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

ii

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

iii

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 subpopulations 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

iv

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

vi

permits 2011-106-NA-90-172, 2012-175-ER-90-172, and 2013-103-ER-90-172. I am extremely grateful to these organizations for the opportunity to conduct this research, especially Julius Keyyu, Victor Kakenge, Angela Mwakatobe, and Kezia at TAWIRI; and from TANAPA, I.A. Lejora, Dominic Njau, Yustina Kiwango, and the staffs of Tarangire and Lake Manyara National Parks.

Financial support for this work was provided by Dartmouth College Graduate Studies, Fulbright U.S. Scholar Program, Sacramento Zoo, Safari West, Cleveland Metroparks Zoo and the Cleveland Zoological Society, Columbus Zoo, Cincinnati Zoo, Leiden Conservation Fund, Dartmouth College Cramer Fund, and the Explorer's Club.

My family and friends were also critical to my work, especially Robert and Irma Bond, Evie and Erik Dykema, Peter and Jessica Bond, Philip Krohn, Tricia Franck, and Lisa Belenky. Special thanks to my parents, Max and Joan Lee, for their unconditional love and unflinching support of my dreams and aspirations.

I dedicate this work to my wife, the beautiful and talented Monica Bond.

TADLE OF CONTENTS

ABSTRACTii
PREFACE vi
TABLE OF CONTENTS viii
LIST OF TABLES ix
LIST OF FIGURESx
LIST OF ACRONYMS xi
Introduction to the dissertation1
Chapter 1. Spatial variation in adult and calf survival and reproduction13
Chapter 2. Functional connectivity among sub-populations
Chapter 3. Seasonal reproductive timing and juvenile survival74
Conclusions
Literature Cited

LIST OF TABLES

Table 1: Model selection for spatial models of apparent survival of adult females	38
Table 2: Model selection for spatial models of apparent survival of adult males	39
Table 3: Model selection for spatial covariate models of apparent survival of calves	40
Table 4: Model selection for spatial models of reproduction	41
Table 5: Vital rates used in Leslie matrix population models	42
Table 6: Existing studies that estimated demographic rates for giraffe	43
Table 7: Model selection for lambda	66
Table 8: Model selection for movement	67
Table 9: Sex-specific population size, and density at five sites	68
Table 10: Seasonal probability of movement between pairs of sites	69
Table 11: Annual flow of individuals out and in of five sites	70
Table 12: Source-sink identification parameters for five sites	71
Table 13: Coefficients in regression explaining variation in lambda for the random a	mong
observed (RAO) matrix population model	72
Table 14: Coefficients in regression explaining variation in lambda for the random v	vithin
range (RWR) matrix population model	73
Table 15: Spatio-temporal covariates of lion predation and alternative prey	92
Table 16: Model selection results for temporal models of calf survival	93
Table 17: Model selection results for covariate models of calf survival	94

LIST OF FIGURES

Figure 1: Tanzanian giraffe aerial survey data from six ecosystems
Figure 2: Study area in the Tarangire Ecosystem of northern Tanzania
Figure 3: Sampling occasions relative to monthly rainfall and precipitation seasons, and
fixed route road transects driven during every sampling event16
Figure 4: Pollock's robust design statistical model and estimated parameters17
Figure 5: Adult male and female giraffe density at five sites
Figure 6: Life cycle graph and Leslie matrix population model
Figure 7: Adult female survival, reproduction, and calf survival at five sites
Figure 8: Demographic estimates across the species' range
Figure 9: Diagram of multi-site matrix population model
Figure 10: Annual net flow of individual adult female giraffe among five sites55
Figure 11: Annual net flow of individual adult male giraffe among five sites
Figure 12: Population projections for 50 years using multi-site matrix models
Figure 13: Diagrams illustrating competing hypotheses of how juvenile survival should
respond to birth synchrony
Figure 14: Survival to 1 year old for calves according to season of birth

LIST OF ACRONYMS

Coefficient of Variation	CV
Game Controlled Area	GCA
Intercalf Interval	ICI
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