Sise 1986; Swanepoel & Swanepoel 1986; Tchamba 1995; Bowland & Yeaton 1997; Jacobs & Biggs 2002; Mtui & Owen-Smith 2006). Since this material has been discussed elsewhere, only those studies that incorporated adequate spatial and temporal controls are discussed in this chapter (Bowland & Yeaton 1997). In an assessment of the effects of elephants on bushveld tree species in KwaZulu-Natal, South Africa, Bowland & Yeaton (1997) demonstrated that the density of nine tree species, that constituted 90% of the diet of elephants, were significantly lower at sites where elephants had access compared to an unused site. Large, mature trees such as *Cassine aethiopica*, Thunb., *Cussonia spicata*, Thunb., and *Sideroxylon inerme*, L. generally occur in bushclumps within the Eastern Cape Province (*Chapter 2*; Low & Rebelo 1996). These trees are usually found close to the centre and in order to access the trees elephants destroy large proportions of bushclumps, particularly when the tree is a highly favoured species such as *C. spicata* (D. Parker, pers. obs.; *Chapter 5*). In my study, although the frequency of occurrence of *C. spicata* and *S. inerme* trees was lower at treatment sites than controls, there was no significant difference between the frequency of these trees or any other mature trees (*C. aethiopica*, *Olea europea*, L., and *Harpephyllum caffrum*, Bernh.) in bushclump savanna at treatments and controls. It is important to remember that treatment sites have experienced a relatively short exposure to elephants at low densities, and it is likely that this explains the non-significant reduction in tree densities. The short exposure of the treatment sites to elephants may also, in part, explain the anomalous results for bushclump size. The original hypothesis predicted a reduction in size resulting from elephant feeding activity, but bushclumps were in fact significantly larger at treatment sites than controls. The significant effect of geographical location suggests that localised climate and site history also influence the size of bushclumps. Sites where past herbivore density was low prior to the re-introduction of elephants, combined with higher rainfall (e.g. Kariega) would have allowed bushclumps to increase in size *sensu* "thicket building" described in *Chapter 4* (Vlok & Euston-Brown 2002). By contrast, sites that experience low rainfall and had high herbivore density in the past (e.g. Kwandwe treatment) would have caused bushclumps to decrease in size, similar to "thicket depletion" described in *Chapter 4* (Vlok & Euston-Brown 2002). It is therefore likely that the observed differences in bushclump volume are a result of differences in biotic and abiotic factors between treatment and control sites, in spite of efforts to ensure that treatment and control sites were as similar as possible.

At a plant community level my results indicated that the species composition of treatment and control sites were similar. However, despite being smaller, bushclumps at control sites had more woody plant species and higher species diversity compared to treatment sites. This is contrary to the theory of island biogeography where larger habitat "islands" (bushclumps) should exhibit higher diversity and species richness than smaller islands (Brown 1978; Quinn & Harrison 1988). However, within a given area, many small habitat patches (or islands) will contain a greater number of species than an area of similar size containing fewer large habitat patches (Loman & Von Schantz 1991). Such a scenario provides a likely explanation for the plant species composition results obtained in my study.

By contrast to the plant community variables discussed above, my results show that although not significant, bird and mammal species richness, diversity and the number of unique species were higher at treatment sites than controls. This supports the theory that larger habitat “islands” will exhibit higher diversity and species richness than smaller islands (Brown 1978; Quinn & Harrison 1988). However, these results must be interpreted with care. The number of taxa utilising bushclumps probably depends on the size and quality of the habitat provided. In addition, the scale and the presence of species rich habitats, neighbouring (~500m) the bushclump savanna, must also be considered. Due to the high mobility of birds and mammals, estimates of species richness and diversity can be inflated if there is a mosaic of habitat/land-use types at the scale of several km^2 (Naidoo 2004; Brotons *et al.* 2005). Furthermore, the high degree of similarity between bird and mammal species composition at treatment and control sites suggests low degrees of habitat specialisation for these two groups. Taxa that have weak habitat specialisation tend to exhibit a stronger relationship between habitat area and species richness (i.e. higher species richness with increasing area) (Ricklefs & Lovette 1999). This suggestion is supported by the lack of any significant differences in the relative abundance of birds with specific food and nesting requirements at treatment and control sites and that all unique species (either at treatments or controls) are fairly wide-ranging in the Eastern Cape Province (A. Craig pers. comm..). However, at present elephant densities, the bird and mammal communities utilising bushclumps are neither negatively nor positively affected.

I have shown that bushclump size varies significantly at a regional scale and that bushclumps are significantly larger where elephants are present compared to control sites. In spite of these differences, bird and mammal communities were similar at treatment and control sites. Thus, the initial hypothesis is only partially supported. Elephants did not decrease the size of bushclumps and woody plant species richness and diversity was higher at control sites than treatment sites. However, bird and mammal communities were similar at treatment and control sites. Thus, I recommend continued intensive research on this aspect of elephant ecology to ascertain whether the results observed in my study persist over an extended time-period.

CHAPTER 7

THE ROLE OF ELEPHANTS IN SEED DISPERSAL WITHIN THE THICKET BIOME OF THE EASTERN CAPE PROVINCE, SOUTH AFRICA

7.1 INTRODUCTION

The dispersal of plant seeds by vertebrates (endozoochory) is thought to have evolved as a mechanism by which propagules are transported away from the parent plant and deposited in favourable microsites to germinate (Samuels & Levey 2005). This dispersal creates spatial heterogeneity within plant communities and increases gene flow, preventing inbreeding depression (Sigwela 1999; Milton & Dean 2001). A second assumed advantage of endozoochory is the enhancement of germination following passage through the gut of the animal (Rodríguez-Pérez *et al.* 2005; Samuels & Levey 2005). This enhancement is achieved through either chemical or mechanical scarification of the seed coat, making it permeable to water, which is required for germination (Roxburgh 2007). Although this aspect of seed dispersal (also termed the quality of treatment) has received much attention in the literature (Lewis 1987; Lieberman *et al.* 1987; Chapman *et al.* 1992; Robertson 1995; Chang *et al*. 2005; Cosyns *et al.* 2005; Rodríguez-Pérez *et al.* 2005; Moolna 2007; Roxburgh 2007) it is not a universal advantage conferred upon plants by endozoochory (Rodríguez-Pérez *et al.* 2005). Other biotic and abiotic factors, such as animal species, microsite and rainfall, can affect the germination success of seeds that have passed through the digestive tracts of animals (Rodríguez-Pérez *et al.* 2005). Sigwela (1999) demonstrated that kudu (*Tragelaphus strepsiceros*, Pallas) dispersed a greater number of viable seeds compared to goats (*Capra hircus*, L.) when feeding in the same habitat. In addition, Rodríguez-Pérez *et al.* (2005) found that seeds that seeds that had passed through the digestive tracts of lizards and birds had increased germination success when planted under controlled (laboratory) conditions compared to those germinated under field conditions.

The Thicket Biome of the Eastern Cape Province (described in *Chapter 1*) is part of a global biome of an ancient (Tertiary) vegetation type that preceded the fire-prone savannas of Africa (Cowling 2006) and plants in the thicket employ both ramet (or vegetative) and seedling recruitment (Cowling 2006). Birds were originally thought to be responsible for the majority of seedling recruitment (through seed dispersal) due to the relatively small sized seeds (~ 4-12mm) produced by most thicket plants (Coates-Palgrave 2000; Kerley *et al.* 2006). In addition, it has been demonstrated that seed mortality increases with a decrease in seed size after passage through the digestive tracts of some mammals (Davis & Kerley 2006), suggesting that mammals are less than ideal candidates for seedling dispersal in thicket. However, unpublished research conducted in the Thicket Biome has shown that mammalian herbivores potentially disperse a greater range of seeds than birds (Kerley *et al.* 2006). According to this research, one of the most important mammalian seed dispersers is the elephant (*Loxodonta africana*, Blumenbach)(Kerley *et al.* 2006).

Records of seed dispersal by elephants exist across Africa (Lewis 1987; Lieberman *et al.* 1987; Chapman *et al.* 1992; Robertson 1995; Yumoto *et al.* 1995; Davis & Kerley 2006; Gonthier 2007; Babweteera *et al.* 2007). The majority of these studies have found that the germination success of seeds passed through the gut of elephants was significantly higher compared to seeds germinated from intact fruits (Lewis 1987; Lieberman *et al.* 1987; Chapman *et al.* 1992; Babweteera *et al.* 2007). However, in all of these studies the fruit consumed and the seeds dispersed by the elephants were relatively large (both between 30 and 180mm). By contrast, according to unpublished reports, seeds passed through the gut of elephants in the Thicket Biome of the Eastern Cape Province are not more likely to germinate (Robertson 1995), presumably due to the higher mortality of the smaller seeds found in the region after passage through the digestive tract (Davis & Kerley 2006).

The aim of this chapter was to determine the extent to which elephants are capable of dispersing seeds in the Thicket Biome. Specifically to assess the diversity, abundance and viability of seeds that had passed through the digestive tract of elephants. In light of the above discussion, it was hypothesized that endozoochory by elephants would not increase the viability and germination success of important Thicket Biome plant species.

7.2 MATERIALS AND METHODS

As this was not a major component of the project as a whole and due to logistical constraints, a once-off (snap-shot) approach to the role played by elephants in seed dispersal was adopted for this part of the work.

7.2.1 Seed identification, collection and assessment

Between April 2005 and March 2007, fruit from all dicotyledonous Thicket plant species encountered at one site (Kwandwe) were collected and oven dried at 60^0C for four days before being cleaned of all pulp (Sigwela 1999). Seeds obtained in this way were stored in Petri dishes, in dark and dry conditions until required and also served as a reference collection (Sigwela 1999; Rodríguez-Pérez *et al.* 2005). During March (late summer) 2007, fresh elephant faecal samples from different individuals (no older than 24 hrs; $n = 30$) were collected from Kwandwe and a 1kg sub-sample (Robertson 1995) oven dried at 60^0C for four days (Sigwela 1999). This time of year was chosen as it is a period characterised by increased rainfall (Stone *et al.* 1998) and a time when several important thicket plant species are known to be in fruit (Coates-Palgrave 2000). The dried faecal samples were passed through a series of graded sieves (Universal Test Sieves; mesh sizes 4.75, 2.36 and 1mm), which ensured efficient isolation of seeds and eliminated unwanted faecal material (Sigwela 1999). Seeds that were smaller than 1mm (i.e. those that passed through the 1mm sieve) and all grass seeds were excluded from further analysis. All remaining seeds were counted and identified under a WILD Heerbrugg dissecting microscope (6X magnification) by referral to the reference specimens and at the Selmar Schönland Herbarium, Albany Museum, Grahamstown. A visual assessment of their quality was made (damaged or intact) and this was recorded. Seeds were defined as being damaged if they appeared to have sustained severe mechanical damage (e.g. split in two) after passage through the digestive tract of elephants (Robertson 1995). The seeds from the two most frequently encountered species in the faecal samples were reserved for further experimentation. Frequency of occurrence was defined as the relative frequency of the seeds of a particular species (presence/absence) in faecal samples divided by the total number of faecal samples examined, expressed as a percentage. Thus, if seeds from *Acacia karroo*, Hayne, were present in 20 samples, *A. karroo* would have had a frequency of occurrence of 66.67%. Only intact seeds were used for the germination trials.

7.2.2 Germination trials

Germination trials were conducted on seeds ingested by elephants (gut passed), field collected seeds (manually extracted control) and whole fruit (intact control) in order to effectively isolate the mechanism responsible for any observed germination patterns (Samuels & Levey 2005). It has been suggested that the flightless dung beetle (*Circellium bacchus*, Fabricius) may play a role in increasing the survival of seeds found in elephant dung by accidentally including them in food or brood balls and thereby removing them from exposed areas where they would be prone to desiccation or trampling (Robertson 1995). Thirty randomly selected seeds from each treatment (described above) were encased in ~ 10g of fresh elephant dung (to simulate incorporation into dung beetle brood balls) and planted in a straight line at a depth of 0.5 – 1 cm, 5 cm apart (Rodríguez-Pérez *et al.* 2005). The elephant dung used for this experiment had been sieved and all other seeds removed. In addition, thirty randomly selected seeds from each treatment were not encased in dung and planted in the same way. Both seeds encased in dung and those not (all treatments) were also planted in two locations, open and closed microsites (Rodríguez-Pérez *et al.* 2005). Microsite was used as a treatment variable as exposure (i.e. open microsites) is known to affect the germination success of seeds (Rodríguez-Pérez *et al.* 2005). The open microsites were located on cleared ($1m^2$) plots and the closed microsites on cleared ($1m^2$) plots under *Portulacaria afra*, Jacq., plants (one of the most dominant plant species in the Thicket Biome)(Low & Rebelo 1996). All plots were located in a fenced off section of Kwandwe to reduce the effects of seed predation and trampling. However, the plots were not protected with a cage of wire mesh to prevent rodent and bird predation. The open and closed locations were 25m apart and the plots containing each treatment were at least 5 m apart. No artificial watering was given and all sites received the same amount of sunlight (Lewis 1987). Germination and seedling survival were monitored bi-weekly from 23 April 2007 – 25 May 2007.

Despite continued monitoring and allowing more than sufficient time for germination (Walters & Milton 2003), none of the seeds from the three treatments germinated. No signs of seed predation were observed over the period of the experiment. It is possible that an unusually cold spell (temperatures below 2^0C) just after the seeds were planted and less than adequate rainfall (11mm in total) caused the observed results. Consequently, only the results from the assessment of seeds from elephant dung are described.

7.2.3 *Data analysis*

Differences between the total number and number of intact seeds from each species identified in the dung were tested using two non-parametric Kruskal-Wallis one-way ANOVAs (Statistica, Statsoft, version 7.0). The categorical predictor in these analyses was “species”. A multiple comparison post-hoc test (using z’ values) was performed to ascertain the source of the variation in each test (Statistica, Statsoft, version 7.0). Differences between the proportions of intact seeds for each species were tested in the same way.

7.3 RESULTS

The seeds from five plant species were identified from the dung of elephants at Kwandwe (Table 7.1). The seeds of *Acacia karroo* were the most abundant, with 2170 individual seeds extracted (Table 7.1). However, only 449 seeds (21%) were intact after gut passage (Table 7.1). The only other seeds extracted from the dung in any great number (217) were from the epiphytic mistletoe (*Viscum rotundifolium*, Trel.), where all seeds appeared to be viable (intact) following gut passage (Table 7.1).

Overall, significantly more seeds from *A. karroo* than any other species were found in the dung of elephants at Kwandwe (Figure 7.1 A; $P < 0.0001$; $H_{4,\,150} = 69.593$). Although significantly more *A. karroo* seeds appeared to be intact ($P < 0.0001$; $H_{4,\,150} = 53.424$) compared to the other species except for those of *V. rotundifolium* (Figure 7.1 B; $P = 1.07$), *A. karroo* had the lowest proportion of intact seeds (% of total found in the dung) of all species (Table 7.1; $P < 0.0001$; $H_{4,\,150} = 38.835$).

Table 7.1: The plant species, total, frequency of occurrence per sample, mean number per sample and proportion of intact seeds (number intact/total number) identified in 30 samples of elephant dung from Kwandwe. Values in parentheses are absolute numbers.

SPECIES	TOTAL	FREQ. OCC.	MEAN	% INTACT
Acacia karroo	2170	80.0 ± 26.32%	14.93 ± 24.21	20.69% (449)
Viscum rotundifolium	217	40.0 ± 49.83%	7.23 ± 16.51	100% (217)
Rhus longispina	26	10.0 ± 34.57%	0.87 ± 3.31	100% (26)
Euclea undulata	6	6.67 ± 20.97%	0.13 ± 0.57	66.67% (4)
Sida sp.	1	3.33 ± 18.26%	0.03 ± 0.18	100% (1)

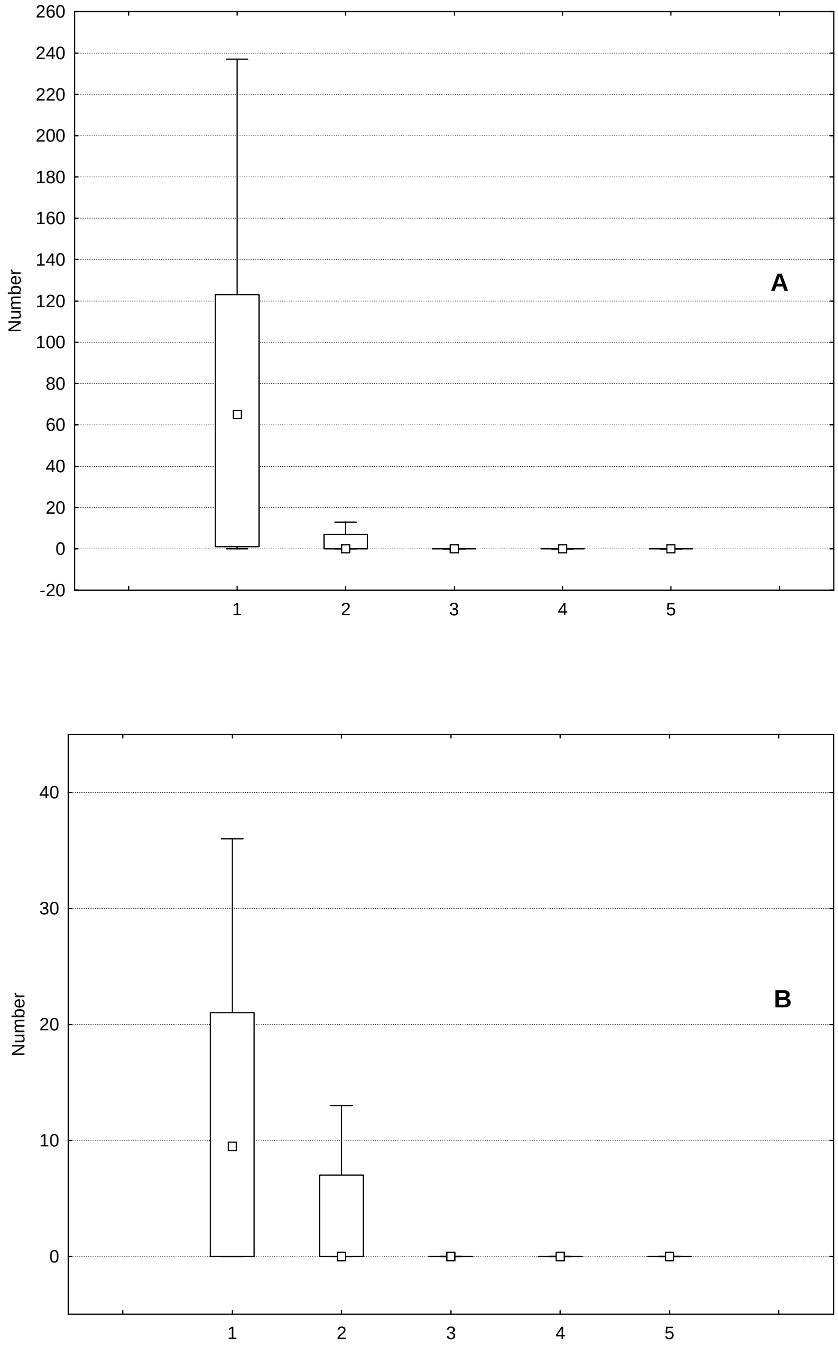

Figure 7.1: The median number per kg of elephant dung of all seeds (**A**) and intact seeds (**B**) extracted from elephant dung at Kwandwe. Boxes indicate percentiles and whiskers indicate non-outlier ranges. 1 = *A. karroo*; 2 = *V. rotundifolium*; 3 = *R. longispina*; 4 = *E. undulata*; 5 = *Sida* sp.

7.4 DISCUSSION

The seeds of five species were recorded in the dung of elephants at Kwandwe in this study, with those of *A. karroo* and *V. rotundifolium* being the most abundant. This is lower than any previous estimate of the species composition of seeds present in elephant dung (Lieberman *et al.* 1987; Robertson 1995; Yumoto *et al.* 1995; Davis & Kerley 2006; Gonthier 2007). Significantly, data from the Eastern Cape Province indicate that seeds from as many as 29 species can occur in elephant dung (Robertson 1995). In addition, Robertson's (1995) survey of the seeds in elephant dung from Addo Elephant National Park and Shamwari Private Game Reserve in the Eastern Cape Province revealed that, although present, neither *A. karroo* nor *V. rotundifolium* seeds were very abundant (both < 0.1%). In the present study, samples were collected during late summer, whereas Robertson (1995) collected dung samples during autumn, mid-winter and early spring. This may explain the observed differences in seed frequency of occurrence. Similarly, by sampling over a broader time scale, when different plant species were in fruit (Coates-Palgrave 2000), Robertson (1995) was more likely to record a greater variety of species in the dung. The species composition results from the present study are not directly comparable with the work from central and western Africa as these studies were conducted in tropical rainforests (Lieberman *et al.* 1987; Yumoto *et al.* 1995).

Notwithstanding the limitations of the current experimental design, it was chosen principally to address whether passage of seeds through the digestive tracts of elephants affected viability and germination success. Research conducted in East Africa has demonstrated that the passage of *Acacia* seeds through the digestive tracts of elephants and other ungulates improved germination rates and reduced seed predation by bruchid beetles (Lamprey *et al.* 1974; Gonthier 2007). However, as suggested by Lamprey *et al.* (1974) and Gonthier (2007), the improved germination rates of *Acacia* seeds in East Africa may be part of a complex mechanism by which the plants escape seed predation by bruchid beetles. By contrast, seed predation by bruchid beetles on *A. karroo* in the Eastern Cape Province is much lower (~20% of seeds) than East Africa (72-99% of seeds)(Lamprey *et al.* 1974; Whittington-Jones 1994; Gonthier 2007). Consequently, *A. karroo* may have evolved alternative mechanisms for successful seedling recruitment. My results indicate that although significantly more *A. karroo* seeds (absolute numbers) were intact compared to the other species, only 21% of all *A. karroo* seeds found in the dung were intact after passage through the gut and very few seeds from the remaining species were found in the dung. In addition, there was no seedling growth during the germination trials. All seeds found in elephant dung during this study were small (all < 8mm; Coates-Palgrave 2000), increasing the likelihood of seed mortality after gut passage (Davis & Kerley 2006). In spite of the unfavourable environmental conditions during the germination trials, as discussed in the methods, the germination trials were conducted under conditions that were as natural as possible in order to effectively assess how the abiotic environment influenced seed germination (Rodríguez-Pérez *et al.* 2005). Significantly, laboratory studies are known to produce inflated estimates of germination success following gut passage (Rodríguez-Pérez *et al.* 2005). Walters & Milton (2003) reported that *A. karroo* seeds should germinate within two months of planting following scarification of the seed coat (*sensu* gut passage) if they are viable. In addition, *A. karroo* seeds are not known to last much more than a year as viable seeds in the seed bank (O'Connor 1995). Furthermore, over the course of more than five years of intensive fieldwork in the Eastern Cape Province I have never recorded anything other than mushrooms germinating from elephant dung in the field (D.

Parker, pers. obs.) Thus, under the conditions experienced in the current germination trial elephants do not increase the viability or germination success of thicket plant species, and the initial hypothesis is accepted.

This part of my study has provided further data on the diversity of plant species potentially dispersed by elephants during austral summer in the Eastern Cape Province of South Africa. In addition, I have shown that elephants do not promote the viability and germination success of thicket plant species during cold and dry conditions that are experienced in the region. However, the role of elephants in the dispersal and germination success of thicket plant species remains unclear and is clearly a topic for future studies in the region.

CHAPTER 8

SUMMARY AND CONCLUDING REMARKS

Due to their large size, high absolute energy requirements, generalist feeding strategy and often wasteful foraging behaviour (Owen-Smith 1992; Cowling & Kerley 2002; O'Connor *et al.* 2007) elephants (*Loxodonta africana*, Blumenbach) are prime examples of ecosystem engineers and keystone herbivores in African ecosystems. Consequently, elephants are capable of causing obvious damage to vegetation, and this has arguably been the root of the so-called "elephant problem" - too many elephants in enclosed reserves and national parks in Africa, irreparably damaging the vegetation and negatively affecting biodiversity (Owen-Smith *et al.* 2006; Van Aarde *et al.* 2006). This perspective has its origin in the early scientific research that was, in some cases, flawed in design and misguided in its interpretation of ecological principles (Owen-Smith *et al.* 2006). Significantly, of the 35 peer-reviewed studies that have reported negative elephant effects, only 23% (8) had adequate controls (Appendix IV). In addition, of the 56 studies that suggested that elephants have both a positive and negative (neutral) effect, only 38% (21) used control sites (Appendix IV). From a pragmatic, scientific point of view this is concerning. In addition, the perceived problem of too many elephants has been taken up by the popular media without due consideration (and critical thought) of the myriad of factors influencing elephants and the way they structure ecosystems in Africa (Owen-Smith *et al.* 2006). However, as Owen-Smith *et al.* (2006) and Van Aarde *et al.* (2006) point out, pragmatism and more rigorous scientific experimental design appear to have returned to elephant research. This is supported by the fact that 14 of the 20 most recent papers on elephant impact (covering a 3 year period) included adequate controls

(Appendix IV). The general consensus amongst ecologists is that certain levels of disturbance (such as elephant impact) are necessary for maintaining ecosystem function and diversity, while too much disturbance will have adverse consequences for biodiversity (Owen-Smith *et al.* 2006; Van Aarde *et al.* 2006; Verdú *et al.* 2007). In addition, severe disturbance will not be dictated by the number of elephants *per se,* but rather by the history or duration of containment of elephants in enclosed areas and the provision of artificial water points (Owen-Smith *et al.* 2006; Van Aarde *et al.* 2006).

In this study, I examined the influence of elephants at low (< 0.5 elephants/km^2) densities, and after short (< 13 years) periods of exposure, on four vegetation types within the Eastern Cape Province, South Africa. Contrary to the third broad null hypothesis, outlined in *Chapter 1* (p. 15), the effects of elephants were most pronounced on aloes, which are highly preferred food items. In the presence of elephants the abundance of aloes declined. In line with research null hypothesis four, elephants did not reduce the size of bushclumps, where mature trees (also preferred food items) are usually distributed, in bushclump savanna. Despite grass being a major component of elephant diet (research null hypothesis one), the presence of elephants neither enhanced nor degraded the physical structure of grassland vegetation. Within the locally important Thicket Biome there was evidence of increased structural heterogeneity and a decrease in vegetation complexity, contrary research null hypothesis two. Although seeds from thicket plant species were recorded in elephant dung, elephants did not promote the germination success of these plants, supporting research null hypothesis five. The cascading effect of elephant foraging or presence on other taxa and ecosystem processes that rely on the vegetation as a resource was variable. Given the short duration of low elephant density occupation at the study sites and the relative mobility of the animal groups surveyed, I expected anthophorid bees (being the least mobile and utilising the inflorescences of a highly preferred food item) to be negatively affected by elephant foraging. However, in general terms, all taxa that were assessed (including these insects) appeared to benefit from elephant foraging across the four vegetation types considered in this study. In addition, ecosystem processes (vegetation patch dynamics and soil surface processes) were neither enhanced nor degraded by the presence of elephants. Thus, using small ($< 300\text{km}^2$), enclosed reserves as experimental units I have demonstrated that where elephant disturbance or impact is low (low density, short occupation time), the species richness and diversity of certain taxa and ecosystem processes are enhanced, consistent with the "intermediate disturbance hypothesis" and facilitation theory (Miller 1982; Bruno *et al.* 2003). In addition, as ecosystem engineers, the large (regional) scale effect of elephants at low densities has enhanced the overall species richness of some taxa by promoting heterogeneity (Jones *et al.* 1997), consistent with the theory of island biogeography (Loman & Von Schantz 1991). While it is tempting to suggest that, at low densities, elephants tend to have an overall, positive influence on the ecosystems of enclosed reserves the Eastern Cape Province, elephants have only been present at each study site for a relatively short period and it is likely that their impact will be cumulative and increase over time, particularly as these are closed systems (Owen-Smith *et al*. 2006).

For large (but not necessarily "open") systems researchers have proposed a number of creative ways to manage elephant populations to ensure that biodiversity is conserved, including the establishment of mega-parks (Owen-Smith *et al.* 2006; Van Aarde *et al.* 2006; Van Aarde & Jackson 2007). However, the basic premise behind all of these proposals is that elephant populations can become “self-limiting” and thereby maintain low levels of elephant-induced disturbance, which will promote the maintenance of biodiversity (Owen-Smith *et al.* 2006; Van Aarde *et al.* 2006; Van Aarde & Jackson 2007). For example, Owen-Smith *et al.* (2006) advocate restricting the availability of artificial water points. The authors argue that because elephants are water dependant, such manipulation will crowd elephants into smaller areas (riparian valleys) during resource limiting periods, such as the dry season, and increase the distance between areas with adequate water and food (Owen-Smith *et al.* 2006). By travelling back and forth between these areas, added stress will be placed on calves and thus reduce their chances of survival (Owen-Smith *et al.* 2006). I would like to augment this approach to propose that, from an evolutionary perspective, riparian valleys have evolved to sustain high levels of disturbance (e.g. browsing and flooding). Consequently, the vegetation growing in riparian valleys may be more capable of regenerating following intensive browsing by elephants in the dry season similar to the results obtained for grasslands and their recovery following a drought in the Kruger National Park, South Africa, following a drought (Kennedy *et al.* 2003).

The containment of elephants on reserves smaller than the typical elephant home range, which restricts their wider movement or migration (Owen-Smith *et al.* 2006), and the provision of artificial water points (Van Aarde *et al.* 2006) is a concern for the conservation of biodiversity in the long-term. Thus, I recommend continued research of elephant impacts at enclosed reserves, particularly as elephant populations and time since re-introduction increase, as this will provide the opportunity to rigorously test the role played by elephants in structuring plant and animal communities. The data obtained from such experimentation will not only be useful for the management of elephant populations on small reserves but will also provide the much needed unequivocal data on the longer-term consequences of high elephant density for the rest of Africa.

CHAPTER 9

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Appendix I: The number of individual points used to survey birds with the point transect technique (see *Chapter 2*) within each of four vegetation types at each treatment and control sites in this study. The total number of points (± SD) per treatment and control within each vegetation type is also given.

	Thicket		**Grassland**		**Aloes**		**Bushclumps**	
	Treatment	**Control**	**Treatment**	**Control**	**Treatment**	**Control**	**Treatment**	**Control**
Pumba	59	65	10	10	55	65	52	32
Kariega	43	52	21	16	45	52	58	53
Amakhala	54	35	15	13	43	46	25	13
Kwandwe	52	18	67	21	87	18	50	35
Shamwari	35	55	16	25	47	55	45	25
Total	243 ± 10	225 ± 19	129 ± 23	85 ± 6	277 ± 18	236 ± 18	230 ± 13	158 ± 15

Appendix II: The relative abundance (birds/Ha.) of the bird species recorded in four vegetation types using the point transect technique at treatment and control sites in this study. SD = standard deviation.

	Thicket				**Grassland**				**Aloes**				**Bushclumps**			
Species	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**
Acacia Pied Barbet	0.018	0.025	0	0	0	0	0	0	0.011	0.180	0	0	0.009	0.021	0	0
African Firefinch	0.008	0.018	0	0	0	0	0	0	0.009	0.019	0	0	0	0	0	0
African Hoopoe	0	0	0.019	0.043	0.005	0.010	0	0	0.007	0.010	0.019	0.043	0.011	0.024	0.067	0.150
African Olive-Pigeon	0.127	0.284	0.027	0.061	0	0	0	0	0.120	0.268	0.027	0.061	0.035	0.079	0	0
African Pipit	0.021	0.048	0	0	0.586	0.561	1.213	1.440	0.041	0.069	0	0	0.177	0.293	1.309	1.831
Amethyst Sunbird	0.047	0.050	0.078	0.095	0	0	0	0	0.043	0.052	0.076	0.095	0.053	0.086	0.047	0.074
Ant-eating Chat	0	0	0	0	0	0	0	0	0.008	0.018	0	0	0.016	0.035	0	0
Bar-throated Apalis	0.287	0.298	0.474	0.242	0	0	0	0	0.201	0.185	0.486	0.246	0.122	0.161	0.439	0.622
Black-collared Barbet	0.024	0.054	0.051	0.071	0	0	0	0	0.026	0.057	0.051	0.071	0.014	0.030	0	0
Black-crowned Tchagra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.029	0.064
Black-headed Oriole	0.146	0.114	0.053	0.081	0	0	0	0	0.129	0.129	0.054	0.081	0.094	0.177	0.075	0.121
Bokmakierie	0.028	0.046	0.017	0.038	0	0	0	0	0.037	0.040	0.017	0.038	0.011	0.024	0.048	0.107
Brown-hooded Kingfisher	0	0	0.009	0.020	0	0	0	0	0	0	0.009	0.020	0	0	0.014	0.031
Burchell's Coucal	0.006	0.014	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cape Bunting	0	0	0	0	0	0	0.027	0.061	0.003	0.007	0	0	0	0	0	0
Cape Glossy Starling	0.045	0.062	0.054	0.078	0.070	0.133	0	0	0.027	0.039	0.051	0.076	0.096	0.094	0.019	0.043
Cape Clapper Lark	0	0	0	0	0.005	0.010	0.218	0.488	0	0	0	0	0	0	0	0
Cape Longclaw	0	0	0	0	0.063	0.141	0.675	1.509	0	0	0	0	0.109	0.244	0	0
Cape Robin-Chat	0.049	0.034	0.064	0.081	0	0	0	0	0.037	0.021	0.066	0.080	0.022	0.028	0.067	0.150
Cape Sparrow	0.005	0.012	0	0	0.311	0.682	0	0	0.024	0.054	0	0	0.064	0.090	0	0
Cape Sugarbird	0	0	0.017	0.038	0	0	0	0	0	0	0.017	0.038	0	0	0	0
Cape Turtle-Dove	0.308	0.096	0.112	0.121	0	0	0	0	0.289	0.125	0.124	0.143	0.182	0.245	0.075	0.121

	Thicket				Grassland				Aloes				Bushclumps			
Species	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**
Cape Wagtail	0	0	0	0	0.009	0.020	0	0	0	0	0	0	0	0	0	0
Cape White-eye	0.038	0.055	0.092	0.205	0	0	0	0	0.051	0.058	0.092	0.205	0.053	0.118	0.056	0.125
Cardinal Woodpecker	0	0	0.008	0.019	0	0	0	0	0.009	0.021	0.008	0.019	0	0	0.010	0.021
Chestnut-vented Titbabbler	0.014	0.032	0	0	0	0	0	0	0.013	0.028	0	0	0.057	0.100	0	0
Chinspot Batis	0.048	0.108	0	0	0	0	0	0	0.051	0.115	0	0	0.014	0.030	0.056	0.125
Common Fiscal	0.080	0.125	0.017	0.038	0.018	0.040	0	0	0.070	0.103	0.020	0.037	0.089	0.121	0.096	0.214
Common Waxbill	0	0	0	0	0.005	0.010	0.300	0.671	0	0	0	0	0.009	0.021	0	0
Crowned Hornbill	0	0	0	0	0	0	0	0	0	0	0	0	0.028	0.063	0	0
Crowned Lapwing	0	0	0	0	0.032	0.071	0	0	0	0	0	0	0	0	0.010	0.021
Dark-capped Bulbul	0.152	0.134	0.098	0.075	0	0	0.135	0.234	0.149	0.173	0.100	0.074	0.180	0.205	0.260	0.261
Emerald-spotted Wood-Dove	0.005	0.012	0	0	0	0	0	0	0.004	0.009	0	0	0	0	0	0
Familiar Chat	0.030	0.042	0.008	0.019	0	0	0	0	0.039	0.054	0.008	0.019	0.019	0.041	0	0
Fiscal Flycatcher	0.121	0.118	0.148	0.127	0	0	0	0	0.135	0.162	0.147	0.128	0.206	0.199	0.086	0.145
Fork-tailed Drongo	0.232	0.201	0.224	0.175	0.080	0.110	0.300	0.671	0.264	0.209	0.219	0.176	0.239	0.269	0.456	0.814
Greater Double-collared Sunbird	0.430	0.321	0.451	0.334	0.005	0.010	0	0	0.475	0.459	0.425	0.278	0.180	0.115	0.313	0.457
Green Wood-Hoopoe	0.051	0.073	0.153	0.300	0	0	0	0	0.034	0.077	0.151	0.301	0	0	0.165	0.232
Green-backed Camaroptera	0	0	0.010	0.022	0	0	0	0	0	0	0.010	0.022	0	0	0.019	0.043
Grey-backed Cisticola	0.020	0.031	0.033	0.073	0.041	0.092	0.164	0.366	0.004	0.009	0.033	0.073	0	0	0	0
Karoo Prinia	0.172	0.135	0	0	0.005	0.010	0	0	0.130	0.103	0	0	0.130	0.094	0.056	0.125
Karoo Scrub-Robin	0.080	0.107	0.017	0.038	0.044	0.098	0	0	0.073	0.068	0.020	0.037	0.019	0.030	0	0
Long-billed Crombec	0	0	0.008	0.019	0	0	0	0	0	0	0.008	0.019	0	0	0	0
Malachite Sunbird	0.391	0.620	0.085	0.142	0	0	0	0	0.426	0.449	0.082	0.141	0.259	0.455	0	0
Neddicky	0.605	0.174	0.495	0.332	0.153	0.273	1.216	1.886	0.886	0.646	0.493	0.333	0.849	0.905	0.472	0.363
Olive Thrush	0.035	0.077	0	0	0	0	0	0	0.033	0.073	0	0	0.007	0.016	0	0
Red-backed Shrike	0	0	0	0	0.027	0.061	0	0	0	0	0	0	0.014	0.031	0	0

	Thicket				**Grassland**				**Aloes**				**Bushclumps**			
Species	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**	**Treatment**	**SD**	**Control**	**SD**
Red-eyed Dove	0.012	0.026	0.010	0.022	0	0	0	0	0.011	0.024	0.010	0.022	0.004	0.008	0	0
Red-faced Mousebird	0.197	0.117	0.221	0.174	0.014	0.031	0.180	0.402	0.161	0.129	0.250	0.197	0.188	0.098	0.478	0.426
Red-fronted Tinkerbird	0	0	0.010	0.022	0	0	0	0	0	0	0.010	0.022	0.009	0.021	0	0
Rufous-breasted Wryneck	0	0	0	0	0	0	0	0	0	0	0	0	0.009	0.021	0	0
Rufous-eared Warbler	0	0	0	0	0.005	0.010	0	0	0	0	0	0	0	0	0	0
Rufous-naped Lark	0	0	0	0	0.014	0.031	0	0	0	0	0	0	0.016	0.035	0	0
Sombre Greenbul	0.431	0.420	0.379	0.242	0	0	0	0	0.364	0.377	0.365	0.220	0.211	0.289	0.089	0.151
Southern Black Tit	0.006	0.014	0.023	0.042	0	0	0	0	0.019	0.042	0.023	0.042	0.026	0.059	0.053	0.076
Southern Boubou	0.178	0.123	0.157	0.182	0	0	0	0	0.165	0.116	0.154	0.183	0.088	0.056	0.171	0.256
Southern Double-collared Sunbird	0	0	0.024	0.054	0	0	0	0	0	0	0.020	0.046	0	0	0	0
Southern Grey-headed Sparrow	0.060	0.100	0.034	0.076	0	0	0	0	0.050	0.095	0.034	0.076	0.023	0.033	0	0
Southern Tchagra	0.031	0.069	0	0	0	0	0	0	0.022	0.041	0.003	0.008	0.011	0.024	0	0
Speckled Mousebird	0.180	0.198	0.097	0.117	0	0	0	0	0.160	0.164	0.098	0.120	0.099	0.094	0.173	0.274
Streaky-headed Seedeater	0.050	0.032	0.130	0.124	0	0	0	0	0.053	0.009	0.129	0.125	0.020	0.028	0.091	0.132
Tawny-flanked Prinia	0	0	0	0	0.005	0.010	0	0	0	0	0	0	0.005	0.010	0	0
Weaver	0.072	0.068	0.225	0.160	0	0	0	0	0.109	0.136	0.223	0.161	0.033	0.057	0.077	0.171
White-browed Scrub-Robin	0.143	0.221	0.074	0.072	0	0	0	0	0.150	0.232	0.073	0.073	0.066	0.094	0.051	0.091
Yellow-breasted Apalis	0.062	0.139	0.056	0.083	0	0	0	0	0.066	0.147	0.059	0.080	0	0	0	0
Yellow-fronted Canary	0.088	0.093	0.054	0.078	0.036	0.080	0.072	0.161	0.062	0.067	0.051	0.076	0.076	0.095	0.078	0.175
Total birds/hectare	5.13	0.08	4.32	0.07	1.53	0.04	4.50	0.12	5.25	0.09	4.32	0.07	4.25	0.08	5.51	0.12

Appendix III: The family, common and scientific name (including authority) of all bird species recorded using the point transect method during this study.

Family	**Common Name**	**Scientific name**
Charadriidae	Crowned Lapwing	*Vanellus coronatus*, Boddaert
Columbidae	African Olive-Pigeon	*Columba arquatrix*, Temminck
	Cape Turtle-Dove	*Streptopelia capicola*, Sundevall
	Emerald-spotted Wood-Dove	*Turtur chalcospilos*, Wagler
	Red-eyed Dove	*Streptopelia semitorquata*, Rüppell
Cuculidae	Burchell's Coucal	*Centropus burchellii*, Hemprich and Ehrenberg
Coliidae	Red-faced Mousebird	*Urocolius indicus*, Latham
	Speckled Mousebird	*Colius striatus*, Gmelin
Halcyonidae	Brown-hooded Kingfisher	*Halcyon albiventris*, Scopoli
Upupidae	African Hoopoe	*Upupa africana*, Linnaeus
Phoeniculidae	Green Wood-Hoopoe	*Phoeniculus purpureus*, Miller
Buceropitidae	Crowned Hornbill	*Tockus alboterminatus*, Büttikofer
Capitonidae	Acacia Pied Barbet	*Tricholaema leucomelas*, Boddaert
	Black-collared Barbet	*Lybius torquatus*, Dumont
	Red-fronted Tinkerbird	*Pogoniulus bilineatus*, Dumont
Picadae	Cardinal Woodpecker	*Dendropicos fuscescens*, Vieillot
Jyngidae	Rufous-breasted Wryneck	*Jynx ruficollis*, Wagler
Alaudidae	Cape Clapper Lark	*Mirafra apiata*, Vieillot
	Rufous-naped Lark	*Mirafra africana*, Smith
Dicruridae	Fork-tailed Drongo	*Dicrurus adsimilis*, Bechstein
Oriolidae	Black-headed Oriole	*Oriolus larvatus*, Lichtenstein
Paridae	Southern Black Tit	*Parus niger*, Vieillot
Pycnonotidae	Dark-capped Bulbul	*Pycnonotus tricolour*, Desfontaines
	Sombre Greenbul	*Andropadus importunes*, Vieillot
Muscicapidae	Ant-eating Chat	*Myrmecocichla formicivora*, Vieillot
	Cape Robin-Chat	*Cossypha caffra*, Linnaeus
	Familiar Chat	*Cercomela familiaris*, Stephens
	Fiscal Flycatcher	*Sigelus silens*, Shaw
	Karoo Scrub-Robin	*Cercotrichas coryphoeus*, Lesson
	Olive Thrush	*Turdus olivaceus*, Linnaeus
	White-browed Scrub-Robin	*Erythropygia leucophrys*, Vieillot
Sylviidae	Chestnut-vented Titbabbler	*Parisoma subcaeruleum*, Vieillot
	Long-billed Crombec	*Sylvietta rufescens*, Vieillot
Cisticolidae	Bar-throated Apalis	*Apalis thoracica*, Shaw and Nodder
	Green-backed Camaroptera	*Camaroptera brachyuran*, Vieillot

	Grey-backed Cisticola	*Cisticola subruficapilla*, Smith
	Karoo Prinia	*Prinia maculosa*, Boddaert
	Neddicky	*Cisticola fulvicapilla*, Vieillot
	Rufous-eared Warbler	*Malcorus pectoralis*, Smith
	Tawny-flanked Prinia	*Prinia subflava*, Gmelin
	Yellow-breasted Apalis	*Apalis flavida*, Strickland
Motacillidae	African Pipit	*Anthus cinnamomeus*, Gmelin
	Cape Longclaw	*Macronyx capensis*, Linnaeus
	Cape Wagtail	*Motacilla capensis*, Linnaeus
Laniidae	Common Fiscal	*Lanius collaris*, Linnaeus
	Red-backed Shrike	*Lanius collurio*, Linnaeus
Malaconotidae	Black-crowned Tchagra	*Tchagra senegalus*, Linnaeus
	Bokmakierie	*Telophorus zeylonus*, Linnaeus
	Chinspot Batis	*Batis molitor*, Hahn and Küster
	Southern Boubou	*Laniarius ferrugineus*, Gmelin
	Southern Tchagra	*Tchagra tchagra*, Vieillot
Sturnidae	Cape Glossy Starling	*Lamprotornis nitens*, Linnaeus
Promeropidae	Cape Sugarbird	*Promerops cafer*, Linnaeus
Nectariniidae	Amethyst Sunbird	*Chalcomitra amethystine*, Shaw
	Greater Double-collared Sunbird	*Cinnyris afer*, Linnaeus
	Malachite Sunbird	*Nectarinia famosa*, Linnaeus
	Southern Double-collared Sunbird	*Cinnyris chalybeus*, Linnaeus
Zosteropidae	Cape White-eye	*Zosterops capensis*, Swainson
Ploceidae	Cape Sparrow	*Passer melanurus*, Statius Müller
	Southern Grey-headed Sparrow	*Passer diffuses*, Vieillot
	Weaver	*Ploceus* spp.
Estrildidae	African Firefinch	*Lagonosticta rubricata*, Linnaeus
	Common Waxbill	*Estrilda astrilda*, Linnaeus
Fringillidae	Cape Bunting	*Emberiza capensis*, Linnaeus
	Streaky-headed Seedeater	*Serinus gularis*, Smith
	Yellow-fronted Canary	*Serinus mozambicus*, Statius Müller

Appendix IV: The 96 studies concerning elephant impact that were reviewed in this study. The author(s), year of publication, the overall impact of elephants as reported by the authors, whether a control site(s) was employed and the biological variable(s) that was assessed in the study are shown. Studies were only included if they had been published in peer-reviewed journals. Review papers were excluded as they were interpretations of previously published data and often included unpublished (un-refereed) data. Ecosystem = any ecosystem process e.g. soil chemistry; and Plants = woody plant and grass communities.

	Authors	**Year**	**Overall impact**	**Control**	**Ecosystem**	**Plants**	**Mammals**	**Birds**	**Insects**
1	Beuchner & Dawkins	1961	Negative	No	0	1	0	0	0
2	Agnew	1968	Neutral	No	0	1	0	0	0
3	Van Wyk & Fairall	1969	Neutral	No	0	1	0	0	0
4	Field	1971	Negative	No	0	1	1	0	0
5	Spinage & Guinness	1971	Neutral	No	0	1	0	0	0
6	Henshaw	1972	Negative	No	0	0	1	0	0
7	Douglas-Hamilton	1973	Neutral	No	0	1	0	0	0
8	Vesey-Fitzgerald	1973	Neutral	No	0	1	0	0	0
9	Anderson & Walker	1974	Negative	No	0	1	0	0	0
10	Croze	1974	Neutral	No	0	1	0	0	0
11	Lamprey *et al.*	1974	Positive	Yes	0	1	0	0	0
12	Penzhorn *et al.*	1974	Negative	Yes	0	1	0	0	0
13	Poche	1974	Negative	No	0	1	0	0	0
14	Thomson	1975	Negative	No	0	1	0	0	0

15	Field & Ross	1976	Negative	No	0	1	0	0	0
16	Leuthold	1977	Neutral	No	0	1	0	0	0
17	Lock	1977	Neutral	No	0	1	0	0	0
18	Coetzee *et al.*	1979	Neutral	No	0	1	0	0	0
19	Barnes	1980	Negative	No	0	1	0	0	0
20	Eltringham	1980	Neutral	No	0	1	0	0	0
21	Guy	1981	Neutral	No	0	1	0	0	0
22	Mwaloyosi	1981	Neutral	No	0	1	0	0	0
23	Yoaciel	1981	Negative	No	0	1	0	0	0
24	Barnes	1983	Negative	No	0	1	0	0	0
25	Pellew	1983	Negative	No	0	1	0	0	0
26	Hatton & Smart	1984	Neutral	Yes	1	1	0	0	0
27	Barnes	1985	Negative	No	0	1	0	0	0
28	Jachmann & Bell	1985	Neutral	No	0	1	0	0	0
29	Lock	1985	Neutral	No	0	1	0	0	0
30	Smart *et al.*	1985	Neutral	Yes	0	1	0	0	0
31	Weyerhaeuser	1985	Negative	No	0	1	0	0	0
32	Okula & Sise	1986	Neutral	No	0	1	0	0	0
33	Swanepoel & Swanepoel	1986	Negative	No	0	1	0	0	0
34	McShane	1987	Neutral	No	0	1	0	0	0
35	Edroma	1989	Neutral	Yes	0	1	0	0	0
36	Dublin *et al.*	1990	Neutral	No	0	1	0	0	0
37	Mwaloyosi	1990	Neutral	No	0	1	0	0	0
38	Ruess & Halter	1990	Negative	No	0	1	0	0	0

39	Jachmann & Croes	1991	Negative	No	0	1	0	0	0
40	Lewis	1991	Neutral	No	0	1	0	0	0
41	Midgley & Joubert	1991	Negative	Yes	0	1	0	0	0
42	Novellie *et al.*	1991	Neutral	Yes	0	1	0	0	0
43	Stuart-Hill	1992	Neutral	Yes	0	1	0	0	0
44	Ben-Shahar	1993	Neutral	No	0	1	0	0	0
45	Lock	1993	Neutral	No	0	1	0	0	0
46	Plumptre	1993	Negative	No	0	1	0	0	0
47	Swanepoel	1993	Negative	No	0	1	0	0	0
48	Barnes *et al.*	1994	Neutral	No	0	1	0	0	0
49	Moolman & Cowling	1994	Neutral	Yes	0	1	0	0	0
50	Ruggiero & Fay	1994	Neutral	Yes	1	0	1	0	0
51	Herremans	1995	Neutral	No	0	0	0	1	0
52	Hoft & Hoft	1995	Negative	No	0	1	0	0	0
53	Tchamba	1995	Neutral	No	0	1	0	0	0
54	Ben-Shahar	1996	Neutral	No	0	1	0	0	0
55	Ben-Shahar	1996	Neutral	No	0	1	0	0	0
56	Leuthold	1996	Positive	No	0	1	0	0	0
57	Bowland & Yeaton	1997	Neutral	Yes	0	1	0	0	0
58	Cumming *et al.*	1997	Neutral	Yes	0	1	1	1	1
59	Musgrave & Compton	1997	Neutral	Yes	0	0	0	0	1
60	Fenton *et al.*	1998	Neutral	Yes	0	0	1	0	1
61	Keesing	1998	Neutral	Yes	0	0	1	0	0
62	Trollope *et al.*	1998	Neutral	Yes	0	1	0	0	0

63	Hiscocks	1999	Neutral	No	0	1	0	0	0
64	Van de Vijver *et al.*	1999	Neutral	No	0	1	0	0	0
65	Styles & Skinner	2000	Neutral	No	0	1	0	0	0
66	Barnes	2001	Neutral	No	0	1	0	0	0
67	Steyn & Stalmans	2001	Negative	No	0	1	0	0	0
68	Birkett	2002	Negative	Yes	0	1	0	0	0
69	Botha *et al.*	2002	Negative	Yes	0	1	0	0	0
70	Brits *et al.*	2002	Negative	No	0	1	0	0	0
71	Duffy *et al.*	2002	Negative	No	0	1	0	0	0
72	Gadd	2002	Negative	No	0	1	0	0	0
73	Jacobs & Biggs	2002	Negative	No	0	1	0	0	0
74	Mapaure & Campbell	2002	Negative	No	0	1	0	0	0
75	Mosugelo *et al.*	2002	Neutral	No	0	1	0	0	0
76	Shaw *et al.*	2002	Neutral	Yes	0	1	0	0	0
77	Goheen *et al.*	2004	Positive	Yes	0	1	0	0	0
78	Loveridge & Moe	2004	Neutral	Yes	0	1	0	0	0
79	Richardson-Kageler	2004	Neutral	Yes	0	1	0	0	0
80	Skarpe *et al.*	2004	Neutral	Yes	1	1	1	0	0
81	Western & Maitumo	2004	Negative	Yes	0	1	0	0	0
82	Wiseman *et al.*	2004	Neutral	No	0	1	0	0	0
83	Botes *et al.*	2006	Neutral	Yes	0	0	0	0	1
84	De Beer *et al.*	2006	Negative	No	0	1	0	0	0
85	Lawes & Chapman	2006	Negative	Yes	0	1	0	0	0
86	Makhabu & Skarpe	2006	Neutral	No	0	1	1	0	0

87	Makhabu *et al.*	2006	Neutral	Yes	0	1	0	0	0
88	Mtui & Owen-Smith	2006	Neutral	Yes	0	1	0	0	0
89	Bonnington *et al.*	2007	Positive	Yes	0	0	0	0	1
90	Dipotso *et al.*	2007	Neutral	No	0	0	1	0	0
91	Hemborg & Bond	2007	Negative	No	0	1	0	0	0
92	Edkins *et al.*	2007	Negative	Yes	0	1	0	0	0
93	Goheen *et al.*	2007	Negative	Yes	0	1	0	0	0
94	Guldemond & Van Aarde	2007	Neutral	Yes	0	1	0	0	0
95	Morgan	2007	Neutral	No	0	1	0	0	0
96	Riginos & Young	2007	Positive	Yes	0	1	0	0	0
	Total				**3**	**87**	**9**	**2**	**5**