

## INTRODUCTION TO THE DISSERTATION

Documenting how temporal and spatial environmental variability influences demographic parameters such as births, deaths, and movements is critical to understanding and affecting changes in animal populations (Emlen 1984, Ratcliffe et al. 1998, Caswell 2001). Mammalian herbivore populations are affected by ‘top-down’ forces such as predation pressure and ‘bottom-up’ factors like food availability, both of which are subject to natural temporal and spatial variability (Coulson et al. 1997, Coulson et al. 1999, Pettorelli et al. 2003b, 2005, Hopcraft et al. 2010). Spatial variability in demography also can be strongly influenced by anthropogenic factors such as habitat loss, degradation, and fragmentation (Fahrig et al. 2003, Wiegand et al. 2005), and hunting (Nilsen et al. 2003). Natural populations often exhibit variation in demographic parameters, and while the examination of temporal variation has long been a central theme in population ecology (Clutton-Brock et al. 1988, Newton 1989), spatial variation among or within populations of the same species has received much less attention (Fredriksen et al. 2005).

Ungulates (hoofed mammals) are important because they shape and maintain the biodiversity and nutrient cycling of ecosystems where they live by consuming and processing vast amounts of vegetation, thereby sometimes acting as keystone species, and by being important prey for numerous predators and scavengers (Simberloff 1995, DuToit and Cumming 1999, Singer et al. 2003, Dobson 2009). Although the vast majority of the world’s ungulate species live in the tropics and sub-tropics, most studies of ungulate demography have taken place in the temperate zone, often in single populations with little or no predation (Gaillard et al. 2000), and few studies have

investigated the demography of large tropical herbivores (Owen-Smith and Marshall 2010).

The goal of this study was to fill this knowledge gap by examining whether spatial variation in demography of giraffe (*Giraffa camelopardalis*) existed in a fragmented ecosystem, and how key demographic parameters of reproduction, adult and juvenile survival, and movements of a large tropical ungulate were affected by spatio-temporal variation in land use, vegetation, poaching (illegal hunting), and predation. Giraffe are an African icon but are believed to be declining across their range (IUCN 2010). Demographic analyses are needed to understand why the species is in trouble, and how conservationists can best maintain viable populations (Caswell 2001, Sibley and Hone 2002). Giraffe also provided a tropical case study to examine whether findings from temperate ungulate demography studies are broadly applicable to the tropics. Spatial variation is important in heterogeneous ecosystems, such as East African savannas, that contain contrasting management regimes, vegetation patterns, and predation pressure. Temporal variation is also important for this asynchronous breeder as conditions for survival and reproduction may vary significantly among seasons and may be influenced by longer-term climactic fluctuations.

### **Research questions**

My research used data from 1,857 individually identified giraffe in the Tarangire Ecosystem of northern Tanzania, East Africa from 2012–2014 to estimate demographic parameters of population size, probabilities of reproduction, calf survival, adult survival, and movements among sites to confirm and understand the suspected declining regional population trend observed in aerial survey data (Fig. 1; Stoner et al. 2006, 2007,

TAWIRI, *unpublished data*). My research was organized around three questions which were addressed sequentially in Chapters 1, 2, and 3:

**1) How does survival, reproduction, and population growth rate vary among sites? Does spatial variation in land management, giraffe density, lion density, or poaching affect adult survival, calf survival, and reproduction? Do patterns of spatial variation reflect the paradigm of ungulate population dynamics from studies of temporal variation?**

Survival, reproduction, and other demographic traits of a species may be markedly variable among populations and sub-populations inhabiting heterogeneous environments (e.g., Paradis et al. 2000, Frederiksen et al. 2005, Grosbois et al. 2008, 2009, Sanz-Aguilar et al. 2009), but this variation has not been well documented for ungulates. Therefore, obtaining reliable estimates of adult female survival, calf survival, and reproduction at 5 sites was the logical first step for understanding population dynamics of this long-lived ungulate species.

At a landscape scale, demography may be linked to spatial variability in habitat availability or quality, food resources, weather, disease, parasites, predator pressure, human activities, and population density (e.g., Jorgenson et al. 1997, Gaillard et al. 1998, Coulson et al. 1999, Dhondt 2001, Ozgul et al. 2006, Sanz-Aguilar et al. 2009). Therefore, I ranked spatial covariate models seeking mechanisms of any observed spatial variation in survival or reproduction according to land-use designation, giraffe density, lion density, and poaching pressure.

Finally, I tested whether the temporal demographic paradigm of stable and high adult female survival with more variable reproduction and calf survival rates can be

applied to giraffe spatial population dynamics at the regional and continental scale. For large, long-lived animals, adult survival has the highest elasticity and therefore incremental changes in adult survival theoretically have the greatest effect on population growth rate (Lebreton and Clobert 1990, Saether and Bakke 2000, Gaillard et al. 1998, 2000). However, long-term ungulate studies from the temperate zone have found the survival rate of adults, particularly prime-aged females, tends to be high and very stable over time, while juvenile survival and reproduction are much more temporally variable than adult survival, and thus may have greater influence on realized population trends (Gaillard et al. 1998, 2000, Gaillard and Yoccoz 2003).

**2) How does movement link the sub-populations in this fragmented landscape? Does land management, predation, or density explain movement rates? How do differences in demography and movement among sub-populations affect the metapopulation?**

Connectivity, the movement of individuals among sub-populations, is essential to landscape-scale population dynamics (Tischendorf and Fahrig 2000, Lowe and Allendorf 2010), such as source-sink dynamics, or the rescue effect (Brown and Kodric-Brown 1977, Holt 1985, Pulliam 1988). Movement among sub-populations in heterogeneous landscapes is one of the most important, yet least understood, ecological processes related to the persistence of animal populations (Bowler and Benton 2005). I quantified connectivity movements among sub-populations in a large, presumed contiguous population of giraffe by estimating site-specific sub-population sizes, sub-population growth rates, and per-capita movement rates among 5 sites defined by land management designations. I also quantified whether and how sub-population growth rates and per-

capita movement rates differed according to land-use designation, giraffe density, lion density, and poaching pressure. Finally, I assessed the source-sink structure of the study area and examined the implications of sub-population demography and movements for metapopulation dynamics.

**3) How do reproduction and juvenile survival vary by season? Do observed seasonal patterns in reproduction and survival relative to changes in vegetation quality and/or predation pressure fit specific theories of synchronous and asynchronous reproduction?**

The timing and success of reproduction is another important aspect of animal demography and population dynamics. In mammals, the timing of reproduction is primarily determined by protein availability during late gestation and early lactation, the most energetically demanding period for reproductive females (Asdell 1964, Bunnell 1982, Oftedal 1984), but also is influenced by other factors such as predation (Aanes and Anderson 1996). Variation in timing of reproduction and juvenile survival may play prominent roles in life history evolution and population dynamics and are major issues for both evolutionary ecologists and wildlife managers (Sæther 1997, Gaillard et al. 2000, Eberhardt 2002). Variation in juvenile survival often explains a large part of the variance in their parents' lifetime reproductive success (Clutton-Brock et al. 1988), and can be regulated by bottom-up or top-down selective forces (Cote and Festa-Bianchet 2001), but few studies have examined the factors affecting juvenile survival in tropical ungulates.

I determined whether and when pulses in birth synchrony occurred in wild giraffe by examining timing of 408 births during 3 precipitation seasons over 2 years. I also estimated juvenile survival according to birth season to discriminate among 3 hypotheses

for birth synchrony and asynchrony. The relative survival of juveniles born during versus outside any observed birth pulse indicated whether “phenological match,” “predator avoidance,” or “temporal resource partitioning” mediated some level of synchrony or asynchrony in this species.

### **Study system**

The Masai giraffe (*G. c. tippelskirchi*) is the most numerous of 9 giraffe subspecies (Dagg and Foster 1976, Dagg 2014), with the majority residing in Tanzania. Aerial surveys of the country’s major ecosystems have indicated that most Masai giraffe populations may be declining (Fig. 1; Stoner et al. 2006, 2007, TAWIRI *unpublished data*).

The Tarangire Ecosystem (TE) is a savanna-woodland ecosystem and a global hotspot of large-mammal diversity (Bourliere and Hadley 1970, Bolger et al. 2008) that supports the second-highest density of giraffe in Tanzania (Stoner et al. 2006, 2007). Habitat outside the TE’s protected areas has been lost or degraded by agriculture, charcoal making, and other uses (Newmark 2008, Msoffe et al. 2011). Giraffe habitat throughout Africa has become similarly lost and fragmented, thus the TE is representative of much of the remaining landscape for these iconic megaherbivores. Most scientific studies of giraffe populations to date have occurred entirely within protected areas (Foster 1966, Leuthold and Leuthold 1978, Pratt and Anderson 1982, Pellew 1983, Strauss and Packer 2013), but much of the current range of the species lies outside of

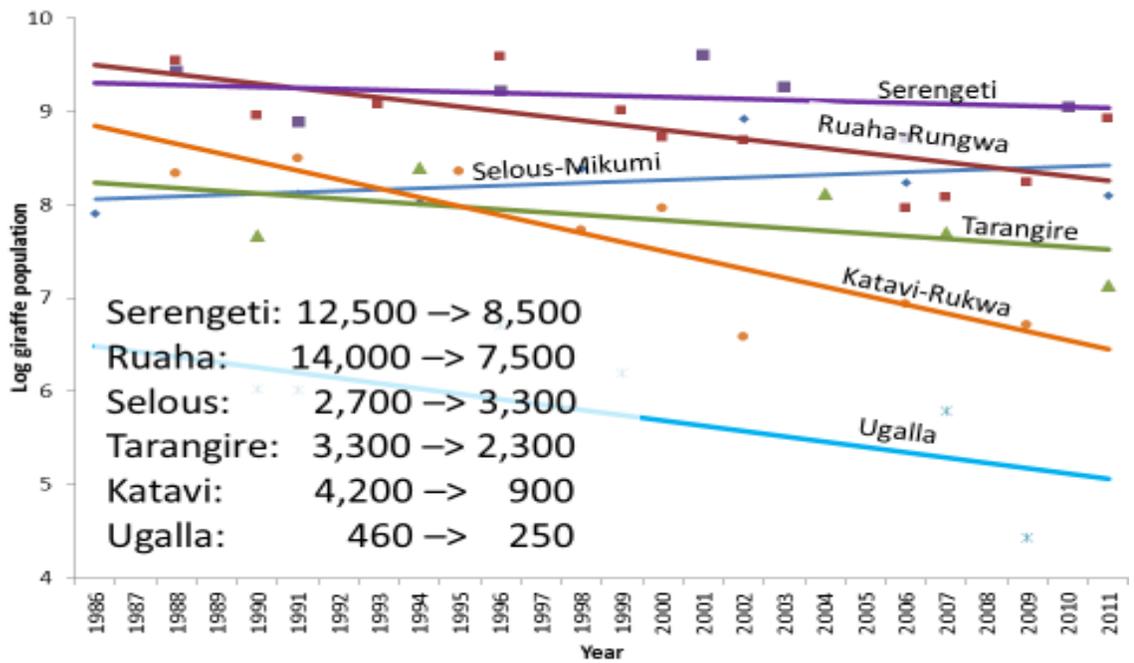


Figure 1. Tanzanian giraffe population estimates (natural log transformed) from aerial survey data in six large ecosystems around the country 1986–2011 (Stoner et al. 2006, 2007, TAWIRI, *unpublished data*). Inset are mean giraffe population estimates from the first and last decades of the time series.

protected areas, and is subject to variation in human land uses. Thus, this study provided important data on how giraffe demography varies across realistic gradients of human land use, poaching, natural predation, and vegetation. The Masai giraffe is the national animal of Tanzania and a highly visible indicator of the health of *Acacia* woodlands, and as such can serve as a flagship species for the conservation of East African savannas.

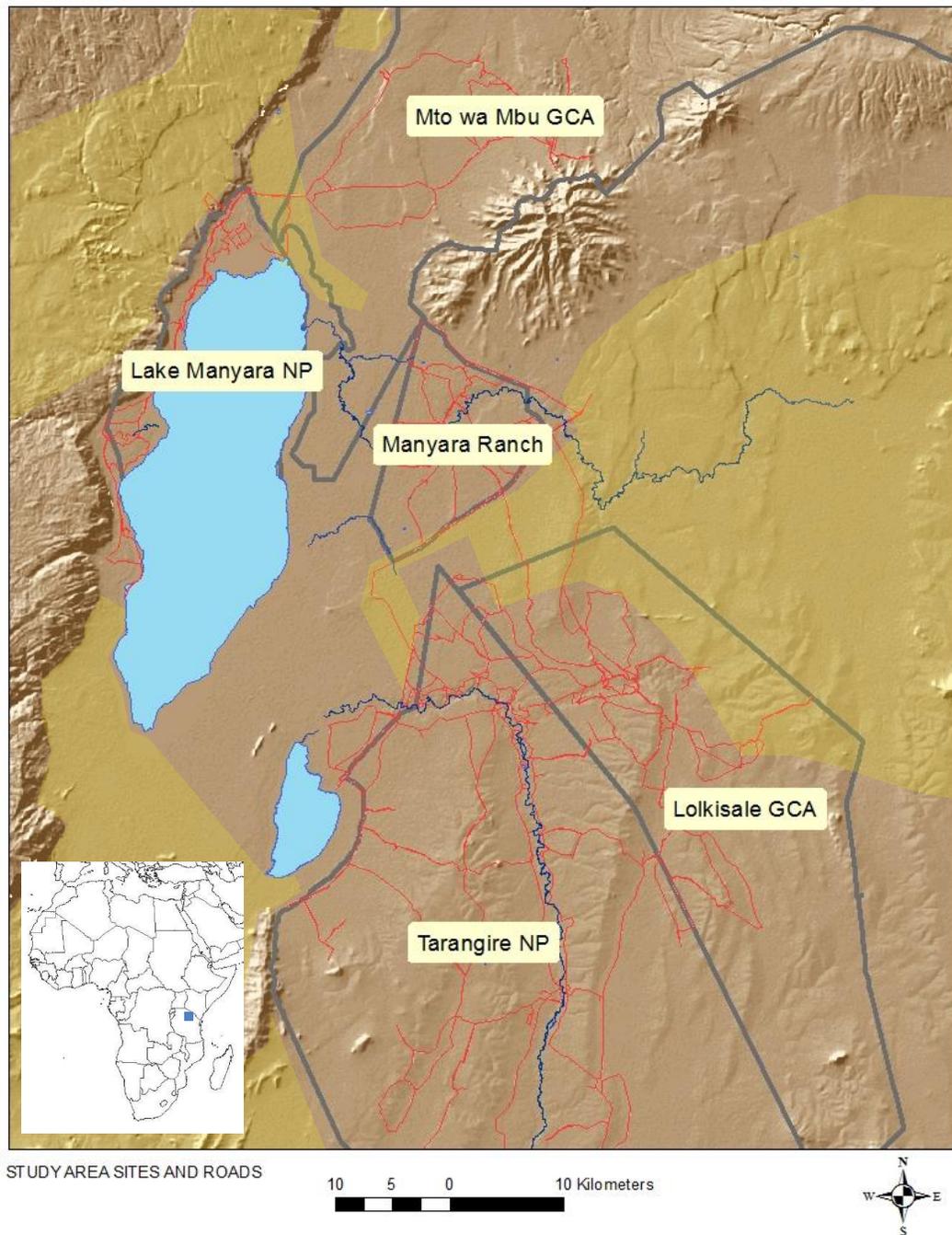


Figure 2. Study area in the Tarangire Ecosystem of northern Tanzania. Grey polygons are the 5 sites sampled, yellow polygons are areas dominated by agriculture, red lines are roads and tracks, blue lines are rivers and watercourses, blue areas are lakes.

The TE is in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km<sup>2</sup> (Borner 1985, Prins 1987). The TE is defined by the migratory ranges of eastern white-bearded wildebeest (*Connochaetes taurinus*) and Burchell's zebra (*Equus quagga*) from their dry-season refuge along the perennial Tarangire River north to Lake Natron, southeast to the Simanjiro plains, and south to the Irangi Hills (Lamprey 1964, Kahurananga and Silkiluwasha 1997, Foley and Faust 2010). Mean total annual rainfall was 650 mm for years 1980–2009, coefficient of variation = 42.6%, range = 312 to 1,398 mm (Foley and Faust 2010, C. Foley *unpublished data*). There are 3 precipitation seasons per year (short rains = Oct–Jan, long rains = Feb–May, and dry season = Jun–Sep). Average monthly precipitation by season was: short rains = 63 mm, long rains = 100 mm, dry = 1 mm (Foley and Faust 2010, C. Foley *unpublished data*).

Our study area in the core of the TE was 4,400 km<sup>2</sup> wherein we sampled a 1,700 km<sup>2</sup> area in 5 geographic sites representing different land-use management regimes (Fig. 2): Tarangire National Park (TNP), Lake Manyara National Park (LMNP), Manyara Ranch Conservancy (MRC), Lolkisale Game Controlled Area (LGCA), and Mtowambu Game Controlled Area (MGCA). Since the 1940s, human population and agricultural development have increased four- to six-fold throughout the TE (Gamassa 1995), causing substantial habitat loss, increasing fragmentation, and reducing connectivity (Newmark 2008, Msoffe et al. 2011). The 2 national parks (Tarangire and Lake Manyara) had strong wildlife protections, anti-poaching efforts, and no legal human encroachment. MRC had livestock grazing and tourism, some human habitation, and anti-poaching patrols. The 2 Game Controlled Areas (Mtowambu and Lolkisale) had agricultural cultivation, pastoralism, and permanent settlement, little or no anti-poaching efforts, and wildlife

harvesting via subsistence and trophy hunting, although hunting of giraffe was legally prohibited (Nelson et al. 2010).

The Rift Valley escarpment formed the western boundary of the study area, because its steep cliff restricts giraffe movements in that direction. The eastern boundary of the study area was a rough line between Makuyuni and Lolkisale towns, and eastward from there large wild mammals were rarely observed due to high human and livestock population density, agriculture, and systematic poaching. Southwest of TNP and south of LMNP were areas of high human population density and intensive agriculture. Two 2-lane asphalt roads crossed the study area.

### **Study species: Giraffe**

Giraffe are large (830–1,000 kg), long-lived, iteroparous, sexually dimorphic, non-migratory, non-territorial, browsing ruminants that eat leaves, twigs, and fruits of *Acacia*, *Balanites*, *Dichrostachis*, and many other species of woody vegetation (Dagg and Foster 1976, Pellew 1984). Their main natural predators are African lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (Dagg and Foster 1976), but giraffe also are targeted by bushmeat poachers. Giraffe have been characterized as asynchronous breeders with a year-round breeding cycle, but in the Serengeti Ecosystem there was some evidence for a small, seasonal birth pulse that coincided with peak protein concentration of new *Acacia* tree leaves during the dry season (Sinclair et al. 2000). Protein is a limiting nutrient for semiarid herbivores, and therefore hypothetically may mediate some degree of reproductive synchrony in giraffe (Bell 1971, Sinclair 1975). Female giraffe attain sexual maturity at ~5 years of age and may breed up to age 20 (Dagg and Foster 1976). Giraffe have a gestation length of  $448 \pm 5$  days (mean  $\pm$  SD),

resume estrous cycling  $103 \pm 46$  days after giving birth (even while still lactating), and cycle  $68 \pm 87$  days before their next pregnancy (del Castillo et al. 2005). Observed birth interval is  $620 \pm 49$  days (Bercovich and Berry 2009), so individual females exhibiting the mean birth interval between sequential births would be out of synchrony with the annual cycle of peak protein in the majority of reproductive attempts. Young typically are weaned at 9 months of age, and are independent at 14 months (Langman 1977).

Giraffe demography has been surprisingly understudied despite their ecological importance, their widespread geographic distribution, and the fact that, as the fourth largest land mammal in Africa, they are actively poached in many areas. Most estimates for giraffe demographic parameters to date have used simple return rates of known animals (Foster and Dagg 1972, Leuthold and Leuthold 1978, Pellew 1983), or ratios of counts (Sinclair and Arcese 1995, Owen-Smith and Mason 2005). We were aware of only one study of giraffe demography that used individually identified animals and modern capture-mark-recapture statistics to estimate population parameters while accounting for imperfect detection probabilities (Strauss 2014), and that study was conducted entirely within a protected national park (Serengeti).

The giraffe population in the TE provided an opportunity to study spatio-temporal factors influencing demography of a tropical ungulate in a fragmented, heterogeneous landscape (Fig. 2) using photographic capture-mark-recapture techniques. Giraffe were numerous in the area, but aerial surveys documented apparent recent population declines, particularly outside protected areas. Giraffe population dynamics may serve as an informative window into savanna ecosystem processes, as the species likely interacts with and responds to many of the factors hypothesized to drive population dynamics seen

in other ungulate species such as changes in vegetation, predators, and poaching.

Furthermore, giraffe provided a tropical, asynchronously breeding case study with which to examine findings from temperate ungulate demography studies.