DEMOGRAPHY OF GIRAFFE IN THE FRAGMENTED TARANGIRE ECOSYSTEM

A Thesis

Submitted to the Faculty

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy
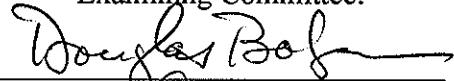
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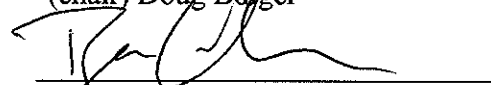
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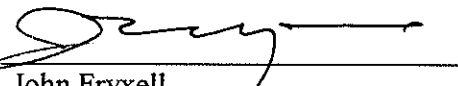15 May 2015

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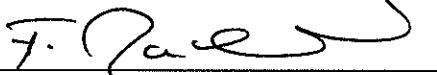Nate Dominy

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ABSTRACT

Documenting whether variation in demographic parameters such as births, deaths, and movements exists, and how temporal and spatial environmental variability influences demography, is critical to understanding and affecting changes in animal populations. Natural populations often exhibit variation in demographic parameters, and while the examination of temporal variation has long been a central theme in population ecology, spatial variation among or within populations of the same species has received much less attention. Although the vast majority of the world's ungulate species live in the tropics and sub-tropics, few studies have investigated the demography of large, tropical herbivores. Giraffe (*Giraffa camelopardalis*) are believed to be declining rapidly, as their habitat throughout Africa has been lost and fragmented, thus the fragmented Tarangire Ecosystem in Tanzania was representative of much of the remaining landscape for these iconic megaherbivores. The goal of this study was to fill this knowledge gap by examining whether spatial variation in demography of giraffe 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 spatial variation in land use, poaching (illegal hunting), and predation. I also assessed the source-sink structure of the study area and examined the implications of sub-population demography and movements for metapopulation dynamics. Finally, I examined temporal seasonal variation in reproduction and calf survival, and whether observed patterns fit specific theories of synchronous and asynchronous reproduction.

My research used data from 1,857 individually identified giraffe at 5 sites within the Tarangire Ecosystem to estimate site-specific population size, probabilities of

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reproduction, calf survival, adult survival, and movements among sites to understand a suspected declining overall population trend. My research was organized around three questions: 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?; 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?; and 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?

I found significant spatial variation in adult female survival, reproduction, movements, and density existed. Only adult female survival was significantly correlated with a spatial covariate (positively correlated with anti-poaching efforts). A matrix population model using site-specific estimates of survival and reproduction showed adult female survival was the highest elasticity parameter, and thus had the greatest proportional effect on population growth rate (*lambda*).

Population growth rate also varied significantly by site, and was best explained by the spatial covariate of distance to Mtowambu, the main bushmeat market town in the area. Population growth rate was ≥ 1.0 (indicating a growing sub-population) only in Tarangire National Park (TNP), but *lambda* at all other sites was less than 1.0 indicating

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decreasing sub-populations. A decreasing metapopulation ($\lambda^M \approx 0.99$) was estimated by two methods of computing the metapopulation growth rate. TNP was identified as the dominant engine of metapopulation growth, but movement of individuals out of TNP and into "attractive sink" sites, where more poaching of adults occurs, is the most likely explanation for the shrinking metapopulation. However, these movements are also responsible for preventing extirpation of giraffe sub-populations in the smaller sites.

I also examined how temporal variation affected calving and calf survival. I found significant seasonal variation in proportion of births, with more births in the short rains and dry seasons relative to the long rains, and calf survival was affected by season of birth in accordance with both the "phenological match" theory of reproductive synchrony and the "temporal resource partitioning" theory of asynchrony. Calf survival also was positively correlated with the seasonal abundance of migratory herds of zebra and wildebeest, the local abundance of which apparently reduced predation pressure on young giraffe.

Based on my results, for conservation of the species and the large-scale processes of giraffe interactions across the landscape, I recommend efforts to disrupt bushmeat markets and expand anti-poaching patrols such as those employed in the Tanzanian national parks, to bring down harvest rates of adult females to sustainable levels, while simultaneously maintaining or improving linkage habitat between all sites to facilitate natural movements. This should increase adult survival to the point where sink sub-populations are less of a drain on the metapopulation, and having multiple linked, healthy sub-populations reduces the risk of total extinction. Additionally, conservation of migratory herds by protecting their calving grounds and migration routes would maintain

their indirect benefit to giraffe calf survival.

Identifying source and sink habitats using the methods described herein is superior to monitoring via abundance or density estimates alone because when managers understand movements, population growth rates, and metapopulation dynamics, they can effectively prioritize actions to ensure the security of sources while addressing the causes of sinks.

PREFACE

It has been a great privilege to work within the Dartmouth community and I am grateful to the many people who contributed to this work and without whom the successful completion of this dissertation would not have been possible. The Ecology and Evolutionary Biology (EEB) faculty, particularly Doug Bolger, Ryan Calsbeek, Nate Dominy, Becky Irwin, Cathy Cottingham, Matt Ayres, and Mark McPeek, along with my external examiner, John Fryxell, provided valuable mentoring, guidance, and feedback. I am also indebted to the incredible staff in Biology and Environmental Studies departments, particularly Kim Wind, Amy Layne, Craig Layne, Paul Zietz, Johnathan Chipman, Nicole Hamilton, Sherry Finnemore, and Mary Poulson. I would like to thank my peers in the EEB program especially Tom Morrison, Mike Logan, Sam Fey, Katie Duryea, Jeff Lombardo, Carissa Aoki, Markus Welker, Tom Kraft and all the rest.

I had the immense pleasure to work in wildlife-rich and incredibly friendly Tanzania where I thank Robert and Niseta Godson, Bernard and Ifura Kissui, Peter Parkepu, Seleivu Meijo, Charles and Lara Foley, John Salehe, Francis Ole Kashe, Sandy Evans, Andrea Athanas and Stefan DelRossi, Julian and Ana Maria Guerrero, Julien Polet, Alvaro Peña, Ethan and Gina Kinsey, Thad Peterson, Krissie Clark, Wayne Lotter, Christian Kiffner, Robert Lawrence, Gasto Rafael, Ramathan Ahmed, and the indefatigable Dassa at the CRC.

This research was carried out with permission from the Tanzania Commission for Science and Technology, Tanzania National Parks (TANAPA), the Tanzania Wildlife Research Institute (TAWIRI), African Wildlife Foundation, Manyara Ranch Conservancy, and the villages of Selela, Lolkisale, and Emboret, under COSTECH

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Coefficient of Variation	CV
Game Controlled Area	GCA
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Lake Manyara National Park	LMNP
Lifetime Reproductive Success	LRS
Lolkisale Game Controlled Area	LGCA
Manyara Ranch Conservancy	MRC
Mtowambu Game Controlled Area	MGCA
National Park	NP
Photographic Capture-Mark-Recapture	PCMR
Tanzania National Parks	TANAPA
Tarangire Ecosystem	TE
Tarangire National Park	TNP

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

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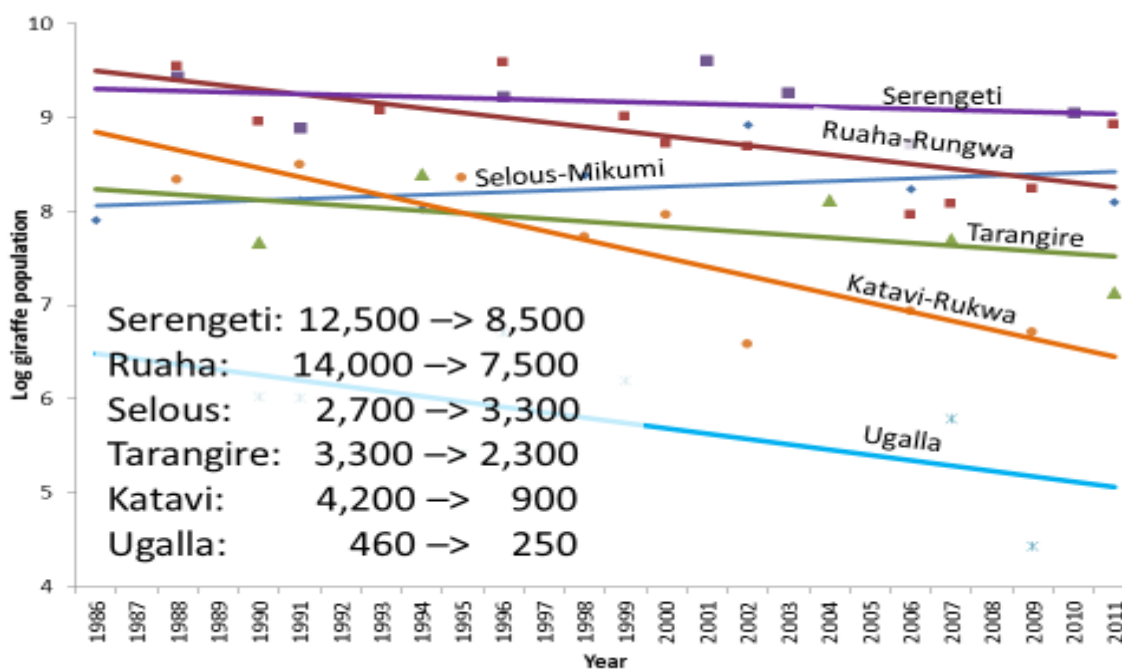
Figure 1. Tanzanian giraffe population estimates (natural log transformed) from
aerial survey data in six large ecosystems around the country 1986–2011 (Stoner et
al. 2006, 2007, TAWIRI, *unpublished data*). Inset are mean giraffe population
estimates from the first and last decades of the time series.

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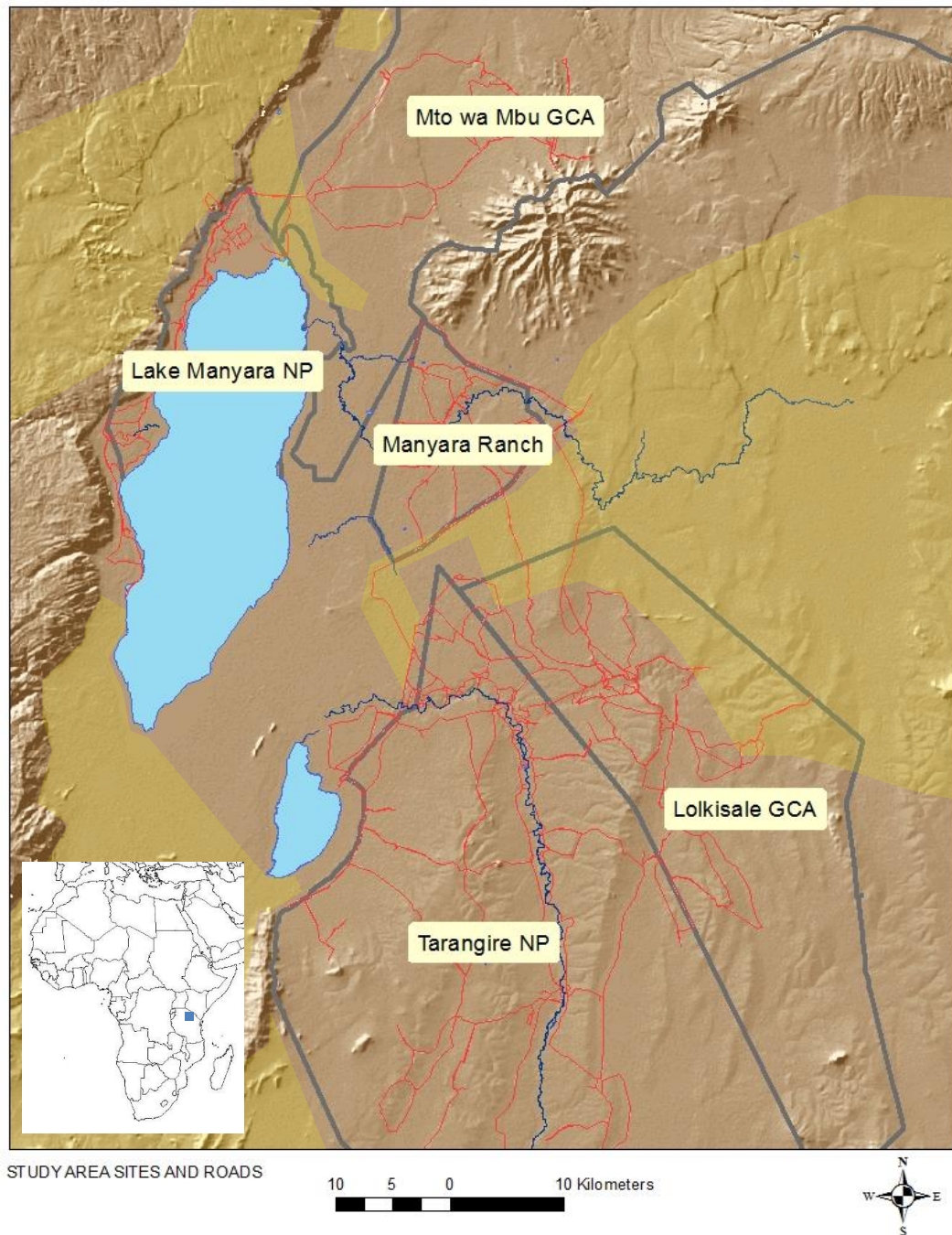
Figure 2. Study area in the Tarangire Ecosystem of northern Tanzania. Grey polygons are the 5 sites sampled, yellow polygons are areas dominated by agriculture, red lines are roads and tracks, blue lines are rivers and watercourses, blue areas are lakes.

The TE is in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km^2 (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^2 wherein we sampled a 1,700 km^2 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 ± 5 days (mean ± SD),

resume estrous cycling 103 ± 46 days after giving birth (even while still lactating), and cycle 68 ± 87 days before their next pregnancy (del Castillo et al. 2005). Observed birth interval is 620 ± 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.

CHAPTER 1.

SPATIAL VARIATION IN GIRAFFE ADULT SURVIVAL, CALF SURVIVAL, AND REPRODUCTION

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). 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.

Across the geographical range of a species, spatial variation is likely to reflect differential climatic conditions (Frederiksen et al. 2005, Grosbois et al. 2008). 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). To more fully understand population dynamics of a given species, demographic parameters for different populations or sub-populations in a large area should be explored and if significant differences are detected, a mechanistic cause should be sought (Bennett and Owens 2002, Kauffman et al. 2004, Frederiksen et al. 2005).

In long-lived animals, elasticities from population models show that population growth rate is most sensitive to changes in adult female survival (e.g., Lebreton and

Clobert 1990, Saether and Bakke 2000, Gaillard et al. 1998, 2000). However, several long-term studies of ungulates have found that because temporal variation in adult survival is low, variability in reproduction and calf survival are typically the most important determinants of observed temporal variation in population growth rates (Eberhardt 1977, 2002, Gaillard 2000). Therefore, obtaining reliable estimates of adult female survival, calf survival, and reproduction is a logical first step for understanding population dynamics of any long-lived ungulate species.

In this study, we tested whether the paradigm of ungulate population dynamics from temporal studies—stable and high adult female survival with highly variable reproduction and calf survival rates—also can be applied to spatial population dynamics. Specifically, we investigated the patterns and mechanisms of spatial demographic structure for Masai giraffe (*Giraffa camelopardalis tippelskirchi*), at 5 sites in the Tarangire region of northern Tanzania, East Africa. We quantified whether reproduction, calf survival, and adult survival probabilities varied among sites, and whether spatial variation in demographic parameters was correlated with spatial differences in land management, giraffe density, lion predation, or poaching. We used our site-specific estimates to parameterize Leslie matrix population models and calculate each site's rate of population growth, λ (Caswell 2001). We also examined variability of demographic rates from across the species' range, and whether that variability at the continental scale supported the temporal paradigm of ungulate population dynamics.

Methods

This study used data from 1,857 individually identified, wild, free-ranging giraffe in a system with nearly the full suite of natural predators and sympatric ungulate species

across a 1,700 km^2 sampled area. We examined spatial variation in density, survival, and reproduction among 5 sites (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). The 5 sites were subject to 3 different management regimes: 2 sites were national parks with stricter enforcement of anti-poaching laws and no permanent settlements, 1 site was a private ranch/wildlife conservancy with some anti-poaching activity and a moderate density of pastoralists and livestock but no permanent settlements, and 2 sites were Game Controlled Areas with few anti-poaching activities, high density of pastoralists and livestock, agriculture and permanent human settlements, and wildlife harvesting via subsistence and trophy hunting, although hunting of giraffe was legally prohibited (Borner 1985, Yanda and Mohamed 1990, Mwalyosi 1991, Gamassa 1995, TCP 1998, Nelson et al. 2010). The sites also differed along several axes: 1) giraffe density, 2) poaching intensity, and 3) lion density.

SAMPLING

We collected data during systematic road transect sampling for photographic capture-mark-recapture (PCMR; Bolger et al. 2012, Morrison and Bolger 2012). We conducted 14 daytime surveys for giraffe PCMR data between Jan 2012 and Feb 2014. We sampled giraffe 3 times per year near the end of every precipitation season (dry, short rains, long rains; see Fig 3A) by driving a network of fixed-route road transects in the study area (Fig 3B). We surveyed according to a robust design sampling framework
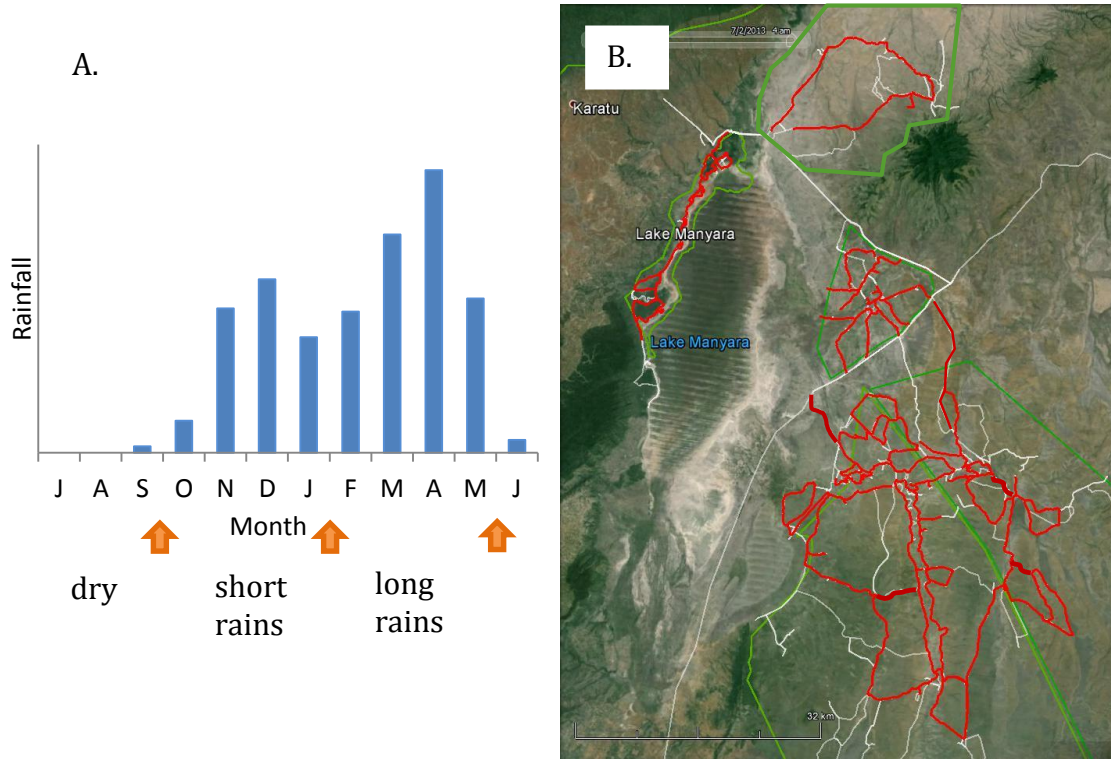
Figure 3. A. sampling occasions (orange arrows) relative to monthly rainfall and precipitation seasons. B. fixed-route road transects (red lines) driven during every sampling event. Rainfall data from Foley and Faust (2010) and C. Foley (*unpublished data*).

(Pollock 1982, Kendall et al. 1995, Kendall and Bjorkland 2001) with 3 occasions per year wherein each sampling occasion was composed of 2 sampling events (see Fig. 4) during which we surveyed all road transects in the study area (3 occ./yr × 2 events/occ. × 2.3 years = 14 survey events). Road density throughout the study area was high relative to giraffe home-range size (~100 km^2 mean female home range). Driving speed was maintained between 15 and 20 kph on all transects, and all survey teams included 2 dedicated observers and a driver. Each road segment was sampled only 1 time in a given
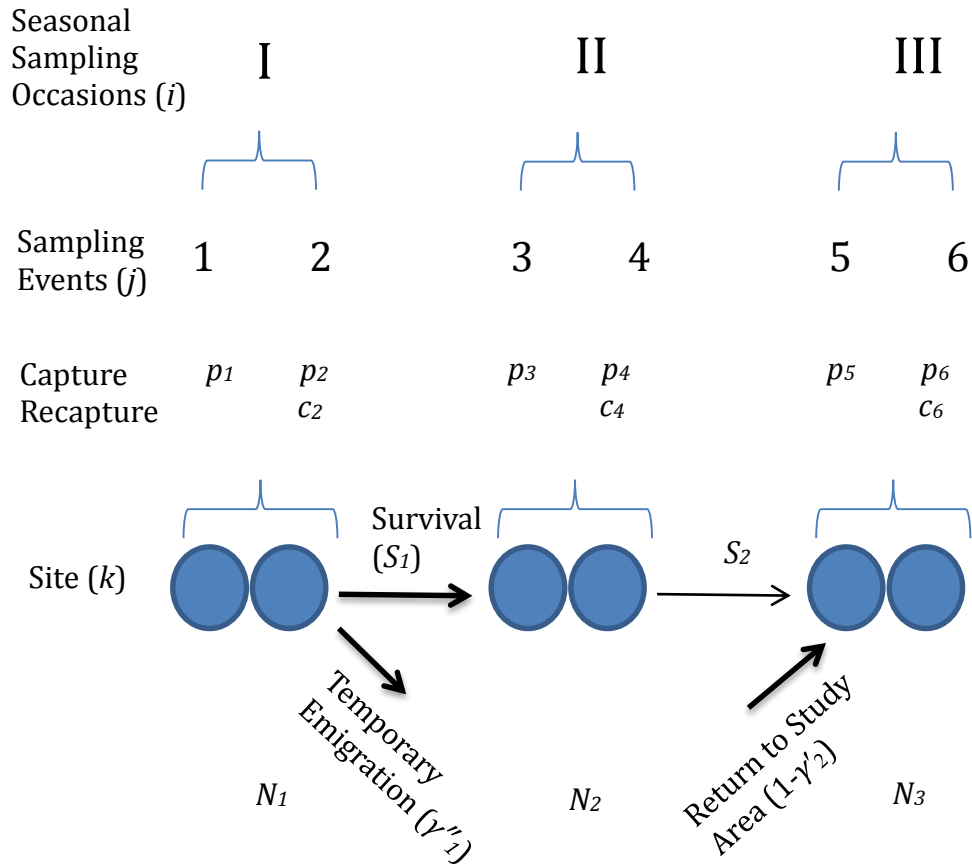
Figure 4. Diagram of Pollock's Robust Design statistical model and associated parameters during one calendar year. Each blue circle represents a sampling event during which all road transects are driven.

event. We systematically shifted the order and direction in which sites and road transects were sampled similar to a Latin Square design to reduce sampling biases.

During PCMR sampling events, the entire study area was surveyed and a sample of individuals were encountered and either "marked" or "recaptured" by slowly approaching and photographing the animal's right side (Canon 40D and Rebel T2i cameras with Canon Ultrasonic IS 100-400 mm lens, Canon U.S.A., Inc., One Canon Park, Melville, New York, 11747). We photographed and later identified individual

giraffe using coat patterns that were unique to each animal and unchanged throughout their lives (Foster 1966). We attempted to photograph every giraffe encountered for individual identification from a distance of approximately 100 m (mean = 90, SD = 39), and recorded sex (male, female), GPS location, and age class. We categorized giraffe into 4 age classes: newborn calf (0–3 months old), older calf (4–11 months old), subadult (1–3 years old), or adult (>3 years for females, >6 years for males) using a suite of physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics, and height (Strauss 2014).

ASSIGNING AGE CLASSES WITH PHOTOGRAMMETRY

Giraffe age classifications were confirmed using photogrammetric measurements of neck length. Photogrammetry, the science of making measurements on photographs (Baker 1960), is now a well-established technique used in a wide range of fields including geology, agriculture, medicine, and mapping (Atkinson 1980), and is a useful, noninvasive method for measuring traits of individual animals (e.g., elephants *Loxondonta africana*, Schrader et al. 2006; gorillas *Gorilla gorilla*, Breuer et al. 2006). For objects oriented parallel with the camera's image sensor, if the focal length of the camera optics and the distance between the camera and the object are known, photographs can be accurately scaled for linear measurements of the object.

For most giraffe we photographed for identification, we measured the distance from the camera to the animal using a laser range finder (Bushnell Scout Arc1000, Bushnell Outdoor Products, 8500 Marshall Drive, Lenexa, Kansas, 66214). Focal length was automatically recorded in the EXIF data stored in every digital photograph. We followed the methods of Shrader et al. (2006) to calibrate our equipment and calculate

formulas for linear photogrammetry measurements. We took 4 digital images (as JPEG files) of a meter stick at 25 meter intervals out to 150 m from the camera. The 4 images were taken with the lens focal length at 100, 200, 300, and 400 mm, respectively. The images comprised 24 different combinations of distance and focal length settings. We downloaded the images onto a personal computer and used GIMP 2.6.11 (GNU Image Manipulation Program, GIMP Development Team, http://www.gimp.org) to count the number of pixels in the length of the meter stick on each of the images. We used simple linear regression analyses to describe the relationship between pixels/m and focal length for each distance to the meter stick. With these functions we computed individuals' neck length (m) from the top of the occipital (posterior) horns to the bottom of C7 vertebra, visible as a chest concavity.

To validate our photogrammetric methods, we photographed 3 objects of known length (1.0, 1.7, and 2.1 m) at 6 distances (38, 52, 74, 90, 123, and 134 m) and 2 focal lengths (300 and 400 mm), and measured them photogrammetrically. Photogrammetric measurements were very close to actual lengths (mean difference = 4.1 cm, SD = 4.1). To determine repeatability of measurements, we used these methods to measure neck length from 16 adult and 11 calf giraffes that were photographed >1 time in TNP during 2 months in spring 2011. Mean difference ($\pm$ SD) between measurements taken from different images of the same animal was adults: 0.6 cm ($\pm$ 9.4), and calves: 4.8 cm ($\pm$ 20.3). We measured and assigned age class at first capture for 1,223 giraffes with observed neck lengths using allometric equations for neck length and total height in Mitchell et al. (2009) and Van Sittert et al. (2010), along with total height at age data from Pellew (1983).

ENCOUNTER HISTORIES AND PARAMETER ESTIMATION

We matched giraffe identification images using WildID, a computer program that matched a large dataset of giraffe images collected using our protocols with a low false rejection rate (0.007) and zero false acceptance rate (Bolger et al. 2012). We created individual encounter histories for all adults and newborn calves for analysis in program MARK 7.1 (White and Burnham 1999). We modeled and estimated parameters using Pollock's (1982) robust design statistical models. For each site, we were interested in estimating adult male and female population sizes (N), adult female and calf survival probabilities (S), as well as nuisance parameters of capture probabilities (p), recapture probabilities (c), and temporary emigration parameters (γ' and γ'') for adults and calves (Fig. 4).

The robust design model is a combination of the Cormack-Jolly-Seber live recapture models (Cormack 1964, Jolly 1965, Seber 1965) and closed capture models. These models are superior to standard Cormack-Jolly-Seber models, which assume all emigration is permanent, because robust design models include estimators for temporary emigration. The emigration probabilities estimated by the robust design models in this study were strictly temporary: in these models, permanent emigration was confounded with mortality. Thus, all temporary emigration probabilities were estimated only for animals that eventually returned to the surveyed area. Temporary emigration movements outside the surveyed area would be primarily associated with animals whose home range was only partially within the surveyed area. The robust design model was described in detail by Kendall et al. (1995, 1997, 2001). For each survey event, we estimated the probability of first capture (p_{ij}) and the probability of recapture (c_{ij}) (where j indexes the

events within the i th occasion). For the intervals between survey occasions, we estimated

the probability of survival (S_i), the probability of emigration from the surveyed area (γ''_i),

and the probability of staying away from the surveyed area given that the animal has left

the surveyed area (γ'_i). This last parameter is the complement of the probability of an

absent animal returning to the study area (1- γ'_i).

CALCULATING DENSITY AND REPRODUCTION

Density and reproduction within each site also were estimated using PCMR data.

Density was computed as adult $\widehat{N}$ / surveyed area (km^2) of each site, with surveyed area

calculated as the minimum convex polygon enclosing our surveyed road network in each

site. We computed a site-specific index of seasonal reproduction as the ratio of newborn

calves (aged 0–3 months) over the site-specific $\widehat{N}$ of adult females. The proportion of

females seen with a calf often has been used as a proxy of birth rate (e.g., elk *Cervus*

canadensis, Eberhardt et al. 1996; white-eared kob *Kobus kob leucotis*, Fryxell 1987;

moose *Alces alces*, Laurian et al. 2000). However, this method is biased unless spatial

and temporal variation in the probability of detection is accounted for, along with

survival from birth to observation (Nichols 1992, McCorquodale 2001, Bonenfant 2005).

Our neck length measurements indicated that we were encountering very few newborn

calves less than 1 mo old, likely due to the solitary hiding strategy employed by mothers

of newborn giraffe calves (Langman 1977). Therefore, we corrected our calf counts for

detectability by dividing the count by site- and season-specific capture probabilities, and

for survival from birth to observation by dividing by the square root of site- and season-

specific survival estimates for the first interval after birth. Thus, corrected count = raw

count / p / $\sqrt{S}$. For comparisons of reproduction among sites we used the mean seasonal reproduction index across all occasions.

COVARIATES

We developed a priori hypotheses about factors that might explain spatial variation in giraffe survival and reproduction, and devised a set of spatial covariate models based on the hypotheses. In addition to the 3 basic models of site-specific parameters (denoted: *site*), constant parameters across all sites (*constant*), and parameter variation according to management authority with 3 levels (*management*), we also constructed 7 spatial covariate models: lion predation (*lion density*), human poaching (*human density*, *anti-poaching*, *distance to paved roads*, *distance to Mtowambu,* and *poaching pressure*), and giraffe density (*giraffe density*), that might explain the observed spatial patterns in survival and reproduction.

Lion predation

Natural predation probability varies across the landscape. Lion population data have been collected by the Tarangire Lion Project since 2003 (B. Kissui, *unpublished data*), but we had no data on hyena or other non-lion predator densities. The Tarangire Lion Project attempted to collect year-round location data for all lion prides every 2 weeks beginning in 2003 (B. Kissui *unpublished data*). Most lion prides in the study area included at least one radio-collared individual, and other prides were located using knowledge of their habitual use areas and information from park rangers and tourism operators. From these data, we created a continuous covariate model of site-specific *lion density* by using pride location and composition data for each site. We averaged across all

seasons by dividing lion population size by the area enclosed by a minimum convex polygon of our surveyed road network in each site.

Density of natural predators like lions was higher in national parks, and lower in areas where trophy hunting removes numerous individual predators from the population and where pastoralists disrupt predator behavior. We expected survival of giraffe calves or reproduction could be negatively correlated with local *lion density* because lions can randomly encounter giraffe calves and kill them (Hayward and Kerley 2005), but adult giraffe in the TE are rarely predated upon by lions (B. Kissui *unpublished data*) so we did not expect *lion density* to affect adult survival.

Poaching

Poaching also varies across the landscape, and poachers have the capacity to greatly reduce populations of resident herbivores (Campbell and Hofer 1995, Ogutu et al. 2009), particularly in less-protected lands (Stoner et al. 2007). The town of Mtowambu is the main market for poached meat in the area (C. Kiffner *unpublished data*), and animals of all age classes can be targeted. We created 5 spatial covariate models related to poaching: *human density*; *anti-poaching* efforts; *distance to paved roads*; *distance to Mtowambu;* and *poaching pressure. Human density* was set to 2 levels based on census data: 45 per km^2 in GCAs, and 0.1 in NPs and MRC (2012 Population and Housing Statistics, United Republic of Tanzania, National Bureau of Statistics, Ministry of Finance, Dar es Salaam). *Anti-poaching* effort was an index score with 3 levels based on the number of encounters we had with anti-poaching patrols during giraffe surveys. *Anti-poaching* was 1 in GCAs, 5 in MRC, and 10 in NPs. *Distance to paved roads* was calculated as the distance from the geographic center of each site directly to the nearest

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paved road. *Distance to Mtowambu* was calculated as the distance from the geographic center of each site directly to Mtowambu town. *Poaching pressure* was an integrated metric computed as the product of the 3 latter models (*poaching pressure = anti-poaching × distance to paved roads × distance to Mtowambu*).

As in other Tanzanian ecosystems (Arcese et al. 1995, Loibooki et al. 2002, Martin et al. 2012), most poachers in the TE are low-income subsistence farmers seeking protein and income (C. Kiffner *unpublished data*). Poaching of giraffe in our study area occurred mainly in GCAs where 2 main methods were employed: (1) wire or rope snares set at ground or neck level that poachers checked regularly; or (2) using vehicles to quickly locate, dispatch, butcher, and remove giraffe (Wildlife Division *pers. comm.*, C. Kiffner *unpublished data*). We expected adult giraffe survival, calf survival, and reproduction could all be positively correlated with *anti-poaching*, *distance to paved roads*, *distance to Mtowambu*, and *poaching pressure*.

Giraffe density

We created a continuous covariate model of site-specific *giraffe density* computed from our estimates of site-specific giraffe population size divided by the area enclosed by a minimum convex polygon of our surveyed road network in each site. Optimal foraging theory predicts animal distribution is influenced by spatial distribution of resources in order to maximize individual fitness (Fretwell and Lucas 1970, Stephens and Krebs 1986). Fitness-maximizing animals are expected to aggregate within the 'most favorable' habitat patches (Bailey et al. 1996). In non-territorial species such as giraffe, individuals may distribute themselves according to the ideal free distribution such that fitness is the same in all areas where they are present. Alternatively, density-dependent effects may
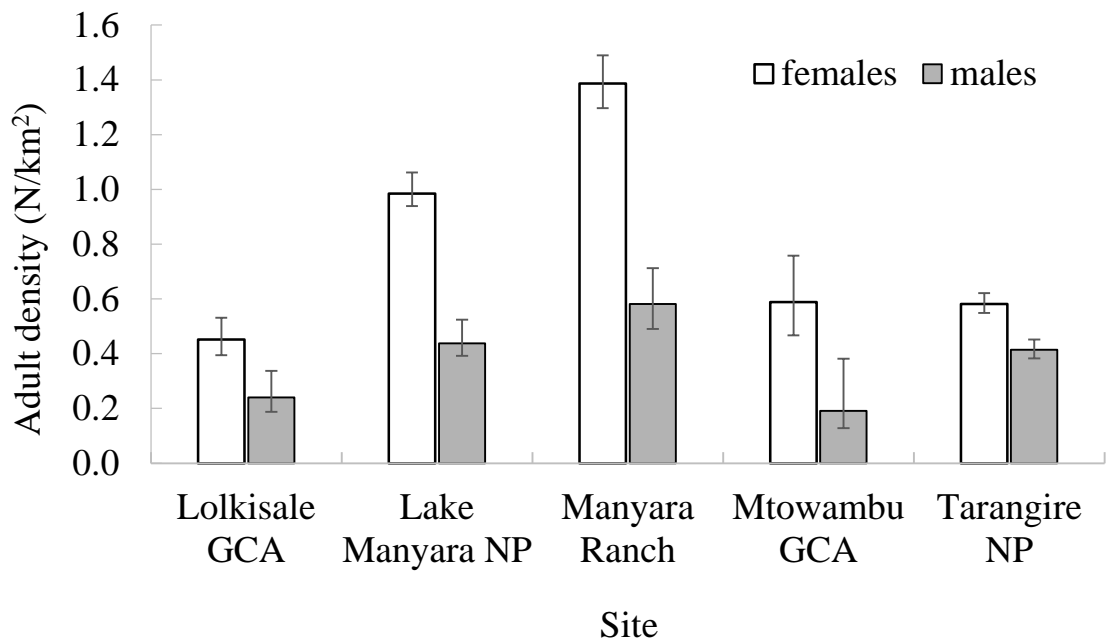
Figure 5. Adult giraffe density (±SE) at 5 sites in the Tarangire Ecosystem 2012 –

2014.

reduce giraffe fitness in areas with either higher giraffe density or of lower habitat

quality. Thus, we expected adult giraffe survival, calf survival, and reproduction could

either be negatively correlated with *giraffe density* if density dependence is in effect, or

not correlated if an ideal free distribution results in equal fitness across a range of

densities.

MODEL SELECTION

We tested goodness-of-fit of encounter histories using U-CARE (Choquet et al.

2009), and adjusted for lack of fit by adjusting $\hat{c} = \chi^2$ / df (Choquet et al. 2009, Cooch

and White, *unpublished*). Throughout model ranking and selection procedures, we ranked

models using qAICc and used model qAICc Weights (*W*) as a metric for strength of

evidence supporting a given model as the best description of the data (Burnham and

Anderson 2002). During survival model selection, we began with the most fully

parameterized model in our set with constraints (site effects) on the main parameters of interest, and with both temporal and site effects in capture (p), recapture (c), and temporal emigration (γ' and γ") rates. We first ranked competing models with reduced temporal complexity of temporary emigration, then detectability parameters. Once the most parsimonious form of temporary emigration and detectability parameters was obtained, we ranked all models of survival, including spatial covariate models, a constant or null model, and a site-specific model.

We ranked models of reproduction using generalized linear models (glm) with a binomial error structure and logit link function in program R (R Core Development Team 2013) with AICc as our metric of model rank and AICc Weights (*W*) as strength of evidence for a given model in the set. Number of neonate calves observed in each survey was corrected for detectability and pre-observation survival using the detection and survival probabilities for the site and season of the observations from survival modeling. Corrected number of neonates in each season-site combination was the numerator (successes) for reproduction analyses, and number of adult females in each site was the denominator (number of trials). Results are reported as mean ±1 SE unless otherwise noted.

SPATIAL VARIATION

We calculated the spatial variability in demographic parameters among sites using the coefficient of variation (CV = SD / mean) of site-specific demographic rates. For comparison with previously published studies, we also calculated spatial variability for the subset of sites with wildlife protection (NPs and MRC). We examined spatial variability at the regional scale and the continental scale by comparing our estimates and

their spatial variability with those from all published demographic studies conducted throughout the species' geographic range in Africa.

LESLIE MATRIX POPULATION MODEL

We constructed a female-based, age-structured, matrix population model for each site (Caswell 2001). The matrix population model has 5 ages, 1-year time steps, and birth flow reproduction (Fig. 6). For each site, we parameterized a matrix population model with fecundity and survival rate estimates from our data and the published literature. Annual calf survival from birth to age class 2 (S_1), and adult female survival (S_A) were computed from our site-specific seasonal survival rates. Subadult survival rates (S_{2-4}) were calculated by increasing survival each year based on our age-specific survival curve from photogrammetrically measured animals (Fig. 6) until it was equal to local adult survival (S_A). Fecundity (F) was calculated as annual estimates of calves/adult female (c/AF) $\times \sqrt{S_A} \times \sqrt{S_1} \times 0.5$ (to represent birth flow reproduction and include only female calves, assuming equal offspring sex ratio).

Results

We analyzed encounter histories for 907 adult females, 542 adult males, and 408 calves. We found evidence for lack of fit in adult female ($\chi^2_{63} = 358$, P < 0.001), adult male ($\chi^2_{76} = 221$, P < 0.001), and calf ($\chi^2_{62} = 97$, P = 0.006) encounter history data. Goodness-of-fit tests are designed to detect departures from model assumptions for (1) independence among individuals, and (2) independence between successive encounters of every individual, by measuring how well observational data fit a simple Cormack-Jolly-Seber or Arnason-Schwarz model. The lack of fit we observed is typical of large datasets where individual differences inherent in any animal population are inevitably detected

F

S_1 S_2 S_3 S_4

1   2   3   4   5

S_A

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 0 & 0 & (c/AF) \times \sqrt{S_A} \times \sqrt{S_1} \times 0.5 \\ S_1 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & S_4 & S_A \end{bmatrix}$$

Annual apparent survival vs Age class (years)
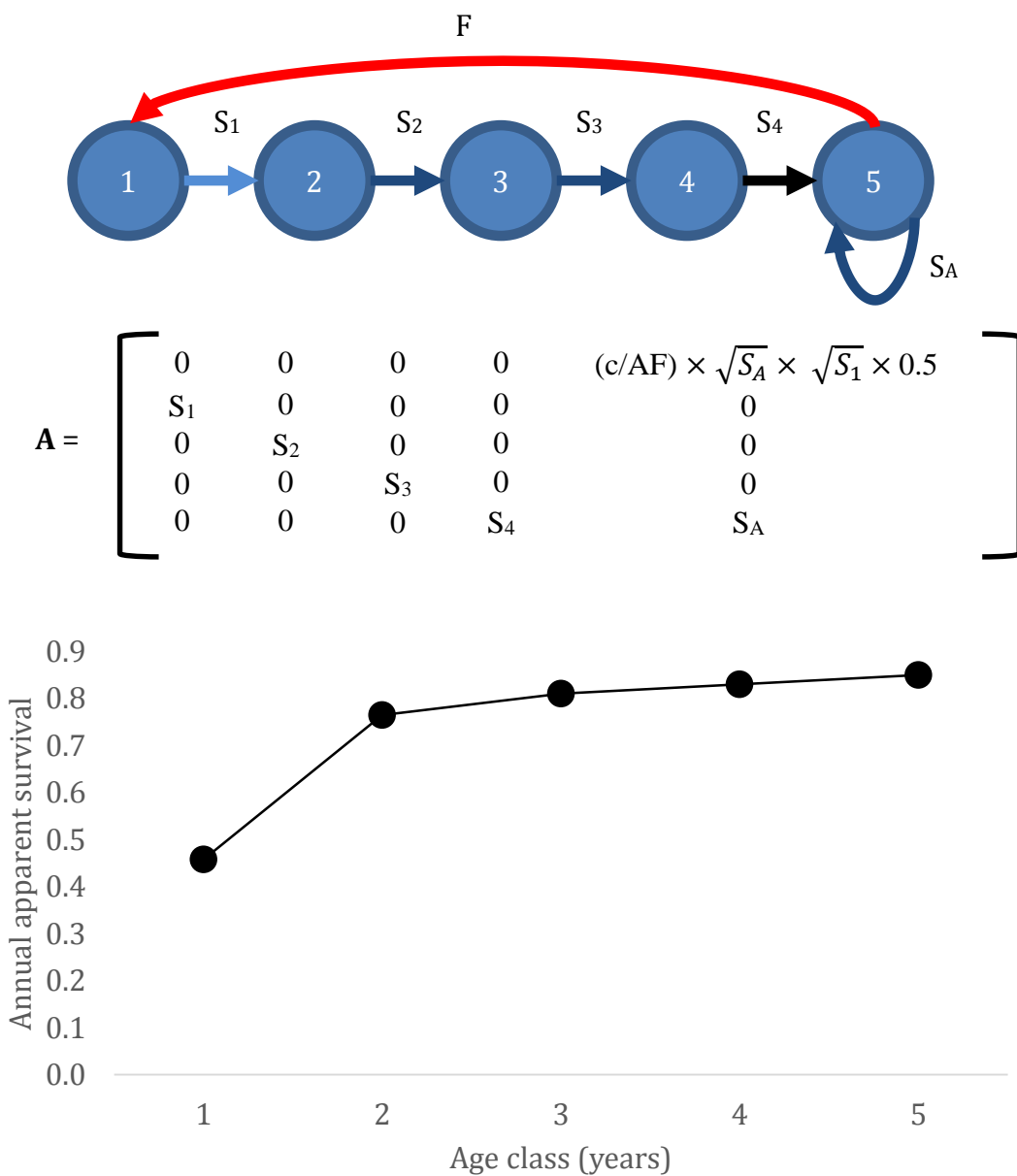
Figure 6. Top: Life cycle graph of female giraffe used to create Leslie matrix population model with vital rates including fecundity (F), calf survival (S_1), sub-adult survival (S_{2-4}), and adult survival (S_A). Middle: Leslie matrix population model. Bottom: Age-specific survival curve.

(Choquet et al. 2009), but we applied $\hat{c}$, a variance inflation factor, that has no effect on parameter estimates, but increases variances to make the model selection process more conservative. We adjusted adult female $\hat{c}$ = 2.0, adult male $\hat{c}$ = 2.9, and calf $\hat{c}$ = 1.5.

We documented significant among-site spatial variation in giraffe density (Fig. 5), adult female survival (Table 1 and Fig. 7), and reproduction (Table 4 and Fig. 7). Adult male survival and calf survival did not vary significantly among sites, evidenced by the *site* model not outranking the *constant* model, and no significant spatial covariates (Tables 2, 3, and 4). Mean values across all sites were: adult female annual survival $\bar{x}$ =
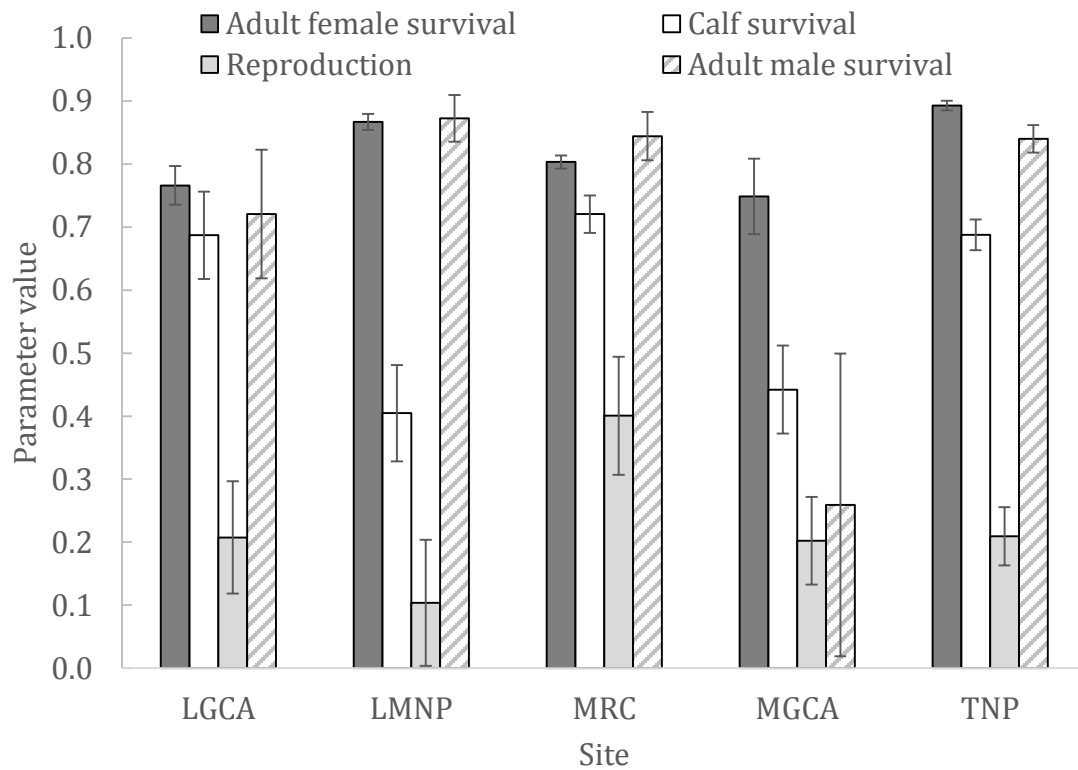
Figure 7. Adult male, female, and calf annual apparent survival probabilities, and annual reproduction index (calves/adult female) at 5 sites in the Tarangire Ecosystem 2012–2014. Error bars are ±1 SE.

0.847 ± 0.016; adult male annual survival $\bar{x} = 0.841 ± 0.045$; calf survival to age 1 year $\bar{x}$

$= 0.588 ± 0.054$; and reproduction (calves/adult female/year) $\bar{x} = 0.22 ± 0.03$.

Spatial covariate models indicated that adult female survival was positively

correlated with *anti-poaching* efforts (Table 1; $\beta = 1.31$, 95% CI = 0.73 to 1.89). Four

adult male spatial covariate models were ranked above the constant model (Table 2), but

none of the covariates were statistically significant as the 95% confidence intervals all

included zero. Calf survival was positively correlated with *distance from Mtowambu*, the

main bushmeat market town (Table 3; $\beta = 0.017$, 95% CI = -0.002 to 0.036), but the

effect was not statistically significant. No covariate models of reproduction explained the

data better than the site-specific model (Table 4).

Matrix population models revealed all populations are likely declining with finite

rates of population growth (λ) < 1.0. The values of λ in NPs and MRC were much higher

than in GCAs. Elasticities in each of the site-specific matrix population models indicated

adult survival (S_A) was by far the highest elasticity parameter (Table 5). Population

growth rate was significantly correlated with adult female survival ($r^2 = 0.81$, $P = 0.04$),

but not reproduction ($r^2 = 0.02$, $P = 0.81$) nor calf survival ($r^2 = 0.17$, $P = 0.48$).

The spatial variability of site-specific demographic rates across all sites in our

regional study area was moderate for adult female survival (CV = 0.21) and calf survival

(CV = 0.26), and high for reproduction (CV = 0.48). When spatial variability was

calculated only using estimates from the 2 national parks and MRC, variability in adult

female survival was much lower (CV = 0.05), while variability in calf survival was

largely unchanged (CV = 0.29), and variability in reproduction was much higher (CV =

0.63). Estimates of adult survival, calf survival, and reproduction rates were available

from national parks across Africa, including the southern, eastern, and western extents of the species' range (Table 6 and Fig. 8). Adult female survival rates from protected areas across the range of giraffe were similar ($\bar{x} = 0.90$, SD = 0.03, CV = 0.03), but there was large range-wide variability in estimates of calf survival to age 1 year ($\bar{x} = 0.45$, SD = 0.14, CV = 0.30), and reproduction ($\bar{x} = 0.31$, SD = 0.10, CV = 0.32).

Discussion

The spatial distributions of individuals and environmental conditions are often heterogeneous, which leads to variation in local population dynamics within larger regional populations. An understanding of these local population dynamics may help explain the dynamics of the larger population (Taylor 1961, O'Neill 1989, Sugihara et al. 1990, Coulson et al. 1997). In our investigation of spatial variation in giraffe fitness components across a 4,400 km^2 area, we found significant spatial variation in adult female survival and reproduction. Spatial variation in adult female survival was positively correlated with the spatial covariate of anti-poaching efforts.

SPATIAL VARIATION IN DEMOGRAPHY AND THE TEMPORAL PARADIGM

Adult female survival is typically the highest-elasticity parameter in ungulate population growth models, including our matrix population model for giraffe. The dominant paradigm for ungulate population dynamics over time holds that adult female survival has the highest elasticity, but its low variation causes it to contribute relatively little to changes in the population growth rate compared to juvenile survival or reproduction, which have low elasticities but high temporal variation, making them the primary determinant of realized population change (Gaillard et al. 1998, 2000, Gaillard and Yoccoz 2003, Raithel et al. 2007). We found that spatial variation of demographic

estimates from generally stable giraffe populations in National Parks across the continental range of the species followed the temporal demographic paradigm. In contrast to this paradigm, in the TE region we found giraffe adult female survival was highly spatially variable and significantly correlated with population growth rate. Similarly, Johnson et al. (2010) found that in 4 of 6 populations of bighorn sheep (*Ovis canadensis sierra*), adult survival explained the highest proportion of variation in population growth. Likewise, Nilsen et al. (2009) examined 8 populations of roe deer (*Capreolus capreolus*) and found variance in population growth rate was mostly driven by low and variable adult survival in declining populations. To date, few ungulate studies have observed such divergence from the temporal paradigm in the importance of different vital rates within or among populations (Albon et al. 2000, Coulson et al. 2005), but the implications of such variation for conservation and management purposes are critical.

Pfister (1998) suggested that demographic rates were unlikely to be both highly variable and have a large effect on the growth rate of a population. However, this observation may be relevant only to stable or increasing populations. In declining populations it might be common for vital rates with the greatest elasticity also to be highly variable and have a large impact on population change, particularly when hunting or predation effects are present (Wisdom et al. 2000, Schmidt et al. 2005, Coulson et al. 2005, Nilsen et al. 2009, Johnson et al. 2010). Our data support other studies on long-lived species that documented population declines associated with decreases in adult survival (Wehausen 1996, Flint et al. 2000, Rubin et al. 2002, Pistorius et al. 2004, Wittmer et al. 2005, Nilsen et al. 2009, Johnson et al. 2010).

The relative contribution of different demographic rates to population growth may vary among populations of the same species, and within the same geographic region, and may not follow expectations from life-history theory (Johnson et al. 2010). Owen-Smith and Mason (2005) found that decreases in adult survival were responsible for African ungulate populations that transitioned from stable trajectories to declining ones. That this pattern was contrary to most other studies of ungulate dynamics was attributed to the fact that most investigations have been conducted in temperate zones with few or no natural predators, not tropical areas with a large suite of predators.

Spatial variability in demography has been related to variability in resource quality (Fretwell and Lucas 1970), and anthropogenic factors have emerged as critically important influences on resource quality and thus animal populations worldwide (Foley et al. 2005). Spatial variation in demographic rates of ungulates has been previously documented for bighorn sheep (Johnson et al. 2010), roe deer (Focari et al. 2002, Nilsen et al. 2009), Soay sheep (*Ovis aries*; Coulson et al. 1999), red deer (*Cervus elaphus*; Coulson et al. 1997), caribou (*Rangifer tarandus*; Wittmer et al. 2007), and wildebeest (*Connochaetes taurinus*; Ndibalema 2009). Our work adds giraffe to the roster of species with documented spatial variation in demographic rates and points to poaching of adult females as a likely mechanism for observed population declines.

SPATIAL VARIATION IN REPRODUCTION

We found reproduction was significantly greater in MRC and lower in LMNP compared with the other sites. Vegetation structure and composition in LMNP are substantially different from that in the other 4 sites due to abundant water supply from the adjacent highlands, and is composed of denser, shrubbier habitat compared with the other

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sites (Greenway and Vesey-Fitzgerald 1969, Loth and Prins 1986, van de Vijver et al.

1999). We were uncertain why reproduction was significantly greater at MRC than other

sites, but it is conceivable that vegetation at this site is of higher quality than the other

sites, leading to greater fecundity. Vegetation differences may be contributing to spatial

variation in reproductive rates at LMNP and MRC: future research might compare forage

species composition and leaf protein levels among sites as potential covariates explaining

differences in reproductive rates. The high variability of reproduction also may play a

role in spatial population dynamics of giraffe, but the observed pattern of reproduction

during this study was not correlated with population growth rates. Perhaps over longer

time spans the role of reproduction in local population dynamics will become clearer.

DEMOGRAPHIC COMPARISONS ACROSS THE SPECIES' RANGE

Overall, spatial variability of demographic rates from protected areas across the

range of giraffe showed a pattern similar to that seen in annual temporal variation for

temperate ungulates—high adult female survival with low variability, and low but

variable reproduction and calf survival (Gaillard et al. 2000). This study examined spatial

variation in demographic rates of adult female survival, calf survival, and reproduction

among 5 sub-populations within a large, continuous, regional population. Our estimates

of adult female survival in the TE were much more variable across sub-populations than

estimates from protected areas across giraffe's range in Africa. However, when we

excluded GCAs from our study and computed variability only across local protected

areas, the CV of survival became similar to the range-wide value. Estimates from across

giraffe's range were available only from protected areas, such as national parks, so the

inclusion of non-protected GCAs could make the resultant regional spatial CV

34
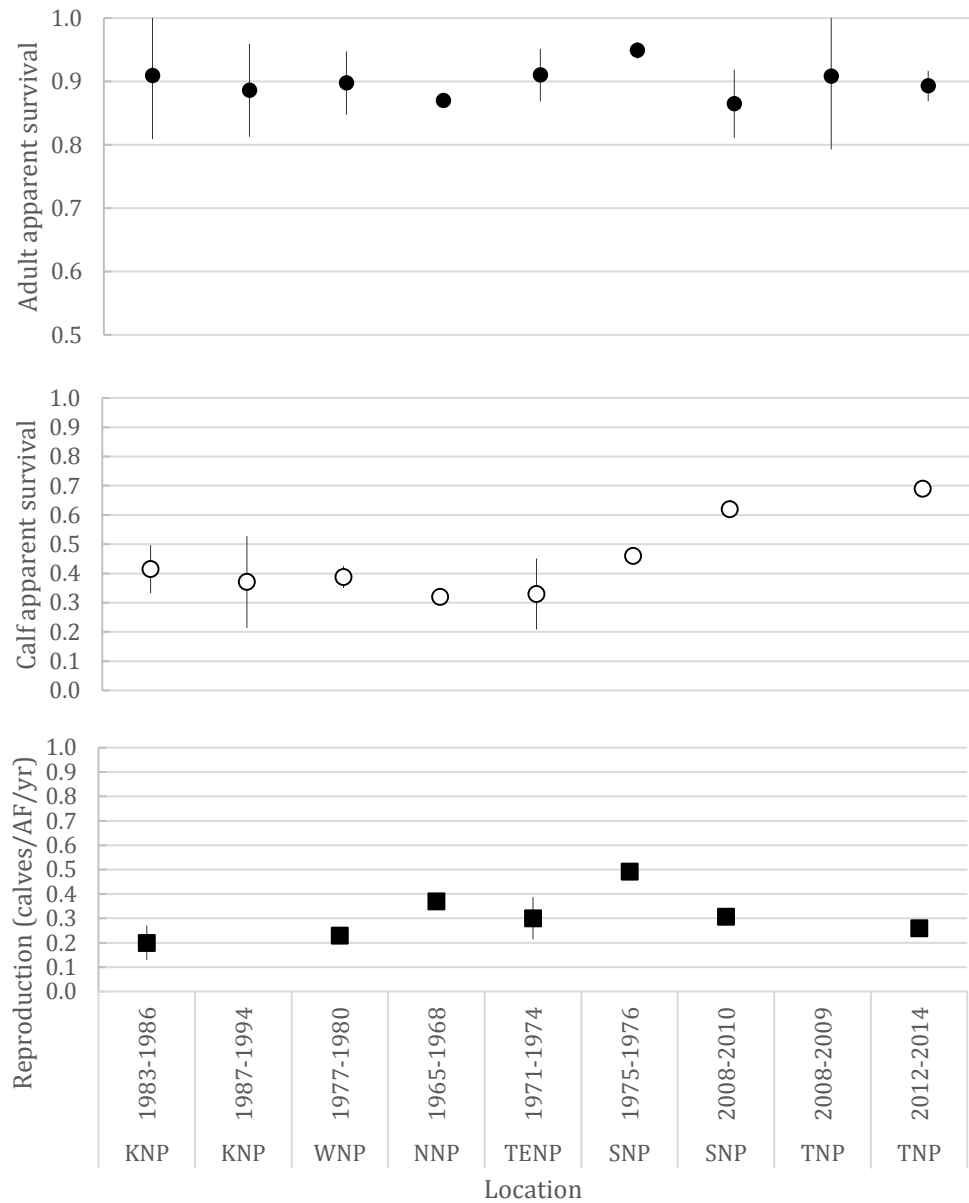
Figure 8. Summary of existing demographic estimates for giraffe in national parks

across the species' range (±SE), data from this study are at far right. Top: adult female

annual survival probability. Middle: calf survival probability to age 1 year. Bottom:

reproduction as number of calves per adult female per year. Location definitions are

given in Table 6.

values incomparable to values from protected areas. However, our estimates likely reflected more realistic conditions faced by most giraffe, as much of their remaining habitat lies outside protected areas, where anthropogenic factors such as poaching and habitat alteration are prevalent. Indeed, even in the Serengeti National Park, adult giraffe survival was believed to be affected by poaching (Strauss 2014). Local and range-wide spatial variability in other regions with increasing habitat fragmentation and human populations actually may be as high as we calculated when we included non-protected areas, because giraffe outside protected areas likely experienced a wider spectrum of environmental and anthropogenic factors that inevitably affected their demographic rates.

The only continent-wide geographic pattern in demographic rates that emerged was that calf survival was significantly greater in East Africa relative to southern and western studies (Fig. 8). This could be due to differences in climate, vegetation, poaching style, or sampling methodology. We recommend the use of standardized PCMR survey and analysis protocols in sites across giraffe's range, along with quantification of climatic, vegetation, and predation factors to clarify this discrepancy.

CONCLUSIONS

This study documented significant spatial variation in giraffe demographic parameters of density, adult female survival, and reproduction. Point estimates of adult male survival and calf survival were also highly variable among sites, but not significantly so due to low precision of those estimates. We caution that data from this study encompassed a short time span and our estimates and conclusions may reflect transient dynamics that do not accurately characterize the longer-term population dynamics of giraffe in the TE. Continued monitoring is required to validate our findings.

Our matrix population models indicated that all sub-populations where we sampled are likely declining in the fragmented Tarangire Ecosystem, with spatial covariate models implicating poaching of adult females as the most likely proximate mechanism of this decline. Thus, the population management actions with highest expected effectiveness would be those aimed at increasing adult female survival, such as anti-poaching patrols and efforts to disrupt bushmeat distribution networks and markets.

Tables

Table 1. Selection results for spatial covariate models of apparent survival of adult female giraffe in 5 sites in the Tarangire Ecosystem, Tanzania, 2012–2014. *ΔqAICc* is the difference in *qAICc* values between a model and the top-ranked model. *W* is model *qAICc* Weight, a metric for strength of evidence supporting a given model as the best description of the data. *K* is the number of parameters in a model. *Anti-poaching* is the only statistically significant covariate ($\beta = 1.31$, 95% CI = 0.73 to 1.89).

Apparent Survival Model	*ΔqAICc*	*W*	*K*
Anti-Poaching	0	0.66	127
Management	2.06	0.24	128
Site	4.52	0.07	130
Human Density	6.61	0.02	127
Poaching Pressure	9.39	0.01	127
Constant	13.88	0.00	126
Distance to Mtowambu	14.69	0.00	127
Distance to Paved Road	14.77	0.00	127
Giraffe Density	15.32	0.00	127
Lion Density	15.42	0.00	127

Table 2. Selection results for spatial covariate models of apparent survival of adult male giraffe in 5 sites in the Tarangire Ecosystem, Tanzania, 2012–2014. $\Delta qAICc$ is the difference in $qAICc$ values between a model and the top-ranked model. *W* is model $qAICc$ Weight, a metric for strength of evidence supporting a given model as the best description of the data. *K* is the number of parameters in a model. No covariate was significant.

Apparent Survival Model	$\Delta qAICc$	*W*	*K*
Giraffe Density	0	0.22	67
Anti-Poaching	0.07	0.22	67
Distance to Mtowambu	0.08	0.22	67
Distance to Paved Road	0.13	0.21	67
Constant	2.83	0.05	66
Human Density	4.48	0.02	67
Poaching Pressure	4.57	0.02	67
Lion Density	4.65	0.02	67
Management	6.64	0.01	68
Site	10.42	0	70

Table 3. Selection results for spatial covariate models of apparent survival of giraffe calves in 5 sites in the Tarangire Ecosystem, Tanzania, 2012–2014. *ΔqAICc* is the difference in *qAICc* values between a model and the top-ranked model. *W* is model *qAICc* Weight, a metric for strength of evidence supporting a given model as the best description of the data. *K* is the number of parameters in a model. No covariate was significant.

Apparent Survival Model	*ΔqAICc*	*W*	*K*
Distance to Mtowambu	0	0.25	109
Constant	0.85	0.16	108
Site	0.88	0.16	112
Human Density	1.60	0.11	109
Distance to Tarmac	2.44	0.07	109
Poaching Pressure	2.93	0.06	109
Lion Density	2.94	0.06	109
Anti-Poaching	3.13	0.05	109
Giraffe Density	3.26	0.05	109
Management	5.45	0.02	111

Table 4. Selection results for spatial covariate models of seasonal giraffe reproduction (calves/adult female/yr) in 5 sites in the Tarangire Ecosystem, Tanzania, 2012–2014. $\Delta AICc$ is the difference in $AICc$ values between a model and the top-ranked model. W is model $AICc$ Weight, a metric for strength of evidence supporting a given model as the best description of the data. K is the number of parameters in a model.

Reproduction Model	$\Delta AICc$	W	K
site	0	1.00	4
AntiPoach	31.6	0.00	2
Management	31.6	0.00	2
lionDens	67.0	0.00	2
TarDist	70.6	0.00	2
PoachPress	70.8	0.00	2
MtoDist	71.6	0.00	2
constant	72.7	0.00	1
HumanDens	74.0	0.00	2
GirDens	74.1	0.00	2

Table 5. Vital rates used in Leslie matrix population models for female giraffe in 5 sites in the Tarangire Ecosystem 2012–2014, finite rate of population growth (λ), and elasticities (E) of vital rates computed from the Leslie matrices.

	LGCA	LMNP	MRC	MGCA	TNP
S_1	0.69	0.40	0.72	0.44	0.69
S_2	0.77	0.70	0.80	0.75	0.89
S_3	0.77	0.80	0.80	0.75	0.89
S_4	0.77	0.87	0.80	0.75	0.89
S_A	0.77	0.87	0.80	0.75	0.89
c/AF	0.21	0.10	0.40	0.20	0.21
λ	0.82	0.88	0.89	0.78	0.94
E S_1	0.05	0.01	0.07	0.03	0.04
E S_2	0.05	0.01	0.07	0.03	0.04
E S_3	0.05	0.01	0.07	0.03	0.04
E S_4	0.05	0.01	0.07	0.03	0.04
E S_A	0.75	0.94	0.64	0.84	0.78
E c/AF	0.05	0.01	0.07	0.03	0.04

Table 6. Summary of existing studies that estimated demographic rates for giraffe.

Abb. is the abbreviated location used in Fig. 8.

Abb.	National Park, Country	years	Source	SN[1]	AN[2]
KNP	Kruger NP, South Africa	1983-1986	Owen-Smith and Mason 2005	A	R
KNP	Kruger NP, South Africa	1987-1994	Owen-Smith and Mason 2005	A	R
WNP	Waza NP, Cameroon	1977-1980	Nje 1983	G	R
NNP	Nairobi NP, Kenya	1965-1968	Foster and Dagg 1972, Dagg and Foster 1976	GI	RC
TENP	Tsavo East NP, Kenya	1971-1974	Leuthold and Leuthold 1978	GI	RC
SNP	Serengeti NP, Tanzania	1975-1976	Pellew 1983	AGI	RC
SNP	Serengeti NP, Tanzania	2008-2010	Strauss 2014	AGI	C
TNP	Tarangire NP, Tanzania	2008-2009	Bolger et al. 2012	GI	C
TNP	Tarangire NP, Tanzania	2012-2014	this study	GI	C

1. Survey Notes: A: aerial counts, G: ground counts, I: individual identification

2. Analyses Notes: R: ratio-accounting, C: capture-mark-recapture

CHAPTER 2.

SOURCE-SINK DYNAMICS AMONG SUB-POPULATIONS OF GIRAFFE

Wildlife scientists and land managers require a solid understanding of spatial population dynamics for animals residing in fragmented ecosystems to develop effective conservation measures (Hansen 2011). Spatial conceptual models have described a large population as composed of a number of local populations with spatial demographic variation (Andrewartha and Birch 1954), or several sub-populations with connecting movements among them (Levins 1969), or a set of local populations which interact via individuals moving among populations (Hanski and Gilpin 1991, Hanski and Simberloff 1997). Within all of these models, a sub-population's size, population growth rate, and connectivity to other sub-populations are the key determinants of its conservation status and extinction risk (Caswell 2001, Sinclair et al. 2006). Population growth rate (*lambda*) is the integrated measure of sub-population fitness (Caswell 2001). Connectivity, the movement of individuals among sub-populations, is essential for understanding landscape-scale population dynamics (Tischendorf and Fahrig 2000, Lowe and Allendorf 2010), such as the potential for sub-populations to buffer each other from the effects of catastrophes or environmental change (Brown and Kodric-Brown 1977, Kokko and Lopez-Sepulcre 2006).

Source-sink theory predicts that individuals in high-quality habitats (sources) should have higher fitness (higher population growth rates) compared to those in low-quality habitats (sinks), with movement rates important to determining whether sub-populations are actually sources or sinks (Holt 1985, Pulliam 1988, Constanti et al.

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2013). Movements of animals among sub-populations in heterogeneous landscapes is one of the most important, yet least understood, ecological processes related to the persistence of the larger population (Bowler and Benton 2005). Investigating processes such as sub-population growth rates and inter-population movement is therefore essential for the development of scientifically based conservation and management plans, particularly in fragmented habitats (Caughley 1977, Gaillard et al. 1998, Martin et al. 2000, Vié et al. 2009).

Given documented evidence for spatial variation in demography and population growth rates of Masai giraffe (*Giraffa camelopardalis tippelskirchi*) among 5 sites in the Tarangire Ecosystem (TE) of northern Tanzania, East Africa (see Chapter 1), there was a need to investigate how movements connect these sites and affect metapopulation dynamics and viability. Our objective here was to quantify connectivity movements among sub-populations in a large, presumed contiguous population of giraffe, using data from an individually based photographic mark-recapture study. We estimated site-specific sub-population sizes, sub-population growth rates, and per-capita movement rates at 5 sites defined by land management designations within the core of the TE (Fig. 2). We also ranked spatial covariate models to quantify whether and how sub-population growth rates and per-capita movement rates differed according to land-use designation, giraffe density, lion density, and human poaching pressure. We assessed the source-sink structure of the study area by calculating the following source-sink statistics (Runge et al. 2006, Sanderlin et al. 2012): the per capita contribution of a member of the focal sub-population to the metapopulation, the growth rate of the metapopulation, the average

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relative contribution of sub-population to the metapopulation, and the average relative contribution of immigrants from outside the metapopulation to metapopulation growth.

To examine the implications of our estimates of among-sub-population movements, we created population projection models. We constructed 3 versions of a multi-site matrix population model for the metapopulation of 5 sites, computed elasticities of parameters (Caswell 2001), and projected forward 50 years to predict how the 5 sub-populations could fare over the next few decades under 3 scenarios: (1) current conditions; (2) with complete loss of connectivity; (3) and with random movement rates (Bessinger and McCullough 2002, Morris and Doak 2002).

The sub-population sites represented a variety of human land uses. Two national parks (Tarangire and Lake Manyara) had strong wildlife protections, anti-poaching efforts, and no legal human encroachment. A private cattle ranch/wildlife conservancy (Manyara Ranch) had livestock grazing and tourism, some human habitation, and anti-poaching patrols. Two 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).

Methods

We collected and organized giraffe encounter data as described in Chapter 1. For this analysis we used adult male and female giraffe only. We used two modeling frameworks to obtain our parameters of interest (Lowe 2003, Peery et al. 2006). We utilized Pradel robust design models to provide site-specific estimates of adult male and female population size (N), and population growth rate without movements (*lambda* [λ];

Pradel 1996, Nichols et al. 2000) and then used multi-site open robust design models (MSORD) to estimate adult movement probabilities (*Psi* [ψ]) among sites (Kendall and Bjorkland 2001, Schwarz and Stobo 1997, Lebreton et al. 2009). Both models also estimate site-specific survival (*S*).

We used the Pradel model parameterization that estimated population size (*N*), seasonal survival probabilities (*S*), population growth rates, *lambda* (λ), capture probabilities (*p*), and recapture probabilities (*c*). For Pradel models, in order to remove the effect of movements among geographic sites, we assigned an individual to one of the 5 sites for the entire study according to where the majority of encounters occurred. When no majority was present, we assigned the animal to the first observed location. Thus, individual movements among sites did not contribute to site variation in *lambda* in the Pradel models.

We used MSORD models parameterized to estimate probabilities for: transition among sites (*Psi*), seasonal survival (*S*), entering the study area (*pent*), remaining in the study area (*Phi*), and capture (*p*). For MSORD models, individuals must remain in the same site within a seasonal sampling occasion (composed of 2 events), but can change sites between occasions. Thus, during each occasion we assigned individuals to a single geographic site according to where the majority of encounters occurred. When no majority was present, we used the first location.

PARAMETER MODELLING AND ESTIMATION

Our focus was on spatial variation in population sizes, population growth rates, and movements among sites, and we strove to maintain a reasonable number of parameters to be estimated and ensure high estimability of all relevant parameters,

therefore we constrained temporal aspects of some models. In all modeling of survival

probabilities, transition probabilities, and lambda, we only considered models where

geographic site was relevant, and included no temporal effects. In the Pradel models, we

allowed capture and recapture probabilities and population sizes to vary by site as well as

temporally, but we ranked models with simplified temporal structure in these parameters

as the first stage in model selection. In the MSORD models, we did not include any

temporal structure, so all parameters were modeled only as site and constant effects. We

fixed some transition probabilities (*Psi*) at zero because there were no observed

movements between these site pairs.

   We tested goodness-of-fit using U-CARE (Choquet et al. 2009), and adjusted for

lack of fit by adjusting $\hat{c} = \chi^2/$df (Choquet et al. 2009, Cooch and White, *unpublished*).

Throughout model ranking and selection procedures, we ranked models using qAICc and

used model qAICc Weights (*W*) as a metric for strength of evidence supporting a given

model as the best description of the data (Burnham and Anderson 2002). In the Pradel

lambda and *N* modeling, we began with the most fully parameterized model in our set

with constraints (site effects) on the main parameters of interest, but with both temporal

and site effects in capture (*p*) and recapture (*c*) rates. We first ranked competing models

with reduced temporal complexity of detectability parameters (*p* and *c*). Once the most

parsimonious form of detectability parameters was obtained, we ranked all possible

combinations of models of site and constant effects in the parameters of interest (*lambda*,

N). In the MSORD models, we began with the most fully parameterized model in our set

(site effects in all parameters), then ranked all possible combinations of site and constant

effects in *S*, *Phi*, and *p*. We then ranked the competing models of *Psi*.

SPATIAL COVARIATES

We ranked 3 basic models of: site-specific parameters (denoted: *site*), constant parameters across all sites (*constant*), and parameter variation according to management authority (*management*). We also constructed 7 spatial covariate models of natural predation (*lion density*), human poaching (*human density*, *anti-poaching*, *distance to paved roads*, *distance to Mtowambu,* and *poaching pressure*), and giraffe density (*giraffe density*), that might explain the observed spatial patterns in population growth and movement (see Chapter 1 for detailed explanations of covariate models).

For spatial covariate models of movement, we calculated values as the difference in each covariate value between the source site and the destination site (destination - origin). We also ranked a model of among-site movement based on distance between sites, denoted (*distance*).

CALCULATING FLOW OF INDIVIDUALS

To calculate total annual flow of individuals out of and into each site, we used the product of: the seasonal movement rate (*Psi*) between origin and destination sites, the population estimate (*N*) at the origin site, and the number of sampling seasons per year (3). We calculated net annual flow of individuals by subtracting total number of emigrants from immigrants for each site.

CLASSIFYING SOURCES AND SINKS

We assessed the source-sink structure of our study area by calculating 4 parameters, C^s, λ^M, $\hat{\bar{c}}^s$, and $\hat{\bar{c}}^0$ using data for female giraffe.

C^s is the per capita contribution of a member of each sub-population s to the metapopulation (Runge et al. 2006):

$$C^S = S_A^S + \sum \psi^{s-k} + B^s\left(S_j^s + \sum \psi^{s-k}\right), \tag{2}$$

where for sub-population s, S_A^S is adult survival, $\sum \psi^{s-k}$ is the sum of per capita emigration movements from the sub-population, B^s is birth rate as calves per adult female, and S_j^s is juvenile survival (the product of S_{1-4}).

λ^M is the growth rate of the metapopulation (Runge et al. 2006):

$$\lambda^M = \sum C^S * \left(\frac{N^S}{N^M}\right), \tag{3}$$

where N^S is sub-population size, and N^M is metapopulation size.

$\hat{\bar{c}}^s$ is the average relative contribution of each sub-population to the metapopulation (Sanderlin et al. 2012):

$$\hat{\bar{c}}^s = \frac{\left(N^S * S_A^s\right) + \left(N^S * \sum \psi^{s-k}\right)}{N^M}, \tag{4}$$

$\hat{\bar{c}}^0$ is the average relative contribution of immigrants from outside the metapopulation to metapopulation growth (Sanderlin et al. 2012).

$$\hat{\bar{c}}^0 = 1 - \sum_{s=1}^{k} \hat{\bar{c}}^s, \tag{5}$$

POPULATON PROJECTION MODELS

We created 4 versions of our population projection multi-site matrix model: one with observed movement rates among sites, one without any movements among sites, and two with random movement rates. Our multi-site matrix population model with movement was based on a single population model (described in Chapter 1), but created one large matrix including each site's population model as well as transition matrices between each pair of sites (Fig. 9). To reflect the indications that TNP population growth was ≥ 1.0 (see Results below), we adjusted $S_A = 0.9$, and female calves / AF $= 0.2$ in TNP.

The diagonal cells are complete site-specific matrix population models, as described in Figure 6, except $S_A' = S_A \times (1 - \Sigma Psi)$, where ΣPsi = sum of *Psi* values leaving that site. The off-diagonals are transition matrices, which in this case are all zeroes except the cell corresponding to $S_A'' = S_A \times Psi$, where *Psi* is the transition probability. The no-movement model was identical to the movement model, but all transition matrices were filled with zeroes. For the random among observed (RAO) movement model we selected a value for each transition probability from among the 20 observed movement parameters using a uniform distribution with replacement. For the random within the range of observed values (RWR) movement model we selected a value for each transition from a uniform random distribution bounded by the highest (0.13) and lowest (0.0) observed transition rates. The random matrices were simulated 100 times and output from each iteration was stored.

We summarized the two simulations (RAO and RWR) by computing correlation coefficients between *lambda* and each transition parameter as well as mean elasticities of

TNP	M-T	L-T	S-T	R-T
T-M	**LMNP**	L-M	S-M	R-M
T-L	M-L	**LGCA**	S-L	R-L
T-S	M-S	L-S	**MGCA**	R-S
T-R	M-R	L-R	S-R	**MRC**

Figure 9. Diagram of multi-site matrix population model. The diagonal cells are complete site-specific matrix population models, the off-diagonals are transition matrices.

all matrix cells using the stored output. To identify the movement rates with the greatest

effect on metapopulation *lambda*, we used AICc to rank all possible subsets regressions

of *lambda* against of transition parameters up to a maximum of 10 terms per regression.

Results

We analyzed encounter histories for 907 adult female, and 542 adult male,

individually identified giraffe. We found evidence for lack of fit in the Pradel model

($\chi^2_{270} = 446$, P < 0.001), and in the MSORD model ($\chi^2_{172} = 293$, P < 0.001), so to account

for model selection uncertainties we adjusted $\hat{c} = 1.65$ in Pradel models, and $\hat{c} = 1.70$ in

MSORD models.

Model selection indicated that there was a single top-ranked model in each set

that performed much better at describing the data than any other model in the sets (Tables

7 and 8). Therefore, we used the top model from each analysis to estimate population

parameters. The top model from the Pradel model selection included the *Distance to*

Mtowambu effect in *lambda* (Table 7), and *site* plus *time* effects in capture and recapture.

The top-ranked model in MSORD model selection included *constant* entry, and *site*

effects in movements, residence, and capture. There was little or no evidence that

management was a good predictor of *lambda*, or movement (Tables 7 and 8).

POPULATION SIZE, DENSITY, AND GROWTH RATE

The total estimated population size for adult females in the study area was 790,

and for males 435 (Table 9). The largest sub-population was in TNP, followed by MRC.

Density varied significantly among sites for both sexes (Fig. 5), with the highest density

in MRC relative to all other sites.

The model for site-specific population growth rate was far superior to the constant model (Table 7), providing strong evidence for significant among-site variation in local population growth rates (Table 12). For females, the 95% confidence interval for population growth rate included 1.0 in TNP and LGCA, but *lambda* at all other sites was significantly less than 1.0 indicating decreasing populations. For males, the 95% confidence interval for *lambda* included 1.0 in TNP, MRC, and LGCA, but *lambda* at all other sites was significantly less than 1.0. This pattern was also reflected in the top-ranked spatial covariate model where *lambda* was positively correlated with *Distance to Mtowambu* ($\beta = 0.002$, 95% CI $= 0.001$ to 0.003).

SURVIVAL

Survival is estimated as an inherent part of the model structures, but survival was not the focus of this paper (see Chapter 1 for detailed analyses of survival).

MOVEMENT AMONG GEOGRAPHIC SITES

Female movement data indicated no sub-population was completely isolated, but movement probabilities (*Psi*) varied among sites (Table 10). Average transition rate among sites was 0.015 (SE $= 0.006$, range $= 0.0$ to 0.127). Based on calculated flow of individuals (Table 11, Fig. 10), female immigration was nearly balanced with emigration at all sites, but net female flow showed that each year, TNP gained a few immigrants, while LGCA, MGCA, and MRC were net exporters of individuals. There was very little movement in or out of LMNP.

Transition probabilities were not significantly correlated with distance between pairs of sites (Table 8). Sub-population annual flows of individuals were not significantly correlated with *lambda* (immigration: $r^2 = 0.67$, $P = 0.08$; emigration: $r^2 = 0.70$, $P = 0.09$;

net: $r^2 = 0.16$, $P = 0.50$), or density (immigration: $r^2 = 0.10$, $P = 0.60$; emigration: $r^2 = 0.10$, $P = 0.61$; net: $r^2 = 0.04$, $P = 0.76$).

Male movement data indicated that LMNP was completely isolated (Table 10). Average transition rate among sites was 0.018 (SE = 0.007, range = 0.0 to 0.10). Net flow of individuals showed that LGCA was the only site that gained male immigrants, while TNP, MGCA, and MRC were net exporters of individuals (Table 11, Fig. 11). As with females, sub-population immigration, emigration, and net flows of males were not significantly correlated with *lambda* (immigration: $r^2 = 0.40$, $P = 0.25$; emigration: $r^2 = 0.26$, $P = 0.38$; net: $r^2 = 0.21$, $P = 0.43$), or density (immigration: $r^2 = 0.14$, $P = 0.54$; emigration: $r^2 = 0.05$, $P = 0.71$; net: $r^2 = 0.23$, $P = 0.41$).

CLASSIFYING SOURCES AND SINKS

Metapopulation growth rate $\lambda^M = 0.996$, indicating a decreasing overall population trend. Parameters calculated to identify source and sink sub-populations indicated that TNP and LGCA were sources, while LMNP, MRC, and MGCA were sinks (Table 12). This result was confirmed by Pradel estimates of sub-population-specific λ as well as calculated average relative contribution of local population s to growth of the metapopulation (C^s; Runge et al. 2006). TNP was the dominant source of population growth in this metapopulation, followed by MRC, and there was negligible contribution of individuals immigrating from outside the metapopulation (Table 12).
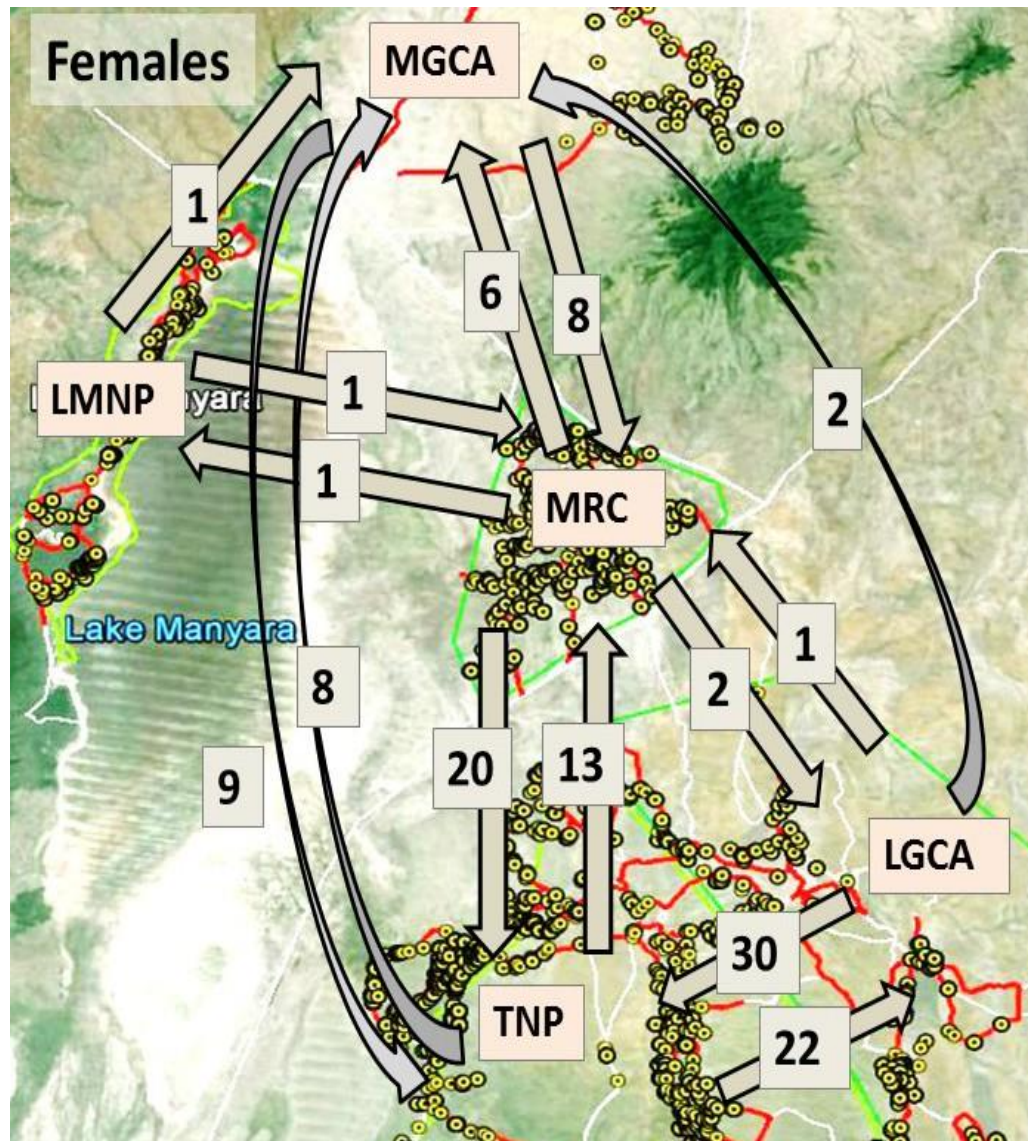
Figure 10. Annual flow of individual adult female giraffe among 5 sites in the Tarangire Ecosystem, Tanzania from 2012–2014. Calculated from per-capita movement rates and current population size in the origin site.
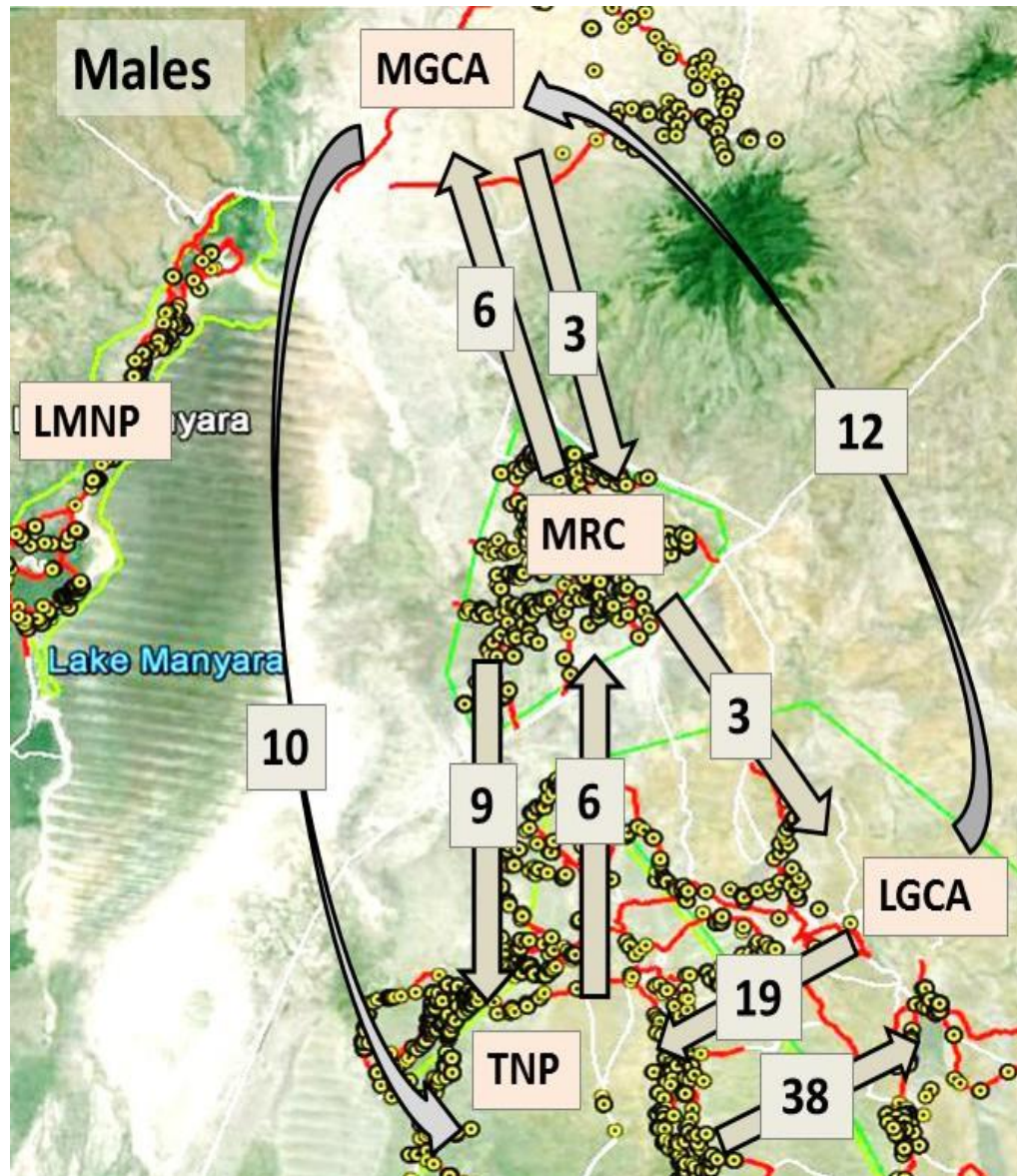
Figure 11. Annual flow of individual adult male giraffe among 5 sites in the Tarangire Ecosystem, Tanzania from 2012–2014. Calculated from per-capita movement rates and current population size in the origin site.

POPULATION PROJECTION AND ELASTICITIES

Population projections over 50 years from the multi-site matrix population model of current movement conditions described a shrinking metapopulation (*lambda* = 0.98), with population declines in all sub-populations (59–97%), but no sub-population ever became extinct within that time frame (Fig. 12, bottom). The multi-site matrix population model with no movement was a stable metapopulation (*lambda* = 1.00), but 3 sub-populations went extinct, while only the TNP population was stable (Fig. 12, top).

Our 2 population projections with random movement probabilities among sites both typically described decreasing populations (mean *lambda* = 0.97 and 0.98, for RAO and RWR models, respectively) with only 1% and 2% of simulations having *lambda* = 1. Significant correlations existed between *lambda* and specific transition movement rates in the simulation output from both random models. All possible regression analysis found the best descriptor of the variance in *lambda* included multiple transition rates. In the RAO model, *lambda* was negatively correlated with the sum of movement rates out of TNP (r^2 = 0.42). The best descriptor of variation in *lambda* for the RAO model was a 8-term model (F_{93}^{7} = 22.4, P < 0.001, r^2 = 0.63) that included 3 negative terms for movements out of TNP, 2 positive terms for movements out of LMNP, and 1 positive and 1 negative term for movements out of LGCA (Table 13). In the RWR model, *lambda* was positively correlated with movements out of LMNP (r^2 = 0.44), and the best descriptor of variation in *lambda* was a 10-term model (F_{91}^{9} = 65.9, P < 0.001, r^2 = 0.87) that included 3 negative terms for movements out of TNP, 2 positive and 1 negative term for movements out of LMNP, and 3 other positive terms (Table 14).

Elasticities computed for the current conditions multi-site matrix model indicated that adult survival in TNP was by far the largest elasticity parameter (0.44), followed by TNP juvenile survival (0.07), TNP fecundity (0.07), MRC adult survival (0.05), LGCA adult survival (0.02), movement from LGCA to TNP (0.02), and movement from TNP to LGCA (0.02). Mean elasticities computed from the random movements multi-site matrix population models were highest in adult survival parameters (RAO: TNP = 0.36, MRC = 0.09, LMNP = 0.08, LGCA = 0.02, MGCA = 0.01; RWR: LMNP = 0.23, TNP = 0.13, MRC = 0.07, LGCA and MGCA = 0.05) followed by juvenile survival and reproduction in TNP (0.05 and 0.02 in RAO and RWR, respectively). Random models' mean elasticities for movement rates were all small (≤ 0.02), but the highest elasticities for movement rates were for movements out of TNP.

Discussion

This study was the first assessment of sub-population and metapopulation growth and movement rates using individual-based demographic data for giraffe in a fragmented savanna ecosystem. We found significantly different population densities and population growth rates among sub-populations, along with significant variation in movements among sub-populations, leading to important implications for the future conservation and management of this metapopulation. Movements out of TNP, likely the only stable or growing sub-population, might avert local extinctions at 3 sub-populations over a 50 year timeframe, but reduced the overall metapopulation and would likely eventually result in total metapopulation extinction. Reducing all connectivity movements to zero might ensure a stable TNP sub-population, but would ensure all other sub-populations become

extinct and leave the sole remaining sub-population susceptible to stochastic events, such as disease outbreak, that could extirpate the population.
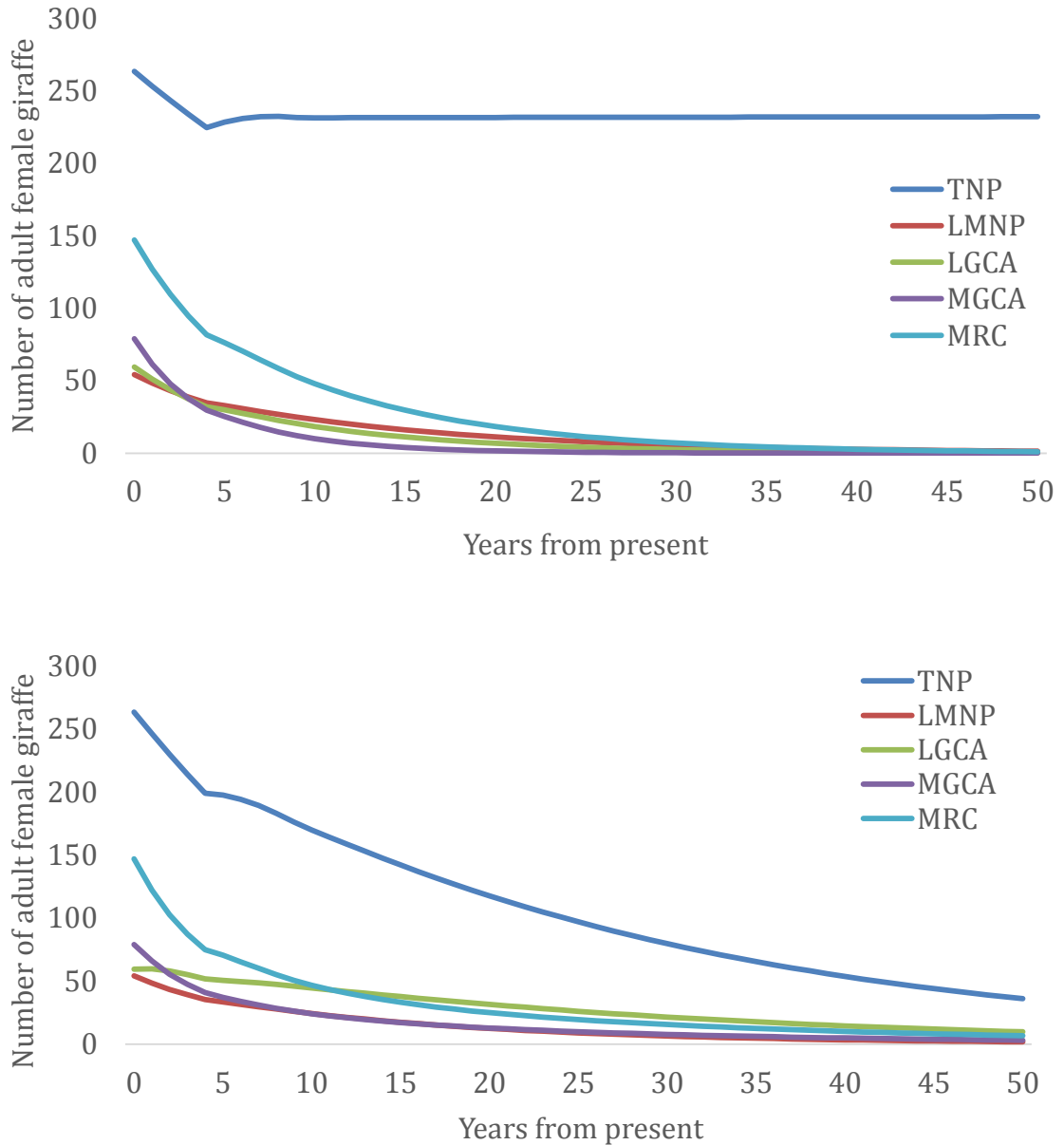
Figure 12. Graphs showing Tarangire adult female giraffe population projections for 50 years from present using multi-site matrix models with no movement (top) and with current among-site movement rates (bottom).

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POPULATION GROWTH RATES AND MOVEMENT PROBABILITIES

Sites with similar land-use designations such as the 2 national parks and 2 game controlled areas did not exhibit similar densities or population growth rates. In this ecosystem, shared land-use designations and management strategies seemed not to result in similar outcomes for giraffe sub-population parameters. Differences in density could indicate differences in habitat quality, typically explained by variation in food quality or predation pressure (Fryxell 1991, Brown and Kotler 2004), or a combination of both. In some species, high population density increases competition for resources (Crawley 1983), and can increase the incidence of attack by parasites (Crawley 1992) and pathogens (Wandeler et al. 1974). We found site-specific density was not correlated with *lambda* or movements, nor was it correlated with site-specific adult survival, calf survival, or reproduction (see Chapter 1), indicating that this system is likely below carrying capacity because density-dependent effects in ungulates often arise only when a population is near carrying capacity (Bonenfant et al. 2009). However, our result showing significant variation in population growth rates among sites supports previous work demonstrating how landscape heterogeneity leads to spatial variation in demography (Naranjo and Bodmer 2007, Contasti et al. 2013). Because we structured our analyses to remove movements between sites when estimating *lambda* directly from PCMR data, the population growth rates from the Pradel models were not influenced by movements among sites.

Our movement data documented that net flow of adult female giraffe in this system is largely into TNP from nearby LGCA and MRC. Our data identified TNP as the site with the highest mean fitness as measured by 2 methods of estimating population

growth rate, and source-sink parameters indicated TNP was a source area, but TNP was also the net recipient of individual movements. The adjacent LGCA was the only other site with a growing female population, and LGCA was the largest net exporter of females, mostly to TNP. These movements may indicate that habitat in TNP is particularly attractive to female giraffe but at present is below carrying capacity. Indeed, giraffe density in TNP was at the lower end of the observed range among sites (Table 9). The African elephant (*Loxodonta africana*) population in TNP has grown rapidly and steadily during the past decade with no evidence of density dependence, suggesting there is likely no local scarcity of megaherbivore browse (Foley and Faust 2010).

Flows of individual male giraffe showed a pattern somewhat different from the female pattern, specifically the net flow of males out of TNP and into the adjacent LGCA. It is possible that high adult male competition for reproductive females was driving younger, less competitive adult males out of TNP. Investigation into male age structure in the different sites could elucidate the reasons for male movement out of TNP.

Observed movement patterns in relation to sub-population growth rates indicate anthropogenic effects. Indeed, illegal hunting of giraffe for bushmeat is common in game controlled areas, particularly MGCA (C. Kiffner, *unpublished data*), and substantial numbers of livestock and humans were present in MGCA, MRC, and LGCA. Both poaching and high densities of humans and livestock may have resulted in low population growth rates in MGCA and MRC, and mediated net flow of females out of those areas and into the relative protection of TNP. Net flows of males were negative at MRC and MGCA as well.

LMNP had a relatively high density of giraffe but almost no net flow into or out of that park, suggesting that habitat fragmentation may have reduced the ability of giraffe to move through the intervening matrix between LMNP and the other sites. LMNP is naturally somewhat isolated by the Rift Valley Escarpment on one side, and on the other side by Lake Manyara, which forms a barrier in the wet season and a >10 km-wide muddy or alkali plain in the dry season that is devoid of woody browse (Fig. 2). Given the rapid expansion of the northern town of Mtowambu, and the intensive agricultural zones northeast and south of LMNP, habitat fragmentation likely negatively affected movement probabilities and has rendered the LMNP sub-population almost completely isolated (Msoffe et al. 2011). Morrison and Bolger (2012) found similar low connectivity for the LMNP wildebeest population. The near-complete isolation of this park and low intrinsic population growth rate of both sexes there suggest the need for immediate conservation measures to protect existing or re-establish historical movement pathways for giraffe between LMNP and other sites.

The current dominant engine of metapopulation growth in this system was clearly TNP. The size and productivity of this sub-population maintained the system as a whole, although overall λ^M <1.0. The contribution of LGCA was also important, but examination of the home ranges of animals in LGCA (D. Lee, *unpublished data*) revealed that many of these females in our sample spend time in both LGCA and TNP, effectively constituting a boundary-inhabiting population. These animals may benefit from their liminal existence by taking advantage of human suppression of predators outside the national park, as well as the protected status of the park and its vegetation.

A well-established tenet of population dynamics is that connectivity among sub-populations influences persistence (Hess 1996, Gilpin and Hanski 1991). Sub-population connectivity benefits viability via compensatory immigration (Turgeon and Kramer 2012), or the 'rescue effect,' where immigration averts a sub-population's extinction (Brown and Kodric-Brown 1977, Stacey and Taper 1992). Our results highlight the importance of connectivity movements among sub-populations of giraffe in the TE for maintaining viability of all sub-populations, particularly the vital role of TNP in sustaining sub-populations with lower local *lambdas* that may be functioning as 'attractive sinks' that deplete even the source population (Delibes et al. 2001). Movements into attractive sinks could result from individuals having incomplete knowledge of the fitness consequences of moving into the sink habitats where poaching is prevalent, resulting in significant sub-population declines even in the effectively protected source sub-population in TNP (Woodroffe and Ginsberg 1998, Gundersen et al. 2001). Continued monitoring will reveal whether increased anti-poaching efforts at MRC established in 2014 ameliorate local adult female survival there and convert the site from a sink to a source.

Our simulated population projections with random movements among all sub-populations showed that the entire metapopulation could be made to grow by increasing movement rates out of LMNP, and/or decreasing movement rates out of TNP. These management actions are unlikely, but demonstrate the importance of maintaining linkages among sub-populations, particularly sub-populations with high adult survival, and by improving efforts such as anti-poaching patrols and efforts to disrupt bushmeat markets to increase adult survival.

Our data represent one of the largest individually based demographic studies of a wild, free-roaming, large mammal ever conducted, both in terms of number of animals identified and geographic scope. However, our data should be considered preliminary, and we acknowledge that stochastic events could have influenced our results. It is also possible that some of the movements we observed were regular movements of individuals whose home range straddled 2 sites. This is most likely between LGCA and TNP because they are adjacent and share a long border, and TNP and MRC because they are relatively close. Seasonal shifts in use patterns could also explain the nearly balanced flow between pairs of sites. However, there was clearly net movement among sites, and even seasonal movements may impart fitness benefits mediated by access to critical resources (Pulliam and Danielson 1991, Rodenhouse et al. 1997). Additional analyses with longer-term data would illuminate the stability of our observed patterns, particularly whether changes in site population growth rates, densities, or survival affect movement patterns. An investigation of natal dispersal patterns also is important for understanding connectivity in this fragmented landscape (Driscoll 2007).

Studies of individually identified animals provide the highest-quality data for estimating population parameters, but are rare because of the time and expense of capture-mark-recapture methods (Clutton-Brock and Sheldon 2010). Such detailed data allow investigations into landscape-level processes to identify if and why local sub-populations are increasing or decreasing and how they are connected through individual movements. By directly estimating population growth rate and movements, we established which sites were sources and which were sinks. Cost-effective methods such as photographic mark-recapture that enable large sample sizes and produce precise

population parameters including density, abundance, movements, and *lambda* are

extremely useful for efficient monitoring and management of wildlife populations

(Yuccoz et al. 2001, Nichols and Williams 2006, Peters 2010, Contasti et al. 2013).

Tables

Table 7. Model selection results for lambda parameters from 2012–2014 in the

Tarangire Ecosystem, Tanzania.

Models	$\Delta qAICc$	W	K
Distance to Mtowambu	0	0.75	128
Site	2.38	0.23	130
Lion Density	7.65	0.02	128
Giraffe Density	16.73	0	128
Distance to Tarmac	21.51	0	128
Management	25.33	0	129
Constant	25.39	0	127
Poaching Pressure	25.82	0	128
Anti-Poaching	26.72	0	128
Human Density	27.15	0	128

Notes: *ΔqAICc* represents the difference between *qAICc* of a given model's and the

highest ranked model (Burnham and Anderson 2002). *qAICc Weights* (*W*) provide

relative likelihood of a given model and sum to 1.0. *K* is the number of parameters in

the model.

Table 8. Model selection results for giraffe movement parameters from 2012–2014 in the Tarangire Ecosystem, Tanzania.

Models	$\Delta qAICc$	W	K
Site	0	1	66
Management	222.56	0	49
Distance	228.01	0	48
Human Density	228.11	0	48
Anti-Poaching	242.36	0	48
Poaching Pressure	255.49	0	48
Distance to Mtowambu	281.47	0	48
Distance to Tarmac	298.33	0	48
Constant	307.50	0	47
Lion Density	308.36	0	48
Giraffe Density	309.51	0	48

Notes: *ΔqAICc* represents the difference between *qAICc* of a given model's and the highest ranked model (Burnham and Anderson 2002). *qAICc Weights* (*W*) provide relative likelihood of a given model and sum to 1.0. *K* is the number of parameters in the model.

Table 9. Estimates of sex-specific sub-population size (N), and density (N/km^2) for adult

Masai giraffe in 5 sub-units of the Tarangire Ecosystem, Tanzania 2012–2014.

Sub-population	area (km^2)	N	SE of N	density
Females				
Lolkisale GCA	175	79	5.9	0.45
Lake Manyara NP	65	64	2.1	0.98
Manyara Ranch	145	201	7.1	1.39
Mtowambu GCA	165	97	12.0	0.59
Tarangire NP	600	349	11.3	0.58
totals	1150	790		
Males				
Lolkisale GCA	175	42	6.4	0.24
Lake Manyara NP	65	28	2.1	0.44
Manyara Ranch	145	84	8.1	0.58
Mtowambu GCA	165	31	9.5	0.19
Tarangire NP	600	248	10.4	0.41
totals	1150	435		

Table 10. Seasonal probability of movement (*Psi*, ψ) for adult female and male Masai giraffe between pairs of sites in Tarangire Ecosystem, Tanzania 2012–2014. Sub-units are: L = Lolkisale GCA, S = Mtowambu GCA, T = Tarangire NP, R = Manyara Ranch, M = Lake Manyara NP.

Sites	Distance (km)	Female *Psi*	SE	Male *Psi*	SE
L to S	39	0.010	0.009	0.068	0.073
L to T	0	0.127	0.026	0.100	0.100
L to R	10	0.005	0.005	0	0
L to M	46	0	0	0	0
S to L	39	0	0	0	0
S to T	34	0.031	0.013	0.078	0.047
S to R	13	0.028	0.012	0.026	0.027
S to M	17	0	0	0	0
T to L	0	0.021	0.005	0.038	0.014
T to S	34	0.007	0.003	0	0
T to R	5	0.012	0.003	0.006	0.003
T to M	45	0	0	0	0
R to L	10	0.002	0.002	0.008	0.010
R to S	13	0.010	0.006	0	0
R to T	5	0.033	0.008	0.027	0.012
R to M	19	0.001	0.001	0	0
M to L	46	0	0	0	0
M to S	17	0	0	0	0
M to T	45	0	0	0	0
M to R	19	0.004	0.004	0	0

Table 11. Estimated annual flow of adult female and male Masai giraffe individuals out (emigration) and in (immigration) for 5 sites in the Tarangire Ecosystem, Tanzania 2012–2014.

Sub-population	Female		Male	
	Out	In	Out	In
Lolkisale GCA (L)	33.5	23.6	31.8	40.7
Lake Manyara NP (M)	0.8	0.9	0.0	0.0
Manyara Ranch (R)	28.3	23.1	11.3	9.4
Mtowambu GCA (S)	17.2	15.9	13.8	12.9
Tarangire NP (T)	42.7	59.1	44.1	38.0

Table 12. Source-sink identification parameters for 5 sub-populations of adult female Masai giraffe in the Tarangire Ecosystem, Tanzania 2012–2014. $\lambda Pradel$ is the estimated sub-population growth rate from capture-mark-recapture models (Pradel 1996). C^s is the per capita contribution of a member of each sub-population s to the metapopulation (Runge et al. 2006). $\hat{\tilde{c}}^s$ is the average relative contribution of each sub-population s to metapopulation growth, and $\hat{\tilde{c}}^0$ is the average relative contribution of immigrants from outside the metapopulation to metapopulation growth (Sanderlin et al. 2012).

	$\lambda Pradel$	C^s	$\hat{\tilde{c}}^s$
Lolkisale GCA	1.02	1.07	0.10
Lake Manyara NP	0.93	0.96	0.08
Manyara Ranch	0.96	0.99	0.26
Mtowambu GCA	0.94	0.97	0.09
Tarangire NP	1.01	1.00	0.47
$\hat{\tilde{c}}^0$			0.01

Table 13. Coefficients in the best descriptive regression model explaining variation in lambda across 100 simulations of the random among observed (RAO) matrix population model of adult female Masai giraffe in the Tarangire Ecosystem, Tanzania.

Term	Coefficient	SE	t	P
Intercept	0.98	0.002	443.37	<0.0001
T-M	-0.08	0.020	-4.09	<0.0001
T-L	-0.12	0.016	-7.74	<0.0001
T-S	-0.10	0.020	-5.11	<0.0001
M-T	0.07	0.019	3.91	0.0002
M-S	0.05	0.020	2.39	0.0188
L-M	0.07	0.017	4.10	<0.0001
L-S	-0.05	0.020	-2.63	0.0100

Table 14. Coefficients in the best descriptive regression model explaining variation in lambda across 100 simulations of the random within range (RWR) matrix population model of adult female Masai giraffe in the Tarangire Ecosystem, Tanzania.

Term	Coefficient	SE	t	P
Intercept	0.94	0.004	244.88	<0.0001
T-L	-0.05	0.018	-3.07	0.0028
T-S	-0.06	0.016	-3.61	0.0005
T-R	-0.05	0.019	-2.63	0.0101
M-T	0.22	0.018	12.24	<0.0001
M-S	0.26	0.018	14.69	<0.0001
M-R	-0.07	0.017	-4.21	<0.0001
L-M	0.18	0.017	10.39	<0.0001
S-M	0.17	0.020	8.81	<0.0001
R-T	0.05	0.018	2.90	0.0047

CHAPTER 3.

SEASONAL REPRODUCTIVE TIMING AND JUVENILE

SURVIVAL OF GIRAFFE

Reproductive synchrony is the tendency of individuals to carry out some aspect of their reproductive cycle at the same time as other members of the population, and is widespread in the plant and animal kingdoms (Ims 1990). Seasonal changes are cyclic, generally predictable sources of environmental variation and are arguably the most ubiquitous external variation in natural systems (Fretwell 1972). Mammalian herbivores in temperate regions generally give birth during a short period that coincides with the spring flush of nitrogen-rich plant growth (Asdell 1964, Bunnell 1982, Bronson 1985), and births outside the summer season are typically not viable due to extreme winter cold (Stearns 1992, Langvatn et al. 2004). In tropical regions, however, births are thermally viable in all seasons due to mild year-round temperatures, thus asynchronous (the opposite of synchronous) reproduction is the norm. Asynchronous reproduction is considered the ancestral state of ruminants, but synchrony has evolved in both temperate and tropical climates (Rutberg 1987, Jabbour et al. 1997, Zerbe et al. 2012).

Timing of reproduction can be an important factor affecting juvenile survival of temperate and boreal ungulates. Survival rates of newborns that are born early or late in the spring (asynchronous from the regional birth pulse) are reduced for many northern species (bighorn sheep, *Ovis canadensis*, Sugden 1961, Festa-Bianchet 1988; caribou, *Rangifer tarandus,* Kelsall 1968, Dauphine and McClure 1974, Nowosad 1975; Dall's sheep, *Ovis dalli*, Bunnell 1980; red deer, *Cervus elaphus*: Clutton-Brock et al. 1982, 1983; and other species, Sadleir 1969, Slee 1971, Santiago-Moreno et al. 2006).

However, other studies have found no effect of birthdate outside the local birth pulse on juvenile survival of temperate ungulates (pronghorn, *Antilocapra americana*, Fairbanks 1993; moose, *Alces alces*, Bowyer 1998; elk, *Cervus elaphus,* Smith and Anderson 1998; mountain goat, *Oreamnos americanus*, Cote and Festa-Binachet 2001; saiga antelope, *Saiga tatarica*, Buuveibaatar et al. 2013). Synchronous births also can lower offspring survival in the presence of a prey-switching predator (roe deer, *Capreolus capreolus*, Aanes and Anderson 1996).

Variation in juvenile survival plays an important role in population dynamics of ungulates (Coulson et al. 1997, Gaillard et al. 2000, Petorelli et al. 2005). For example, juvenile survival is consistently lower and more sensitive to environmental variation than adult survival in populations of large herbivores (Gaillard et al. 2000, Eberhardt 2002, Gaillard and Yoccoz 2003, for reviews). Variation in juvenile survival also often explains a large part of the variance in their parents' lifetime reproductive success (Clutton-Brock et al. 1988) and other fitness measurements (Gaillard et al. 1998). Identifying the sources of variation in early survival therefore constitutes a major issue for both evolutionary ecologists and land managers. Juvenile survival can be regulated by bottom-up (vegetation) or top-down (predation) selective forces (Cote and Festa-Bianchet 2001), but few studies have examined the factors affecting juvenile survival in tropical ungulates.

Reproductive synchrony is adjusted through estrus timing (Berger 1992), mediated by maternal condition (Ryan et al. 2007), and may be selected for via reduced juvenile survival in asynchronous individuals (Findlay and Cooke 1982, O'Donoghue and Boutin 1995). Recent studies of reproductive synchrony indicate that timing and synchrony of parturition in large mammals is primarily regulated by climate, and only

secondarily by predation on newborns (Bowyer et al. 1998, Post et al. 2003, Moe et al. 2007, Barber-Meyer et al 2008, Ogutu et al 2010). However, most investigations into breeding synchrony and asynchrony have focused on small deviations from a generally synchronous birth pulse in temperate-zone populations. Breeding generally becomes less synchronous with decreasing latitude (Bronson 1989, Zerbe et al. 2012), and although the vast majority of the world's ungulate species live in the tropics and sub-tropics, few studies have investigated the demography of large tropical herbivores (Owen-Smith and Marshall 2010). Tropical latitudes also exhibit clear seasonal peaks in herbivore food supply and quality, usually determined by the onset of seasonal rainfall patterns (Rutherford 1980, Desmukh 1984, Ogutu et al. 2007, Wittemyer et al. 2007), and although most species of tropical ungulates give birth year-round, most have a more or less distinct seasonal birth pulse (Owen-Smith and Ogutu 2013). Giraffe (*Giraffa camelopardalis*) provide a tropical, asynchronously breeding case study for testing reproductive synchrony/asynchrony hypotheses in comparison with temperate ungulate demography studies.

Our objective here was to determine whether and when pulses in birth synchrony occur in wild giraffe in the Tarangire Ecosystem (TE) of northern Tanzania, East Africa by examining timing of 408 births during 3 precipitation seasons over 2 years. Previous research in the Serengeti Ecosystem of Tanzania suggested giraffe there may exhibit a small birth pulse during the phenological protein peak of *Acacia* trees (Sinclair et al. 2000). We investigated whether a birth pulse was evident in the TE, indicating some level of reproductive synchrony within the broader asynchronous strategy. To elucidate possible causes and consequences of birth synchrony and asynchrony, we estimated

juvenile survival according to birth season to see whether calf survival was higher, lower, or the same for calves born during versus outside the birth pulse, if such a pulse were observed. The relative survival of juveniles born during versus outside any observed birth pulse indicates whether phenological match, predator avoidance, or temporal resource partitioning mediates some level of synchrony or asynchrony in this species (Fig. 13; see also "synchrony and asynchrony" below).

This system has large seasonal variation in ungulate biomass and predation pressure as migratory herds of thousands of wildebeest (*C. taurinus*) and zebra (*Equus quagga*) move between wet and dry season ranges, and predators follow or commute to access these herds. Therefore, to examine whether and how this change affects giraffe calf survival and is a factor mediating birth synchrony or asynchrony, we constructed spatio-temporal covariate models of lion density, alternative prey density, and lion predation pressure.

SYNCHRONY AND ASYNCHRONY

Three hypotheses have been offered as explanations for the evolution of birth synchrony in wild ungulates: (1) "phenological match" is timing births to coincide with periods of optimal resource conditions such as the protein concentration peak at the beginning of the growing season (Rutberg 1987); (2) "predator swamping" reduces the individual probability of being predated upon (Darling 1938, Kruuk 1964, Estes 1976, Puliam and Caraco 1984, Ims 1990a); and (3) "optimization of social development" maximizes the number of like-age playmates and learning opportunities (Brown 1985, Pfeifer 1985).

The evolution of reproductive asynchrony (the opposite of synchrony) may be explained by (1) "temporal resource partitioning" among sympatric adult females to share food resources during gestation and lactation (McShea 1989, Ims 1990b); (2) "predator avoidance" to reduce the probability of detection of vulnerable neonates (Ims 1990b); and (3) "optimal mate choice" which permits females to choose from a larger pool of male mates (Ims 1988). These hypotheses are not mutually exclusive, so two or more may be operating simultaneously. Here, we only considered synchrony hypotheses of phenological match and predator swamping, but not social development. Asynchrony hypotheses we considered here were temporal resource partitioning and predator avoidance, but not mate choice.

In most mammals, the timing of reproduction is primarily determined by seasonal peaks in protein availability during late gestation and early lactation, the most energetically demanding period for reproductive females (Oftedal 1984, Rutberg 1987, Sinclair et al 2000). "Phenological match," or timing reproduction to coincide with seasons of maximum resource quality can increase juvenile survival and therefore increase lifetime reproductive success (Pianka 1976, Kennish 1997, Langvatn et al. 2004). There are 2 periods of elevated protein concentration in the TE and phenological match could occur during either one or both. Protein concentration in *Acacia* trees peaks at the end of the dry season, when *Acacia* trees flush with new growth in anticipation of the coming short rains. Protein concentration in all non-*Acacia* woody plants is highest during the early growing season at the beginning of the short rains. Protein concentration declines in all woody plants as biomass increases during the long rains (Pellew 1984).

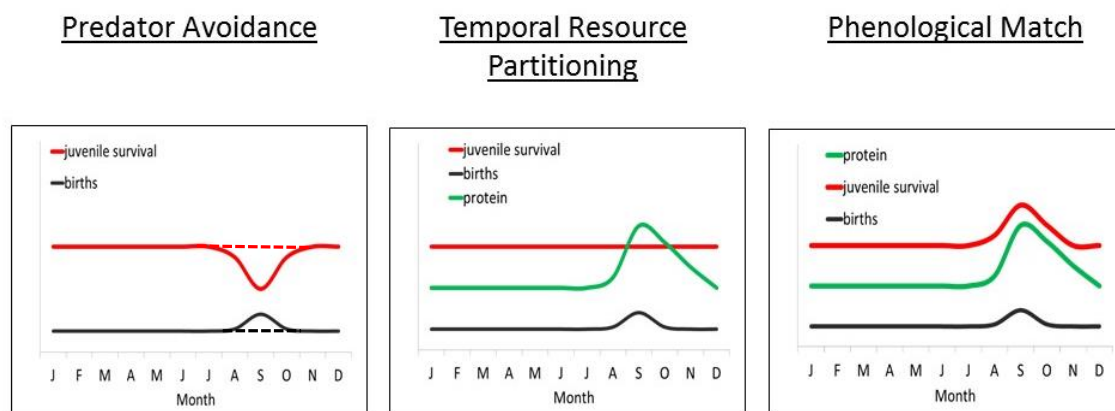| Predator Avoidance | Temporal Resource Partitioning | Phenological Match |

Figure 13. Diagrams illustrating competing hypotheses of how juvenile survival should respond to instances of birth synchrony in a generally asynchronous breeder. Left: Number of births and juvenile survival should both be constant over time (dashed lines), but if a birth pulse occurred by chance, a negative correlation between number of births and survival of juveniles born in that season would support the predator avoidance theory of asynchrony. Center: No change in juvenile survival during a birth pulse due to a resource peak would indicate temporal resource partitioning theory of asynchrony. Right: Positive correlation between protein concentration, number of births, and survival of juveniles born in a given season would support the phenological match hypothesis of synchrony.

"Temporal resource partitioning" asynchrony could be an adaptation to limited resources where individual females' resource requirements oscillate during the reproductive cycle. When resources are limited but available year-round and associated females can readily exchange socially mediated cues, fitness of sympatric females might be enhanced if they reproduce out of synchrony with each other to temporally partition resources (McShea 1989). Competition for resources needed to support more than one

breeding female giraffe would be reduced if parturition dates were staggered so that they reached the later stages of lactation (the most energetically demanding) at different times. Giraffe meet the assumptions for testing this hypothesis because females can breed year-round, and form fission-fusion associations (Shorrocks and Croft 2009, Carter et al. 2013), enabling the exchange of pheromonal reproductive stimuli (Ims 1990).

"Predator avoidance" asynchrony posits that reproductive timing could be influenced by mortality regimes induced by predators, as determined by the behavior and spatial distribution of predators and prey (Ims 1990, Sinclair et al. 2000). "Predator avoidance" asynchrony reduces risk of offspring predation when predators target prey according to their relative abundance and accessibility (Aanes and Andersen 1996) and should be favored in species such as giraffe that hide their newborn young and are not sufficiently abundant to "swamp" predators (Ims 1990, Sinclair et al. 2000). Lions and hyenas are generalist predators that consume juvenile giraffe and other prey according to accessibility (Hayward and Kerley 2005, Hopcraft et al. 2005, Owen-Smith and Mills 2008). Our study area encompasses 5 distinct but connected sites with spatio-temporally contrasting levels of lion density and alternative prey density, offering an opportunity to examine how these covariates affect reproductive timing and juvenile survival thus supporting one or more of these hypotheses.

Methods

DATA COLLECTION

We collected giraffe data and created individual encounter histories for analysis as described in Chapter 1. We only utilized data from newborn calf-age animals born in the 4-mo interval before each survey.

Lion densities were computed from lion location data collected in TNP, LGCA, and MRC during 2010–2013. All lion prides in northern TNP and adjacent areas of LGCA have been identified and monitored regularly since 2003 (Packer et al. 2010). B. Kissui attempted to locate all known lion prides and individuals in TNP, LGCA, and MRC every 2 weeks using regular surveys, radio collars, GPS collars, and ancillary information from national parks staff, tourism operators, and local informants. LMNP has monitored lion prides since 2005 during monthly surveys of all large mammals with ancillary information from national park staff, tourism operators, and local informants. Lion density in MGCA was estimated from irregular surveys of the area by professional hunting operators augmented with estimates from LGCA with similar habitat and land-use management. Seasonal site-specific densities of alternative lion prey (wildebeest, zebra, and buffalo, *Syncerus caffer*) were computed from road transect distance-sampling surveys we performed during giraffe surveys. Covariate values were combined density (number of individuals per km^2) of all alternative prey species rounded to the nearest 5.

PREDATION COVARIATES

Our covariate model set included models of lion density, alternative prey density, and lion predation pressure (lion density / prey density). Table 15 presents the spatio-temporal covariates of lion predation used in model selection. Three sites (NPs and MRC) have higher lion densities due to active predator protection policies. Trophy hunting and pastoralist activities in 2 GCA sites resulted in lower lion and hyena densities in these sites (Davidson et al. 2011, Kolowski and Holcamp 2009). Large herds of alternative prey species (~ 20,000 wildebeest, zebra, and buffalo) migrate seasonally into TNP in the dry season, and out of the study area during the long rains. This migration

attracts some predators out of TNP and into LMNP and the 2 GCAs, while MRC

maintains a relatively constant prey and predator population. A covariate of lion

predation pressure on giraffe calves was computed by dividing the density of lions by the

density of alternative prey.

REPRODUCTION ANALYSIS

We computed seasonal reproduction (calves / adult female) using known

population size of adult females as the denominator, and the number of newborn calves

(aged 0–3 months) detected during each seasonal survey (corrected for site- and season-

specific capture (p) probabilities, and survival ($\sqrt{S_1}$) between birth and first PCMR

encounter) as the numerator. We analyzed seasonal reproduction rates using generalized

linear models with a Poisson distribution and log link function to determine mean

seasonal birth distribution among all years and sites.

SURVIVAL ANALYSIS

We modeled and estimated parameters using Pollock's (1982) robust design

statistical models in program MARK 7.1 (White and Burnham 1999). We modeled and

estimated probabilities of capture (p), recapture (c), survival (S), and temporary

emigration parameters (γ' and γ''). We tested goodness-of-fit using U-CARE (Choquet et

al. 2009), and adjusted for lack of fit by adjusting $\hat{c} = \chi^2/\text{df}$ (Choquet et al. 2009, Cooch

and White, *unpublished*). Throughout model ranking and selection procedures, we ranked

models using qAICc and used model qAICc Weights (*W*) as a metric for strength of

evidence supporting a given model as the best description of the data (Burnham and

Anderson 2002). Due to model selection uncertainty, we present only model-averaged

parameter values and based all inferences on these model-averaged parameters (Burnham

and Anderson 2002). We considered covariates to be statistically significant if the 95%

confidence interval of the beta coefficient did not include zero.

We began with the most fully parameterized model in our set. Our most-

parameterized model included survival as a linear effect of calf age, varying categorically

by site, by birth season, and by season, and with site and time effects in all other

parameters: {S(age + site + birth season + season) γ'(site × time) γ''(site × time) p(site +

event + season) c(site + event + season)}. In young ungulates, survival generally

increases with age (Gaillard et al. 2000) and may also differ by sex (Clutton-Brock et al.

1985). Preliminary analyses indicated that age, but not sex, was a significant factor in

juvenile giraffe survival.

We first ranked competing models with reduced temporal complexity of

detectability parameters (p and c), and temporary emigration parameters (γ' and γ''). Once

the most parsimonious form of detectability and temporary emigration parameters was

obtained, we ranked 7 additional models of survival with site, birth season, and seasonal

effects (Table 16). During survival model selection, we kept detectability and temporary

emigration parameters in their most parsimonious form, and including age and sex effects

on survival throughout. The *site* effect modeled survival as site-specific in all 5 sites.

Season modeled survival different in each of the 3 seasons (short rains, long rains, and

dry). *Birth season* is a cohort-like intercept effect where all calves born in a given season

(short rains, long rains, and dry) have similar survival probabilities throughout their lives.

We also ranked a *constant* model with no effects of site, season, or birth season. Finally,

we ranked survival models with spatio-temporal covariates of browse protein, lion

density, alternative prey density, and lion predation pressure during birth season and subsequent seasons.

SIMULATIONS OF PHENOLOGICAL MATCH-MISMATCH

We examined the costs and benefits of phenological match using simulated life histories of adult female giraffe over their reproductive lifetime. We computed lifetime reproductive success (LRS) as number of calves surviving to age 1 year for mothers who reproduced according to 2 schedules of intercalf intervals (ICI): the mean intercalf interval (ICI = 20 months); and mothers who delay reproduction to give birth to every calf during the short rains (ICI = 24 months). We assumed mothers in both reproductive schedules lived 10 years as reproductive adults and both gave birth to their first calf in January (during the short rains). Calves survived to age 1 year according to the birth-season-specific estimated probabilities of survival (see Results). We used these simulations to determine what level of calf survival during the short rains was required to make LRS ICI_{24} > LRS ICI_{20}.

Results

We analyzed 408 encounter histories for individually identified neonatal calves. Seasonal variation in reproduction was significant (Fig. 14; $F_{32}^2 = 4.29$, $P = 0.031$), with fewer births in the long rains (0.23 ±0.02), and more births during the short rains (0.39 ±0.02) and the dry season (0.38 ±0.02).

We found evidence for lack of fit in encounter history data ($\chi_{62}^2 = 97$, $P = 0.006$), so to account for model selection uncertainty we adjusted $\hat{c} = 1.5$. Survival modeling indicated evidence for variation due to birth season (Table 16). Compound probabilities of survival (estimated using model-averaged parameters of models in Table 16) up to 1

year old for calves born in each of the 3 seasons indicated that calves born during the short rains had a slightly higher probability of surviving to 1 year of age (0.53 ±0.08), relative to those born during the long rains or dry season (0.43 ±0.08), but the effect was not statistically significant (Fig. 14).

Spatio-temporal covariate models of calf survival (Table 17) found that local density of alternative prey was positively correlated with calf survival (alternative prey β = 0.028, SE = 0.017, 95% CI: -0.005 to 0.061). This top-ranked model was 3 times more likely to be the best in the set than the second-ranked model (Table 17), but the covariate effect was not statistically significant (95% CI includes zero).
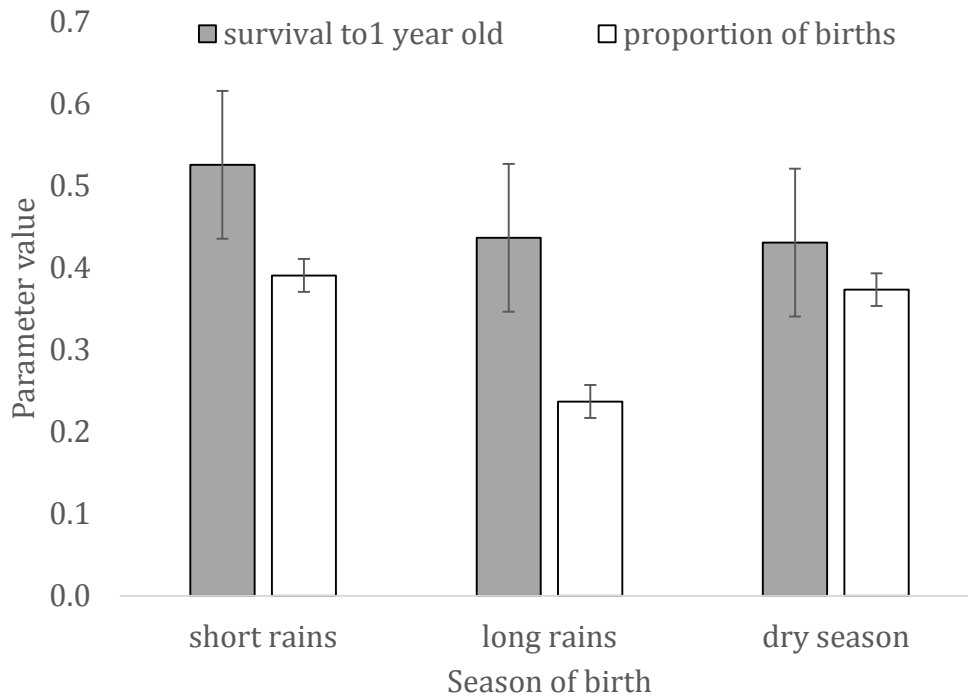

Figure 14. Probability of survival from birth to 1 year old for giraffe calves born during 3 precipitation seasons as computed from compound seasonal survival rates estimated using model-averaged parameters of models in Table 16.

Match-mismatch simulations using observed birth-season-specific survival rates (0.53 and 0.43) indicated the ICI_{20} mothers had 3 calves in the short rains and 4 in other seasons, while ICI_{24} mothers had 6 calves all in the short rains resulting in ICI_{20} having higher LRS than ICI_{24} mothers (LRS: ICI_{20} = 3.31; ICI_{24} = 3.18). Increasing survival of calves born in the short rains to 0.58 changed the outcome so LRS ICI_{24} > LRS ICI_{20} (LRS: ICI_{20} = 3.46; ICI_{24} = 3.48). This survival rate for calves born in the short rains is within 1 SE of the observed estimate.

Discussion

SYNCHRONY AND SURVIVAL

We found evidence that this population of giraffe exhibited 2 seasonal pulses in reproduction, one during the short rains and another during the dry season. Calves born during the reproductive pulse in the short rains have higher survival probability relative to calves born in other seasons. This positive correlation between seasonal births and juvenile survival supports the "phenological match" theory of reproductive synchrony (Fig. 13), with the season of highest survival occurring when protein content was highest for non-*Acacia* woody browse species. Calves born during the second birth pulse in the dry season had equivalent survival to calves born during the long rains, which is the signal for "temporal resource partitioning" theory of asynchrony (Fig. 13).

Phenological match describes offspring born in the season when high-quality food is abundant (Rutberg 1987, Sinclair et al 2000). In tropical and subtropical areas, ungulate birth peaks may coincide with seasonal rainfall and the subsequent appearance of green foliage (Owen-Smith and Ogutu 2013), but an advantage in juvenile survival has not been previously demonstrated for tropical phenological match. Our giraffe data

suggest that phenological match does confer a juvenile survival advantage to offspring of tropical ungulate browsers born during the early growing season protein peak for non-*Acacia* woody plants.

Temporal resource partitioning reduces competition for local browse resources needed to support multiple breeding female giraffe if parturition dates are staggered such that they reach the most energetically demanding stage at different times. The local giraffe population in the TE is likely below carrying capacity because density-dependent effects are not apparent (Chapters 1 and 2), and the local African elephant (*Loxodonta africana*) population has grown rapidly and steadily during the previous decade, and continues to grow with no evidence of density dependence (Foley and Faust 2010, C. Foley, *unpublished data*), indicating there is currently no local scarcity of megaherbivore browse. However, over evolutionary time, the strongest selective forces would be acting during periods when the giraffe population was at or near carrying capacity and browse resources were scarce, and those conditions could have shaped the temporal resource competition adaptation for asynchrony. Further study of whether females with overlapping home ranges have lower synchrony of reproduction than females that do not share resources would shed light on this topic.

The positive relationship we found between seasonal number of births and calf survival does not rule out predator avoidance as another factor influencing giraffe reproductive asynchrony. The negative effect of predation during the birth peak could be present, but masked by the positive survival effect of birth season due to vegetation quality. Similarly, the equal survival of calves born during long rains and dry seasons

could also include predation effects that, if removed, would result in higher survival during one of those seasons.

PREDATION

We found seasonal calf survival was positively correlated with local density of wildebeest, zebra, and buffalo during post-natal seasons. The seasonal availability of alternative prey can modulate the predation experienced by giraffe via the predator's behavior (Holt 1977, Holt and Lawton 1994). The positive survival effect of local ungulate density on giraffe calf survival could therefore be due to predator swamping through dilution or prey switching (Estes 1976, Sekulic 1978, Estes and Estes 1979, Testa 2002). However, local lion density was not a good correlate of calf survival, nor was lion predation pressure, perhaps illustrating the importance of hyena predation in this population. Local lion prides often develop specialized hunting tactics and target species, so broad measures such as lion density may not accurately reflect true lion predation pressure due to the behavioral variation in hunting strategies among lion prides (Hayward and Kerley 2005).

MATCH-MISMATCH

Interbirth interval is one of the most variable aspects of a female giraffe's lifetime fitness. The coefficient of variation in interbirth interval is 25% in captive, and 27% in wild giraffe, and is largely determined by length of time between parturition and conception (Bercovich et al. 2004, Bercovich and Berry 2009). Giraffe have a 20-month intercalf interval, so subsequent births are one season earlier than the previous birth, and mothers who delay conception would reduce their lifetime reproductive output. On the other hand, females whose previous calf was born during the short rains may benefit from

delaying estrous in order to synchronize their next pregnancy with the short rains calf survival peak. The presence in the TE of a giraffe birth pulse, together with the large potential for individual variation in time between parturition and estrous suggests that some giraffe may be delaying estrous to achieve phenological match between their calf's birth and the short rains survival peak.

Population simulations indicate that mothers who delay estrous to give birth to every calf during the short rains (ICI_{24}) will have slightly lower lifetime reproductive success than mothers who reproduce according to the mean reproductive schedule (ICI_{20}), if birth-season-specific calf survival is the mean estimated value. However, survival of calves born during the short rains needs to be only 0.58 (versus the mean 0.53) before mothers delaying to achieve phenological match would achieve higher lifetime reproductive success. Thus, our observed variation in survival of giraffe calves born in the short rains is theoretically sufficient to confer some LRS advantage to mothers who delay birth timing. Additionally, if giraffe suffer any costs of reproduction, ICI_{24} mothers that delay might also benefit from achieving the same LRS with 1 fewer birth during their lifetime relative to ICI_{20} mothers.

However, the timing of the birth pulse is determined many months earlier when females undergo estrous cycling, mate, and conceive. Several studies have demonstrated a correlation between rainfall, animal condition, or resource availability during the time of conception with the timing of mating or births (Estes 1976, Adams and Dale 1998, Post 2003, Moe et al. 2007, Ryan et al. 2007, Ogutu et al. 2010, 2011, Burthe et al. 2011). Giraffe may be adjusting estrous based upon climatic cues during the rains (Hall-Martin et al. 1975). Periodic reproduction triggered by resources, particularly rainfall events, is

considered the least understood phenomenon in mammalian seasonality (Bronson 2009).

Adult female giraffe likely are in optimal condition during the long rains, when browse

biomass is at maximum (Pellew 1984), particularly if the previous years' precipitation

was below average. East African elephants, another mega-herbivore species with a long

mean intercalf interval (ca. 4.5 years) and year-round calving, exhibit condition-

dependent conception mediated by rainfall-dependent primary productivity anomalies

(Wittemyer et al. 2007). Conception in giraffe is also dependent on maternal condition,

and may be mediated by browse biomass in a manner similar to that documented for

elephants (Hall-Martin et al. 1975). Thus, any period of extended drought that reduces

maternal condition such that many adult females are unable to breed until the drought

ends could result in a synchronous return to condition and estrous with a subsequent

synchronous birth pulse during the short rains.

CONCLUSIONS

This study documented seasonal variation in giraffe calf production and calf

survival, potentially mediated by seasonal changes in vegetation quality. Our covariate

models focused on predation, but none of the covariates were significantly correlated

with observed patterns of calf production and survival. This implies that seasonal

variation in vegetation characteristics, rather than natural predation, is the most likely

proximate mechanism underlying the observed patterns in giraffe reproduction. However,

there was some evidence that the presence of large migratory herds of alternative prey

might increase local calf survival, perhaps due to predator swamping or prey switching.

These migratory herds are threatened by increasingly restricted connectivity between

calving grounds and dry-season range along the Tarangire River (Morrison and Bolger

2012). Therefore, it is conceivable that if wildebeest, zebra, and buffalo populations crash as a result of disrupted migrations, then giraffe calves might face increased predation pressure from local lions and hyenas responding to reduced availability of large ungulate biomass. Asynchrony is believed to be the ancestral state of all ungulates (Zerbe et al. 2012), and this investigation has illustrated how seasonal variation in vegetation quality and predation pressure may both play a role in the evolution of synchronous births.

Tables

Table 15. Spatio-temporal covariates of lion predation and alternative prey densities in 5 sites and across 3 seasons.

	LMNP	MRC	TNP	LGCA	MGCA
Lion density					
Dry	20.5	14	9.3	1.4	1.4
short rains	22.5	14	8.3	1.4	1.4
long rains	22.5	14	8.3	2.4	2.4
Alternate prey density					
Dry	10	15	100	0	0
short rains	5	15	0	10	10
long rains	5	15	0	15	15
Predation pressure					
Dry	2	1	0.01	1	1
short rains	5	1	10	0.1	0.1
long rains	5	1	10	0.2	0.2

Table 16. Selection results for spatio-temporal models of survival of 408 neonatal giraffe in Tarangire Ecosystem, Tanzania 2012–2014. The *site* effect modeled survival as site-specific in all 5 sites. *Season* modeled survival different in each of the three seasons (short rains, long rains, and dry). *Birth season* is a cohort-like effect where all calves born in a given season (short rains, long rains, and dry) have similar survival probabilities throughout their lives. The *constant* model has no effects of site, season or birth season. All models included the additional effect of *age* in survival, and *site* and *time* effects in detectability and temporary emigration parameters in the form {S(age) $\gamma' = \gamma''$ (constant) p = c(site + sampling event + season)}.

Model #	Survival Models	ΔqAICc	W	k
1	birth season	0	0.27	72
2	season	0.26	0.24	72
3	constant	0.43	0.22	69
4	birth season + season	0.83	0.18	75
5	site + birth season	3.28	0.05	77
6	site + birth season + season	4.32	0.03	80
7	site + season	6.77	0.01	77
8	site	7.10	0.01	74

Table 17. Selection results for covariate models of lion predation pressure on survival of neonatal giraffe. Data from 408 neonatal calves in Tarangire Ecosystem, Tanzania 2012–2014. *Alternative prey density* modeled calf survival as a function of the local density of wildebeest and zebra, *lion density* modeled survival as a function of local lion density. *Lion predation pressure* modeled survival according to predation pressure (*lion density / alternative prey density*). *Birth season*, *season*, and *constant* are as described in Table 16. All models included the additional effect of *age* in survival, and *site* and *time* effects in detectability and temporary emigration parameters in the form $\{S(\text{age}) \, \gamma' = \gamma''(\text{constant}) \, p = c(\text{site} + \text{sampling event} + \text{season})\}$.

Model #	Model	ΔAICc	W	K
1	alternative prey density	0	0.54	70
2	birth season	3.22	0.10	72
3	season	3.48	0.09	72
4	constant	3.66	0.09	69
5	birth season + season	4.06	0.07	75
6	lion predation pressure	5.60	0.03	70
7	lion density	5.79	0.03	70

CONCLUSIONS

I found that my study area in the Tarangire Ecosystem was a spatially structured metapopulation of giraffe with significant variation in adult survival, reproduction, density, and lambda among sub-populations. Spatial covariate models for adult female survival and reverse-time lambda indicated that covariates associated with poaching explained some of this spatial variation. I found site-specific density was not correlated with lambda, movements, adult survival, calf survival, or reproduction, indicating that this system is likely below carrying capacity; density-dependent effects in ungulates often arise only when a population is near carrying capacity (Bonenfant et al. 2009).

The dominant paradigm for ungulate population dynamics over time holds that adult female survival has the highest elasticity, but its low variation causes it to contribute relatively little to changes in the population growth rate compared to juvenile survival or reproduction, which have low elasticities but high temporal variation, making them the primary determinant of realized population change (Gaillard et al. 1998, 2000, Gaillard and Yoccoz 2003, Raithel et al. 2007). I found that spatial variation of demographic estimates from generally stable giraffe populations in National Parks across the continental range of the species did follow the temporal demographic paradigm. In contrast, in the fragmented TE region I found adult female survival was highly spatially variable and significantly correlated with population growth rate. My data support other studies on long-lived species that documented population declines associated with decreases in adult survival (Wehausen 1996, Flint et al. 2000, Rubin et al. 2002, Pistorius et al. 2004, Wittmer et al. 2005, Nilsen et al. 2009, Johnson et al. 2010).

Multiple analyses pointed to TNP as the engine of this metapopulation, with movements among sites maintaining linkage among all sub-populations. Those movements had important implications for the future of this metapopulation and its management. The rescue effect of TNP insulates all sub-populations from short-term extinctions, but would eventually result in a metapopulation crash as the sink sub-populations deplete the source. At the same time, having multiple linked sub-populations increases the resilience of the metapopulation to stochastic catastrophes by hedging extinction risk among multiple sub-populations. The loss of all linkage movements could grow the metapopulation over the medium term, but would create effectively a single population in TNP that holds the only giraffe in the landscape.

Based on my results, for conservation of the species and the large-scale processes of giraffe interactions across the landscape, I recommend efforts to reduce poaching and disrupt bushmeat markets to bring down harvest rates of adult females to sustainable levels, while simultaneously maintaining or improving linkage habitat between all sites to facilitate natural movements. This should increase adult survival to the point where sink sub-populations are less of a drain on the metapopulation, and having multiple linked, healthy sub-populations reduces the risk of total extinction. Identifying source and sink habitats using PCMR methods is far superior to monitoring via abundance or density estimates because when managers understand movements and population growth rates, they can effectively prioritize actions to ensure the security of sources while addressing the causes of sinks (McCoy et al. 1999, Schwartz et al 2010).

Conservation of the Masai giraffe in the Tarangire Ecosystem will likely require the cooperation of all stakeholders from Wildlife Division (who conduct anti-poaching

patrols on Game Controlled Areas), National Parks, private landowners, and village leadership, to enhance population growth rates in MGCA and MRC and maintain or enhance habitat connectivity throughout this fragmented landscape. Anti-poaching strategies employed by Tarangire and Lake Manyara national parks appear to be effective in protecting adult female giraffe at these sites, and this model could be expanded to areas outside the parks. Giraffe are important to savanna ecosystems because the presence of browsers benefit *Acacia* growth and survival (*sensu* Palmer et al. 2008), and maintaining landscape connectivity for giraffe, a non-migratory, charismatic, keystone and flagship species, would also benefit threatened migratory species and preserve ecosystem integrity and functions (Crooks and Sanjayan 2006, Morrison and Bolger 2014).

I found evidence that this population of giraffe exhibited 2 seasonal pulses in reproduction, one during the short rains and another during the dry season. Calves born during the reproductive pulse in the short rains have higher survival probability relative to calves born in other seasons. This positive correlation between seasonal births and juvenile survival supports the "phenological match" theory of reproductive synchrony, with the season of highest survival occurring when protein content was highest for non-*Acacia* woody browse species. Calves born during the second birth pulse in the dry season had equivalent survival to calves born during the long rains, which is the signal for "temporal resource partitioning" theory of asynchrony. I also found seasonal calf survival was positively correlated with local density of wildebeest, zebra, and buffalo during post-natal seasons. The seasonal availability of alternative prey can modulate the predation experienced by giraffe via the predator's behavior (Holt 1977, Holt and Lawton 1994). The positive survival effect of local ungulate density on giraffe calf survival could

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be due to predator swamping through dilution or prey switching (Estes 1976, Sekulic 1978, Estes and Estes 1979, Testa 2002). Therefore, it is conceivable that if wildebeest, zebra, and buffalo populations crash as a result of disrupted migrations, then giraffe calves might face increased predation pressure from local lions and hyenas responding to reduced availability of large ungulate biomass. Asynchrony is believed to be the ancestral state of all ungulates (Zerbe et al. 2012), and this investigation has illustrated how seasonal variation in vegetation quality and predation pressure may both play a role in the evolution of synchronous births.

The unique detail and landscape-level perspective offered by this extensive set of photographic capture-mark-recapture data from >1,800 individual giraffe illustrated the spatial complexity of tropical large-mammal demographics at the scale of one order of magnitude greater than the mean individual home range of giraffe (1,000 km^2 study area vs. 100 km^2 mean female home range). Precisely and efficiently estimating sub-population sizes, adult survival, calf survival, reproduction, and movement probabilities made this detailed spatial and temporal demographic analysis possible and provided detailed insight into sub-population and metapopulation dynamics in this fragmented ecosystem.

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