Chapter 1. General Introduction

Wildlife population management is often a central component of both theoretical and applied ecological research. Ecologists are confronted with problems of augmenting small, isolated populations (e.g. Hedrick and Fredrickson 2010; Meretsky et al. 2000) and of reducing large populations that are damaging their resource base (e.g. Fortin et al. 2005; McCullough et al. 1997). With African savannah elephants (*Loxodonta africana*), both of these problems occur; populations that are exposed to poaching can quickly become diminished (Barnes 1999; Barnes and Kapela 1991; Ntumi et al. 2009); whereas, those in protected parks that are given supplemental water can boom and alter woodland structure (Asner et al. 2012; Dunham 1988; Skarpe et al. 2004). Managing elephant population demography then becomes costly and time consuming for managers and can place stress on the animals through culling, relocation, and immunocontraception (i.e. Kerley and Shrader 2007; Pimm and van Aarde 2001; van Aarde et al. 2006).

To alleviate some of these management issues, the idea of managing elephants as a metapopulation was first introduced by van Aarde and Jackson (2007). The metapopulation theory was first developed for small, discrete, and isolated populations (Hanski 2004), but has since grown into a potential management scheme to regulate populations and maintain connectivity. For large mammals, the metapopulation concept relies on having discrete local breeding populations with asynchrony in demography and dispersal between populations (Driscoll 2007; Olivier et al. 2009). Source populations supplement the mortality in sink areas, resulting in a net stable population (Pulliam 1988; van Aarde and Jackson 2007). Managing large mammals in this manner is rare due to their large spatial requirements (Olivier et al. 2009), but in southern

Africa, the spatial location of parks and the large roaming distances of elephants make this idea feasible (van Aarde and Jackson 2007). However, Armstrong (2005) noted that managing wildlife populations based on metapopulation theory alone could result in a failure to identify positive management strategies and potentially make erroneous management recommendations. For instance, ignoring the quality of habitat patches might cause patches of poor quality to be incorrectly included in the metapopulation network (Armstrong 2005; Battin 2004). Armstrong (2005) therefore recommends a metapopulation concept be integrated with a habitat-based approach, to ensure appropriate management of species across broad spatial scales.

Integrating the metapopulation concept with a habitat-based approach first requires a basic understanding of habitat utilization by elephants. While much research has been done to describe the resource requirements of elephants, these studies have generally focused on selection at a single location (e.g. de Knegt et al. 2011; Vanleeuwe 2010) or for a single habitat feature (e.g. Loarie et al. 2009; Smit and Ferreira 2010; Young et al. 2009). However elephants are habitat generalists, whose wide ecological tolerances make them well suited to survive in a variety of habitat conditions. Across southern Africa, elephants occur in the deserts of northern Namibia to the mesic forests of Mozambique (van Aarde et al. 2008). Under these varying conditions, habitat selection is expected to change as a function of local resource availability. Selection for water, for example, may be an important predictor of elephant habitat selection in arid environments or in the dry season when water is limited, but as water increases on the landscape, it may become a poor predictor of habitat selection patterns. When habitat selection changes as a function of the availability of a resource, this is known as a functional response (Boyce and McDonald 1999; Mysterud and Ims 1998). While functional responses in habitat selection can be a hindrance to the applicability of these models at the local scale, they provide insights into limiting and key resources at large spatial scales when selection is examined across a gradient of resource availabilities (Boyce and McDonald 1999; Gillies et al. 2006; McLoughlin et al. 2010). Using the information gained from habitat selection estimations, habitats can then serve as a foundation to answer a variety of ecological questions pertaining to the feasibility of the metapopulation concept for elephants across southern Africa.

A key criterion for the existence of a metapopulation is dispersal between sub-populations (Driscoll 2007; Olivier et al. 2009). Yet dispersal is often difficult to quantify for wildlife, largely because long-distance dispersal events are rare (Hoffman et al. 2006; Sutherland et al. 2000). Generally only a few individuals within a population carry telemetry collars, further decreasing the odds of observation. Yet using information gained for habitat selection models, we can identify areas of potential connectivity based on habitat requirements. If, for example, we know that elephants need to be close to water and far from people, we can use this information to create a probabilistic model of habitat use, called a resource selection function (Manly et al. 2002). This probability surface can then be used to analyzed landscape connectivity to identify the path of least resistance between two inhabited areas using least cost path analysis (Chetkiewicz and Boyce 2009) or, going further, to identify the permeability of habitats across the entire study area using circuit theory (McRae et al. 2008). Habitats then become the foundation for connectivity in a spatially-structured metapopulation, identifying important corridors or barriers to dispersal. Areas of high connectivity can be given priority for future research, and considerations can be made to manage these areas collectively.

While habitat selection is an important predictor of elephant distribution across the landscape, mortality also plays a vital role in both the habitat and metapopulation concepts. Habitat selection alone does not yield increased survival and fitness. If the habitat is an ecological trap, for example, animals may be attracted to a habitat which ultimately increases their mortality risk (Battin 2004). Invariably, habitat selection studies try to identify high-quality habitats; those that are used by the species, enhance their lifetime survival and recruitment, contribute to demographic performance, and incur limited mortality risk. However, habitat selection studies often fall short on all but the first objective, unless critical life history parameters are also incorporated (Nielsen et al. 2006). This integration is necessary in linking the habitat-based approach to a second criterion of metapopulations, asynchronous population dynamics. Heterogeneity in habitat quality and mortality risk across the landscape creates population sources (high use, low mortality), sinks (high use, high mortality), and non-habitat (low use). The interplay between these habitat classes is ultimately what leads to population stability in a metapopulation. While this asynchrony in dynamics has been observed in elephant populations in different parks and protected areas (Olivier 2009), the next step is to link these demographic observations to the habitat components that regulate population processes. Then, habitat heterogeneity becomes a central component promoting net stable population growth within a metapopulation.

Using a habitat-based approach, critical assumptions of the metapopulation theory can be tested, but in reality the landscape is also inhabited by humans. For many large mammal species, including elephants, humans play an integral role in species distribution (Morrison et al. 2007), and our tolerance or intolerance of a species ultimately plays a large role in species persistence (Woodroffe 2000; Woodroffe et al. 2005). Humans contribute to direct changes in habitat suitability (Hoffman and O'Riain 2012), fragmentation (Crooks 2002), mortality (Nielsen et al. 2004), and indirect changes in animal behaviour (Harju et al. 2011). Humans and wildlife may also be in direct competition for resources or for space, which could result in increased human-wildlife conflict. These cumulative pressures imposed by humans will likely play an integral role in the success or failure of the metapopulation concept for elephants in southern Africa. Understanding how human distribution on the landscape influences elephant habitat use and mortality is necessary to insure effective elephant management, particularly if human populations continue to increase.

Management of any wildlife species is ultimately complex and requires inputs from a variety of information sources. In the past, managers often relied on expert opinion and common sense to design population targets and conservation plans, but as our knowledge of wildlife systems increase, these methods are proving insufficient. Worldwide, wildlife is encountering threats from many sides; habitats are being fragmented, human populations are increasing, and global climate change is creating unknown future environments. Consequently, ecologists are increasingly using advanced modelling techniques to inform management actions. This thesis attempts to inform one such management plan for elephants.

In this study, I will use habitat selection theory to test the feasibility of managing elephants as a spatially-structured metapopulation in southern Africa. Following this general introduction, chapters in this thesis are organized into independent papers, two of which have been published (Chapter 2 and 3). I begin by describing elephant habitat selection across southern African and examine functional response to resource availability (Chapter 2). I use these models as a foundation to next examine connectivity between elephant populations (Chapter 3). Mortality also plays a role in the functionality of habitat, so I then examine the habitat associations of elephant mortalities in northern Botswana using elephant carcass data (Chapter 4). Finally, I then explore the consequences of human-elephant competition for resources (Chapter 5). Taken together, this works forms the first steps towards creating a habitat-based management plan for elephants in southern Africa using metapopulation theory.

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