

DEMOGRAPHY AND MOVEMENT OF MIGRATORY WILDEBEEST
(*CONNOCHAETES TAURINUS*) IN NORTHERN TANZANIA

A Thesis

Submitted to the Faculty

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

in

Biological Sciences

by

THOMAS ANDREW MORRISON

DARTMOUTH COLLEGE

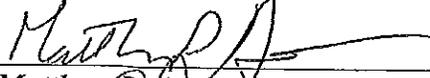
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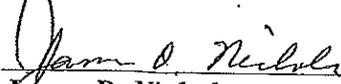
Douglas P. Bolger (Chair)



Matthew P. Ayres



Ryan Calsbeek



James D. Nichols

Brian W. Pogue, Ph.D.
Dean of Graduate Studies

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SUMMARY ABSTRACT

The study of ungulate migrations remains unavoidably rooted in population biology, a discipline that often makes the simplifying assumption that all individuals within populations, or within certain life history categories, are effectively equivalent. Of course, individuals, and the areas that they inhabit, vary in ways that influence their behavior and impact their probabilities of surviving and reproducing in the future. Given the widespread declines observed in many migratory ungulate populations, there is a growing call for identifying sources of demographic and behavioral variation in these populations with greater resolution. Here, I examine individual-level variation of two recently declining populations of wildebeest (*Connochaetes taurinus*) in Northern Tanzania using a noninvasive photographic capture recapture methodology.

Photographic sampling yielded a total of 8968 high quality photographs of adult wildebeest across 2.5 years, with 884 recaptures between sampling periods. We estimated the expected level of misidentification using a test set of known-identity images and developed a simple data conditioning technique that involved discarding the first photograph of every encounter history. Applying this technique resulted in very low levels of bias in simulated parameter space, but also reduced precision, particularly at low sampling intensities. We found that wildebeest in the Tarangire population exhibit relatively high but variable fidelity to their wet season ranges across years. Animals from Lake Manyara National Park rarely mixed with the Tarangire animals, confirming that Lake Manyara animals exist in relative isolation. Many of the observed switches between wet season in Tarangire wet season ranges involved breeding females. Breeders in Tarangire also exhibited large survival costs of reproduction, but no cost in terms of

future probability of recruitment. This result contrasts past studies of temperate populations that suggest current reproduction more likely affect future reproduction than survival. Finally, we found considerable variation in recruitment and survival rates across the different wet and dry season ranges. Lake Manyara animals consistently exhibited the highest calf recruitment rates, while Simanjiro animals exhibited the lowest rates. Survival was more variable across time and space. My results expand our understanding of wildebeest migration, and highlight the need to examine dynamics at the individual level.

PREFACE

People often ask me, “why study wildebeest?” While any species that migrates hundreds of miles across a human-dominated landscape while subsisting on a diet of grass is fascinating in its own right, I recognize that the reason why *I* study wildebeest has less to do with the fact that wildebeest make an appealing study organism than it does with the many people who first got me interested in wildlife in East Africa in the first place, as well as all of those people who have helped me along the way. First, I want to thank Susan Alberts (Duke University) and Beth Archie (University of Notre Dame) who, for some reason, hired me as a field assistant on their project studying elephants in Amboseli National Park, Kenya in 2002. Susan and Beth served as role models for how to navigate the many challenges of working in East Africa while conducting rigorous and powerful science. I owe an enormous debt of gratitude for the unplanned direction that my life took after they hired me. Secondly, I thank Dan Doak (another former employer, collaborator and friend) who directed me to Dartmouth during a key time in my graduate school decision-making process. Dan then served as an examiner on my thesis proposal committee, providing his keen insight to the demographic aspects of my project.

In Tanzania I thank the researchers and staff at the Tanzania Wildlife Research Institute, Tanzania National Parks, the Tanzania Commission for Science and Technology for permission to conduct this fieldwork and the African Wildlife Foundation for permission to work on Manyara Ranch. I received a considerable amount of scientific guidance and practical advice from Bill Newmark, Charles and Lara Foley and Bernard Kissui, to whom I cannot say enough thanks. To a large extent the successful execution of my fieldwork, and perhaps my dissertation as a whole, is due to Robert Mollé

Godson. Robert was as close to an ideal field assistant as I could imagine, and I feel tremendously fortunate to have found him during the early stages of my research. Sarah Wallis, Alicia Davis, Paula Gremley and others provided much needed reality checks and support (not to mention housing) throughout my fieldwork.

While at Dartmouth, I was extremely lucky to be surrounded by a diverse and superb group of mentors, colleagues and friends. I'm especially indebted to the Dartmouth EEB faculty staff, in particular Matt Ayres, Becky Irwin, David Peart and Ryan Calsbeek, all of whom provided guidance as committee members at one time or another. I especially thank Matt Ayres for challenging me to think critically about the topic of scientific advocacy and for his practical advice to avoid chaining myself to any trees (or wildebeest). I also received extremely valuable support from collaborators at the Patuxent Wildlife Research Center, especially Jim Nichols, Jun Yoshizaki, Jim Hines and Bill Kendall. Jim Nichols served as my outside thesis examiner and was exceedingly generous with his time at all stages of my project, agreeing to come to Dartmouth on two occasions and providing detailed comments on many chapter drafts. Bennet Vance and Hany Farid were instrumental in helping to develop the computer-assisted identification software used for identifying female wildebeest ('WILD-ID'). I also thank the graduate students and postdocs in the EEB program, in particular Jeff Garnas, Susan Elliott, Laura Burkle, Jim Kellner, Sharon Martinson, Alicia Ellis, Melissa Callahan, Laurel Symes, Bob Cox, Sam Fey, Ernesto Ruelas and my lab mates, Lizzie Wolkovich and Emilio Gabbai-Saldate. In particular at Dartmouth, I thank my advisor Doug Bolger, whose creativity and broad perspective on asking ecological questions in human-dominated landscapes enabled its success. Doug was more generous with his time and feedback than

a graduate student could hope for and I look forward to our future collaborations in East Africa.

Finally, I want to thank my family for their unconditional support throughout this entire process. I can only believe that my achievements so far in life are reflection upon, at least to a small degree, a combination of my father's intellectual curiosity and my mother's good sense.

Generous funding for my doctoral research was provided by the Wildlife Conservation Society Research Fellowship Program, the Robert and Patricia Switzer Foundation, the Dartmouth College Graduate Alumni Fund, the Dartmouth College Gilman Fund, Dartmouth College Cramer Fund, the Marion and Jasper Whiting Foundation, the Nelson A. Rockefeller Center at Dartmouth College, and NSF grant DBI-0754773 to Doug Bolger and Hany Farid.

I dedicate this dissertation to the loving memory of D. Anoop Sharma, whose fascination with the many mysteries of this world continues to inspire me.

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INTRODUCTION

Migration is unique among animal movement strategies because of the impressive distances over which animals move, the predictability that they will eventually return and (for many species) the sheer number of individuals involved (Dingle 1998; Milner-Gulland et al. 2011). Ungulate migration is typically portrayed as an adaptive behavior that provides animals with greater access to seasonally-available resources than could otherwise be obtained from a sedentary lifestyle (Fryxell & Sinclair 1988). The fact that fragmentation, habitat loss, the construction of barriers and overhunting are increasing within portions of many migratory landscapes lends urgency to demographic monitoring efforts and to investigations of the relative costs and benefits of migratory behavior (Bolger 2008; Harris et al. 2009). One such landscape is the Tarangire-Manyara Ecosystem (TME) in Northern Tanzania, which supports both a diverse assemblage of migratory ungulates and a growing human population. In this study, we focus on the TME wildebeest (*Connochaetes taurinus*) population, which has undergone a large decline in observed abundance since the late 1980's (Figure 1), presumably due to an array of anthropogenic factors.

In many ways, ungulates make model organisms for studying demography and movement. These animals tend to be relatively easy to locate and count, which provides opportunities to relate migratory movement to large-scale environmental gradients (Boone et al. 2006; Mueller et al. 2008), predator distributions (Creel et al. 2005; Hebblewhite & Merrill 2009), and heterogeneity in landscape structure (Fryxell et al. 2005; Kie et al. 2005). The long distances over which these animals travel each year in absolute terms (Berger 2004) and the disproportionate effect they can have on community

and ecosystem processes (Sinclair 1979; Sinclair et al. 2007; McNaughton 1984; Frank 2005) also make them important focal organisms in landscape conservation planning (Thirgood et al. 2004). However, compared to other migratory taxa, such as birds and amphibians, ungulates have been relatively poorly studied at the individual level (Bolger et al. 2008), particularly in tropical ecosystems which comprise roughly 90% of ungulate diversity (Galliard et al. 2000). While telemetry data is becoming increasingly inexpensive and accurate, studies that rely on this technology tend to only follow a small number of individuals due to the cost and effort required to attach the devices. In this study, we developed and employed an inexpensive, noninvasive methodology for following individual ungulates over time: computer-assisted photographic identification. This technique has been increasingly used to identify individual animals and to compile encounter histories within capture recapture frameworks for an array of species that have variable natural marking patterns (e.g., Holmberg et al. 2008). However, the method is prone to causing misidentification errors (i.e., failures to correctly identify individuals), which can severely bias capture recapture parameters estimates (Yoshizaki et al. 2009). Therefore, in Chapter I, we develop a simple data conditioning method for minimizing the effects of misidentifications on survival rate estimates. Using simulations, we examine the expected accuracy of this conditional approach alongside an approach in which misidentification errors are ignored.

In Chapter II, we address the question of whether wildebeest exhibit fidelity to their wet season ranges. Site fidelity has important implications for the conservation, management, genetic structure and dynamics of migratory populations. Ungulate migration in general, and wildebeest migration in particular, have been characterized as

strategies that allows individuals and herds to track dynamic and patchily distributed resources (Fryxell & Sinclair 1988; Albon & Langvatn 1992). While many ungulates appear to exhibit strong site fidelity (e.g., White et al. 2010), particularly to wet season ranges in the tropics and summer ranges in temperate latitudes, these studies often lack large sample sizes or a clear definition of site and scale. Our study overcomes these issues by relying on a large multi-year capture recapture dataset and three well-defined wet season ranges, between which animals do not move within the same wet season.

Chapter III looks more closely at one potential source of variation in survival and reproductive rates: those related to trade-offs due to reproduction in females (i.e., reproductive costs). We evaluate whether reproduction in the current year impacts a female's probability of reproducing and survival in the future. These costs are predicted because reproductive activities (mate choice, copulation, gestation, lactation and parental care) generally require a large investment in time and energy (Oftedal 1984) which can reduce the capacity for mothers to locate food and avoid predators. Long-term studies of temperate ungulates suggest that reproduction rarely incurs an observable future cost in survival and only occasionally influences future reproduction (Hamel et al. 2010). However, these costs have not been examined in any tropical ungulate. These species likely live with different physiological constraints than temperate species.

In Chapter IV, I examine patterns of spatial and temporal variation in calf recruitment, and calf and adult survival. Like many savannah ecosystems, the TME is characterized by high spatial and temporal heterogeneity in biotic and abiotic conditions, and supports a variety of human land-use activities, including two national parks used extensively for safari-based tourism (Tarangire (TNP) and Lake Manyara (LMNP)), a

private wildlife conservancy which permits livestock grazing and limited tourism (Manyara Ranch (MR)), and a number of Game Controlled Areas (Mto wa Mbu, Simanjiro Plains and Lolkisale) which permit wildlife harvesting (subsistence and trophy hunting), agricultural cultivation and permanent settlement (Nelson et al. 2007). High intra and inter seasonal variation in rainfall (coefficient of variation in annual rainfall in Tarangire National Park = 36% over 26 years; Foley et al. 2010) produces large variation in primary production over time (Prins and Loth 1988). Survival and recruitment rates should reflect the integration of this environmental heterogeneity and increasing human utilization across the landscape, thereby providing a starting point for identifying major sources of variation in demographic rates.

In the concluding section, we focus on highlighting the aspects of this work that are relevant to the management and conservation of wildebeest in general, and wildebeest in the Tarangire-Manyara Ecosystem in particular. We then use this information to identify potential management policies that we believe could be leveraged to moderate the recent downward population trends.

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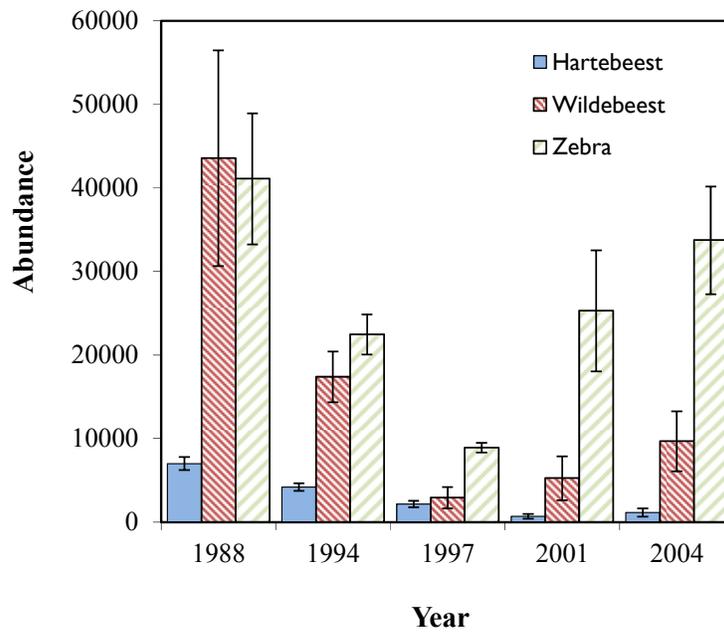


Fig 1. Population trends of three migratory ungulates in the Tarangire-Manyara Ecosystem, Tanzania: wildebeest, hartebeest and zebra. Both wildebeest and hartebeest have declined in abundance, whereas zebra likely declined between 1988 and 1997 but have since seemingly recovered (TAWIRI 2001).

CHAPTER I

**ESTIMATING SURVIVAL IN PHOTOGRAPHIC CAPTURE-RECAPTURE STUDIES:
OVERCOMING MISIDENTIFICATION ERROR**

Authors:

Morrison, Thomas A.¹

Yoshizaki, Jun² (junrossetti@gmail.com)

Nichols, James D.² (jnichols@usgs.gov)

Bolger, Douglas T.³ (douglas.t.bolger@dartmouth.edu)

¹Department of Biological Sciences, Dartmouth College, Hanover, NH 03755

²U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland 20708

³Environmental Studies Program, Dartmouth College, Hanover, NH 03755

In press at *Methods in Ecology and Evolution*

Abstract

For many species, noninvasive photographic identification offers a powerful and cost-effective method for estimating demographic parameters and testing ecological hypotheses in large populations. However, this technique is prone to misidentification errors that can severely bias capture-recapture estimates. We present a simple *ad hoc* data conditioning technique that minimizes bias in survival estimates across all rates of misidentification. We use simulated data sets to characterize trade-offs in bias, precision and accuracy of survival estimators for a range of misidentification probabilities, sampling intensities, survival rates and population sizes using this conditional approach. Misidentification errors resulted in mean survival estimates that were negatively biased by as much as -24.9% when errors were ignored. Applying the conditional approach resulted in very low levels of bias across parameter space. However, the main cost of conditioning is a loss of precision, which was particularly severe at low sampling intensities. Overall, the conditional approach was superior to the non-conditional approach (in terms of root mean square error (RMSE) of survival estimates) in 51% of the parameter combinations that we explored. We apply the data conditioning technique to a 3-sample capture-recapture data set compiled from 2551 images of a migratory wildebeest, *Connochaetes taurinus*, population in northern Tanzania. We estimate the false rejection rate (i.e., the probability of failing to match two photographs of the same individual) using a test set of ‘known-identity’ individuals. With this information, we compare survival estimates derived from conditioned data ($\hat{\phi}=0.698 \pm 0.176$), unconditioned data ($\hat{\phi}=0.706 \pm 0.121$) and simulated data to illustrate some of the key considerations for deciding whether to apply a conditional approach to a photographic

data set. These analyses demonstrate that ignoring misidentification error can lead to substantial bias in survival estimates. When sampling intensity and misclassification error rates are both relatively high, use of our conditioned data approach is preferred and yields survival estimates with lower RMSE. However, when sampling intensity and misclassification error are both small, the standard approach using unconditioned data yields smaller RMSE.

Introduction

The ability to identify and follow animals over space and time is fundamental to the study of animal populations. Recognizing individuals allows researchers to estimate vital rates, to quantify fitness and life-history tradeoffs, and to describe social behavior. Traditionally identification is accomplished by physically capturing and marking animals (Williams et al. 2002). However these invasive techniques can alter the behavior and physiology of captured animals (Wilson and McMahon 2006) and are often expensive and difficult to implement, particularly when the study population is large. As an alternative, species with variable marking patterns can be identified noninvasively with photographs. This has involved studies of small populations using hard copy photo catalogs that are matched “by eye.” However, the advent of sophisticated software packages that integrate pattern-recognition algorithms with digital photographic databases provides a promising new avenue for identifying individuals noninvasively over multiple years and multiple sites (Gamble et al. 2008; Hastings et al. 2008; Holmberg et al. 2008). A growing number of species with variable natural marking patterns has been studied using computer-assisted photo identification, including cheetah,

Acinonyx jubatus Schreber (Kelly 2001), whale sharks, *Rhincodon typus* Smith (Arzoumaniann et al. 2005), spotted ragged-tooth shark, *Carcharias taurus* Rafinesque (Van Tienhoven et al. 2007), tigers, *Panthera tigris* Linnaeus (Karanth et al. 2006), African elephants, *Loxodonta africana* Blumenbach (Ardovini 2007), cetaceans (Hastings et al. 2008), African penguins, *Spheniscus demersus* Linnaeus (Sherley et al. 2010) and salamanders (Table S1; Church et al. 2007; Gamble et al. 2008).

As image-analysis software applications improve, there will be a growing opportunity to apply photo-ID to capture-recapture (CR) studies of large populations (Langtimm et al. 2004; Church et al. 2007; Holmberg et al. 2008). Encounter histories can be constructed from photographs taken over time, and together these histories can be used to estimate abundance in closed populations and survival and state transition probabilities in open populations (Williams et al. 2002). However, CR models typically assume that all individuals are correctly identified, which is rarely the case in computer-assisted photo identification, particularly when photo libraries are large. Of the few studies that have estimated demographic rates using photographic identification, most have not explicitly addressed the issue of misidentification (Langtimm et al. 2004; Church et al. 2007; Hastings et al. 2008). However, even low rates of misidentification can bias parameter estimates in standard CR models (Mills et al. 2000; Stevick et al. 2001; Lukacs and Burnham 2005; Yoshizaki et al. 2009). Given the great potential of photographic identification and its increasing use, we feel it is imperative to develop analytical approaches that address misidentification errors. Our focus is on estimation of survival probability in the face of misidentification errors.

Source of Misidentification

Most computer-assisted photo matching systems are only partially automated and do not return simple ‘match’ or ‘no match’ decisions, (though see Burghardt 2008 and Sherley et al. 2010 for an automated example with African penguins). Rather, they provide a standardized similarity score for all pair-wise combinations of photos. To find matches for a particular photo, users must visually inspect the highest ranking potential matching photos defined by a specified threshold of similarity. False rejection errors (i.e., failing to match two photos of the same individual) are produced when either the identification system fails to rank true matching photos above the threshold level *or* when human observers fail to identify true matches that have been ranked above the threshold. In contrast, false acceptance errors (i.e., falsely matching two photos of different animals) occur only when observers incorrectly match a high-ranking pair of photos from different individuals. Thus, while false acceptances are caused by the observer’s inability to discriminate between photos of the different individuals, false rejections are a product of both computer and human abilities to detect true matches. Both types of misidentification will occur more frequently when study organisms have low variability in natural marking patterns across individuals (Ottensmeyer and Whitehead 2003), when patterns are not stable in time (Hastings et al. 2008; Yoshizaki et al. 2009), or when pattern-matching algorithms inadequately characterize or compare pattern topology. However, if marking patterns are sufficiently variable among individuals and stable over time, and observers receive adequate training, the incidence of false-acceptance should be relatively rare (Vincent et al. 2001). Therefore, our analytical approach focuses on minimizing the effects of false rejections.

False rejections occur when photographs contain external sources of variation (e.g., lighting, foreground objects, photographic perspective, mud or dust on fur etc.) that alter the visible pattern in the photo so that either the computer algorithm or human observer cannot detect the true pattern. Because the number of factors that introduce variation into the quality of a photograph is large, we assume that when low quality photos are compared to subsequent photos of the same individual (regardless of quality of the second photo), those photos will fail to match. Thus, false rejections should produce two encounter histories, at least one of which is represented in the data set as a single encounter event (called ‘ghosts’ or ‘ghost histories’; Yoshizaki 2007).

The problem of ghost histories is at least superficially analogous to that of ‘transients,’ in terms of effects on standard capture-recapture estimators and approaches to dealing with the problem (Pradel et al. 1997). Transient individuals appear in the study area for a single period only and have no chance of being recaptured at later time periods. However, transients and residents have independent detection probabilities whereas ghosts and non-ghosts produced from false photo rejections do not. Indeed as long as it is possible to assume that all encounter histories in a data set are independent, standard multinomial models can be adapted to incorporate misidentification errors (see Lukacs and Burnham 2005; Lukacs et al. 2009). In photographic CR, however, detection histories of a correctly identified individual and its ghost counterparts are not independent, as they represent the same individual. This dependency between ghosts and non-ghosts is problematic because the sum of the expected marginal probabilities of all encounter histories will be greater than one (for a full description of this problem, see Yoshizaki 2007). Therefore, traditional CR models that assume data are drawn from

multinomial distributions are inappropriate, preventing the derivation of a multinomial likelihood function.

Several alternative modeling frameworks have been proposed to deal with misidentifications. Link et al. (2010) developed a Bayesian approach for closed-population data that identifies the latent multinomial distribution of encounter histories containing misidentification errors. This approach can incorporate auxiliary information on error rates. Moreover, Yoshizaki et al. (2009) used unweighted least squares and minimum χ^2 to estimate capture probabilities and abundance in data sets with ‘evolving’ natural tags. While both of these approaches could theoretically be extended to open population situations, they assume that individuals can only be photographed once per sampling occasion. In many cases with photographic data, individuals may be photographed and misidentified multiple unknown times within the same sampling occasion. Explicitly modeling the within-interval sampling process is possible, but non-trivial, because it requires knowledge of the sampling distribution of expected number of photographs per individual per sampling occasion (e.g., λ , if we were to assume a Poisson sampling process). Determining this sampling distribution, in turn, requires an estimate of population size.

Due to these obstacles, we propose an alternative for survival estimation in the face of misidentification. The approach is to simply censor all initial photographs (thus all encounter histories with a single photograph will be excluded; these include all misidentifications) from the encounter history data set. This approach has been used several times as a way to minimize the effects of transient individuals that appear in the data set on single occasions (Paradis et al. 1993; Pradel et al. 1997). Using simulated

encounter histories, we estimate the bias, precision and accuracy of survival estimators when ignoring misidentification error in a Cormack-Jolly-Seber model (CJS) (Cormack 1964; Jolly 1965; Seber 1965) and compare these to results from our alternative approach. We also illustrate the approach using encounter history data from a photo-identified population of migratory wildebeest *Connochaetes taurinus* Burchell. These data were collected as part of a larger effort to examine spatial and temporal demographic variation in a declining wildebeest population in Northern Tanzania (TAWIRI 2001). We compare survival estimates of wildebeest using our proposed approach to those obtained from an unconditioned (full) data set. Throughout, we attempt to clarify some of the central problems and potential solutions associated with using large-scale photo identification in the context of CR survival estimation.

Methods

Basic Approach

Because survival estimates in CJS models are conditioned on the initial release of an animal (Williams et al. 2002), one approach to minimizing bias in survival is to condition the data on “releases” of sets of encounter histories known to contain no or few ghosts. Given our assumption that ghosts’ identities are based on single photo captures, we can eliminate ghosts by discarding all initial photographs, a filtering process that we refer to as the “conditional approach.” While this process also eliminates initial photo captures of non-ghosts, it allows us to use standard CJS estimation techniques, where the expected probability of recapture at time i becomes the product of the true probability of recapture (p_i) and the probability of correct identification (α_i), given an encounter:

$$E(\hat{p}_i) = p_i \alpha_i$$

Thus, under this conditional approach, misidentification occurs with a probability of $[1 - \alpha_i]$ and simply lowers the expected probability of detecting real individuals ($E(\hat{p}_i)$), which should result in unbiased survival estimates.

To illustrate the conditional approach, consider an open-population sampling design where photographs are collected over three sampling periods. The sampling periods are sufficiently separated in time that we expect the possibility of gains and losses between sampling occasions. For purposes of this example, we assume that an animal may be photographed up to three times within a given sampling occasion. Observed data summarize the number of photo captures identified for each individual in each sampling occasion. The “unconditional approach” involves reducing the observed data into encounter histories where each entry in the resulting vector represents detection (“1”) of a known (because it was detected previously) individual or not (“0”) in each of the 3 sampling periods. In the “conditional” encounter history, all initial photo captures from observed data are censored (i.e., ignored in the modeling), and the data set is once again reduced to binary responses for individual sample periods. Consider the following possible histories and their translation into unconditional and conditional encounter histories for use in CJS models:

Individual	Observed data		Unconditional data	Conditional data
A	100	→	100	000
B	110	→	110	010
C	201	→	101	101
D	131	→	111	011

Individual A was photographed only once (period 1) and will be removed from the data set after conditioning. B was photographed once in period 1 and once in period 2 and will have a single encounter (during period 2) in the conditional data set. C was photographed twice in the first period and once in the third, so after conditioning will have encounters in periods 1 and 3. D's initial capture will be censored after conditioning because it was only photographed once during period 1. The purpose of the conditioning is thus to produce a set of encounter history data that contains no ghosts. This objective is achieved by restricting the data to individuals detected at least twice, because we assume that ghost individuals cannot be re-identified.

Simulated data sets

We simulated capture-recapture data across 3 open periods using both conditional and unconditional approaches and evaluated the relative performance of the approaches in terms of the bias, precision and accuracy of survival estimators. We approximated photographic sampling in each sample occasion using a Poisson distribution. Poisson sampling assumed that individuals were photographed at random from a homogenous population with replacement. Photographs were drawn from two population sizes: $N = 3000$ and $10,000$ individuals. We applied five sampling intensities (λ) that resulted in the expected number of photographs per individual per sampling period of 0.36, 0.51, 0.69, 0.92 and 1.20. These sampling intensities correspond to encounter probabilities (i.e., the probability of an individual being photographed at least once within a sample period) of $1 - e^{-\lambda} = 0.30, 0.40, 0.50, 0.60$ and 0.70 respectively. Note that (λ) represents the

expected number of photos per individual per sampling period and that some of these photos may be misidentified.

We used a random Bernoulli process to apply three levels of true survival ($\phi = 0.50, 0.75$ and 0.90) to each individual in the population between sampling occasions. Populations were maintained at a constant population size by setting the simulated recruitment rate of new individuals equal to mortality. We assumed that misidentification of individual photographs followed a Bernoulli process with six possible probabilities ($1 - \alpha = 0.01, 0.05, 0.10, 0.20, 0.30, 0.40$). All correctly identified photos with the same unique identity constituted a single encounter history, whereas misidentified photos generated encounter histories with single a encounter event (i.e., ghosts).

For each set of parameter combinations, we simulated 2500 encounter history data sets, a sufficient number to provide stable mean estimates. Each run produced an estimate of survival between sampling periods 1 and 2, and 2 and 3. The survival estimates from all iterations were used to estimate relative bias, standard error (a measure of precision) and root mean square error (a measure of bias and precision) across each parameter combinations. Bias was estimated using the general formula:

$$RBias(\hat{\phi}) = \frac{\sum_{i=1}^n (\hat{\phi}_i - \phi) / \phi}{n},$$

where $\hat{\phi}$ is a survival estimate from a single iteration, ϕ is the true survival and n is the number of iterations. Standard error was estimated as:

$$SE(\hat{\phi}) = \sqrt{\frac{\sum_{i=1}^n (\hat{\phi}_i - \hat{\phi})^2}{n-1}},$$

where $\hat{\varphi}$ is the mean of the n survival estimates. Root mean square error was estimated as:

$$RMSE(\hat{\varphi}) = \sqrt{\frac{\sum_{i=1}^n (\hat{\varphi}_i - \varphi)^2}{n-1}}$$

In all simulation runs we used a time-invariant CJS survival and recapture model (ϕ, p) and modeled parameters with an identity link function. Data sets were generated and compiled using R (R: Development Core Team 2009; Appendix S1), and maximum likelihood estimates of survival were computed with program MARK (White and Burnham 1999). We experienced some convergence failures in simulations that used a combination of high misidentification probability, low sampling intensity and small population size (i.e., in five parameter combinations, 1-5% of runs failed to converge). Because these failed iterations did not appear to be a random subset (i.e., they had particularly low numbers of recaptures), simply discarding them would have produced slightly biased mean estimates. Therefore, we do not report these five parameter combinations in the simulation results.

Wildebeest data set

We collected photographs of adult male wildebeest (aged 24 months or older) during three sampling periods – October-December 2006, May-July 2007 and October-November 2007 – in the Tarangire-Lake Manyara Ecosystem in Northern Tanzania. This population is geographically isolated from other wildebeest populations in Northern Tanzania (i.e., it is closed to emigration and immigration) and consists of roughly 2200 adult males (Morrison, *unpub data*). Males were used rather than both sexes because of

small differences in the photo-matching process between sexes that would have required additional interpretations. Males were photographed from a stationary vehicle at a distance of between 10-100 meters during daylight hours using a 6.1 megapixel Pentax *istD* camera and 400mm Sigma telephoto zoom lens. For each herd encountered, we attempted to take as many photographs as there were individuals in the herd. In some cases, herds moved out of range before we had collected the target number of photographs. On average we encountered 110 herds per sampling period and photographed 70.3% of males within these encountered herds. We tried to avoid photographing individuals multiple times, though it was impossible to distinguish individuals by eye in herds larger than about 10-15 individuals.

We utilized natural variation in shoulder stripe patterns to discriminate among individuals (Figure 1). Patterns were not symmetrical along the wildebeests' two flanks, so we photographed their right sides only, perpendicular to the length of the animal. We used a computer-assisted identification system developed by Conservation Research Ltd. <conservationresearch.co.uk> to identify matching photographs. Photo-matching involved the following steps: 1) new photographs were downloaded into an image library, 2) the user placed markers on each image to identify the upper and lower margins of the body and a few recognizable features such as the nose and base of the tail, 3) the software used the markers to superimpose a three-dimensional surface model, 4) it then extracted a planar sample of the shoulder stripe pattern that compensated for viewpoint and posture differences and, 5) it used two algorithms to calculate similarity scores between the focal photo and every other photo in the photo pattern library, and 6) the observer (T. Morrison) then manually compared the focal photo to the top ten potential

matching photos (ranked by similarity score) for each algorithm and noted each true match (Hiby et al. 2009). Once matching was complete, we compiled encounter histories across the three sampling periods for all individuals and used program MARK to estimate apparent adult male survival for the unconditioned and conditioned data sets under a simple model (ϕ, p) with constant survival and recapture probabilities (White and Burnham 1999). We were also interested in asking whether our simulations were doing a reasonable job of approximating the actual processes that generated the wildebeest data. We thus tailored simulations to the wildebeest sampling situation and compared simulation results with the actual estimates for the unconditioned and conditioned approaches. To do this we generated 5000 additional simulated data sets using the observed conditioned survival rate, and assumed that adult male population size (N) was 2200 individuals (Morrison, *unpub data*), sampling intensity was 0.30 (based on the number of photographs when $N = 2200$) and probability of misidentification ($1-\alpha$) was 0.04 (see results).

To characterize misidentification error ($1-\alpha$) in our system, we first estimated the false rejection rates (FRR). We also estimated the false acceptance rates (FAR), as both metrics are conventionally used in biometric performance assessments and are akin to false negative and false positive error, respectively (Jain 2007). Importantly, our estimate of FRR using a subset of known images is not equivalent to the probability of misidentification used in our simulation ($1-\alpha$). Specifically, the conventional FRR (Jain 2007) is calculated using pairs of photos of the same individuals, so that $FRR = 1-\alpha^2$. However, we assume that photographic misidentifications (i.e., ghosts) are actually produced on a per photo basis whenever a single photo is of insufficient quality to be

matched with any other photo. We used this FRR estimate to calculate our per-photo misidentification probability ($1 - \alpha$).

We calculated FRR and FAR using a test set of images of positively identified individuals ($N = 198$ true matching photo pairs) taken between June 2005 and November 2007. A portion of photos in this test set was taken of individuals with unique horn abnormalities that were easily recognized by eye ($N = 69$ true matching photo pairs). An additional group of photos ($N = 129$ true matching photo pairs) was collected from an isolated herd that we visited multiple times over a month, the photos of which were visually matched 'by eye' (i.e., without the aid of the computer-matching software). Both types of data were pooled in the analysis of FRR and FAR to increase the sample size of positively identified individuals. All individuals in the test set had been photographed at least twice. In all cases, the photos of each pair in the test set were collected on different days (range in number of days between photo pairs: 1-863 days) and contained levels of variation in photo quality (i.e., lighting, foreground objects, perspective, etc.) that were comparable to those of non-test set photos.

We quantified FRR by running all photos through the computer matching software and calculated the proportion of true matching photos that failed to appear above a particular threshold specified as the number of top ranked photos to be examined. The threshold ranged from 1-40 images. Our estimate of FRR did not include human error produced when observers falsely reject matches above the threshold value. Estimating this value would have required training an additional observer who was unfamiliar with the test images. However, we believe this is a minor source of misidentification error relative to the computer-generated error because wildebeest

patterns contain a great deal of inter-individual variability, and to a trained eye matches are easy to identify. FRR was calculated as the number of falsely rejected photo matches divided by the total number of true matching photo pairs.

In contrast to FRR which is determined by the software constraints, the false accept rate (FAR) is determined solely by the observer's ability to avoid matching two photos of different individuals. Therefore, we used an inexperienced observer to make our estimate of FAR as conservative as possible. The inexperienced observer (J. McGrew) visually matched 100 test photos by eye. This test set contained twenty five matching photo pairs from the above test set and 50 randomly selected unmatched photos. FAR was calculated as the number of incorrectly matched photos divided by the total number of identification attempts (for 100 photos, the number of identification attempts = 4950).

Results

Simulations

Without conditioning, survival estimates were negatively biased across all treatments, with values of relative bias as low as -0.25, when $N=10,000$, $\lambda=1.20$, $\hat{\phi}=0.5-0.9$, $1-\alpha=0.4$. High probabilities of misidentification (0.2, 0.3 and 0.4) and high sampling intensities (0.92-1.20) produced the most severe bias. At low probabilities of misidentification (0.01) unconditioned data consistently produced estimates with small bias (<0.01). True survival rate had little effect on the magnitude of bias, while population size had only a small effect on bias. In contrast the conditional approach minimized bias across the entire parameter space (Figs 2).

However, conditioning increased the standard error of survival estimates relative to those from unconditioned data. This relative difference was magnified at low sampling intensities and high probabilities of misidentification. Standard error estimates were positively related to the probability of misidentification and to the true survival rate for both unconditioned and conditioned approaches, though these relationships were stronger in the conditional approach. The smaller population size (3,000) produced substantially higher standard errors, particularly in the conditional approach (Figs 2).

Root mean square error was lower for the conditional approach in 51% of the parameter combinations that we explored. The conditional approach outperformed the unconditional approach in terms of RMSE when the probability of misidentification was high, as long as sampling intensity was also high. Overall, RMSE of estimates from conditioned data were positively related to misidentification rate and negatively related to sampling intensity, true survival rate and population size. Unconditioned data sets produced relationships in similar directions as conditioned data sets, with the notable exception that RMSE from unconditioned data was positively related to sampling intensity.

Wildebeest Example

Across the three sampling periods, we collected 2900 photographs of adult males, of which 2571 were of sufficiently high quality to be used for identification. From these, we identified 1539 unique individuals. The computer-assisted identification method required roughly 3.08×10^4 visual (i.e., manual) photo comparisons, compared to the over 1.18×10^6 comparisons that would have been necessary in the absence of computer-

matching software, thus representing a 38-fold labor savings. The FRR among our 198 pairs of test photos decreased as the threshold number of photos inspected increased and was 7.6% at the threshold level used in the survival analyses (i.e., top 10 highest scoring matches; Figure 3). This FRR value corresponded to a probability of misidentification of 0.039. The FAR was extremely low: 8.1×10^{-4} . Conditioning eliminated 62% of the total number of releases ($\text{releases}_{\text{uncon}} = 1698$, $\text{releases}_{\text{con}} = 640$; Table 1). We estimated apparent 7-month survival rate ($\hat{\phi} \pm \text{SE}$) between the first and second sampling periods (October 25-December 15, 2006 and May 25-July 14, 2007), as 0.698 ± 0.176 for the conditional approach and 0.706 ± 0.121 for the unconditional approach. Probability of recapture, \hat{p} , was estimated as 0.214 ± 0.055 for the conditioned and 0.164 ± 0.030 for the unconditioned data sets.

Discussion

Misidentification error in the photographic matching process produces a systematic violation of CJS model assumptions (i.e., that all individuals are correctly identified) that negatively biases survival estimates across sampling conditions (Figs 2). Our results support the use of the conditional approach as a way to minimize this bias, particularly when the probability of misidentification and the sampling intensity (expressed, e.g., as λ , the mean number of photos per individual per sample period) are moderate or high. By discarding all first photo captures from an encounter history data set, conditioning removes ghost identities and yields a data set that produces unbiased estimates. However, conditioning incurs a cost in terms of precision, yielding higher standard errors relative to an unconditional approach, particularly at low sampling

intensities, small population sizes and low survival rates. These latter parameter combinations produce smaller numbers of recaptures across sampling periods, which in a CJS modeling framework, generates large variances (Williams et al. 2002). At the lowest sampling intensity ($\lambda=0.36$), SE based on the conditional approach was 2.32-3.06 times larger than for the unconditional approach. In this situation RMSE was 1.49-2.54 times larger for the conditional approach relative to the unconditional approach. Therefore, when the number of recaptures is low and cannot be augmented with additional sampling, we advise against using the conditional approach.

Past photo identification studies have reported probabilities of misidentification as low as 0.03 (reported FRR=6.4%; Kelly 2001) and as high as 0.10 (reported FRR=20.2%; Foster et al. 2006). Our simulations suggest that if the probability of misidentification is low (0.01-0.05), unconditioned data generally produce better survival estimates than conditioned data (in terms of RMSE). In our example of wildebeest photographic data, we estimated a 0.039 misidentification rate for the identification system (based on FRR of 0.076; Figure 3). Given this FRR value, if we assume that the adult male population size (N) was 2200 individuals (Morrison, *unpub data*) and that the 7-month adult survival rate (ϕ) was 0.70, the sampling intensity (λ) should be roughly 0.36 photos per individual per sampling period. At these values, the conditional approach produces survival estimates that have 3-5 times higher RMSE values than the unconditional approach, indicating that the unconditional approach is preferable for our wildebeest data set. Indeed, conditioning eliminated 62% of the total number of releases (Table 1), which increased the SE of survival by 45% ($SE_{\text{uncon}} = 0.121$, $SE_{\text{con}} = 0.176$) relative to unconditioned data. Because of the low misidentification rate, most of these losses

represent actual individual animals, rather than ghosts. This loss in the total number of releases illustrates the major cost of using a conditional approach: lower precision. Based upon these results we accept the unconditioned estimate of apparent survival of 0.706 ± 0.121 . Our simulations suggest that the expected bias is only -0.01 . In this particular case, our observed conditioned estimate (0.698 ± 0.176) was slightly lower than the unconditioned estimate, likely due to sampling variance, though on average, conditioned survival estimates will be higher than unconditioned ones.

Weighing the tradeoff between bias and precision, and therefore between conditional and unconditional approaches, ultimately depends on the goals of the study and the uses of the estimates. In some situations, such as monitoring of survival trends, choosing precision over bias may be a sensible option as long as it can be reasonably assumed that bias remains relatively constant over time. In other situations (e.g. life history analysis, population projection) highly precise, but biased estimates may be unacceptable. Regardless of the study, we recommend that researchers estimate the false rejection rate prior to sampling so that they can select an appropriate sampling intensity. If FRR is high and cannot be reduced by other measures, relatively high sampling intensity will be necessary to ensure that estimates based on conditioned data have sufficient precision. Fortunately, photographic CR is especially well-suited for increasing sampling intensity and sample sizes because of the relative ease with which additional individuals can be photographed. Photographing individuals twice (or more) in quick succession on the same day would be one possible way to do this as long as the two photos were as challenging to match as ones taken on different days or years. However, in wildebeest (and probably other species) we believe that processes acting across days

and years (e.g. lighting, variation in the visibility of coat patterns, etc.) contribute more to the probability of photo matching success than processes within single encounters (e.g. slight differences in camera perspective). If researchers have prior knowledge of approximate population size and survival rates, simulations can be valuable for exploring the sampling intensity needed to generate accurate and precise survival estimates (see Appendix S1).

If FRR is unknown or not possible to estimate, a useful rule-of-thumb for gauging the magnitude of FRR (i.e., high or low) would be to compare conditioned and unconditioned survival estimates, as long as both estimates are relatively precise and transient individuals are unlikely to be present in the population. Under this situation, survival estimates that are precise and similar would be expected to reflect low FRR. Survival estimates that are precise but different would be expected to reflect high FRR. However, if one or both sets of estimates have large SE's, or if transient individuals are likely in the population, this comparison would likely not provide insight into the magnitude of FRR.

One of the major assumptions of our study is that misidentifications result in encounter histories with single ghost encounters (i.e., a ghost cannot be recaptured). In reality, ghosts may be recaptured under some conditions. If this was to occur, conditioning would only remove a portion of ghosts from the data set, producing negatively biased survival estimates. Moreover, if the variability in marking patterns across the study population is not sufficiently high to discriminate some individuals by eye, photographs of different individuals may be falsely matched (i.e., false acceptance errors or the “shadow effect”; Mills et al. 2000). The removal of potentially erroneous

encounters in these data sets would not be possible in a way analogous to the conditioning approach outlined above. If false acceptance error rates can be estimated using a data set for which truth is known, then it may be possible to develop joint models that incorporate such errors explicitly.

We believe that it should be possible to develop model-based approaches that are more efficient than the *ad hoc* approach that we have suggested. In some sampling circumstances, it may be possible to use existing models to cope with misidentification errors. The Link et al. (2010) model is based on a similar set of assumptions as our data within a closed population framework, with the exception that animals can only be photographed once per sampling period. As long as animals are rarely photographed multiple times within periods, the Link et al. (2010) approach could in theory be extended to open population situations. To this end, one sampling approach for mobile species, such as wildebeest, might involve photographing animals as they migrate in one direction past a particular vantage point. Additionally, territorial species might be relatively easy to sample in a way that avoids multiple captures within periods (e.g., salamanders; Church et al. 2007).

The use of computer-assisted matching reduced by ~38-fold the number of matches “by eye” that had to be performed. Moreover, computer assisted photo-identification was far less costly and invasive than identification methods that involved physically marking a similar number of individuals. For instance, immobilizing an adult wildebeest costs roughly \$250 per individual for field operations and veterinary drugs (Morrison, *unpub. data*). To capture and mark 1539 males (the number followed in our photographic study) would have cost roughly 50 times more than we expended to

photographically ‘mark’ male wildebeest in the Tarangire ecosystem (\$384,750 vs. \$7500), assuming capture costs increase linearly. Evidence that immobilizing and handling animals can influence behavior and survivorship of study organisms (Côté et al. 1998; Oosthuizen et al. 2009) furthers the call for an expansion of noninvasive methodologies and analytical techniques that can be used in individual identification studies (Wilson and McMahon 2006).

Our results demonstrate that ignoring misidentification in photo capture-recapture studies can lead to substantial negative bias in survival estimators. We also show that misidentification can be handled with appropriate analytical techniques and data conditioning so that methods of photographic recognition do not need to be error free (or nearly so) to be useful. Despite misidentification errors, with a sufficient number of recaptures, photographic identification can be useful for fitting more complicated models, such as multi-state or robust design models (Nichols et al. 1994; Kendall et al. 2004). Our work, and that of Link et al. (2010), Yoshizaki (2007), Yoshizaki et al. (2009) and Lukacs et al. (2009), provide a number of techniques as well as guidance on the performance of the techniques under different sampling conditions. We believe that there is great potential for photographic capture-recapture to allow cost effective, fine-scale demographic monitoring of many species. Indeed, the rapidly expanding field of computer vision technology calls for a broader application of existing analytical techniques as well as the development of new techniques that can allow researchers to exploit these technologies to provide precise and unbiased estimates of demographic parameters, even when they technologies generate non-negligible error rates.

Acknowledgements

We thank the Commission for Science and Technology and the Tanzania Wildlife Research Institute for permission to conduct research in Tanzania, and the Tanzania National Park for permission to work in Tarangire and Lake Manyara National Parks. We are grateful to J.E. Hines for assistance with the simulation study, R. Mollel for immense energy in the field, J. McGrew, N. Brown and C. Biggs for help analyzing wildebeest photos, L. Hiby for technical assistance with the matching software, and three anonymous reviewers for helpful suggestions about an early draft of the manuscript. This work was funded by the Wildlife Conservation Society Research Fellowship Program and Dartmouth College, the Marion and Jasper Whiting Foundation, the Nelson A. Rockefeller Center at Dartmouth College and NSF grant DBI-0754773 to DTB and H. Farid.

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TABLES

Table 1. Summarized encounter history data of Tarangire adult male wildebeest. The middle column is the number of individuals for each encounter history retaining first photo captures. The right column is conditioned data where the initial photo capture has been deleted.

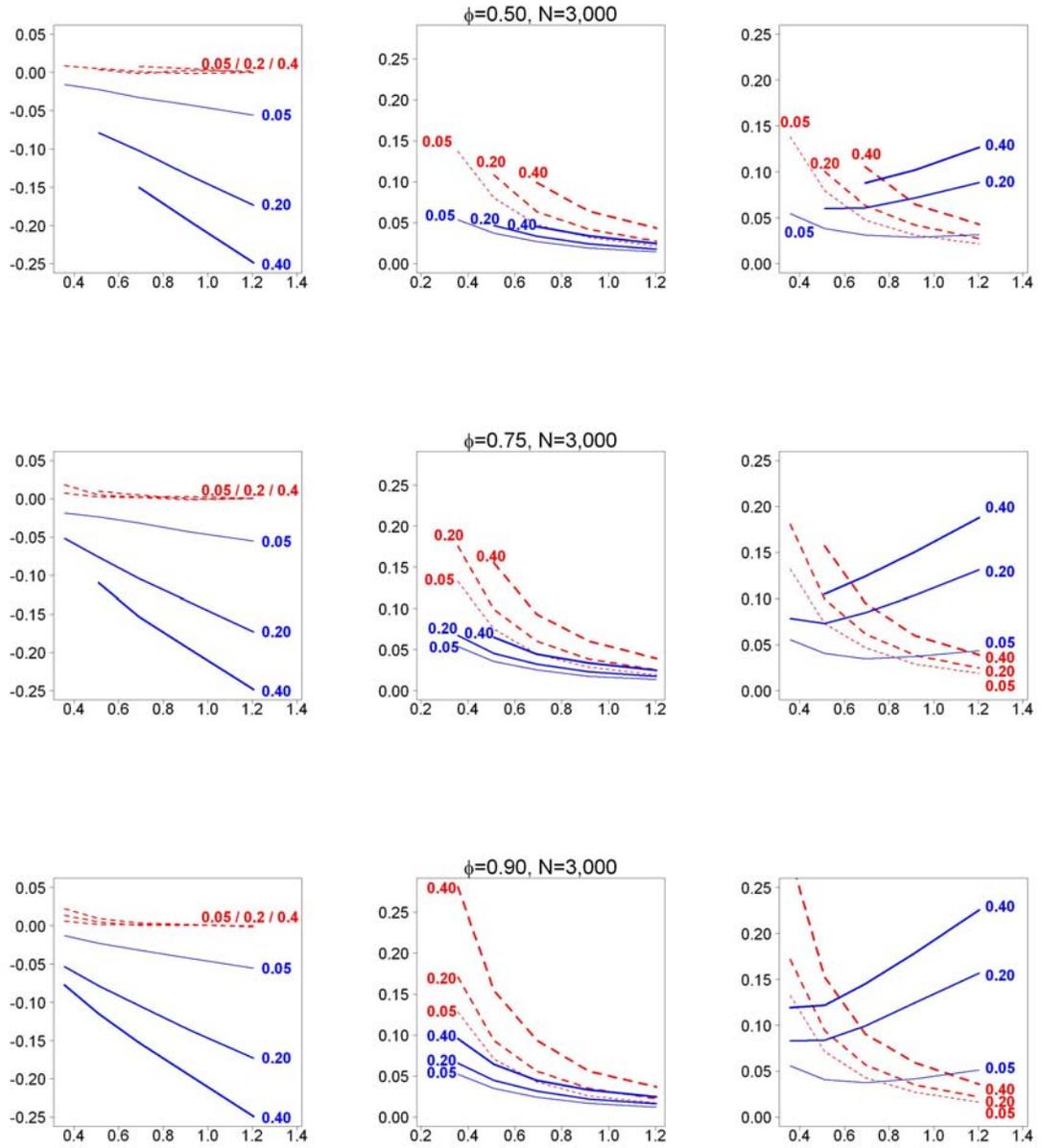
Capture histories	Unconditioned	Conditioned
001	516	181
010	569	228
100	302	85
011	89	51
101	31	12
110	25	7
111	7	2
Individuals:	1539	566
Releases:	1698	640

FIGURES

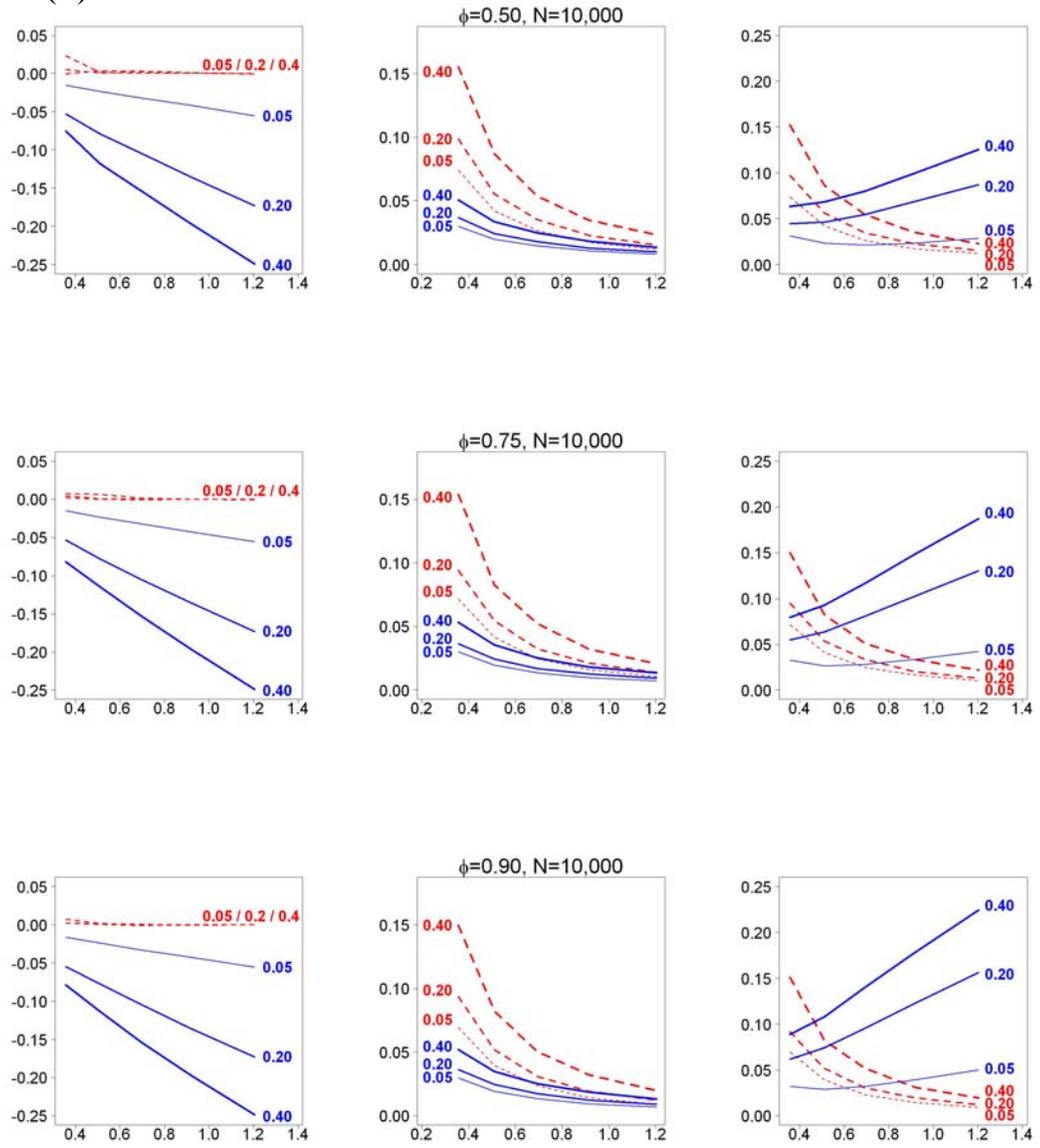


Figure 1. Lateral view of an adult male wildebeest with unique stripe patterns.

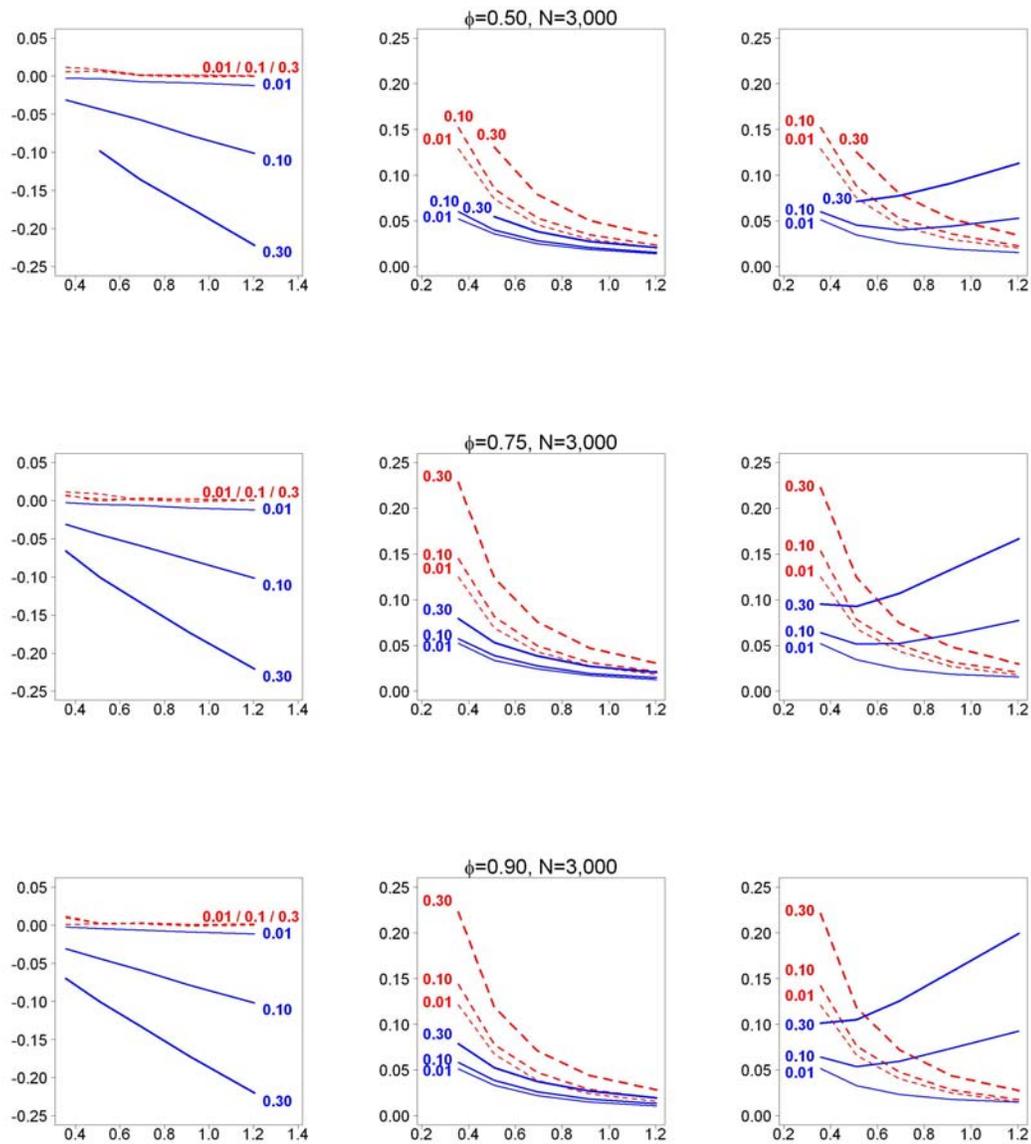
(A)



(B)



(C)



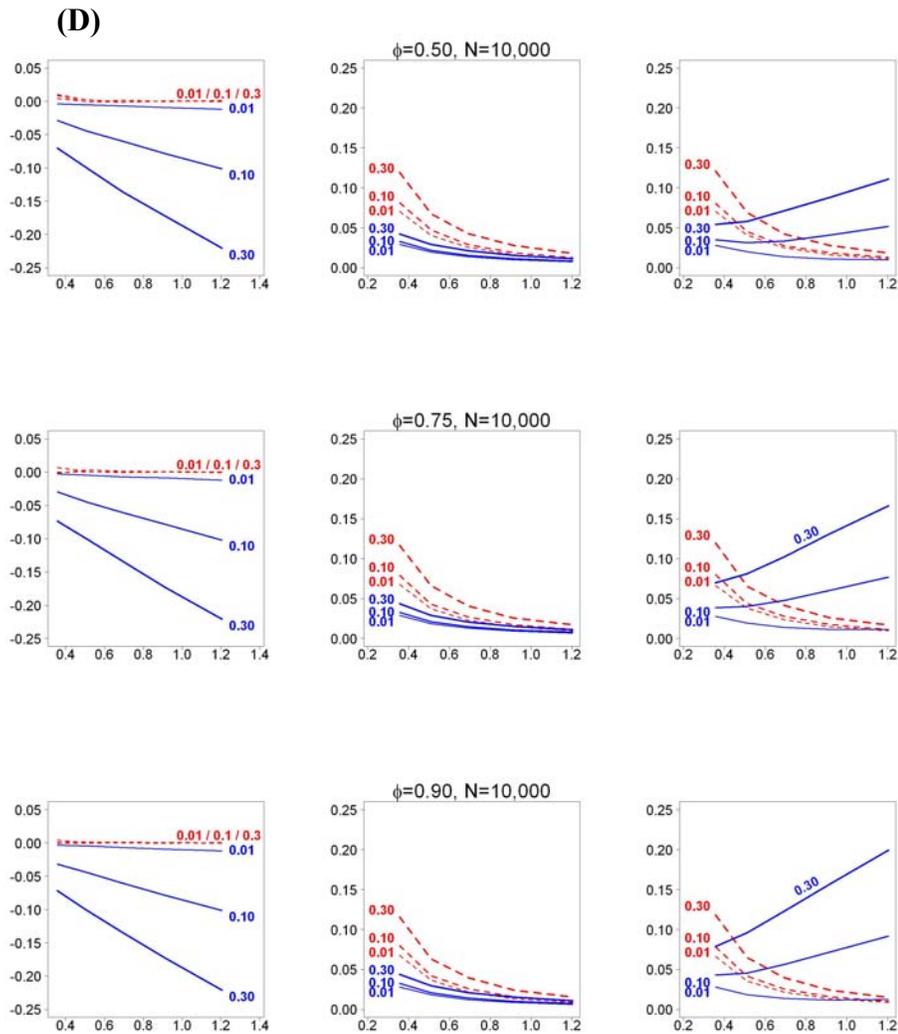


Figure 2. Trade-off between conditional (red dotted lines) and unconditional (blue solid lines) approaches in terms of the relationships between photographic sampling intensity (λ) and bias, standard error and root mean square error of survival estimates. Each curve represents a specific photographic misidentification probability ($1-\alpha$). Intersection of RMSE curves (black dots) indicate the sampling intensity above which the conditional approach provides better accuracy. Results based on 2500 runs per parameter combination over $K = 3$ sampling periods for two population sizes (N): (A, C) 3000 and (B, D) 10,000 individuals where true survival (ϕ) is either 0.50, 0.75 or 0.90.

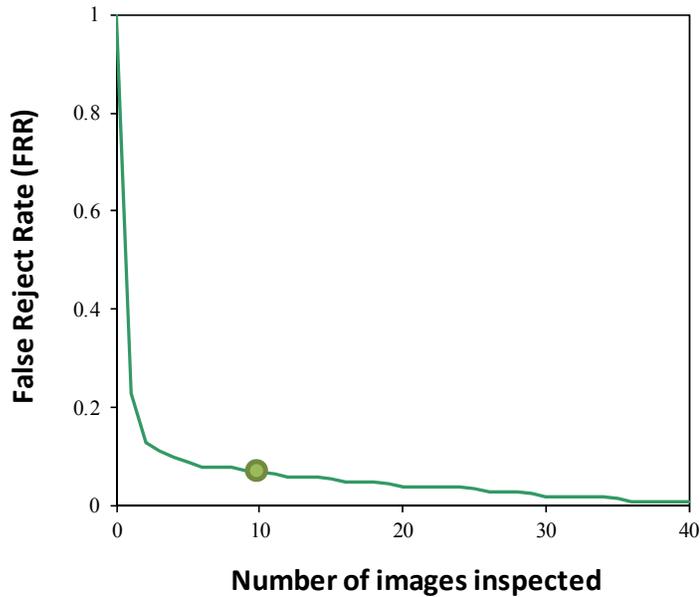


Figure 3. False reject rate (FRR) of the photo identification system for a test set of 198 true matching photo pairs of adult wildebeest from the Tarangire Ecosystem, Tanzania. The number of incorrectly identified matching pairs over true matching pairs is plotted as a function of the number of photos that were visually inspected (i.e., the threshold for inspection). The green dot indicates the threshold value (top 10 highest scoring photos) used for assembling the wildebeest encounter history data set. Based on the resulting FRR value (0.076), our estimated misidentification rate ($1-\alpha$) for comparison to the simulations was 0.039.

Supporting Information

Appendix S1.

R code for simulating open-population capture-history data sets with misidentification.

Found online at: <<http://www.methodsinecologyandevolution.org/view/0/index.html>>

under *Supporting Information*.

Table S1 Summary of computer-assisted photographic identification studies where false rejection rate (FRR) and false acceptance rate have been estimated. We list only the minimum FRR and FAR values for each study, as well the sample sizes (parentheses). For giraffe, we differentiated FRR due to computer-generated error (top FRR) and observer error (bottom FRR).

Species	Pattern type	FRR (sample size)	FAR (sample size)	Image comparison method	Patterns change over time?	Reference
African elephant (<i>Loxodonta africana</i>)	Ear edge	0.150 (200)	--	Inspect 10 highest ranking candidate images	Yes	Ardovini et al. 2008
African penguin* (<i>Spheniscus demersus</i>)	Ventral spots	0.080 (797)	<0.001 (73,600)	Automated matching; threshold 0.01% false accept rate	--	Shirley et al. 2010
Bottlenose dolphin (<i>Tursiops truncatus</i>)	Dorsal fin edge	0.250 (NR)	--	Inspect 30 highest ranking candidate images	Yes	Gope et al. 2005
Cheetah (<i>Acinonyx jubatus</i>)	Lateral spots	0.064 (72)	--	Inspect all excellent and medium quality images with 'similarity coefficients' ≥ 0.45	No	Kelly 2001
Common wall lizard (<i>Podarcis muralis</i>)	Ventral scales	0.020 (50)	--	Inspect 5 highest ranking candidate images	--	Sacchi et al. 2010
Giraffe (<i>Giraffa camelopardis</i>)	Reticulated polygons	0.000 (1103) 0.007 (300)	0.000 (516)	Inspect top ranked candidate image	--	Bolger et al., <i>In review</i>
Grey whale (<i>Eschrichtius robustus</i>)	Fluke edge	0.250 (NR)	--	Inspect 23 highest ranking candidate images	Yes	Gope et al. 2005
Harbor seal (<i>Phoca vitulina</i>)	Ventral spots	0.042 (1020)	--	Inspect top 0.3% of ordered list of good/excellent quality images	Seasonal	Hastings et al. 2008
Humpback whale (<i>Megaptera novaeangliae</i>)	Fluke patches	0.174 (42)	--	Inspect 3 highest ranking candidate images	--	Ranguelova et al. 2004
Marbled salamander (<i>Ambystoma opacum</i>)	Dorsal spots	0.05 (101)	--	Inspect 10 highest ranking candidate images	--	Gamble et al. 2008
Plains zebra (<i>Equus burchelli</i>)	Lateral stripes	0.202 (NR)	--	Inspect top ranked candidate image	No	Foster et al. 2006
Spotted ragged-tooth shark (<i>Carcharias taurus</i>)	Spots	0.193 (NR)	--	Inspect 10 highest ranking candidate images; Repeated 100 times to correct for random effects	--	van Tienhoven et al. 2007
Sea-lion (<i>Eumetopias jubatus</i>)	Flipper edge	0.250 (NR)	--	Inspect 28 highest ranking candidate images	Yes	Gope et al. 2005
Whale shark (<i>Rhincodon typus</i>)	Lateral spots	0.080 (27)	--	Inspect moderate or high confidence match categories	--	Arzoumanian et al. 2005
		0.070 (50)	--	Inspect 50 highest ranking candidate images; Images inter- annual	--	Speed et al 2007
White-bearded wildebeest (<i>Connochaetes taurinus</i>)	Shoulder stripes	0.076 (198)	<0.001 (4925)	Inspect 10 highest ranking candidate images	--	This study

*Fully automated matching, which provides a true trade-off between false acceptances and false rejections

CHAPTER II

WET SEASON RANGE FIDELITY IN WILDEBEEST (*CONNOCHAETES TAURINUS*)

Authors:

Morrison, Thomas A.¹
Bolger, Douglas T.² (Douglas.T.Bolger@dartmouth.edu)

¹Department of Biological Sciences, Dartmouth College, Hanover, NH 03755

²Environmental Studies Program, Dartmouth College, Hanover, NH 03755

Abstract

One of the striking features of migratory ungulates is their tendency to return to the same wet season ranges each year. Because fidelity to wet season ranges defines both management units and evolutionarily significant units, selection of seasonal ranges is a critical aspect of migratory behaviour with consequences for a population's demography, sensitivity to habitat change and adaptation to local environmental conditions. In ungulates, characterizing patterns of breeding site fidelity is difficult because it requires following large numbers of marked individuals across multiple migratory cycles. We used photographic capture-recapture to examine patterns of fidelity to wet season ranges in a declining population of wildebeest (*Connochaetes taurinus*) in northern Tanzania. Among 2557 uniquely identified adult wildebeest, we observed 150 recaptures across consecutive wet seasons. Between the two main migratory population subunits, the probability of switching wet season areas ranged between 0.00 and 0.18. Animals from the isolated Lake Manyara sub-population were rarely observed in other wet season areas, despite close spatial proximity to one of the migratory pathways. We found no effect of sex on switching between wet season ranges. However, breeding status in females (breeders vs. non breeders) had a strong influence on patterns of range fidelity, with breeders nearly four times as likely to switch ranges as non-breeders. Social-group associations between pairs of recaptured animals were random with respect to an individual's wet season range during the previous or forthcoming wet seasons, suggesting that an individual's herd identity during the dry season does not predict their wet season range.

Introduction

Migratory wildlife often exhibit a remarkable tendency to return to the same sites, ranges and routes each year, a behaviour referred to as ‘fidelity’ (Greenwood 1980; Waser & Jones 1983; Johnson 1986). Examples are widespread, and include many birds (Greenwood 1980), fish (Thorrold et al 2001; Block et al. 2005), amphibians (Reading et al. 1991; Sinsch 1992) and mammals (Johnson et al. 1986; Wedikin et al. 2010). Because the expression of fidelity can have important demographic, genetic and management and conservation implications (Saunders et al. 1991; Doligez et al. 2003; Bolger et al. 2008), there has been considerable interest in characterizing patterns of fidelity in wild migratory populations, and identifying potential mechanisms that generate those patterns (Milner-Gulland et al. 2011). An inflexible migratory strategy, where individuals return to the same area each year, can result in suboptimal habitat use in some or all years if habitat quality of breeding sites varies from year to year or if site quality deteriorates deterministically (e.g., because of habitat degradation) (Wiens et al. 1986; Watkinson & Sutherland 1995; Sutherland 1998; Cooch et al. 2001). Over multiple generations, high fidelity should promote local adaptation and assortative mating by effectively isolating demographic subunits within larger populations (Esler 2000; McNamara & Dall 2011). Genetic and demographic substructure play important roles in the stability and long-term viability or recovery of populations (Lande & Barrowclough 1987; Campbell et al. 2008) and imply that population subunits should be managed independently (Templeton & Georgiadis 1996; White et al. 2010).

Characterizing patterns of ‘fidelity’ in wild populations, however, remains challenging for a number of reasons. First, measuring fidelity requires the ability to follow a relatively large number of marked individuals across multiple migratory cycles in multiple sites or ranges (Belisle 2005). Even with large samples, separating mortality from dispersal can be difficult or impossible if individuals move over large areas and not all locations are sampled (Faaborg et al. 2010). Furthermore, defining the scale and boundaries of ‘sites’ can be arbitrary, particularly in highly mobile species that have large, potentially overlapping, seasonal ranges (Schaefer et al. 2000). Because non-territorial herbivores, such as many ungulates, move over relatively large ranges within any given season and are unattached to nesting or denning sites, fidelity for these species may be most appropriately measured at the scale of the entire range (Hansen et al. 2010). Linear displacement and range overlap across years have been used as measures of fidelity (Sweaner & Sandegren 1989) or as measures of habitat use following disturbance (Fallie et al. 2010). However, many such approaches suffer from a lack of an appropriate null model (Schaeffer et al. 2000). Only when sites or ranges are spatially non-overlapping does ‘fidelity’ unambiguously describe an animal’s faithfulness to a particular area. The Tarangire-Manyara Ecosystem (TME) provides a convenient location to study annual wet season range fidelity patterns because wildebeest occupy three spatially and ecologically discrete ranges during the wet season and congregate in two discrete ranges during the dry season (TCP 1998). At their furthest extent, wet season ranges are several hundred kilometres apart and individuals cannot easily switch to alternative areas until the next breeding cycle (Figure 1).

A number of hypotheses have been proposed to explain patterns of fidelity (or dispersal) in migratory species. Extremely high fidelity is presumed to be controlled by genetics, memory or cultural imprinting (Sutherland 1998) because animals do not act adaptively when conditions change. For instance, several migratory shrubsteppe bird species exhibit extremely high fidelity to breeding sites despite the experimental removal of up to 75% of their habitat, presumably to the detriment of their fitness (Wiens et al. 1986). In many populations, however, only a portion of individuals return to the same range or site in consecutive years. While this pattern does not preclude the possibility that genetics or cultural imprinting still play a role in determining when and where animals move, it suggests that animals may follow conditional decision rules (Hoover 2003), such that fidelity or dispersal is based on past experiences or environmental cues. For instance, a considerable number of studies on birds (e.g., Haas 1998; Switzer 1997; Hoover 2003) and some ungulates (e.g., Tremblay et al. 1997) have shown that successful breeders are often more likely to return to breeding sites or ranges in the following wet season, though this pattern does not always hold (Paton & Edwards 1996). Switzer (1993) termed this the 'win-stay: lose-switch' strategy. An alternative to basing range selection decisions on past experiences is to respond to reliable environmental cues that predict the quality of habitats in future. This strategy could involve responses to either extrinsic factors, such as recent rainfall and plant growth (Holdo et al. 2009), or intrinsic forces such as density-mediated habitat selection (Morris 1987).

Individuals may experience varying motivations for selecting certain types of habitat. For example, sex and age are also often correlated with patterns of fidelity and dispersal (Greenwood 1980; Harvey et al. 1984; Holmes et al. 1996). In polygynous

mammals, males and juveniles (of either sex) often have a greater probability of dispersing than females and older individuals, presumably either as a way to reduce inbreeding, lowering mate competition or retaining preferred sites (Dobson 1982). In female ungulates breeding state (i.e., whether or not a female is nursing a calf) is thought to play particularly important roles in influencing resource selection and local movement decisions (Fischhoff et al. 2007). Identifying causes of fidelity and dispersal becomes more complicated in gregarious species, where attraction to a social group may override an individual's directional bias (Couzin et al. 2005). For example, if an individual that selects area 'A' one year later joins a social group composed mostly of individuals from area 'B', the individual may be more likely to migrate to area 'B' during the following year. This type of behaviour could be facilitated by either leadership by a few well-informed or experienced individuals, or by group consensus decision-making (Conradt & Roper 2005).

To a large extent, ungulate migration has been viewed as a strategy to provide individuals with greater access to seasonally-available forage resources during the breeding season (i.e., 'summer' in temperate latitudes and 'wet' season in tropical latitudes; Fryxell & Sinclair 1988; Albon & Langvatn 1992). This view emphasizes the importance of environmental cues in determining where and when animals migrate to their breeding grounds (Albon & Langvatn 1992; Hebblewhite et al. 2008). The low fidelity to breeding sites or ranges exhibited by many migratory ungulate populations (Fancy & Whitten 1991; Rettie & Messier 2001; Wiseman et al. 2006) may reflect an initial or repeated movement towards resources that are available within the perceptual range of the animals. If this were the case, we would expect not only low seasonal

fidelity, but also directional dispersal, i.e., individuals favouring a particular range (the one with the highest quality resources) in a given year. Nonetheless, many ungulates appear to exhibit relatively high fidelity to ranges or routes (e.g., Sawyer 2009; White et al. 2010). For example, in Yellowstone National Park, 96% of migratory elk (*Cervus elaphus*; $n=52$ individuals followed for 2-4 breeding cycles) returned to the same summer grounds in consecutive years across 12 possible summer ranges (White et al. 2010). In these populations, mechanisms other than perceptual cues likely determine the long-range seasonal movements.

Wildebeest (*Connochaetes taurinus*) are one of the best studied migratory ungulates due to long-term monitoring records in the Serengeti-Mara Ecosystem in East Africa (Sinclair et al. 2007). However, the large population size in the Serengeti (~1.2 million individuals) and the lack of geographically discrete seasonal ranges has made it difficult to characterize patterns of fidelity across the landscape. Serengeti wildebeest appear to respond to forage and nitrogen availability in new grass growth within the perceptual range of individuals (80-100 km) (Holdo et al. 2009). Holdo et al. (2009) did not reject behavioural cues, past experiences and memory from influencing long-range movement (i.e. outside of wildebeest' perceptual ranges), but they concluded that environmental cues strongly influenced intermediate scale movements. Others have suggested that movements at the large scale may be a strategy to maximize energetic intake (Wilmshurst et al. 1999) or ingestion of new grass growth (Boone et al. 2006). Notably, most recent explanations for the Serengeti migration have focused on animal responses to environmental cues. Just east of the Serengeti ecosystem, wildebeest in the Tarangire-Manyara Ecosystem (TME) migrate between 40 and 120 km between seasonal

areas, a distance which falls on the edge of their perceptual range for predicting resource quality (Holdo et al. 2009). The TME population is sufficiently small (6000 individuals) that we can use photographic capture-recapture methods to individually identify animals in the different wet season ranges (Morrison et al., *in press*).

We characterize range fidelity in wildebeest by acquiring capture histories across three breeding cycles and develop multistate capture-recapture models to estimate the probability of transitioning to alternative wet season ranges. The use of multistate capture-recapture models in our analysis provides a robust method for estimating transition probabilities, while accounting for potential survival and recapture differences between different ranges (Brownie et al. 1993). We quantify fidelity at the scale of the entire wet season range, and measure it along a continuum of possible inter-annual movement strategies, from active dispersal (i.e., a lower probability of returning to the same range than chance predicts), random movement (i.e., an equal proportion of individuals from a given range in one year move to all ranges the following year) and fidelity (i.e., a higher probability of returning to the same range than chance predicts). We use the model of range fidelity to test four hypotheses. If environmental cues influence wet season range selection, we would expect that the probability of switching ranges is greater towards one range than others in a particular year (here called ‘directionality’). We also test whether sex or breeding success (among females) during the previous wet season influences an individual’s probability of returning to the same wet season area in consecutive years. Finally we examine the role of social forces in determining where individuals spend the wet season by comparing pairs of individuals recaptured within the same herd during the dry season and testing whether they come from, or move to, the

same wet season ranges. If individuals associate at random during the dry season, it supports the hypothesis that social group identity does not influence an individual's decision about where to migrate in the wet season.

Method

Study Area

The Tarangire-Manyara Ecosystem (TME) lies in the eastern branch of the Great Rift Valley in northern Tanzania and encompasses roughly 20,000 km² (Figure 1). TME is a savannah-woodland ecosystem that supports one of the most diverse communities of migratory ungulates in the world (Bolger et al. 2008). Precipitation in TME is highly variable from year to year (mean: 656mm year⁻¹; coefficient of variation: 36.4%), and largely falls (98% on average, $n=31$ years) between November and May (Foley & Faust 2010). Both calving and mating are highly synchronous in wildebeest and occur within short periods during the wet season (Figure 2; Estes 1976). In most years, calving occurs in three spatially distinct wet season ranges: the Northern Plains (NP), the Simanjiro Plains (SP), and along the northern shore of Lake Manyara (LM) (Kahurananga & Silkiluwasha 1997; TCP 1998). Once surface water dries out, animals migrate in herds to Tarangire and Lake Manyara National Parks, where the only perennial sources of water in the ecosystem are located. The Simanjiro Plains and Northern Plains lie roughly 150 km apart and are separated by a chain of forested volcanic mountains (Losiminguri, Burko and Mondouli mountains). Therefore, movements between SP and NP (or vice versa) within wet seasons are unlikely, and would require passing through Tarangire National Park (Figure 1). Movements of wildebeest from or to LM, in contrast, are unknown,

despite some speculation that this population is non-migratory and that individuals do not mix with the migratory population (Borner 1985; Prins & Douglas-Hamilton 1990; Mwalyosi 1991a).

Historically, TME wildebeest migrated to four or five distinct breeding (i.e., ‘wet’) season wet season ranges (Lamprey 1964; Borner 1985). However, since the 1940s, human population and agricultural expansion outside of Tarangire and Lake Manyara National Parks have increased four to six-fold (Mwalyosi 1991b; Gamassa 1995), reducing the connectivity in the ecosystem and causing substantial habitat loss and fragmentation (TCP 1998). Between 1988 and 2001, wildebeest in TME have experienced an estimated six-fold decline, from roughly 40,000 to 5000 individuals (TAWIRI 2001). Emigration from the study areas is an unlikely explanation for this decline because it would require large movements over forested habitat or through areas where surface water is typically unavailable. On the western edge of TME, the Gregory Rift Wall forms a major geographic barrier which has prevented any significant gene flow between the TME wildebeest and the adjacent Serengeti-Ngorongoro population (Geogriadis 1995).

Study Design and Data

The presence of natural variation in shoulder stripe patterns of adult (>2 years old) wildebeest allowed us to use computer-assisted photographic identification methods to compile capture histories across three breeding cycles in 2005-2007 (Figure 2). In each study year, we began photo sampling in May, ~2.5 months after the calving pulse, during which time wildebeest were on their wet season ranges. Sampling of each range took

between 2-14 days, depending on conditions and local animal densities. Each range was sampled twice per wet season within a robust design framework (see below). We also collected photographs during the dry season in Tarangire and Lake Manyara National Parks. These photos were not used in the capture-recapture analysis, but were necessary for the analysis of social-group associations during the dry season.

Each primary sampling period ($k=3$) encompassed two closed secondary periods within a robust-design framework (Figure 2; Pollock 1982). Sampling involved collecting photographs of animals in the Simanjiro Plains (encompassing Emboreet, Terat, Sukuro and Loiborsoit villages), the Northern Plains (encompassing Esilalei, Ol Tukai, Selela, Engaruka, Gelai Lumbwa villages and Manyara Ranch) and Lake Manyara National Park. We drove all roads and main tracks within a site once per secondary period and collected photos of all herds that we encountered. We first aged and sexed all animals within a herd on the basis of horn shape and body size (Watson 1967; Attwell 1982; Mduma et al. 1999) and collected a GPS location of each herd. Herds were defined as groups of wildebeest in which no individual was greater than 100m from the next individual (Archie et al. 2007). We then photographed individuals on their right sides only (stripe patterns were not symmetrical on both sides) perpendicular to the length of the animal. Photos were collected from a stationary vehicle at a distance of 10-100 meters during daylight hours using a 6.1 megapixel Pentax *istD* camera with a 400mm Sigma telephoto zoom lens (Figure 3). For each herd, we attempted to collect as many photographs as there were adults in the group. In some cases, herds moved away or joined other herds before we had collected the target number of photographs. Because the identity of individuals and herds was not known at the time of sampling, some

individuals and some herds were undoubtedly photographed multiple times while others were not photographed at all. Overall, we aimed to photograph 40-50% of all adults within each site to balance sample size and coverage. Actual capture rates (i.e., the percentage of the population identified) were much lower (capture probabilities (p) ranged from 0.02-0.22) because (i) some individuals were unknowingly photographed multiple times, and (ii) approximately 30% of images were too poor in quality to be used for matching.

We used two pattern recognition computer programs to identify individuals based on stripe patterns within images: one for adult males and one for adult females. The program used for males was developed by Conservation Research Ltd. <conservationresearch.co.uk> (Hastings et al. 2008). This system involved preprocessing images in three steps: (i) The user digitally outlined the margins of each individual within an image and placed reference markers on several key features, such as the nose and base of the tail. (ii) The software used these markers to fit a three-dimensional surface model on the animal which helped compensate for variation in viewpoint, posture changes and body shape of the animal across photographs. (iii) The software extracted a standard region of the shoulder stripe and created a planar black-and-white image which was then used for pattern-recognition. For female images, we switched to a simpler identification program (Wild-ID; <http://dartmouth.edu/~envs/faculty/bolger.html>) that required only one preprocessing step: cropping a rectangular region of the torso of each animal (Figure 3).

Both software programs processed and scored images along four similar steps: (i) SIFT features were extracted for each of the two images (Lowe 2004). (ii) The program

identified candidate matched pairs of SIFT features from the two images. (iii) A subset of geometrically self-consistent matched image pairs obtained in step 2 were selected, from which the program calculated a 2D affine transform mapping the first image to the second image. (iv) The program assigned a standardized score between 0 and 1 describing the strength of match between the two images. (v) Images were ranked based on the standardized score. For each photograph, an observer (T. Morrison) visually compared the top twenty ranking photos and recorded any matches. We then compiled the resulting set of matched photographs into capture histories that denoted whether individuals were seen or not seen (1 or 0) during each sampling period.

The two software programs yielded similar probabilities of misidentification (Fig S1), based on a test set of 198 images of known-identify animals (Morrison et al., *in press*). This was unsurprising, given that both programs used the same pattern-characterization algorithm ('SIFT') and processed and scored images in a similar manner. Furthermore, any slight differences in male and female datasets due to the software should be reflected in the recapture probabilities and not in the transition probabilities of the multistate capture recapture model. Because of these factors, we felt comfortable combining both male and female datasets and using them in a single analysis.

Range fidelity models

We fit two sets of capture history data to multistate robust-design capture-recapture (MSRD) models (Pollock 1982; Brownie et al. 1993). 'State' in this model corresponded to the three wet season ranges that individuals occupied at the time of sampling: Simanjiro (state SP), Northern Plains (state NP), or Lake Manyara National

Park (state LM). However, because we observed very few switches to, or from, Lake Manyara National Park, we excluded LM data from the multi-state model. We report the observed transitions involving LM animals and discuss this smaller population separately.

The ‘all-adults’ model examined the effect of sex and wet season range in year i on the probability of transition to an alternative wet season range (SP or NP) at year $i+1$. We define ψ_i^{SP-SP} and ψ_i^{NP-NP} as the probabilities that an animal present in the Simanjiro and Northern Plains, respectively, in the wet season of year i and alive in year $i+1$, selects the same wet season range in $i+1$. Models in which wet season range was random with respect to the site used in the previous year (i.e., ‘non-Markovian transitions’; Nichols et al. 1994) included the following constraints: $\psi_i^{SP-SP} = \psi_i^{SP-NP}$, and $\psi_i^{NP-NP} = \psi_i^{NP-SP}$.

These constraints implied that individuals first captured in SP or NP have the same probability of returning to those same ranges as they do of migrating to the alternative range (i.e., that movement between ranges is random). Models lacking this constraint indicate that individuals exhibit either fidelity (i.e., $\psi_i^{X-X} > \psi_i^{X-Y}$) or dispersal (i.e.,

$\psi_i^{X-X} < \psi_i^{X-Y}$). Directionality occurs in areas X and Y when $\psi_i^{X-Y} > \psi_i^{Y-X}$ or

$\psi_i^{X-Y} < \psi_i^{Y-X}$.

The second model (‘female-only’) used female captures across two wet seasons (2006 and 2007) to examine whether a female’s breeding status (breeder (B) or non-breeder(N)) influenced the probability of selecting either wet season range (SP or NP). Breeding status of females was recorded at the time of photo capture (i.e., May-July, 2.5-4.5 months post-calving), and females occupied four possible states (SP^B, SP^N, NP^B,

NP^N). Females were classified as either breeders or non-breeders on the basis of whether or not they had visible mammary glands (i.e., teats), indicating that they were nursing a calf. Any adult female that had lost their calf within ~10 days of being photographed would likely still have visible teats and would thus be recorded as a breeder (Watson 1967). Similarly, ‘non-breeders’ included both females that had failed to breed and females that had reproduced during that current breeding cycle but had lost their calf or foetus ~10 or more days before being photographed. In 24.5% of captures, we were unable to discern breeding status because females moved away too quickly, so these females have unclassified breeding statuses. We could not use a state misclassification model due to low recapture rates within primary periods (Morrison et al., *in press*). Therefore, any individual that had an unclassified state (always due to unknown breeding status) was censored from the dataset ($n = 41$ individuals). We assumed that all breeding statuses were classified correctly and that unclassified females were random with respect to transition probability and survival.

Other assumptions were similar for both the ‘all-adults’ and ‘females-only’ models: (i) there was no heterogeneity in capture or survival probabilities within wet season ranges and sexes, (ii) that within primary periods, survival was 1.0 and individuals could not transition between states, and (iii) that the population was open to transitions between states, mortality and recruitment (but not immigration to, or emigration from, other areas) between primary periods (Brownie et al. 1993). One of the significant issues for photographic capture-recapture data is that they violate the assumption that all marks (i.e., photos) are correctly identified. False acceptance errors (i.e., falsely matching two photos of different animals) are relatively rare in the wildebeest encounter history

datasets (estimated FAR was 8.1×10^{-4} , based on 100 test images; Morrison et al., *in press*), and we assume these errors did not have a significant impact on the data structure. However, encounter histories contained moderate numbers of false rejection errors (i.e., failures to match two photographs of the same individual, ‘FRR’) which inflate the number of observed encounter histories (Morrison et al., *in press*; Yoshizaki et al. 2009). Further, FRR is slightly different in the two identification programs; overall the program used for matching female photos had a 2.1% higher false rejection rate, based on tests using the same 198 image pairs (Morrison et al. *in press*). For these reasons, we do not report estimates of survival in our results. However, misidentification errors should not strongly bias transition probabilities. Because transition probabilities (i.e., the probability of moving between different wet season ranges in different years) are already conditioned on individuals being available for capture at least twice, they should be robust to false rejections and differences in FRR between males and females.

Model selection

In the ‘all-adult model’, we compared 20 candidate models where survival (ϕ), transition (ψ), and capture probabilities (p) varied by sex (g), state (s), primary periods (T) and secondary periods (t). In the ‘females-only model’, 18 candidate models were developed in a similar fashion, though in these we varied all model parameters by breeding status. We developed parameterizations of ϕ , ψ and p based on a priori model sets in order to reduce the list of potential models to a manageable number. For the ‘all-adults model’, we used the global model, $\{\phi(g,s,T), \psi(g,s,T), p(g,s,T,t)\}$, indicating variation in survival (ϕ), transition probability, and capture probability across sex,

breeding states, primary periods and secondary periods. For the ‘females-only model’, we used the global model: $\{\varphi(g,s), \psi(g,s), p(g,s,T,t)\}$. We assessed whether our data met the assumptions of multistate capture-recapture models by running Goodness of Fit tests on the global models using the program MSSURVIV (Hines 1994). This program estimates a pooled G^2 goodness-of-fit test statistic which can be used to assess the amount of dispersion in the data (\hat{c}) by dividing G^2 by model degrees of freedom (Lebreton et al. 1992). We compared competing models using the Quasi-Akaike Information Criteria corrected for small sample sizes (AICc, Akaike 1973; Burnham & Anderson 2002; Lebreton et al. 1992). AICc weights determined the strength of support for a particular model within a model set (Burnham & Anderson 2002). All model selection steps and estimation procedures were conducted using the “Open Robust Design MultiState” model with Huggins Closed Capture data structure in Program MARK, ver 5.1 (White & Burnham 1999).

Social-group associations in the dry season

We identified all pairs of individuals captured in the same herd during the dry (non-breeding) season. We classified each of these pairs into one of three categories: 1) Simanjiro Plains pair (i.e., both individuals within a pair used Simanjiro in the wet season), 2) Northern Plains pair (i.e., both individuals within a pair used the Northern Plains in the wet season) or 3) mixed pair (i.e., one individual from Simanjiro Plains and one from the Northern Plains). In all cases, herds contained other unidentified individuals whose wet season range affiliations were unknown. If social-group associations (i.e., pairs) in herds during the dry season were random with respect to their wet season range,

we expected the number of herds in each of the three categories to approximate a binomial distribution. We tested this hypothesis in each transition period using a χ^2 -test. We generated the expected frequency of herd category in each transition using the relative frequency of individuals from either wet season range. All estimates are reported as mean \pm SE.

Results

Overall, we collected 5657 images from 2557 unique individuals. We observed 150 recaptures (involving 136 unique individuals) between different wet season ranges in consecutive years (Figure 4). Wildebeest exhibited relatively high fidelity to wet season ranges. Wildebeest in Lake Manyara National Park were isolated from the other population subunits and exhibited near absolute fidelity. The most parsimonious model in the ‘all-adult’ dataset $\{\varphi(. , g , .) \psi(t , . , .) p(t , g , s)\}$ estimated annual wet season range fidelity as 1.0 from 2005-2006 (no SE due to estimates lying at the edge of parameter space) and 0.82 ± 0.06 from 2006-2007 (Table 1). We found a strong effect of year on the probability of switching wet season ranges between year i and year $i+1$, with switching more likely between 2006 and 2007, but no effect of sex nor of directionality in year i (summed QAICc weights for models with an effect of year = 0.94, for models with sex = 0.28, and for models with directionality (i.e., a state effect) = 0.08; Table 2). The effect of year may have been, at least partially, an artefact of lower power to a smaller sample size in 2005 (2005: 384 unique captures; 2006: 1178 captures, and 2007: 1230 captures). The global ‘all-adult’ model did not suffer from a significant lack of fit ($\chi^2=11.60$, $df=10$, $P=0.37$).

In the ‘females-only’ dataset, 86.6% females remained faithful to their previous year’s range. The probability of returning to, or of switching, wet season ranges from year i to year $i+1$ depended on breeding status in year i (Table 3). The top eight models ranked by QAICc all included an effect of breeding status on the transition probability (Table 3; summed QAICc weights for models with an effect of breeding status = 1.0). Breeders in year i were nearly four times as likely to switch ranges between year i and $i+1$ than were non-breeders. Estimated switching probability among breeders in year i was 0.203, while non-breeders was only 0.050 (Table 4). Overall, we observed 9 out of 32 breeders in year i switching wet season ranges in year $i+1$, while 0 out of 10 non-breeders switched between years (Figure 5). While eight out of nine observed range switches involved breeders moving from SP to NP (all between 2006 and 2007), we found little support for an effect of directionality on switches (summed QAICc weights for models with an effect of year = 0.07). The global ‘female-only model’ did not suffer from lack of fit ($\chi^2 = 38.54$, $df = 28$, $P = 0.09$) and had a c-hat value of 1.38.

Individuals coming from, or going to, the two wet season ranges appear to associate at random within dry season herds in Tarangire National Park (Table 4). The distribution of pair-wise within-herd associations in the dry season did not differ significantly from a random null model of associations in all transitions, except in the early dry season of 2007. During this transition (3A in Table 4), pairs of animals in Tarangire National Park were significantly segregated by the identity of their wet season ranges during the previous wet season. However, by the late dry season sample (i.e., immediately prior to migrating to wet season ranges), social-group associations were random with respect to the identity of their previous wet season.

Discussion

In tropical ungulates, wet season ranges provide animals with seasonally-available high quality forage that is critical for reproductive activities (Fryxell & Sinclair 1988) and play central roles in adaptive explanations of the causes or the timing of migration patterns (McNaughton 1990; Fryxell 1995; Murray et al. 1995; Holdo et al. 2009; Voeten et al. 2010). Fidelity to these ranges constrains migration patterns at the seasonal scale, promotes genetic differentiation among population subunits (assuming that breeding occurs on these ranges) and furthers the importance of managing each subunit independently. However, wet season range fidelity has not been well documented in wildebeest, or any tropical ungulate populations (Bolger et al. 2008). Adult wildebeest in the TME exhibited high but variable patterns of fidelity to wet season ranges, with no observed switches between 2005 and 2006 and an estimated 18% of individuals switching between 2006 and 2007 in the migratory population subunits. High range (or site) fidelity has been reported in temperate migratory ungulates, including pronghorn (White et al. 2010), woodland caribou (Schaefer et al. 2000), barren-ground caribou (Cameron 1986), sika deer (Sakuragi et al. 2004) and bighorn sheep (Festa-Bianchet 1986). Other ungulate populations exhibit much lower fidelity to all or portions of their ranges (Wiseman et al. 2006; Fallie et al. 2010). For instance, in the Porcupine caribou (*Rangifer tarandus*) herd which migrate hundreds of kilometres each year in northern Canada and Alaska, Fancy & Whitten (1991) found low fidelity to calving sites when comparing occupied calving sites to randomly selected calving sites in consecutive years

(n=245 transitions across years). Unfortunately, the mechanisms that control fidelity in ungulates have been poorly studied.

Surprisingly, migratory breeding wildebeest were responsible for roughly four times as many range switches as non-breeders (Table 2). This result runs contrary to past research that has found either no correlation or a positive correlation between reproductive success and fidelity (Haas 1998; Schaefer et al. 2000; Hoover 2003; Tremblay et al. 2007). One possibility is that females that switched ranges lost their calves after we had observed them as breeders, and their decision to switch was based on this failure to wean a calf. In several ungulates, predation on calves appears to increase the likelihood of moving to new calving sites the following year (Testa et al. 2000; Welch et al. 2000). However, we feel this explanation is unlikely because we sampled reproductive success at the end of the wet season. Any predation on calves that occurred following our observations would largely be unlinked to their wet season ranges, unless it occurred while animals were on migration back to dry season grounds in Tarangire National Park. An alternative explanation is that breeders were in relatively poor body condition by the end of the dry season, which increased their probability of switching ranges. This type of condition-dependent dispersal is common in many species (Ims & Hjermann 2001). While we could not measure body condition, annual rainfall was below average in TME during the course of our study (2005-2007) and was particularly low during April in both 2005 and 2006 when lactating wildebeest are under their greatest energetic demands (Sinclair 1977). These poor rainfall conditions could have placed surviving breeders in a large nutritional deficit by the end of the dry season, which may have induced them to migrate to a new range the following wet season. Unfortunately,

relatively little is known about the dynamics of body condition and its relationship with migration strategies in ungulates (Albon & Langvatn 1992).

In the Lake Manyara population, we three observed transitions to alternative wet season ranges, all involving adult females, two of which were breeders during the first year. Our larger encounter history dataset, which includes wet-to-dry dry-to-wet season transitions in 2006 and 2007, involved a total of 18 individuals transitioning to or from Lake Manyara NP and other areas in the ecosystem. Fourteen (78%) of these transitions were adult females, though because of the variable time span between these recaptures, the influence of breeding state could not be assessed among these females. Nonetheless, these data as well as the greater observed number of female transitions in the Tarangire population, support the hypothesis that female wildebeest, particularly breeders, are the most likely to disperse to new ranges. While male wildebeest are known to establish semi-permanent territories during the rutting season (Estes 1969), it remains unclear whether this territoriality extends across seasons and explains the pattern of greater male fidelity in the TME.

While there were a greater absolute number of observed range shifts from the Simanjiro Plains to the Northern Plains, we found little support for directionality in range selection (i.e., a greater proportion of individuals moving one direction than the other) which would be expected if wildebeest were responding to strong differentials in resource quality between the two migratory ranges in the early wet season (Boone et al. 2006; Holdo et al. 2009). Past work on ungulates has largely characterized migration patterns (particularly during the transition from the dry/winter to wet/summer seasons) as a response to heterogeneity in resource quality within the perceptual range of individuals or

herds (Albon & Langvatn 1992; Hebblewhite et al. 2008; Holdo et al. 2009). Wildebeest in the Serengeti may be nomadic rather than migratory (Holdo et al. 2009), a strategy that firmly emphasizes the ability of individuals and herds to track ephemeral resource patches that vary in time and place across years (Mueller et al., *in press*). Serengeti wildebeest appear to perceive variation in resource quality at scales of 80-100 km (Holdo et al. 2009), which is roughly the distance between the dry and wet season ranges in the migratory areas of the TME. However, the perceptual range of wildebeest in the Serengeti is likely much larger than elsewhere because herds can number in the tens of thousands of individuals. Larger herds may be able to improve navigational accuracy by allowing ‘many wrong turns’ (Simons 2004). Serengeti herds are an order of magnitude larger than any aggregation we observed in TME, and suggests that the ability of TME wildebeest to locate resource patches may be much lower than in the Serengeti. Moreover, in some years there may be a low differential in forage quality at the beginning of the wet season between ranges, because of, for example, simultaneous rainfall in all directions. To explore this further, one would need to closely monitor rainfall and new grass growth during the early onset of the wet season.

Social-group associations during the dry season did not appear to play a role in patterns of wet season range fidelity (Table 5). Individually-based movement models in group-forming animals have assumed that individual movement is a consequence of social forces and directional biases of one or more leaders in a herd (Gueron et al. 1996; Couzin et al. 2005). While our results cannot rule out the influence of social forces in influencing wet season range selection, they do suggest that wildebeest herds are not stable over the dry season, and that herd identity may not influence wet season range

selection. Early in the non-breeding (dry) season of 2007, individuals in Tarangire National Park were still segregated according to their wet season affiliations. However, this pattern disappeared by the late dry season (October-November) and pair-wise associations within herds become random with respect to the identity of an individual's previous or forthcoming wet season range.

Despite relatively high fidelity to wet season ranges, the fact that a moderate proportion of surviving individuals switch ranges between years demonstrates a degree of flexibility in migratory behaviour in wildebeest. Furthermore, we show that wildebeest in the TME exhibit variation in patterns of range fidelity. Adults that reside along the shore of Lake Manyara were rarely captured in other areas of the ecosystem (Figure 3). This confirms earlier speculations that the Lake Manyara wildebeest form an isolated population (Borner 1985; Prins & Douglas Hamilton 1990; Mwalyosi 1991a). Prins & Douglas Hamilton (1990) report that wildebeest went locally extinct in the Lake Manyara basin in the mid 1960's due to rising lake levels, but that a small number of animals ($n=80$) repatriated the area in the mid 1970's. Their residency near the northern boundary of Lake Manyara National Park is intriguing in light of the fact that the Northern Plains migration lies within ~5 km of the LM population, near the vicinity of Manyara Ranch. While the area between this Northern migration corridor and Lake Manyara is inhabited by a growing pastoralist community, much of the area remains relatively open rangeland and other wildlife populations are known to migrate through this human-dominated matrix (e.g., elephants; C. Foley, *pers comm.*). Nonetheless, the dichotomy in movement strategies between Lake Manyara and Tarangire animals highlights the need for comparative analysis that quantify the costs and benefits of migratory versus residency

strategies in populations such as those found in the TME (Bolger et al. 2008; Hebblewhite & Merrill 2009; Holt & Fryxell 2011).

The high range fidelity that we observed has several important implications for the long-term management and viability of wildebeest in the Tarangire-Manyara Ecosystem. The TME is undergoing rapid conversion of rangelands for agricultural use (TCP 1998). Most historical migratory pathways first described by Lamprey (1964) are no longer available for use and the population declined 8-fold between 1988 and 2001 (TAWIRI 2001). If wet season range fidelity remains consistently high over many years, wildebeest will have limited capacity to overcome rapid habitat changes or severe fluctuations in environmental conditions. Thus, populations may not have been able to rapidly shift to alternative ranges when a migratory pathway was eliminated. Wildlife managers should not assume that wildebeest can easily switch to new wet season ranges if previously inhabited ranges deteriorate or experience particularly poor conditions in a certain year. High range fidelity should also promote genetic differentiation among groups of animals using the different wet season ranges (Esler 2000; Campbell et al. 2008). This differentiation could be beneficial for adaptation to local environmental conditions (Skov et al. 2010). More data are needed to assess variability in range fidelity across multiple years, especially in years where strong differences occur in the prevailing environmental conditions between the two remaining migratory wet season ranges (SP and NP).

Acknowledgements

We thank the Commission for Science and Technology and the Tanzania Wildlife Research Institute for permission to conduct research in Tanzania, and the Tanzania National Park for permission to work in Tarangire and Lake Manyara National Parks. We thank R. Mollé for assistance in the field, to J. McGrew and N. Brown for help analysing wildebeest photos, and to J. Nichols and J. Hines for their assistance with the capture-recapture modelling. The work was funded by the Wildlife Conservation Society Research Fellowship Program and Dartmouth College, the Marion and Jasper Whiting Foundation, the Nelson A. Rockefeller Centre at Dartmouth College and NSF grant DBI-0754773 to DTB and H. Farid.

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Figures and Tables

Table 1. Summary of candidate models fit to ‘all-adults’ dataset. Survival (ϕ) and transition probabilities (ψ) were varied across years (T), sex (g) and wet season range (s). Capture probability (p) varied within primary periods (t), across years (T), with sex (g) and with wet season range (s). “nonMARK” indicates a model where transitions were random with respect to wet season range at year i . All other models followed a first-order Markovian process (i.e., wet season ranges at year i dependent upon wet season range at year $i+1$).

No.	Model	K	QAICc	Δ QAICc	w	QDeviance
1	$\phi(T,g,.)\psi(T,.,.)p(T,t,g,s)$	22	2278.38	0.00	0.36	2231.92
2	$\phi(T,g,.)\psi(T,g,.)p(T,t,g,s)$	24	2280.34	1.97	0.14	2229.80
3	$\phi(.,g,.)\psi(T,.,.)p(T,t,g,s)$	20	2280.45	2.08	0.13	2238.07
4	$\phi(.,g,s)\psi(T,.,.)p(T,t,g,s)$	22	2281.01	2.64	0.10	2234.55
5	$\phi(T,g,.)\psi(T+g,.)p(T,t,g,s)$	25	2282.28	3.90	0.05	2229.69
6	$\phi(T,g,.)\psi(T,.,s)p(T,t,g,s)$	24	2282.44	4.06	0.05	2231.90
7	$\phi(.,.,s)\psi(T,.,.)p(T,t,g,s)$	20	2282.52	4.15	0.05	2240.14
8	$\phi(.,g,.)\psi(T,g,.)p(T,t,g,s)$	22	2282.55	4.18	0.04	2236.09
9	$\phi(T,g,.)\psi(.,g,.)p(T,t,g,s)$	22	2283.87	5.49	0.02	2237.41
10	$\phi(T,g,.)\psi(.,.,s)p(T,t,g,s)$	21	2284.24	5.87	0.02	2239.82
11	$\phi(.,.,s)\psi(T,g,.)p(T,t,g,s)$	22	2284.32	5.95	0.02	2237.86
12	$\phi(T,g,.)\psi(.,.,s)p(T,t,g,s)$	22	2285.22	6.85	0.01	2238.76
13	$\phi(.,.,s)\psi(T,.,s)p(T,t,g,s)$	22	2286.12	7.74	0.01	2239.66
14	$\phi(T,g,.)\psi(.,g,s)p(T,t,g,s)$	24	2286.18	7.81	0.01	2235.64
15	$\phi(.,.,s)\psi(T,g,s)p(T,t,g,s)$	25	2289.54	11.17	0.00	2236.96
16	$\phi(T,g,s)\psi(T,g,s)p(T,t,g,s)$	31	2291.76	13.39	0.00	2226.88
17	$\phi(T,g,.)\psi(T,g,nonMARK)p(T,t,g,s)$	22	2293.27	14.89	0.00	2246.81
18	$\phi(.,g,s)\psi(T,g,nonMARK)p(T,t,g,s)$	24	2298.55	20.17	0.00	2248.01
19	$\phi(.,g,s)\psi(T,.,.)p(T,t,g,.)$	14	2300.39	22.02	0.00	2270.19
20	$\phi(T,g,.)\psi(T,.,.)p(T,.,g,s)$	14	2561.70	283.32	0.00	2531.50

Table 2. Estimates of range fidelity (i.e., transition probabilities) between Simanjiro Plains (SP) and the Northern Plains (NP), Tanzania between 2005-2006 and 2006-2007. These estimates are derived from a time-varying model of transition probability (Model 2, Table 1). Note that we could not estimate SE for transition probabilities that fell near the boundary of parameter space (0.0 and 1.0). Overall, the probability of staying in the same wet season range (in a model lacking effects of sex; Model 1, Table 1) was 1.0 in 2006 and 0.824 (± 0.06).

		Behaviour	Parameters	Estimate	SE
Females	2006	‘Switch’	$\psi^{SP-NP}, \psi^{NP-SP}$	0.00	0.00
		‘Stay’	$\psi^{SP-SP}, \psi^{NP-NP}$	1.00	0.00
	2007	‘Switch’	$\psi^{SP-NP}, \psi^{NP-SP}$	0.24	0.08
		‘Stay’	$\psi^{SP-SP}, \psi^{NP-NP}$	0.76	0.08
Males	2006	‘Switch’	$\psi^{SP-NP}, \psi^{NP-SP}$	0.00	0.00
		‘Stay’	$\psi^{SP-SP}, \psi^{NP-NP}$	1.00	0.00
	2007	‘Switch’	$\psi^{SP-NP}, \psi^{NP-SP}$	0.07	0.06
		‘Stay’	$\psi^{SP-SP}, \psi^{NP-NP}$	0.93	0.06

Table 3. Summary of candidate models fit to ‘females-only’ dataset. We varied survival (ϕ) and transition probabilities (ψ) across breeding status (b) and wet season range (s). Capture probability (p) varied across breeding status (b), wet season range (s) and secondary periods (t). ‘Switch’ implied that transitions across breeding status was dependent on whether animals were switching wet season ranges or remaining faithful to wet season ranges.

No.	Model	K	AICc	Δ AICc	w	Deviance
1	S(s,.) ψ (.,b(switch)) p (t,s,.)	14	1589.29	0.00	0.73	1558.89
2	S(s,b) ψ (.,b(switch)) p (t,s,.)	16	1593.07	3.78	0.11	1558.55
3	S(s,.) ψ (s,b) p (t,s,.)	22	1594.17	4.88	0.06	1547.24
4	S(.,.) ψ (.,b(switch)) p (t,s,.)	13	1594.94	5.65	0.04	1566.59
5	S(.,b) ψ (.,b(switch)) p (t,s,.)	14	1595.83	6.54	0.03	1565.43
6	S(s,b) ψ (s,b) p (t,s,.)	24	1597.85	8.56	0.01	1546.76
7	S(s,.) ψ (.,b) p (t,s,.)	12	1598.62	9.33	0.01	1572.31
8	S(.,.) ψ (s,b) p (t,s,.)	21	1600.96	11.67	0.00	1556.11
9	S(s,.) ψ (s(state),.) p (t,s,.)	12	1602.43	13.14	0.00	1576.13
10	S(s,b) ψ (s(state),.) p (t,s,.)	13	1603.74	14.44	0.00	1575.38
11	S(s,.) ψ (s,.) p (t,s,.)	14	1605.06	15.77	0.00	1574.66
12	S(.,.) ψ (s(state),.) p (t,s,.)	11	1607.67	18.38	0.00	1583.41
13	S(.,b) ψ (s(state),.) p (t,s,.)	12	1608.52	19.23	0.00	1582.22
14	S(s,b) ψ (s,.) p (t,s,.)	16	1608.62	19.33	0.00	1574.11
15	S(.,.) ψ (s,.) p (t,s,.)	13	1609.06	19.77	0.00	1580.71
16	S(.,b) ψ (s,b) p (t,s,.)	22	1609.68	20.39	0.00	1562.75
17	S(s,b) ψ (s,b) p (t,s,b)	32	1610.21	20.92	0.00	1542.30
18	S(.,b) ψ (s,.) p (t,s,.)	14	1610.26	20.97	0.00	1579.86

Table 4. Transition probabilities for the ‘Female-only’ model. Adult females (breeders (B) and non-breeders (N)) between two wet season range (Simanjiro Plains (SP) and the Northern Plains (NP)), Tanzania in June 2006 and June 2007. Estimates were derived from Model I (Table 3), which indicated that transitions across wet season ranges from year i to $i+1$ were dependent upon breeding status of females at year i . Estimates with asterisks were calculated by subtraction; no SE or CI could be estimated.

		Parameter	Estimate	SE	LCI	UCI
Non-breeder at 1 st capture	‘Stay-do not breed’	$\psi^{SP_N-SP_N}, \psi^{NP_N-NP_N}$	0.109*			
	‘Stay-breed’	$\psi^{SP_N-SP_B}, \psi^{NP_N-NP_B}$	0.844	0.110	0.514	0.965
	‘Switch’	$\psi^{SP_N-NP_N}, \psi^{SP_N-NP_B}$	0.025	0.026	0.003	0.171
		$\psi^{NP_N-SP_N}, \psi^{NP_N-SP_B}$				
Breeder at 1 st capture	‘Stay-do not breed’	$\psi^{SP_B-SP_N}, \psi^{NP_B-NP_N}$	0.042	0.041	0.006	0.244
	‘Stay-breed’	$\psi^{SP_B-SP_N}, \psi^{NP_B-NP_N}$	0.752*			
	‘Switch’	$\psi^{SP_B-NP_N}, \psi^{SP_B-NP_B}$	0.103	0.040	0.048	0.210
		$\psi^{NP_B-SP_N}, \psi^{NP_B-SP_B}$				

Table 5. Social-group associations within dry season herds are random with respect to wet season range in the prior or forthcoming wet season.

	Transition Type	Date range	No. of associations	χ^2	df	p-value
1	Non-breeding to Breeding	October 2006 - July 2007	9	0.44	2	0.80
2	Breeding to Non-breeding	June 2006 - November 2006	28	0.05	2	0.97
3a	Breeding to Non-breeding	May 2007 - November 2007	39	9.68	2	0.01
3b	Breeding to Non-breeding	May 2007 - November 2007	14	2.12	2	0.35

*Transition 3a included 25 associations that were observed within a month of animals migrating back to the non-breeding range. If these associations are excluded so that we only include mid or late non-breeding season observations (3b), the relationship is not significant

Figure 1. Map of the Tarangire-Manyara Ecosystem, Tanzania. Dotted lines denote the two primary migratory pathways used by wildebeest as they migrate between Tarangire National Park in the dry season and the Simanjiro Plains (SP) and Northern Plains (NP) during the wet season. The non-migratory population in Lake Manyara National Park (LM) is outlined on the western margin.

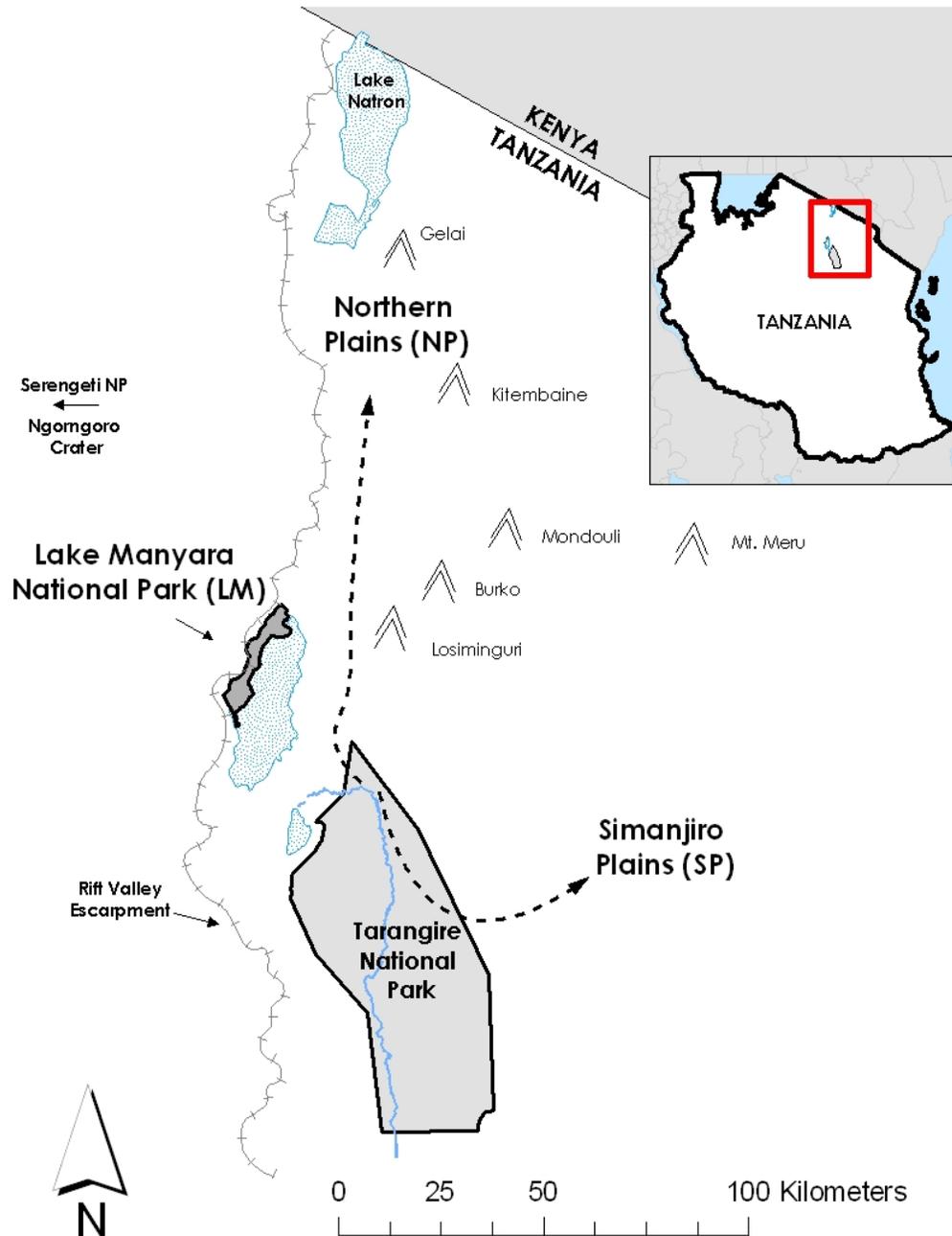


Figure 2. Generalized annual cycle for wildebeest in the Tarangire-Manyara Ecosystem, Tanzania.



Figure 3. Example of an adult female wildebeest photo captured on two occasions in different wet season ranges: A) in the Simanjiro Plains in June 2006 and B) in the Northern Plains in June 2007. Female was a breeder in both years. Dashed lines show the approximate cropped region of the torso used for pattern analysis and image matching in adult females.



Figure 4. Observed transitions between wet season ranges in adult migratory wildebeest in the Tarangire-Manyara Ecosystem, Tanzania, summed across two wet-wet season transitions (2005-2006, and 2006-2007). Black squares indicate instances where individuals returned to the same wet season range, while white squares are instances of switching wet season ranges.

		<i>t</i>		
		SP	NP	MNP
Females	SP	46	2	0
	NP	10	6	2
	MNP	1	0	36
Males	SP	23	1	0
	NP	2	12	0
	MNP	0	0	9

Figure 5. Observed transitions among adult females only, summed across three wet seasons (2005-2007). Breeding status was classified at year i . Black squares indicate instances where individuals returned to the same wet season range, while white squares are instances of switching wet season ranges.

		t	
		SP	NP
Breeders	SP	21	1
	NP	8	2
Non-breeders	SP	9	0
	NP	0	1

CHAPTER III

SEVERE REPRODUCTIVE COSTS IN A FEMALE TROPICAL UNGULATE

Morrison, Thomas A.¹

Bolger, Douglas T.² (Douglas.T.Bolger@dartmouth.edu)

¹Department of Biological Sciences, Dartmouth College, Hanover, NH 03755

²Environmental Studies Program, Dartmouth College, Hanover, NH 03755

Abstract

Life history theory predicts a tradeoff between current reproductive effort and future survival and reproduction. We examine four hypotheses related to reproductive costs in adult female wildebeest: 1) that reproduction incurs survival costs, 2) that survival costs are largely incurred during the dry season (June-October) when food is limited and calves are still nursing, 3) that reproduction in any given year lowers the probability of reproducing the following year, and 4) that survival of breeding females varies with wet season rainfall. We followed 895 females over three breeding cycles in the Tarangire Ecosystem, Tanzania using computer-assisted photographic capture-recapture, which resulted in 496 observed recaptures. We develop a robust-design multi-state capture-recapture model that allows for misclassification of breeding state. This framework provides a robust statistical approach for overcoming biases caused by uncertainty in breeding states of females, a common problem in analyses of reproduction-survival trade-offs. We observed over 50% higher survival in non-breeders than in breeders, indicating severe survival costs of reproduction. Survival did not vary over time in the best fitting models, nor did we find evidence that current breeding state affects the probability of reproducing the following breeding season. The severe survival costs were unexpected given the relatively long life spans of wildebeest and the fact that a majority of adults reproduce every year. We propose that low rainfall and rapid human-induced habitat change are the most plausible explanations for the observed costs during the study period. The high degree of calving synchrony in wildebeest and their low capacity to buffer survival costs with stored body fat (relative to temperate ungulates) should in theory amplify costs when environmental conditions for breeders become poor.

Introduction

A central tenant of life history theory proposes a tradeoff between current reproduction and an organism's future survival and reproductive output (Reznick 1985; Stearns 1992). This 'cost of reproduction' (sensu Williams 1966) shapes an assortment of life history traits and behaviors, including population age structure (Proaktor et al. 2007), age of first reproduction, age of senescence (Festa-Bianchet & King 2007) and strategies for parental care (Klug & Bonsall 2010). Reproductive costs are predicted because individuals face constraints in their ability to allocate limited resources towards both their offspring and their own survival (Gittleman & Thompson 1988). In female mammals, for example, reproductive activities (mate choice, copulation, gestation, lactation and parental care) require a large investment in time and energy (Ofstedal 1984) which can reduce the capacity for mothers to locate food and avoid predators.

In long-lived iteroparous vertebrates, adults should favor their own survival over that of their offspring (Sæther et al. 1993; Festa-Bianchet and Jorgenson 1998). This diminishes the chances of observing survival costs in wild populations (Hamel et al. 2010). Adult survival enables future breeding attempts while investment in juvenile survival or fecundity – two vital rates that vary considerably from year to year in large ungulates (Gaillard et al. 2000) – is a risky strategy. However, numerous studies have found that reproduction reduces the probability of reproducing the following breeding season (Hamel et al. 2010). These patterns of infrequent survival costs but relatively frequent reproductive costs of reproduction are predicted in capital breeders whose breeding success relies on stored body fat reserves (i.e., their 'capital') (Stephens et al. 2009). These stored reserves can remain depleted following a reproductive bout; future

reproduction tends to be more sensitive to losses in body fat than adult survival (Cook et al. 2004).

Costs of reproduction have received considerable attention in ungulates (Hamel et al. 2010), due to a number of long-term studies using individually identifiable animals (Clutton-Brock et al. 1996; Festa-Bianchett et al. 1998; Tavecchia et al. 2005; Moyes et al. 2006; Berube et al. 1996; Weladji et al. 2008; Hamel et al. 2009). In general, survival costs of reproduction have only been documented under severe environmental conditions, such as high density and harsh weather (Clutton-Brock et al. 1996; Tavecchia et al. 2005; Bardsen et al. 2008) while costs in terms of future reproduction are comparatively common (Hamel et al. 2010). Under favorable environmental conditions (i.e., low population density and mild winters), survival and future reproduction can be positively correlated with current breeding states in females, typically because the highest quality individuals have the highest probability of both reproducing *and* surviving (Cam et al. 2002; Weladji et al. 2008).

Nonetheless, the period of lactation is generally the costliest stage in the reproductive cycle of ungulates (Clutton-Brock et al. 1989). During the first month post-partum, for example, lactating females increase their energetic demands between 65 and 215%, relative to gestation (Oftedal 1985; Robbins 1993). Many ungulates time their reproductive activities to coincide with periods of the year when forage is most abundant and reliable (Sinclair et al. 2000). In the tropics, this period occurs in the wet season during which time animals congregate in breeding ranges that have been found to contain grasses high in protein and nutrients such as phosphorus and calcium (McNaughton 1990;

Voeten et al. 2010). Both nutrients are essential to the nutritional state and milk production of reproductive female bovids (McDowell 1985; Read et al. 1986).

Studies of reproductive costs in ungulates are strongly biased towards temperate, non-migratory species, mostly inhabiting areas with few or no large predators (Gaillard et al. 1999; Hamel et al. 2010). Despite the greater species diversity of ungulates in the tropics, these animals have been poorly studied from a life-history perspective and few populations have been studied at the individual level (Gaillard et al. 1999). For example, understanding of the demography of the >90 species of large herbivores in Africa (over 5kg) is based almost entirely on (i) intermittent transect-based surveys that do not identify individuals, or (ii) data from a small number of individuals carrying radio or GPS-collars (McNaughton & Georgiadis 1986; though see Owen-Smith 1990 and Prins 1996).

Among tropical ungulates, wildebeest (*Connochaetes taurinus*) are probably the best-studied species at the population-level due to over 50-years of monitoring in the Serengeti Ecosystem (Mduma et al 1999; Sinclair 2007). One of the key insights from the Serengeti is that dry season rainfall, through its effect on forage production, limits the total abundance of the migratory population (Sinclair et al. 1985; Mduma et al. 1999; Sinclair 2002). Nonetheless, we still know very little about reproductive costs in wildebeest and its interaction with rainfall and seasonality, largely due to the difficulty of following individuals over time and space (e.g., the Serengeti population includes over 1 million animals, most of whom travel roughly 2000 km per year). The recognition that migratory populations are declining throughout East Africa (Homewood et al., 2001; Stoner et al. 2006; Estes 2009; Harris et al. 2009) and that current boundaries of protected

areas often do not encompass migratory breeding grounds (Thirgood et al. 2004; Bolger et al. 2008; Voeten et al. 2010) lends urgency to investigations of reproductive costs in these populations.

In this chapter, we investigate four hypotheses related to reproductive costs in adult female wildebeest: 1) that reproduction incurs survival costs, 2) that survival costs in the dry season (June-October) are higher than in the wet season when food is limited and calves are still nursing, 3) that past reproduction increases costs in terms of future reproduction, and 4) that survival of breeding females varies with wet season rainfall. We predict that breeding females will have a lower survival rate than non-breeders, that this difference will be largest in the dry season, and that breeders will experience lower reproductive rates the following breeding season. Using a large dataset of individually recognizable animals, we develop a robust-design multi-state capture-recapture model to compare competing reproduction models. We use a model that accounts for misclassification of breeding state which provides a robust statistical approach for overcoming biases caused by uncertainty in breeding states of females (Kendall et al. 2004), a common occurrence in analyses of reproduction-survival trade-offs (Nichols et al. 1994).

Methods

Study Area

The Tarangire-Manyara Ecosystem (TME) is situated in the eastern branch of the Great Rift Valley in northern Tanzania and encompasses roughly 20,000 km² (Figure 1). TME is a savannah-woodland ecosystem that supports one of the most diverse

communities of migratory ungulates in the world (Bolger et al. 2008). Precipitation in TME is highly variable across time and space, with an average of 656mm year⁻¹ in Tarangire National Park (SD = 239 mm; Foley & Faust 2010). Migratory wildlife in TME have historically congregated in and near Tarangire National Park during the dry season (June to October) and migrated to four or five distinct pathways during the wet season (November to May) (Lamprey 1964; Borner 1985). This pattern of migration appears to be driven by water limitation during the dry season and forage quality or quantity during the wet season (Kahurananga & Silkiluwasha 1997; TCP 1997, 1998). One of the two remaining breeding grounds, the Simanjiro Plains, contains high concentrations of phosphorous during the wet season relative to dry season areas sampled concurrently (Voeten et al. 2010). Phosphorous is an important element for lactating female bovids (Murray 1995).

TME supports a variety of human land-use activities, including a national park used exclusively for safari-based tourism (Tarangire), a private wildlife conservancy which permits livestock grazing and limited tourism (Manyara Ranch), and a number of Game Controlled Areas and Open Areas, which permit wildlife harvesting (subsistence and trophy hunting), agricultural cultivation and permanent settlement (Nelson et al. 2007). Since the 1940s, human population expansion and agricultural cultivation have increased four to six-fold throughout the TME (Yanda & Mohamed 1990; Mwalyosi 1991; Gamassa 1995), reducing the connectivity in the ecosystem and causing substantial habitat loss and fragmentation (TCP 1998). Among the largest of the ungulate declines in the ecosystem (in terms of absolute number) are the wildebeest whose population has

decreased an estimated eight-fold between 1988 and 2001 (from roughly 43,000 individuals to 5300 individuals) based on aerial censuses (TAWIRI 2001).

Study Design and Data

We used photographic identification to compile capture-recapture data of adult female wildebeest (>2 years old). We photographed female wildebeest adults during five primary periods between May 2005 and November 2007, providing four intervals during which the population was ‘open’ to mortality (Figure 2). The first interval corresponded to a 12-month period (June 2005-June 2006) and the latter three intervals corresponded roughly to two dry seasons (June-October 2006 and June-October 2007) and one wet season (November 2006-May 2007). Using a ‘robust-design’ framework (Pollock 1982), each primary period consisted of two secondary periods, with the exception of periods 1 and 3 which each had only one secondary period. During secondary periods, we sampled in four different areas: (i) Tarangire National Park, (ii) Manyara (consisting of Esilale and Ol Tukai villages, and Manyara Ranch) (iii) Simanjiro Plains (Emboreet, Terat, Sukuro and Loiborsoit villages), and (iv) the Northern plains (Selela, Engaruka and Gelai villages). Prior to sampling, we conducted preliminary driving surveys and spoke with local informants (game scouts, wildlife managers and Masai residents) to identify which areas were currently occupied by wildebeest herds.

Photographic sampling involved driving all roads and main tracks within a site once per secondary period and approaching any herds encountered. We aged and sexed all animals within a herd on the basis of horn shape and body size prior to photo sampling (Watson 1967; Attwell 1982; Mduma et al. 1999). For each herd, we attempted to collect

as many photographs as there were adults in the group. In some cases, herds moved away or joined other herds before we had collected the target number of photographs. Because the identity of individuals and herds was not known at the time of sampling, some individuals and some herds were undoubtedly sampled multiple times while others were not photographed at all. Overall, we aimed to photograph 40-50% of all individuals (adult males and females) within each site to balance sampling effort and coverage. Actual capture rates (i.e., the percentage of the population identified) were likely lower because (i) some individuals were unknowingly photographed multiple times and (ii) some images were too poor in quality to be used for matching.

Animals were photographed perpendicular to their torso on their right sides (Figure 3) from a stationary vehicle at a distance of 10-100 meters during daylight hours using a 6.1 megapixel Pentax *istD* camera with a 400mm Sigma telephoto zoom lens. We recorded the breeding state (breeder (SB) or non-breeder (FB)) of females on the basis of whether or not they had visible mammary glands (i.e., teats). In 76.4% of the sightings, females with teats were also accompanied by a calf within a few meters. However, we found that the presence/absence of teats was a more reliable indicator of breeding state than having an associated calf. In all cases where mothers with teats but lacking calves were observed long enough, their calves eventually returned. Moreover, mother-calf associations are difficult to discern in dense herds and calves become more independent during the dry season, though they still nurse occasionally (Watson 1967). Any adult female that had lost their calf within ~10 days of being photographed would likely still have visible teats and would thus be recorded as a breeder (Watson 1967). Similarly, ‘non-breeders’ included both females that had failed to breed and females that had

reproduced during that year but had lost their calf or fetus ~10 before being photographed. In 24.5% of the photographs, we were unable to discern breeding state because individuals moved away too quickly; these females received an ‘unobserved’ classification.

We used the program WILD-ID to assist in the photo-matching process (Bolger et al. *in prep*; <<http://www.dartmouth.edu/~envs/faculty/bolger.html>>). While this software program was different than the one used for adult male wildebeest in Chapter I, the photo-matching procedure was effectively the same so will only be covered briefly here. WILD-ID used the SIFT algorithm to identify information-rich locations in the wildebeest stripe patterns in each photo (called ‘keypoints’; Lowe 2004). A pattern-matching algorithm was then used to provide a standardized score similarity between each new photo and all previously processed photos of adult females in the library database.

We compiled each unique animal ID into a capture history and then conditioned the full dataset by discarding all initial captures (Chapter I). This conditional approach was necessary because the dataset contained misidentification errors (i.e., failures to match two photographs of the same individual). These misidentifications created additional capture histories, which we assumed contain single encounters. The conditional approach removes these erroneous capture histories (i.e., ‘ghosts’) and reduces the resulting bias in survival estimates, so long as the capture rates are relatively high.

In the capture history data, all captures of females with teats were denoted as breeders (State B). However, because females lacking teats could not be unambiguously

classified as non-breeders (State N), we assumed that unless a female was observed with teats, their breeding state was unknown (denoted ‘u’ in the capture history data). This approach is identical to one used by Kendall et al. (2004) for adult female Florida manatees (*Trichechus manatus latirostris*). Females with unknown states included animals lacking teats and those whose state were ‘unobserved’. Because captures that lacked observations of breeding state may not have been random with respect to their state, we included time-specific covariates in the capture history data corresponding to whether or not breeding state was recorded at each capture.

Statistical model

We analyzed the mark-recapture data using a robust-design multistate model with misclassification (RDMSmis) (Kendall et al. 2004). This framework helps overcome three main problems that often confound studies of reproductive costs. First, the probability of capturing breeders may differ from that of non-breeders. Any difference will produce biased estimates of breeding probability and survival if ignored (Nichols et al. 1994). Multistate capture-recapture models account for these differences by estimating a separate capture probability, p , for each breeding state (Nichols et al. 1994). Secondly, the probability of classifying a female’s true breeding state, given that the female was observed, may be <1.0 . In our dataset, females lacking teats could not be unambiguously classified as non-breeders. Failing to accurately classify state produces underestimates of breeding probability and potentially biases survival estimates (Kendall et al. 2004). Finally, breeding states may be unobserved at the time of sampling; typically, any capture history with unobserved states would have to be discarded. RDMSmis models correct for

both misclassified states and unobserved states by estimating the probability of observing an individual's true state, given that the individual was observed (Kendall et al. 2004). This is made possible with the robust-design framework. To determine the probability of correctly classifying breeding state we rely on females whose breeding state is observed multiple times during a single primary period.

Our model also assumed that (i) there was no heterogeneity in capture probabilities within breeding states and no heterogeneity in survival rates across the ecosystem (e.g., that reproductive costs were the same across the four sampling areas), (ii) that secondary periods were closed with respect to breeding state and female survival (i.e., no calves are born or lost, and no females are recruited, die or leave the population between secondary periods within a primary period), (iii) that the population was open between primary periods (Brownie et al. 1993) and (iv) that all females observed as breeders were truly breeders (Kendall et al. 2004). This final assumption is necessary to resolve breeding state misclassifications. In the case of wildebeest, the assumption is supported by the distinct visual difference between those with and without lactating teats. Photographs for which there was any doubt were classified as unknown.

Females in breeding states B and N survived with probabilities S_i^B and S_i^N between primary periods i and $i+1$, respectively. We assume that females transition between state B and state N with a probability of ψ_i^{B-N} and from state N to state B with a probability of ψ_i^{N-B} . This transition occurs immediately prior to the second sampling interval and is conditioned on their surviving the interval. We constrained this transition probability in several ways. Surviving females could either transition to the alternate state or remain within the same state, (i.e., $\psi_i^{B-N} + \psi_i^{B-B} = 1$, and $\psi_i^{N-B} + \psi_i^{N-N} = 1$).

Secondly, because wildebeest have a highly synchronized birth pulse and are extremely unlikely to breed at other times of the year (Estes 1976), we added the constraint that $\psi_2^{N-B} = \psi_4^{N-B} = 0$, indicating that non-breeders could not transition to become breeders between the end of the wet season and the end of the dry season.

During each secondary period, j , of primary period i , females had a state-specific capture probability of $p_{i,j}^B$ and $p_{i,j}^N$ for breeders and non-breeders, respectively. Poor field conditions prevented us from collecting photos during the latter secondary periods of primary periods 1 and 3. During these periods we coded the encounter histories of all individuals as zeros to maintain the robust design structure and set capture probabilities in the model equal to zero, i.e., $p_{1,2} = p_{3,2} = 0$. Given that females were captured and observed as breeders or non-breeders, the probability of correctly classifying their true breeding state was $\delta_{i,j}^B$ and $\delta_{i,j}^N$, respectively. Since non-breeders were recorded as belonging to an ‘unknown’ state, we constrained the model so that the classification probability of non-breeders was always zero (i.e., $\delta_{ij}^N = 0$). The classification probability of breeders, δ_{ij}^B , can be estimated by relying on breeders encountered during multiple secondary periods in the same primary period. The model also defined π_i as the probability that a female first captured as a non-breeder in primary period i indeed had no calf (Kendall et al. 2004). Finally, the unconditional breeding probability, ω_i , provided an estimate of the fraction of females that were breeders in primary period i (Kendall et al. 2004). Because time intervals varied between sampling periods (5, 7 and 12-month intervals; Figure 2), we standardized all intervals to a 6-month (i.e., seasonal) scale.

The most general first model was $\{S(T,s) \psi(T,s) p(T,t,s) \omega(T) \pi(T) \delta(T,t)\}$, indicating variation across breeding states (s), secondary periods (t) and primary periods (T). However, due to data sparseness, this model produced a number of poor estimates so we collapsed several parameters that we expected to vary mostly across, rather than within, season (i.e., capture probability, p , and state classification probability, δ) and used the resulting reduced model $\{S(T,s)\psi(T,s)\pi(t)\omega(t)p(T(\text{season}),s)\delta(t(\text{season}))\}$ as our global model (Kendall et al. 2004). We could not determine goodness-of-fit for this general model (Lebreton et al. 1992) because no appropriate procedure has been developed for multistate capture-recapture models with state classification errors and individual covariates. Goodness of fit is a diagnostic test that examines whether our data meet the assumptions of the model and is typically measured using a χ^2 test. This test also allows us to estimate a variance inflation factor, $\hat{c} = \frac{\chi^2}{df}$, with which we can adjust model output to accommodate overly dispersed data (Lebreton et al. 1992). Therefore, we proceeded by assuming that our data did not suffer from lack of fit (other subsets of wildebeest capture-recapture data did have lack-of-fit problems) but we compared competing models across three levels of \hat{c} (1.0, 2.0, 3.0) to ensure that excessive data dispersion did not strongly affect the qualitative results of our models.

Overall we developed a set of 26 competing models that constrained parameters across time (primary or secondary intervals), season (all dry and wet intervals set equal) and breeding state (breeder or non-breeder in time i). We also examined whether breeding probability is independent of breeding state during the previous sampling period. This involved comparing models where $\psi_i^{B-B} = \psi_i^{B-N}$ and $\psi_i^{N-N} = \psi_i^{N-B}$ (i.e., a ‘non-Markov’ transition, where breeding state at time $i+1$ was independent of the state at

time i) to models lacking this constraint. Our study encompassed two transitions from non-breeding seasons to breeding seasons (June 2005- June 2006 and November 2006- June 2007), so we only applied ‘non-Markov’ constraints to these two intervals (Figure 2).

Using the most parsimonious time- and state-varying model from above, we examined whether total rainfall during the month of April preceding the survival interval explained variation in survival of breeders by incorporating rainfall covariates and comparing these models to one lacking the covariate. April is, on average, both the month of highest rainfall and the month of greatest energetic demand in lactating female wildebeest (Sinclair 1977). Monthly precipitation was recorded in Tarangire National Park at park headquarters from 1979-2009.

We sequentially developed parameterizations of p , ψ and S based on a priori model sets in order to reduce the list of potential models to a manageable number (Anthony et al. 2006). We compared competing models using the Akaike Information Criteria corrected for small sample sizes (AICc, Akaike 1973; Burnham and Anderson 1998; Lebreton et al. 1992). AICc weights determined the strength of support for a particular model within a model set (Kendall et al. 2004; Burnham & Anderson 1998). All model selection steps and estimation procedures were conducted using the “Robust Design MultiState with Misclassification” model in Program MARK, ver 5.1 (White & Burnham 1999).

Results

We collected 5574 high-quality photographs of adult female wildebeest over the five primary sampling periods. After conditioning on individuals photographed at least twice, our capture history dataset consisted of 895 individual capture histories and 496 recaptures across sampling periods. Most sites required multiple days of sampling (4.71 ± 0.68 days per site per secondary period, $\bar{x} \pm SE$), and the mean number of days to sample *all* sites within a secondary period was 24.9 days (range = 13-48 days). The secondary periods (during primary periods 2, 4, 5) were separated by 2 days each, except during the 2006 wet season (primary period 4) which had a separation of 16 days between secondary periods.

As predicted, we found a strong effect of breeding state on survival. However, breeding state was not dependent upon state the previous year or season. Increasing the variance inflation factor (\hat{c}) from 1.0 and 3.0 in the model output did not alter these qualitative results. For $\hat{c} = 1.0, 2.0$ and 3.0 , the summed weights (AICc or QAICc) of models that included a state effect on survival were: $w = 1.0, 0.93$ and 0.87 , respectively, while those including a non-Markov transition are $w = 0.95$ across all \hat{c} values (Table 1). In the most parsimonious model, $S(.,s)\psi(T(\text{non-Markov}),s)\pi(t)\omega(t)p(.,s)\delta(t(\text{season}))$, the estimated 6-month survival rate of non-breeders was over twice as high as breeders: 1.0 (no SE estimate) compared to 0.47 ± 0.06 respectively (Table 2). The standard error of non-breeder survival could not be estimated because it was on the boundary of parameter space. A model with no time dependence was 37.2 times more likely than a neighboring model that included time-dependence, $S(T,s)\psi(T(\text{non-Markov}),s)\pi(t)\omega(t)p(.,s)\delta(t(\text{season}))$ and 10.7 times more likely than a model that

included season (dry or wet) dependence. Thus, survival differences between breeders and non-breeders did not interact strongly with season or time.

Transitions between breeding states followed a non-Markov process, such that breeding state in a previous primary period did not impact the probability of transitioning into the opposite state during the following period during the two transitions that we observed across breeding cycles (Table 1). Between the dry-season 2006 and wet-season 2007, all non-breeders became breeders ($\psi_{2007}^{N-B} = 1.0$; Table 2). The two transitions that did not span different breeding cycles yielded large differences in the probabilities of transitioning from breeder to non-breeders: $\psi_{2006}^{B-N} = 0.94 \pm 0.06$ and $\psi_{2007}^{B-N} = 0.28 \pm 1.6$.

Capture rates were nearly twice as high for breeders ($p^B = 0.13$) than for non-breeders ($p^N = 0.07$). Based on model weights, the top model was 2.19 times more likely than a neighboring model that included both breeding state and season as effects on capture probability $p(\text{season},s)$, 2.44 times as likely as a model that included time and state ($p(t,s)$) and 28.4 times as likely as a model where capture probability was constant across all main effects ($(p(.,.))$) (Table 1). Given that a female was captured and breeding state observed, the probability of correctly classifying breeders was remarkably high rate ($\delta_{wet}^B = 0.99$ and $\delta_{dry}^B = 0.95$ for the wet and dry seasons, respectively). Finally, the proportion of breeders (ω) in the female population varied considerably across year and season. In the top model, unconditional breeding proportion ranged between 0.52 ± 0.06 and 0.85 ± 0.10 in the wet season (2 month after calving) and between 0.34 ± 0.07 and 0.37 ± 0.06 in the dry season (7 months after calving).

Total annual precipitation in Tarangire National Park during the course of our study was between 0.72 (August 2006-July 2007) and 0.95 (August 2005-July 2006)

times the average annual amount and annual rainfall had not been at or above the average since 2000-2001 (Figure 4; Supplemental Material). In each of the three study years (2005-2007), April was the month with the greatest rainfall deficit (between 44-77% below normal). Over a long time frame (1979-2008) April was consistently the wettest month for precipitation and the most reliable ($\bar{x} = 143.80\text{mm}$, coefficient of variation = 0.74). Nonetheless, time and state-varying models that included April rainfall covariates were less supported than a model lacking the covariates, as ΔAICc for models including covariates were all >8.0 .

Discussion

We found large reproductive costs in terms of future survival in adult female wildebeest (Table 2). Overall, non-breeders were nearly twice as likely to survive as breeders. However, current reproduction did not affect future reproduction, as both breeders and non-breeders contributed a proportionally equal number of females to either state the following year or season. Thus, most reproductive costs were paid through their effect on survival rather than future reproduction. The magnitude of the survival costs and lack of future reproductive costs are surprising given that in wildebeest, like many long-lived iteroparous organisms, adults are predicted to favor their own survival over that of their offspring (Stearns 1992). Generally, adult survival is high and invariable across years, whereas fecundity and juvenile survival is variable and strongly influenced by environmental conditions (Gaillard et al. 1998; Gaillard et al. 2000). Our estimate of non-breeder survival (1.0 ± 0) is comparable to adult 6-month survival reported elsewhere: 0.84 ± 0.01 (adult females only; Mills & Shenk 1992), and 0.93 ± 0.02 (adult

males and females combined; Mduma et al. 1999), while survival of breeders (0.47 ± 0.06) is far lower.

This result contrasts with past studies of reproductive costs in temperate populations. In a review of reproductive costs in ungulates, Hamel et al. (2010) found only 2 of 7 populations (29%) experienced survival costs, while 9 out of 18 populations (50%) experienced costs in terms of future reproduction. However, these studies all focus on temperate ungulates, which may face different constraints than tropical ones (Gaillard et al. 1998). As capital breeders that invest heavily in stored body fat reserves prior to winter (Hamel & Cote 2009), temperate adult ungulates may have greater capacity to buffer their own survival against variation in environmental conditions than tropical species, which, maintain comparably low body fat reserves throughout the year (Owen-Smith 1970).

Long-term research in the Serengeti Ecosystem provides some evidence that breeding wildebeest experience large and immediate changes in body condition during severe weather years, which may incur survival costs. Sinclair (1977, Figure 65) found lactating females to have only $1/5$ of the femur fat reserves of non-lactating females in the month of April (typically the wettest and most reliable month of rain) during a year of unusually low rainfall. Marrow fat is a reliable indicator of body condition in ungulates and is generally the last fat deposit to be metabolized (Sinclair & Duncan 1972). Furthermore, energetic models show that lactating wildebeest operate at a net energy deficit in normal rainfall years because energy intake does not match expenditures (Sinclair 1977). During our study, rainfall was below average, and particularly low each April (Figure 5). However, precipitation covariates (i.e., total monthly precipitation, dry

season precipitation and April precipitation) did not help explain variation in survival among breeding females when included in time-varying survival models. This analysis was limited to only four periods, so our power to detect a relationship, if one exists, was quite low.

The severity of the observed costs diminish any possibility that the costs represent an adaptive life history trade-off. Given that the majority of females bred each year of the study ($\omega = 0.52-0.85$ breeding proportion during the wet season, ~2 months post-partum; Table 2), such low survival of breeders, if sustained, would quickly drive the population to extinction. Nonetheless, the TME population is known to have declined approximately 8-fold between 1988 and 2001 (TAWIRI 2001) and high mortality of breeders could have certainly contributed to this decline. Additionally, mortality from natural predators (lions, leopards and hyena) is an unlikely explanation for these reproductive costs. Wildebeest rarely defend their young from predators (Kruuk 1972) and Tarangire animals spend a substantial proportion of the year outside of Tarangire NP in areas where lion densities are relatively low (Kissui, *pers comm*).

The potential for human disturbances on wildebeest breeding ranges to play a role in observed reproductive costs has expanded in recent years. Since the 1940s, human population growth and agricultural cultivation have increased four to six-fold throughout the TME (Yanda & Mohamed 1990; Mwalyosi 1991; Gamassa 1995), reducing the connectivity in the ecosystem and causing substantial habitat loss and fragmentation (TCP 1998). Breeding grounds, such as the Simanjiro Plains, contain forage material that contains relatively high concentrations of certain nutrients (particularly phosphorus) (Voeten et al. 2010). Because these nutrients are critical for milk production in lactating

females (McDowell 1985), they are believed to be a major driver of migratory behavior in the Tarangire Ecosystem (Voeten et al. 2010) and elsewhere (McNaughton 1990; Murray 1995). Additionally, both legal and illegal wildebeest harvesting occur outside of the national park in key breeding areas (Sachedina 2008). While selective harvesting by humans is known to bias mortality of reproductively valuable females in some elk populations (Wright et al. 2006), there is no evidence from Tarangire that breeders are specifically targeted.

Given i) these landscape changes to breeding areas, ii) the costs associated with early-stage lactation in breeding females (Clutton-Brock et al. 1989), and iii) the fact that the dry season is the critical season for limiting population growth (Sinclair 1977; Sinclair et al. 1985; Mduma et al. 1999; Ogutu & Owen-Smith 2003), we had expected to observe higher reproductive costs during the interval between June and October, which encompasses the end of the wet season and all of the dry season. We found only mild support for an effect of season or time on survival. In the fully time-dependent model (Figure 4), the difference between breeders and non-breeders was larger in the wet season interval (November 2006-May 2007) than the two dry season intervals, indicating that the wet season may have been the more costly period.

Our findings should represent conservative estimates of reproductive costs on survival because wet season sampling occurred in June, 2-3 months after most births (Sinclair et al. 2000). The average quality of breeding females during our wet season sample was likely greater than the average quality at birth or conception because lower quality females would be more likely to abort or lose calves prior to being classified as breeding females (Cameron et al. 1993; Tveraa et al. 2003). Thus, reproductive costs

should have been more difficult to detect by starting at this later time period (Hamel et al. 2010). In contrast, the high degree of birthing synchrony seen in wildebeest (Sinclair et al. 2000) should improve our ability to detect a signal of reproductive costs when, and if, they exist. By using a modeling framework that estimates the probability of classifying the true breeding state of individuals given that breeding state was observed (i.e., MSRDMis), we limited the amount of error due to misclassifications in breeding states (Kendall et al. 2004).

In light of the magnitude of survival costs, we consider several other error processes that could potentially produce spurious survival differences between successful and non-breeder. First, if breeders were more likely to be misidentified than non-breeders during the photo matching process, their observed survival would appear lower. This could occur if breeding activity somehow altered an individual's stripe patterns, making it more difficult for the SIFT pattern-recognition algorithm to characterize and match an individual's pattern before and/or after a reproductive bout. However, we examined photos matches involving individuals that were first captured as breeders or non-breeders and then later resighted in either breeding state. Each match had an associated rank value within the listed of visually inspected images (from 1 to 20). If differences in survival were driven by greater difficulty in matching photos of breeders than non-breeders, we hypothesized that breeders would have higher ranks within the top twenty visually inspected images than non-breeders. However, we found no difference between the distributions of ranks in breeders and non-breeders (no. matching pairs: $n^B = 143$, $n^N = 72$; Wilcoxon signed rank test: $\chi^2 = 1.26$, $df = 1$, $p = 0.026$). This analysis was limited to photo matches that were collected across primary sampling periods. Permanent

emigration by breeders to unsampled areas would also potentially produce similar differences in survival to those observed. However, we did not detect any segregation by breeding state within herds that we encountered (i.e., the distribution of the proportion of breeders in herds was unimodal within and across seasons). Our selection of sampling areas was also extensive and covered the large-scale seasonal range of migratory animals within the ecosystem (TCP 1997, 1998). Moreover, during the dry season, the ecosystem only contains a few sources of permanent water. Because wildebeest are drought intolerant (Estes 1992), most or all individuals in the population should be within several kilometers of one of these sources, and are thus relatively easy to locate.

In conclusion we observed higher reproductive costs in terms of future survival than in any other ungulate previously reported (Hamel et al. 2010). The fact that population growth rates in ungulates are most sensitive to changes in adult survival is particularly worrisome (Gaillard et al. 2000). Given that the TME wildebeest population has experienced substantial declines over the recent past and is threatened by increasing rates of habitat loss and fragmentation to breeding ranges (Borner 1985; Voeten et al. 2010), we advocate continued monitoring of demography in this population and as well as further work on identifying the mechanisms that cause these costs.

Acknowledgements

We thank the Commission for Science and Technology and the Tanzania Wildlife Research Institute for permission to conduct research in Tanzania, and the Tanzania National Park for permission to work in Tarangire and Lake Manyara National Parks. We thank R. Mollé for assistance in the field, to J. McGrew and N. Brown for help analyzing

wildebeest photos, and to W. Kendall, J. Nichols and J. Hines for their assistance with the capture-recapture modeling. The work was funded by the Wildlife Conservation Society Research Fellowship Program and Dartmouth College, the Marion and Jasper Whiting Foundation, the Nelson A. Rockefeller Center at Dartmouth College and NSF grant DBI-0754773 to DTB and H. Farid.

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Tables and Figures

Table 1. Model selection results of 26 candidate models of adult female wildebeest (>2 years old) capture-recapture data in Tarangire Ecosystem, Tanzania, between 2005 and 2007. Model notation follows Kendall et al. (2004): survival (S), transition probability (ψ), capture probability (p), state classification probability (δ), unconditional breeding proportion (ω) and the probability that a female who first captured as a non-breeder in primary period i indeed had no calf (π). These parameters can vary across primary periods (T), secondary periods (t), season ('state'; all wet or dry season sampling periods are set equal), and breeding state (s), or they can be held constant ("."). Additionally, transition probabilities can be non-Markov (i.e., breeding transitions are random with respect to breeding state) or Markov (i.e., breeding states at time $i+1$ are dependent on states at time i). All main effects and interactions are multiplicative except for two models where survival across breeding states was additive (i.e., $S(T+s)$). 'April Rainfall' indicates models in which total rainfall during the month of April (88 mm in 2005, 76 mm in 2006 and 46 mm in 2007) as an effect on breeder survival. Because GOF could not be assessed (see methods), we ranked models by AICc for the case where \hat{c} (the variance inflation factor) equals 1.0. We also provide the relative model ranks for $\hat{c} = 2.0$ and 3.0. \hat{c} did not strongly affect the two main results: survival varied by breeding state and current breeding state at time $i+1$ did not depend upon past breeding state at time i .

Model	Model Rank for given c-hat				c-hat=1.0			
	1.0	2.0	3.0	K	AICc	Δ AICc	Weight (w)	Deviance
S(.,s)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(season))	1	2	2	20	4946.70	0.00	0.33	4905.90
S(.,s)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(.))	2	1	1	19	4947.41	0.71	0.23	4908.69
S(.,s)ψ(T(non-Markov),s)π(t)ω(t)p(t(season),s)δ(t(season))	3	4	7	22	4948.27	1.57	0.15	4903.31
S(.,s)ψ(T(non-Markov),s)π(t)ω(t)p(t,s)δ(season)	4	22	24	34	4948.48	1.78	0.14	4878.19
S(.,s)ψ(T,s)π(t)ω(t)p(.,s)δ(t(season))	5	5	8	22	4950.54	3.84	0.05	4905.58
S(T+s)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(season))	6	7	10	23	4951.17	4.48	0.04	4904.12
S(T(season),s)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(season))	7	9	13	24	4951.43	4.74	0.03	4902.29
S(.,s)ψ(T(non-Markov),s)π(t)ω(t)p(.,)δ(t(season))	8	3	3	19	4953.39	6.70	0.01	4914.67
S(T,s)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(season))	9	15	19	26	4953.93	7.23	0.01	4900.59
S(T+s)ψ(T,s)π(t)ω(t)p(.,s)δ(t(season))	10	14	17	25	4955.22	8.52	0.00	4903.98
S(T,s)ψ(T,s)π(t)ω(t)p(.,s)δ(season)	11	20	21	28	4957.35	10.65	0.00	4899.80
S(T,.)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(season))	12	11	11	22	4957.78	11.08	0.00	4912.82
S(.,)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(season))	13	6	4	19	4958.30	11.61	0.00	4919.58
S(T(season),.)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(season))	14	10	9	21	4958.46	11.76	0.00	4915.58
S(.,s)ψ(T(non-Markov,season),s)π(t)ω(t)p(.,s)δ(T(season))	15	8	6	19	4959.64	12.94	0.00	4920.92
S(.,s)ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t)	16	21	23	28	4960.05	13.35	0.00	4902.50
S(T,.)ψ(T,s)π(t)ω(t)p(.,s)δ(t(season))	17	19	18	24	4961.94	15.24	0.00	4912.80
S(.,)ψ(T,s)π(t)ω(t)p(.,s)δ(t(season))	18	13	12	21	4962.43	15.73	0.00	4919.56
S(T(season),.)ψ(T,s)π(t)ω(t)p(.,s)δ(t(season))	19	16	16	23	4962.60	15.90	0.00	4915.55
S(.,s)ψ(T(non-Markov),s)π(t)ω(t)p(t(season),.)δ(t(season))	20	24	22	26	4966.53	19.83	0.00	4913.19
S(.,Breeder(April rainfall))ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t)	21	25	25	32	4966.75	20.05	0.00	4900.72
S(.,s)ψ(T(non-Markov),s)π(.,)ω(t)p(.,s)δ(t(season))	22	11	4	16	49.68.93	22.23	0.00	4936.41
S(.,s)ψ(T,.)π(t)ω(t)p(.,s)δ(t(season))	23	17	14	20	4968.95	22.25	0.00	4928.15
S(.,)ψ(T,s)π(t)ω(t)p(.,)δ(t(season))	24	18	15	20	4968.96	22.26	0.00	4928.16
S(.,Breeder(April rainfall))ψ(T(non-Markov),s)π(t)ω(t)p(.,s)δ(t(season))	25	23	20	24	4969.71	23.01	0.00	4920.57
S(T,s)ψ(T,s)π(t)ω(t)p(.,s)δ(season)	26	26	26	49	4971.44	24.74	0.00	4868.66

Table 2. Parameter estimates and standard error (SE) derived from the best-fitting model (Table 1) of photographic capture-recapture data of adult female wildebeest in the Tarangire Ecosystem, Tanzania, 2005-2007: survival (S), transition probability (ψ), capture probability (p), state classification probability (δ), unconditional breeding proportion (ω) and the probability that a female who first captured as a non-breeder in primary period i indeed had no calf (π). Breeders are denoted as state B and non-breeders as state N. Survival is standardized to a 6-month interval.

Parameter	Estimate	SE	Parameter	Estimate	SE
S^N	1.00	0.000	δ_{Wet}	1.00	0.000
S^B	0.47	0.058	δ_{Dry}	0.95	0.046
ψ_1^{NB}	0.75	0.181	$\omega_{June\ 2005}$	0.85	0.096
ψ_2^{NB}	0.00 ^a		$\omega_{June\ 2006}$	0.52	0.060
ψ_3^{NB}	1.00 ^b	0.000	$\omega_{Oct\ 2006}$	0.34	0.066
ψ_4^{NB}	0.00 ^a		$\omega_{June\ 2007}$	0.70	0.051
ψ_1^{BN}	0.25	0.181	$\omega_{Oct\ 2007}$	0.38	0.063
ψ_2^{BN}	0.94	0.056	$\pi_{June\ 2005}$	0.84	0.448
ψ_3^{BN}	0.00 ^b	0.000	$\pi_{June\ 2006}$	0.00 ^b	0.003
ψ_4^{BN}	0.28	0.157	$\pi_{Oct\ 2006}$	0.33	0.259
p^N	0.07	0.012	$\pi_{June\ 2007}$	1.00 ^b	0.000
p^B	0.13	0.016	$\pi_{Oct\ 2007}$	0.00 ^a	

^a These parameters were fixed due to known constraints in the model.

^b These parameters could were poorly estimated due to data sparseness.

Figures

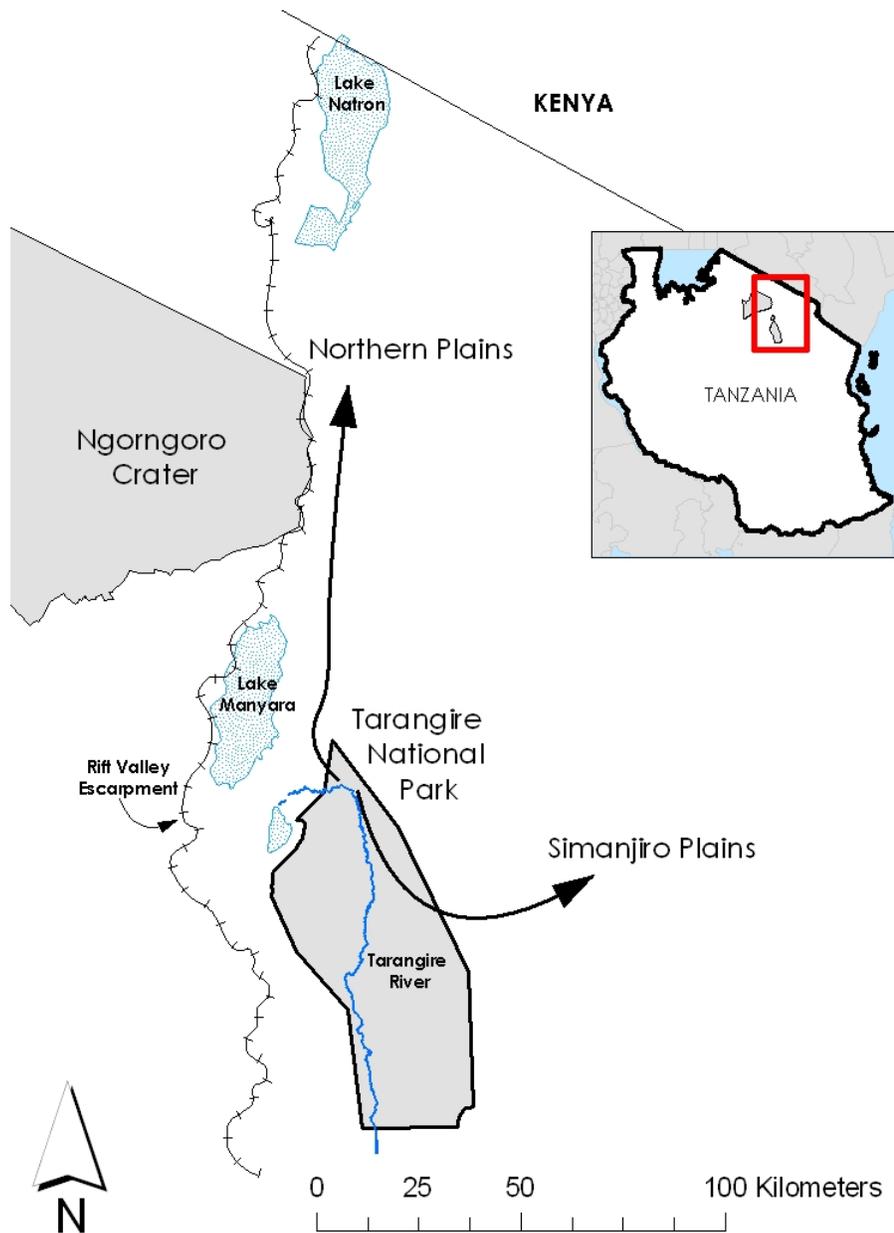


Figure 1. Map of the Tarangire Ecosystem, Tanzania. Arrows indicate the two primary migratory pathways used by wildebeest as they migrate between Tarangire National Park in the dry season and the Simanjiro and Northern Plains during the wet season.

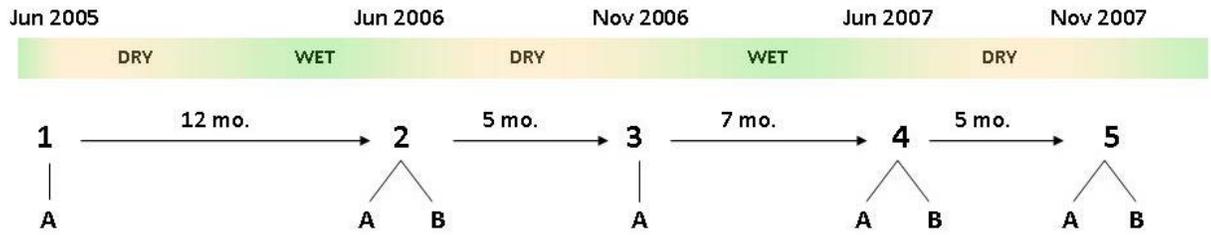


Figure 2. Sampling design and survival estimates for CR data collection. Note that there was only one secondary period in primary periods 1 and 3. Samples 1, 2, and 4 occurred at the end of the wet season and samples 3 and 5 occurred at the end of the dry season.



Figure 3. Adult female wildebeest displaying lateral stripe pattern, followed by her calf. Dashed line shows the approximate cropped region of the torso used for pattern analysis and image matching.

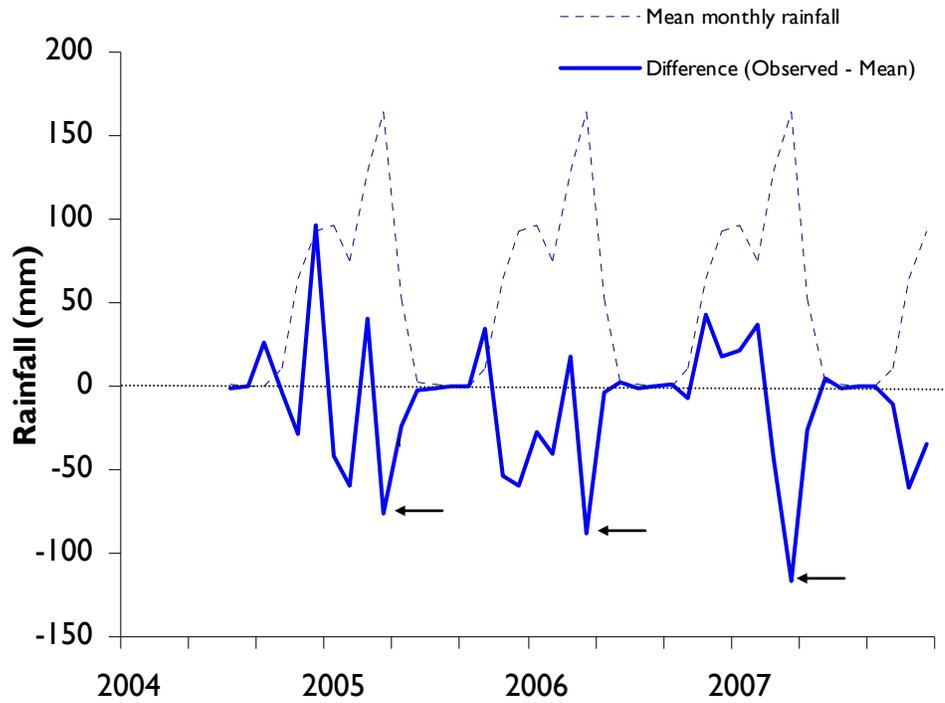


Figure 4. Difference between observed monthly rainfall and mean monthly rainfall (solid line) in Tarangire National Park, Tanzania. Mean monthly rainfall (dotted line) from 1978-2008 included as a reference. Arrows indicate rainfall during the month of April. April accounted for the largest negative difference between observed and expected rainfall during each year of the study (2005-2007).

CHAPTER IV

**SPATIO-TEMPORAL DEMOGRAPHIC VARIATION IN THE TARANGIRE-MANYARA
WILDEBEEST (*CONNOCHAETES TAURINUS*) POPULATION**

Author:

Morrison, Thomas A.

Department of Biological Sciences, Dartmouth College, Hanover, NH 03755

Abstract

An important first step in understanding and managing populations of wildlife is to characterize demographic variation across space and time. Migratory populations are particularly challenging in this respect because they range over large, ecologically-diverse landscapes that can encompass multiple types of land-uses and forms of protection. I examine patterns of spatial-temporal variation in vital rates in a recently declining population of migratory wildebeest (*Connochaetes taurinus*) in Northern Tanzania between the years of 2005 and 2007. This population migrates through areas experiencing high rates of human-induced habitat change, particularly on wet-season habitat which largely lies within communal land. I estimate seasonal, age and sex-specific survival and recruitment rates in three areas, two of which are connected by a shared dry season range (Tarangire National Park) and one of which is largely non-migratory and isolated in the Lake Manyara basin. Recruitment was consistently highest in the Lake Manyara population, followed by the Northern Plains population subunit. The Simanjiro Plains population subunit consistently had the lowest recruitment rates. Survival rate estimates were more variable across years and sites, but generally showed higher survival in the wet season than dry season in the Tarangire population. In Lake Manyara, the best model was one that did not include an effect of season, which was predicted given the low degree of seasonality in food quality and quantity provided by lake-edge grasses. I contrast variation in this population to other wildebeest populations, particularly those inhabiting the well-studied Serengeti-Ngorongoro ecosystem. I stress the importance of continued demographic monitoring of this population, particularly as human activities outside of protected areas continue to expand.

Introduction

Population models that identify sources of demographic variation are increasingly valuable to conservation and ecology (Wootton 1992; Doak 1995; Kauffman 2004). Certain areas, seasons, years or age-sex classes may contribute disproportionately to a population's overall growth rate. Identifying demographic heterogeneity can not only improve population models, but also help wildlife managers prioritize resources towards particular segments of the population. In the context of migratory ungulates, characterizing demographic variation has been a considerable challenge due to the difficulty of following large numbers of individual animals across their entire migratory cycle and separating seasonal from spatial effects (Bolger et al. 2008).

Migratory populations in particular may show spatial and temporal demographic variation. In many landscapes, anthropogenic habitat loss, fragmentation and barriers (e.g., fences, roads etc) have caused significant range contractions and reduced the number of possible routes available for migration (Bender et al. 1998; Bolger et al. 2008), and in some cases, they have prevented populations from migrating altogether (e.g., Williamson et al. 1985). The disruption of migrations can have severe population consequences, as exemplified in Southern Africa where the erection of livestock fences during the 1980's caused rapid declines in a number of migratory ungulate populations (Williamson et al. 1985; Whyte & Joubert 1988; Spinage 1992; Ben-Shahar 1993; Berry 1997). The widespread decline in numbers of many migratory populations (Berthold et al. 1998; Harris et al. 2009) underscores the importance of examining more closely spatial patterns in the demography and movement of migrations. This allows for the

identification of particular areas or segments of the population which may play proportionally greater roles in the overall dynamics of the population (Bolger et al. 2008). A high degree of connectivity between different areas could in theory provide a degree of demographic buffering if certain population subunits act as demographic source (Gill et al. 2001).

In this study, I investigate seasonal, spatial and age-sex related variation in demographic rates in two populations (Tarangire and Lake Manyara) of Eastern white-bearded wildebeest (*Connochaetes taurinus albojubotus*) in Northern Tanzania. The goal of the analysis is to identify particular periods of the migratory cycle, or components of the population, that may have disproportionate effects on the overall population trends. I employ a combination of photographic capture-recapture (for adult male and female survival and movement) and ratio-based techniques (for juvenile survival and reproduction) to estimate demographic parameters. The use of a multistate capture-recapture model in the Tarangire population allows us to differentiate between ‘seasonal’ (i.e., dry versus wet) variation in survival and variation across the two wet season calving grounds (Simanjiro Plains versus Northern Plains). The Tarangire population has declined roughly 5-8 fold over the last several decades (TAWIRI 2001) and is now a major focus of landscape and local-level conservation planning efforts (Sachedina 2008; Nelson et al. 2010). The Lake Manyara wildebeest population size has remained relatively stable over that period (Prins and Douglas-Hamilton 1990). During the course of this study, animals in the Lake Manyara basin remained relatively isolated from other areas (Chapter II). The striking contrast between the Lake Manyara population and the migratory Tarangire population (which move up to 300 kilometers per year) provided an

opportunity to tentatively evaluate the potential for changes in life history strategies due to differing migratory strategies.

Methods

Study Area

The Tarangire-Manyara Ecosystem lies in the eastern branch of the Great Rift Valley in northern Tanzania and encompasses roughly 20,000 km² (Figure 1). The Tarangire-Manyara Ecosystem is a savannah-woodland ecosystem that supports one of the most diverse communities of migratory ungulates in the world (Bolger et al. 2008). Precipitation is highly variable from year to year (mean: 656mm year⁻¹; coefficient of variation: 36.4%), the majority of which (98% on average, $n = 31$ years) falls between November and May (Foley & Faust 2010). I define the interval between December to June as the ‘wet-season’, and the interval between July and November as the ‘dry-season.’ The Tarangire-Manyara Ecosystem supports two distinct wildebeest populations: 1) the Tarangire population, which inhabits Tarangire National Park (‘TP’) in the dry season and two spatially discrete wet season ranges in the Simanjiro Plains (‘SP’) and the Northern Plains (‘NP’) (Kahurananga & Silkiluwasha 1997; TCP 1998), and 2) the Lake Manyara population, which inhabits grasslands around the shore of Lake Manyara (‘LM’; Figure 1). The Tarangire population migrates up to 300 kilometers per year, while individuals from the Lake Manyara population are effectively year-round residents in the Lake Manyara basin (Chapter II).

Historically, wildebeest in the Tarangire population migrated to four or five distinct wet-season breeding ranges (Lamprey 1964; Borner 1985). However, since the

1940s, human population and agricultural expansion outside of Tarangire and Lake Manyara National Parks have increased four to six-fold (Yanda & Mohamed 1990; Mwalyosi 1991; Gamassa 1995), reducing the connectivity in the ecosystem and causing substantial habitat loss and fragmentation (TCP 1997, 1998). Between 1988 and 2001, wildebeest in the Tarangire-Manyara Ecosystem have experienced an estimated six-fold decline, from roughly 40,000 to 5000 individuals (TAWIRI 2001). Emigration from the study areas is an unlikely explanation for this decline because it would require large movements over forested habitat or through areas where surface water is typically unavailable. On the western edge of the ecosystem, the Gregory Rift Wall forms a major geographic barrier which has prevented any significant gene flow between the Tarangire-Manyara wildebeest and the adjacent Ngorongoro-Loliondo population (Geogriadis 1995).

Study Design and Data

Population parameters (age structure, survival and reproduction) of ungulates are often derived by examining how the ratio of the number of calves or yearlings to the number of cows within herds changes over time (White et al. 1996). This method is widespread in ungulate studies because of the relative ease with which these data can be collected. However, the approach is often criticized as a way of inferring trends within a population because both sides of the ratio (number of calves and number cows) can vary over time, confounding interpretations of demographic change in a particular vital rate (Caughley 1974; Harris et al. 2008). Because I had independent estimates of adult female survival from capture-recapture models, I could adjust for variation in female survival to

derive estimates of calf (<2-14 months old) and yearling (14-19 months old) dry season survival. More formally, I estimated the probability of survival between time i and $i+1$

for calves and yearlings as: $S_i^C = \frac{calf_{i+1} : female_{i+1}}{calf_i : female_i} \times (S_i^f)$, and

$S_i^Y = \frac{yearling_{i+1} : female_{i+1}}{yearling_i : female_i} \times (S_i^f)$, respectively (Paulik & Robson 1969), and used the

‘delta method’ to estimate error terms. Because animals migrated between sampling periods in the Tarangire population, I could not differentiate female survival rates by site. Therefore I averaged values across estimates from the most parsimonious model, adjusted for the number of months encompassed by a particular interval. I used separate female survival rates for Lake Manyara animals. During each of the three wet season samples (2005-2007), I also estimated the recruitment rate (R) of new calves as the proportion of calves to adult females ($R_i^C = calf_i : cow_i$). Because sampling occurred approximately two months after the calving season (May-June), calf recruitment was a product of both fecundity rate and early survival (i.e., $f_i^f S_{0-2months}^C$). These ratios should theoretically be the same as those estimated in the breeding model in Chapter III (i.e., the probability of an adult female having a calf, ω). Therefore, I report both ratio and ω estimates, and provide a qualitative comparison of the two methods.

Survival estimates

I utilized natural variation in shoulder stripe patterns of adult (>2 years old) wildebeest and computer-assisted photographic identification to compile capture histories between May 2005 and November 2007 (Figure 2). Photographic sampling occurred in the Simanjiro Plains (SP), encompassing the villages of Emboreet, Terat, Sukuro and

Loiborsoit villages, the Northern Plains (NP), encompassing the villages of Esilalei, Ol Tukai, Selela, Engaruka, Gelai villages and Manyara Ranch, Tarangire National Park (TP) and Lake Manyara National Park (LM). I divided sampling intervals in SP, NP and TP into six primary periods and in LM into five primary periods. I attempted to collect two secondary periods per primary period within a robust-design framework, though on a number of occasions I could not collect the final secondary period because animals had moved to a new area (Figure 2; Pollock 1982). Photographic sampling involved driving all roads and main tracks within a site once per secondary period and approaching any herds that I encountered. Prior to sampling, I first aged and sexed all animals within a herd on the basis of horn shape and body size (Watson 1967; Attwell 1982; Mduma et al. 1999) and collected one GPS location per herd. Herds were defined as groups of wildebeest where no individual was greater than 100 m from the next individual (Archie et al. 2008). I photographed individuals on their right sides only (stripe patterns were not symmetrical on both sides) perpendicular to the length of the animal. Photos were collected from a stationary vehicle at a distance of 10-100 meters during daylight hours using a 6.1 megapixel Pentax *istD* camera with a 400mm Sigma telephoto zoom lens (Figure 3). For each herd, I attempted to collect as many photographs as there were adults in the group. In some cases, herds moved away or joined other herds before I had collected the target number of photographs. Because the identity of individuals and herds was not known at the time of sampling, some individuals and some herds were undoubtedly photographed multiple times while others were not photographed at all. Overall, I aimed to photograph 40-50% of all adults within each site to balance sample size and coverage. Actual capture rates (i.e., the percentage of the population identified)

were much lower (capture probabilities (p) ranged from 0.02-0.22) because (i) some individuals were unknowingly photographed multiple times, and (ii) some images were too poor in quality to be used for matching.

I used two separate pattern recognition computer programs to identify individuals based on stripe patterns within images: one for adult males (Chapters I and II) and one for adult females (Chapters II and III). The program used for males was developed by Conservation Research Ltd. (Hastings et al. 2008; <conservationresearch.co.uk>). This system involved preprocessing images in three steps: (i) the user digitally outlined the margins of each individual within an image and placed reference markers on several key features, such as the nose and base of the tail. (ii) The software used these markers to fit a three-dimensional surface model on the animal which helped compensate for variation in viewpoint, posture changes and body shape of the animal across photographs. (iii) The software extracted a standard region of the shoulder stripe and created a planar black-and-white image which was then used for pattern-recognition. For female images, I switched to a simpler identification program (WILD-ID; <http://www.dartmouth.edu/~envs/faculty/bolger.html>) that required only one preprocessing step: cropping a rectangular region of the torso of each animal (Figure 3).

Given a pair of preprocessed images, both image-matching programs proceeded similarly along four steps: (i) SIFT features were extracted for each of the two images (Lowe 2004). (ii) The program identified candidate matched pairs of SIFT features from the two images. (iii) A subset (ideally a maximal subset) of geometrically self-consistent matched pairs obtained in step 2 were selected, from which the program calculated a 2D affine transform mapping the first image to the second image. (iv) The program then

assigned standardized scores to the goodness of the fit between the images. (v) Images were ranked based on the standardized score. For each photograph, an observer (T. Morrison) visually compared the top twenty ranking photos and recorded any matches.

I compiled the resulting set of matched photographs into capture histories that differentiated captures as occurring in one of the four sites (TP, SP, NP, and LM; Table 1). I observed only three consecutive-year transitions between Lake Manyara National Park and other areas in the ecosystem (Chapter II). Therefore I separated LM data and ran separate analyses for the LM population and the Tarangire population. The three shared capture histories were excluded from either dataset. I then ‘conditioned’ the dataset by censoring all initial captures (Morrison et al., in press). This conditional approach was necessary because the dataset contained misidentification errors (i.e., failures to match two photographs of the same individual). These misidentifications created additional capture histories, which I assumed contain single encounters. The conditional approach removes these erroneous capture histories (i.e., ‘ghosts’) and reduces the resulting bias in survival estimates, so long as the capture rates are relatively high.

Capture-Recapture Modeling

I fit the Tarangire capture history dataset to a robust-design multistate capture-recapture (RDMS) model (Pollock 1982; Brownie et al. 1993). I assumed individuals occupied one of three states (i.e., ‘sites’; TP, SP and NP) during each primary sampling period. Between primary sampling periods, individuals survived with a probability of $S_i^{g,s}$, where g was the individual’s sex (male or female) and s was the site in which they were captured at time i . Given their survival, individuals could transition within or

between the three sites with a probability of $\psi_i^{g,s_i^j - s_{i+1}^j}$, where g was the individual's sex (male or female) and s_i^j was the site, j , in which they were captured at time i and s_{i+1}^j was the site in which they were captured at time $i+1$.

This model examined the effect of sex, site and time and season on the probabilities of surviving, transitioning to alternative sites and being captured. In addition to simply differentiating by sex and sites (TP, SP and NP), I set the two wet season sites equal to evaluate whether they varied. Note that survival in a particular site refers to those animals first captured in that site. These animals could (and often did) move elsewhere shortly after they were captured, and site-specific survival may not have been a reflection of interactions occurring on that particular site. This is one of the main challenges of study spatial demographic variation in a migratory species. The 'seasonal' effect, in contrast, involved differentiating *dry* season intervals (June-October 2006, June-July 2007 and July-October 2007), a single *wet* season interval (November 2006 – May 2007) and a single *annual* survival (June 2005-June 2006) within the capture-recapture design matrix. 'Time' was modeled so that all intervals could vary. Transition probabilities between wet season sites (SP and NP) were estimated with greater precision in Chapter II using a larger (i.e., 'unconditioned') dataset. However, I were interested in the transition probabilities from the dry season site (TP) to the two wet season sites as these would provide understanding of variation in wet season selection among those individuals that had survived to the dry season. Some of the transitions were impossible due to the absence of animals (and thus sampling) in particular sites during particular periods (Figure 2). For example, during the fourth sampling period, no animals were captured in Tarangire National Park (TP) because animals were still on their wet season grounds (SP

and NP). I constrained the model so that individuals could not transition to TP during the previous time period: $\psi_3^{SP-TP} = \psi_3^{NP-TP} = \psi_3^{TP-TP} = 0$, and all TP animals had to transition to either SP or NP: $\psi_3^{TP-SP} + \psi_3^{TP-NP} = 1$. In total, 72 parameters (out of a possible 168 in the most general model) were constrained due to either impossible or inevitable transitions. The general model was $S(T,g,s)\psi(T,g,s)p(T,t,g,s)$, indicating variation in survival (S) and transition probabilities (ψ) across primary sampling periods (T), sex (g) and site (s). Capture probability (p) also varied across secondary sampling periods.

I also developed a single state robust-design model for the Lake Manyara National Park (LM) dataset. I compared models where survival (S) varied across sex (g), season ($T(\text{season})$) and primary periods (T) and where capture probability also varied across secondary periods (t). This led to a general model of $S(T,g)p(T,t,g,s)$.

Assumptions were similar for both models: (i) that all individuals of a particular sex occupying a particular area in a given sampling period had an equal probability of being captured, (ii) that primary periods were closed with respect to mortality or migration and (in the TP-SP-NP model) that individuals could not transition between states, and (iii) that the population was open to transitions between states, mortality and recruitment (but not immigration or emigration from other areas) between primary periods (Brownie et al. 1993). Finally (iv) these models assume that all individuals were correctly identified at the time of capture. While capture-recapture using photographs is prone to violating this assumption (Yoshizaki et al. 2009; Morrison et al., *in press*), I minimize the effects of these errors by conditioning capture-histories on being captured at least twice and censoring the first capture (see above).

Model Selection

I developed parameterizations of S , ψ and p based on *a priori* model sets in order to reduce the list of potential models to a manageable number (Anthony et al. 2006). For the Tarangire population, I compared 30 candidate models and for the Lake Manyara model I compared 13 candidate models. I assessed whether these data met the assumptions of multistate capture-recapture models by running Goodness of Fit tests on the global models using the program MSSRVRD for the Tarangire model and program SRVRD for the Lake Manyara model (Hines, *pers comm.*). These programs estimate a pooled G^2 goodness-of-fit test statistic which can be used to assess the amount of dispersion in the data (\hat{c}) by dividing G^2 by model degrees of freedom (Lebreton et al. 1992). I compared competing models using the Akaike Information Criteria corrected for small sample sizes (AICc, Akaike 1973; Burnham and Anderson 1998; Lebreton et al. 1992). AICc weights determined the strength of support for a particular model within a model set (Burnham & Anderson 1998). All model selection steps and estimation procedures were conducted using the Huggins closed capture data type model in Program MARK, ver 5.1 (White & Burnham 1999). Estimates are reported as mean \pm SE.

Results

I collected 8968 high quality photographs of adult male and female wildebeest across five primary sampling periods in the Lake Manyara population and six sampling periods in Tarangire population. After identifying matches and conditioning the encounter histories on individuals having been sighted at least twice, the resulting dataset yielded 1778 unique capture histories. This included 2230 captures (individuals were

only counted once per secondary period) and 453 recaptures (Table 1). In the Tarangire population, the general model did not suffer from lack of fit ($G^2 = 62.01$, $df = 180$, $p > 0.10$). The most parsimonious model indicated survival was strongly influenced by season (annual vs. dry vs. wet), sex and site (no. parameters = 55, AICc model weight = 0.76; Table 2). This top model had 11.3 times more support than the next best model, which had an identical parameterization but lacked an effect of season on survival. In the Lake Manyara population, the top model $S(\cdot, \cdot)p(T, t, g)$ had no effect of sex or time on survival and had 3.22 times greater support than the next best model (according to model weights). The general model for Lake Manyara data also did not suffer from lack of fit ($G^2 = 12.58$, $df = 12$, $p > 0.10$). Estimates of capture probabilities varied considerably across sampling periods, but were generally low in both models and suffered from relatively low precision. For instance, in the Northern Plains, female capture rate was $p = 0.02 (\pm 0.15)$, though in Tarangire NP during the same period, female capture rate was estimated as $p = 0.88 (\pm 0.34)$.

Seasonal Variation

I found a strong effect of season on adult survival in the Tarangire population, but not in the Lake Manyara population (Table 2). Actual survival estimates varied considerably between 0 and 1 in the Tarangire population and suffered from low precision (Table 3). In general, dry season survival rates were lower than wet season survival across all sex-site categories, except among Northern Plains females for which dry season survival was slightly higher, though confidence intervals for the two estimates had considerable overlap (Table 3). Adult survival in the non-migratory Lake Manyara

population was particularly low, though these estimates were more precise than those in Tarangire (12-month survival: 0.37 ± 0.08). Season had only a small effect on survival in this population (AICc model weight = 0.16; Table 2).

Contrary to predictions, in both the Tarangire and Lake Manyara populations, monthly calf survival during the dry season (ages ~2-7 months, June-November) in 2006 and 2007 was lower than calf survival during the wet season (ages ~7-14 months, November-May) in 2006-2007. Comparisons of yearling survival across season were not possible. I could not obtain a wet season yearling survival rate because yearlings could not be differentiated from adults at the end of their second year (age 26 months).

Variation among Calving Grounds

Adult survival varied across the two calving grounds in the Tarangire population (SP and NP). In general, the adults inhabiting the Northern Plains appear to have higher mean survival than those inhabiting the Simanjiro Plains, with the exception of females during the wet season. During the wet season, female survival was over twice as high in the Simanjiro Plains than in the Northern Plains. Again, adult survival estimates suffered from relatively low precision (Table 3). The Northern Plains also produced higher calf recruitment than the Simanjiro Plains in two out of the three years (2005-2007; Table 4). These areas had similar recruitment in 2005. However, calf recruitment in Lake Manyara was between 10-50% higher than either SP or NP across all years. In the Tarangire population, the proportion of females with calves, ω , estimated from the female breeding model in Chapter III was roughly twice as large as age-ratio based estimates of recruitment in 2005. However, the proportions were nearly the same in 2006 and 2007, if

estimates from the ratio-base method were averaged across SP and NP. We could not estimate ω in 2005 because we collect capture-recapture data during only one secondary sampling period within this primary period (Chapter III)

Variation in survival across sex

While I found no difference in adult male and female survival in the Lake Manyara population, females in the Tarangire population had on average 22% higher survival than males ($S_f = 0.69 (\pm 0.13)$ vs. $S_m = 0.568 (\pm 0.12)$) based on a model where survival only varied by sex. However, in the Northern Plains female survival was lower than males during both the dry and wet season intervals (Table 3).

Tarangire vs. Lake Manyara populations

In contrast to the Lake Manyara population which has a constant survival across sex and season, the migratory Tarangire population had high but variable adult survival rates across most intervals and sex-site categories. The main exception to this pattern was during the dry season, when adults (both males and females) first captured in Tarangire National Park and the Simanjiro Plains had lower survival than those in Lake Manyara (Table 3). As noted, recruitment was higher in the Lake Manyara population than the Tarangire population across all three years (Table 4). Calf survival between the two populations varied across years in terms of which had a greater magnitude. Yearling survival was considerably lower in the Lake Manyara population than the Tarangire population in 2006 (monthly dry season survival: 0.62 ± 0.08 vs. 0.95 ± 0.05 for LM and TP, respectively; Table 4).

Discussion

A major focus in population biology over the last several decades has been to incorporate an understanding of spatial variation in demographic rates and movement probabilities into models of populations (Turchin 1998). This emphasis has led to numerous insights in conservation (Wootton 1992; Doak 1995), ecology (Holt 1985; Pulliam 1988; Kareiva 1990), and evolutionary biology (Morris 1991; McPeck & Holt 1992). In the context of migratory ungulates, characterizing demographic variation has been a considerable challenge because of the difficulty of following large numbers of individual animals across their entire migratory cycle (Bolger et al. 2008). To my knowledge, this study represents the first capture-recapture of a migratory ungulate population to quantify demographic variation across an entire ecosystem and multiple migration cycles.

In ungulates, fecundity and early calf survival are expected to be the most variable fitness components and have the greatest degree of sensitivity to environmental variation (Gaillard et al. 2000). I observed higher calf recruitment (the product of fecundity and early calf survival) in Lake Manyara than either of the other two calving grounds across all years. Among migratory population subunits, Northern Plains animals had higher recruitment than Simanjiro Plains in all years, though the difference was only significant in 2006. Estimates of recruitment in the Tarangire population were similar to those from the breeding state model in Chapter III. Wildebeest have been well recognized for their high annual reproductive output (Talbot & Talbot 1963). In other monitored populations, fecundity of prime aged adults ranged between 0.74 and 1.0 calves adult⁻¹ year⁻¹ (Talbot

& Talbot 1963; Watson 1967; Mills & Shenk 1995; Mduma et al. 1999). Our measure of recruitment, however, includes both fecundity and early calf survival (between 0 and ~2 months old). The consistent spatial patterns in recruitment, with highest recruitment in Lake Manyara, followed by the Northern Plains and then Simanjiro Plains, indicates that Simanjiro was a relatively poor location for producing calves. Further comparisons of demographic rates between the migratory Tarangire population and the non-migratory Lake Manyara population may provide useful insights into the trade-offs between these substantially different migratory strategies (Bolger et al. 2008).

I found substantial variation in adult wildebeest survival rates across the four study sites. However, these estimates suffered from poor precision. In the Tarangire population, models that differentiated survival by season (i.e., dry, wet and annual), sex were best supported by the data. Lower survival in the dry season is a result that is well supported in other wildebeest populations (Mduma 1996) and tropical ungulates in general. During the dry season, food becomes limiting due to the concentrations of digestible energy in forage falling below the levels required to maintain body weight (Mduma et al. 1999). In the Lake Manyara population there was no effect of season or time. These animals forage largely along the north side of the lakeshore on perennial 'a-seasonal' grasses (Prins 1996). Because of groundwater from the lake, these grasses resist wilting and provide a relatively stable source of forage throughout the year (Prins 1996).

Estimates of adult survival ranged between 0.09 ± 0.15 (TP males during the dry season) and 1.0 (NP males; Table 3). These lower estimates were substantially below adult wildebeest survival rates reported elsewhere, even compared to a particularly severe drought in the Serengeti (1993) in which adult survival was 0.64 (Mduma 1996).

Exploratory analysis of a reduced single-state model of the Tarangire population estimated low survival rates, particularly of females in the dry season, though with narrower confidence limits (Morrison, *unpub*), though precision was still generally poor. Thus, the low survival estimates observed during the dry season in TP and annually in LM are difficult to accept at face value. One possibility is that survival estimates were biased low during these periods due to transient effects in which a portion of the population is photographed once then moves to unsampled areas in the ecosystem (Pradel et al. 1997). However, LM wildebeest were relatively easy to locate within the Lake Manyara basin because the landscape is flat and open with a limited number of locations that contain sufficient freshwater and forage for grazing. Furthermore, I observed very few recaptures (3 out of 48) involving LM animals in other portions of the ecosystem. Thus, in the Lake Manyara dataset, bias caused by movement to unsampled areas seems unlikely. In the migratory TP population, transient effects are more likely because the landscape is much larger, making it conceivable that some individuals were captured only once then moved to unsampled areas. Nonetheless, the dry season range in Tarangire National Park is relatively constricted because animals must stay within close proximity to water. Thus, it would be more likely that transiency would bias wet season survival lower than dry season survival, yet wet season survival rates were relatively high. An alternative possibility is that misidentification probability is higher in the dry season than in the wet season and that conditioning the dataset did not remove the effects of these misidentifications. However, if we were to assume that true adult survival was nearer to the lowest value reported elsewhere (e.g., 0.64; Mduma et al. 1999), misidentification rates still would have to be extremely high to produce such biased results (Morrison et

al., *in press*). Thus, we are uncertain if and to what extent our reported survival values are biased low.

Calf survival was higher in the dry season than the following wet season in both Lake Manyara and Tarangire (Table 4). In contrast, in Serengeti National Park Mduma (1996) reported lower survival during the wet season (ages ~12-18 months; mean monthly survival: 0.98 ± 0.01 , $n = 4$ years) than the dry season (ages ~6-12 months; monthly mean survival: 0.93 ± 0.02 , $n = 7$ years). Wet season calf survival was particularly low in the Tarangire population. Monthly dry season yearling survival, in contrast, was 1.53 times higher in Tarangire than in Lake Manyara. However, I caution that a difference in yearling survival could be influenced by dispersal between the Lake Manyara and the Tarangire populations. The identification technique, which focused on adults, would not have detected such movements. Further, estimates of yearling survival as well as dry and wet season calf survival would have been highly sensitive to any inaccuracies in TP and LM adult female survival estimates, as female survival was used to calculate the proportion of surviving calves and yearlings. If female survival was biased low, calf and yearling survival rates would also likely have been biased low. This highlights one of the central issues with ratio methods (Caughley 1974).

Acknowledgements

I thank the Commission for Science and Technology and the Tanzania Wildlife Research Institute to conduct research in Tanzania, and the Tanzania National Park for permission for permission to work in Tarangire and Lake Manyara National Parks. I am grateful to

R. Mollel for helping to collect data in the field and to B. Vance and L. Hiby for technical assistance with the matching software. The work was funded by the Wildlife Conservation Society Research Fellowship Program and Dartmouth College, the Marion and Jasper Whiting Foundation, the Nelson A. Rockefeller Center at Dartmouth College and NSF grant DBI-0754773 to DTB and H. Farid.

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Tables and Figures

Table 1. Number of captures by site and sampling period ($n = 2330$). Data were conditioned on individuals who were captured at least twice, and all first captures were then censored (Morrison et al., *in press*). Primary periods 1 and 5 contained only a single secondary period.

SITE	DATES and SAMPLING PERIODS									
	May-Jul 05	May-Jun 06	Jun-Jul06	Oct-Nov 06	Nov-Dec 06	May-Jun 07	Jun 07	Jul 07	Oct 07	Nov 06
	1	2A	2B	3A	3B	4A	4B	5	6A	6B
Tarangire Nat'l Park (TP)	30		68	158				337	202	218
Simanjiro Plains (SP)	52	217		42		144				
Northern Plains (NP)		34	101	59		168	36		9	13
Lake Manyara (LM)	12	29	32	22	48	49	41		43	66

Table 2. Summary of model selection results from the an open robust design multi-state capture-recapture models of Tarangire and Lake Manyara wildebeest populations.

Model	Parameter	Model Component	Structure	Summed AICc weights (w)
Tarangire population	Survival (S):	Season (dry vs. wet vs. annual) x gender x site	S(T(d!=w!=a),g,s)	0.76
		Gender x Site	S(.,g,s)	0.07
		All constant	S(.,.,.)	0.06
		Time x Site([SP = NP])	S(T,.,s(season))	0.05
		Gender	S(.,g,.)	0.03
		Gender x Site([SP = NP])	S(.,g,s(season))	0.02
		Season (dry vs. wet vs. annual)	S(T(d!=w!=a),.,.)	0.01
		Site	S(.,.,s)	0.01
		Time	S(T,.,.)	0.01
	Transition probability (ψ):	Time x Gender x Site	$\psi(T,g,s)$	1.00
Capture probability (p):	Time(primary) x Time(secondary) x Site	p(T,t,.,s)	1.00	
Lake Manyara population	Survival (S):	All constant	S(.,.)	0.58
		Gender	S(.,g)	0.18
		Season (dry vs. wet vs. annual)	S(T(d!=w!=a),.)	0.16
		Time	S(T,.)	0.06
		Season (dry vs. wet vs. annual) x Gender	S(T(d!=w!=a),g)	0.01
	Capture probability (p):	Time(primary) x Time(secondary) x Gender	p(T,t,g)	1.00

Note: AICc weights were summed across all candidate models that included each model component for a given parameter. Weights add to 1.0 for each parameter (S, ψ or p). Site([SP = NP]) indicates models where survival in wet season sites (SP and NP) were set equal to one another but differed from the dry season site (TP). T(d != w != a) indicates a model where the parameter varied by across wet and dry seasons, as well as the one annual period (June 2005-June 2006).

Table 3. Summary of adult survival estimates from the top model of the Tarangire wildebeest population ($S(\cdot, g, s)\psi(T, g, s)p(T, t, \cdot, s)$), standardized to a 12-month time scale. Transition and capture probabilities (p) were excluded for brevity. Asterisks (*) denote parameters that were held constant due to an absence of animals in that site (TP) during that sampling interval.

Site	Sex	Label	Estimate	SE	L95CI	U95CI
Tarangire Nat'l Park	Females	$S_{annual}^{F,TP}$	0.73	0.36	0.07	0.99
		$S_{dry}^{F,TP}$	0.13	0.04	0.07	0.24
		$S_{wet}^{F,TP}$	*			
	Males	$S_{annual}^{M,TP}$	0.35	0.33	0.03	0.91
		$S_{dry}^{M,TP}$	0.09	0.06	0.02	0.28
		$S_{wet}^{M,TP}$	*			
Simanjiro Plains	Females	$S_{annual}^{F,SP}$	1.00	0.00	1.00	1.00
		$S_{dry}^{F,SP}$	0.22	0.19	0.03	0.70
		$S_{wet}^{F,SP}$	1.00	0.00	1.00	1.00
	Males	$S_{annual}^{M,SP}$	0.50	0.25	0.12	0.88
		$S_{dry}^{M,SP}$	0.23	0.19	0.03	0.71
		$S_{wet}^{M,SP}$	0.70	0.43	0.04	0.99
Northern Plains	Females	$S_{annual}^{F,NP}$	1.00	0.00	1.00	1.00
		$S_{dry}^{F,NP}$	0.56	0.61	0.01	0.99
		$S_{wet}^{F,NP}$	0.47	0.30	0.08	0.90
	Males	$S_{annual}^{M,NP}$	1.00	0.00	1.00	1.00
		$S_{dry}^{M,NP}$	0.96	0.16	0.01	1.00
		$S_{wet}^{M,NP}$	1.00	0.00	1.00	1.00

Table 4. Summary of parameters derived from herd composition ratios. Breeding model indicates estimates of ω (i.e., proportion of adult female breeders) from SP and NP females (Chapter III). Note that calf recruitment is the product of fecundity and early survival of calves, from ~0-2 months.

PARAMETER	AGE	TIME PERIOD(S)	METHOD			
			Breeding model (ω)		Composition ratios	
			SP & NP	SP	NP	LM
Calf recruitment	~2 months	Jun 2005		0.45 ± 0.02	0.46 ± 0.06	0.58 ± 0.05
		Jun 2006	0.52 ± 0.06	0.46 ± 0.01	0.57 ± 0.03	0.69 ± 0.03
		Jun 2007	0.70 ± 0.05	0.64 ± 0.01	0.67 ± 0.04	0.74 ± 0.02
				SP & NP		LM
Monthly dry season calf survival	~2-7 months	Jun - Nov 2006		1.00		0.90 ± 0.06
		Jun - Nov 2007		0.83 ± 0.05		0.92 ± 0.02
Monthly wet season calf survival	~7-14 months	Nov 2006 - Jun 2007		0.58 ± 0.02		0.73 ± 0.05
Monthly dry season yearling survival	~14-19 months	Jun - Nov 2006		0.95 ± 0.05		0.62 ± 0.08
		Jun - Nov 2007		1.00		1.00

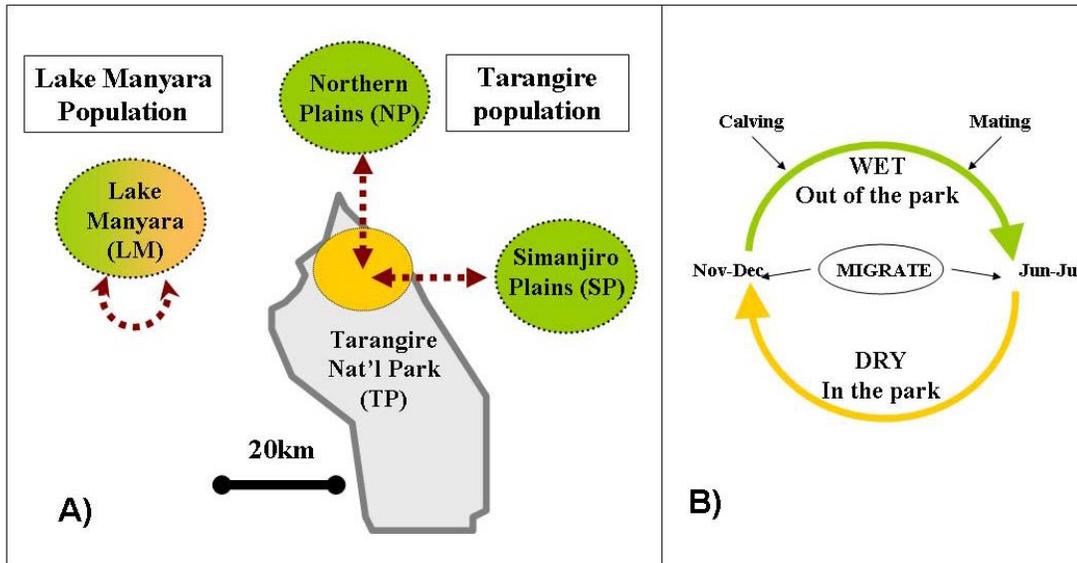


Figure 1. Generalized seasonal movement patterns of wildebeest in the Tarangire-Manyara Ecosystem, Tanzania (not drawn to scale). A) Dotted lines denote observed migratory transitions between different sites used during the wet season (green) and dry season (orange). Movement between the two wet season areas in Tarangire (SP and NP) involves moving through or near to Tarangire National Park (TP) along the way due to geographic and ecological barriers between the two areas. B) Diagram of phenology of the annual cycle in the migratory Tarangire population. In the non-migratory Lake Manyara population, the timing of calving and breeding occur at roughly the same time as in the Tarangire population. They stay in or near the boundary of Lake Manyara National Park throughout the year.

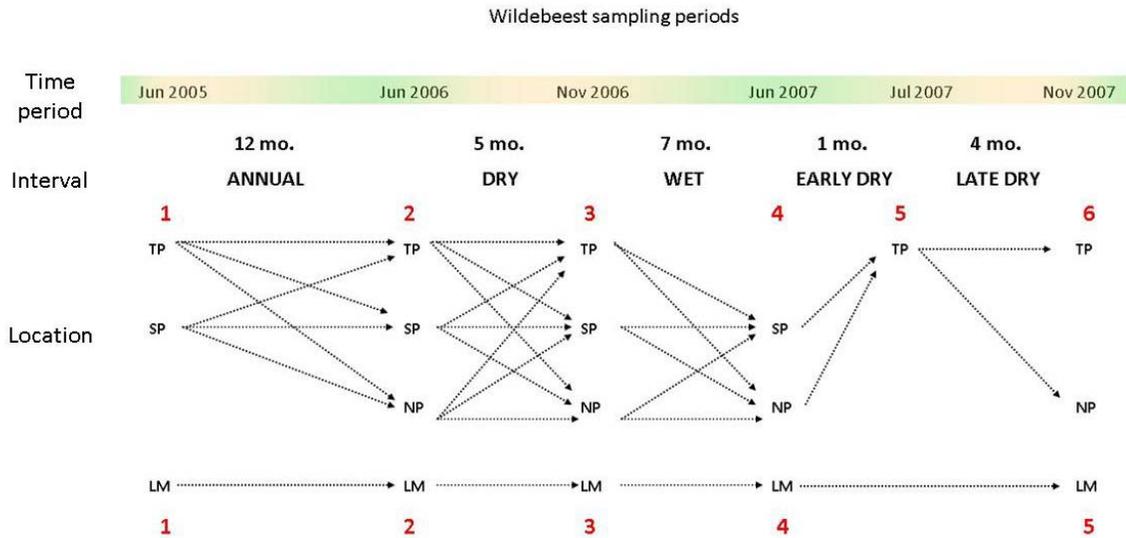


Figure 2. Sampling framework showing possible transitions during this study. The four sites are: Tarangire National Park (TP), Simanjiro Plains (SP), Northern Plains (NP) and Lake Manyara (LM). The absence of arrows pointing to a particular site indicates that no animals were captured in the site at the time of sampling. Note that LM was only sampled on five primary sampling periods. Because sampling intervals varied in length, all survival and transition probabilities reported in text were standardized to a 12-month rate.



Figure 3. Example of an adult female wildebeest photo captured on two occasions in different breeding ranges: A) in the Simanjiro Plains in June 2006 and B) in the Northern Plains in June 2007. Female was a breeder in both years. Dashed lines show the approximate cropped region of the torso used for pattern analysis and image matching in adult females.

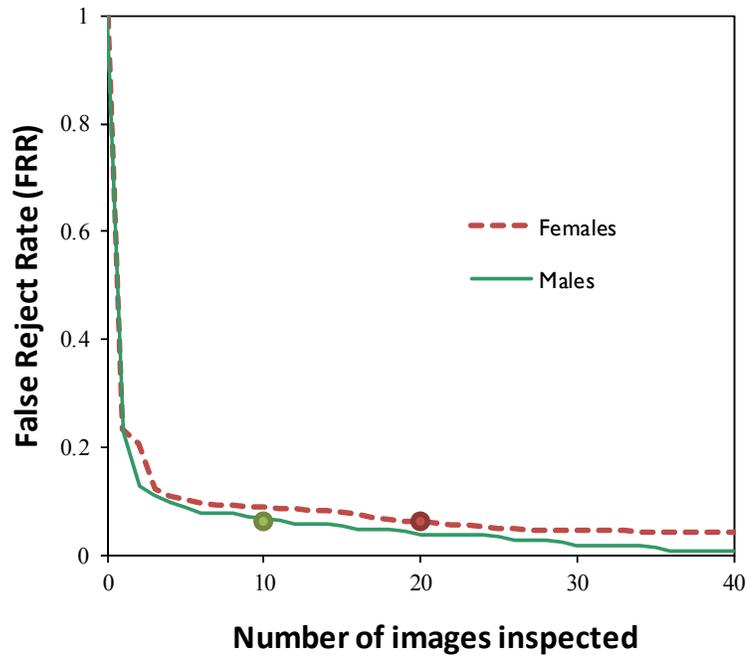


Figure S1. False reject rate (FRR) of the two photo identification systems (Wild-ID used for females and Hiby system used for males), based on a test set of 198 true matching photo pairs of adult wildebeest from the Tarangire Ecosystem, Tanzania. The number of incorrectly identified matching pairs over true matching pairs is plotted as a function of the number of photos that were visually inspected (i.e., the threshold for inspection). The circles indicate the threshold values (20 images for females and 10 for males) used for assembling the female and male encounter history data sets in this study, representing FRR's of 0.064 for females and 0.069 for males.

CONCLUSIONS:

MANAGEMENT IMPLICATIONS FOR THE TARANGIRE-MANYARA WILDEBEEST POPULATION

This section highlights the aspects of this dissertation that are most relevant to the management and conservation of wildebeest in the Tarangire-Manyara Ecosystem. We integrate our research results with existing background knowledge to identify potential management policies that we believe could be leveraged to moderate the recent downward population trends and to ensure the long-term viability of this population.

The importance of continued population-level research on ungulates in the TME

Basic information on demographic and spatial dynamics of migratory ungulates is lacking in the Tarangire-Manyara Ecosystem. This makes it difficult to prioritize conservation decisions. Over the last 25 years, to my knowledge only five population-wide large mammal surveys have been conducted in the ecosystem, and none since 2004 (TAWIRI 2004). These surveys suggest that wildebeest, hartebeest and oryx have declined by 88%, 90%, and 95% between 1988 and 2001, while other ungulate populations (eland, Grant's gazelle, zebra) have remained relatively stable. In the mid 1990's the Tarangire Conservation Project (i.e., 'the OIKOS Project') studied the seasonal distributions of many of the large-bodied species in TME and characterized the underlying forage composition and nutrient distribution across the landscape (TCP 1997, 1998). While the OIKOS project provided important baseline information about the large mammal community in TME, among some stakeholders in this area there has been a

tendency to assume that the project provided a comprehensive description of the dynamics of migratory wildlife in TME. However, we believe that, if anything, the project highlights how little we know about the migratory populations in this ecosystem, both in the past and presently. For instance, it is difficult to assess whether habitat loss, habitat degradation, poaching or some other factor is most responsible for the recent population declines. Further, we do not know how individual animals respond behaviorally when changes do occur, whether animals migrate to new areas, whether the phenology of migration changes and whether these changes have demographic consequences. Finally, this ecosystem is characterized by high spatial and temporal heterogeneity in environmental conditions. In such a system any short-term study of demographic dynamics (including this one) can, at best, only provide an approximation of the mean dynamics of the system. Nonetheless, demographic parameters (survival, calf recruitment and movement) should reflect the integration of environmental heterogeneity and increasing human utilization across the landscape. Therefore, demographic research, particularly if it includes an understanding of individual variation, can providing a starting point for identifying important factors that drive the dynamics of populations. Below we outline how the current study contributes to this understanding.

Calf recruitment is lowest in the Simanjiro Plains

Of the three wet main season ranges (Simanjiro Plains, Northern Plains and Lake Manyara National Park), calf recruitment – which in our study includes the product of fecundity and early (~0-2 months) survival – was lower in Simanjiro than elsewhere between 2005-2007 (Chapter II, Table 4). Lake Manyara National Park had the highest

recruitment levels in all years, with between 0.64 (0.01) and 0.74 (0.02) of females recruiting calves. This translates to 15-50% higher calf recruitment in Lake Manyara than in the Simanjiro Plains. While population growth rates of ungulates are less sensitive to variation in calf recruitment and survival (Gaillard et al. 2000), consistent differences in recruitment between area can drive local population trends and suggest divergent ecological or human-related pressures across ranges.

Adult mortality is highest in the dry season

We found higher mortality rates in the dry season (June-October) than the wet season (November-May) (Chapter II), which is consistent with past observations in the Serengeti ecosystem that wildebeest populations tend to be dry season limited (Mduma et al. 1999). In addition to food limitation, in Tarangire National Park large predators such as lions spend a majority of their time inside the park (B. Kissui, *pers comm.*), where they interact with large herbivores during the dry season. Nonetheless, lower survival during the dry season does not necessarily imply that wet season ranges are unimportant to the overall population growth rate. In migratory systems, nutritional states can carry over between seasons and impact an individual's probability of survival the following season (Studds & Mara 2005).

The importance of the Northern Plains dispersal area

The majority of past research on wildebeest in the TME ecosystem has focused on animals that migrate between Tarangire NP and the Simanjiro Plains (Kahuranganga 1981; Kahuranganga & Silkiluwasha 1997; TCP 1998; Voeten 1999; Msoffe et al. 2010).

However, during each of the three years of this study (2005-2007), a large portion of Tarangire wildebeest were observed in the Northern Plains dispersal area, which stretches from Manyara Ranch to the southern shores of Lake Natron. During the late wet season (May-June) in 2006, for example, ~50% of the adult wildebeest were found on the Simanjiro Plains, based on a preliminary Bayesian analysis of the capture-recapture data (Morrison and Link, *in prep*). In December 2006, over three thousand wildebeest were counted in the Plains north of Engaruka Village from a single vantage point. Large numbers of zebra, and smaller numbers of Thompson gazelle, Grants gazelle, oryx, eland, lesser kudu, and giraffe were also observed in these areas. Photo recaptures of wildebeest in this area confirm that at least some of these animals originated from Tarangire and Lake Manyara National Parks. With the exception of impressive efforts to preserve connectivity and habitat in Manyara Ranch, the Kwa Kuchinja corridor and Ol Tukai Village, we believe that the Northern Plains dispersal area has not been fully appreciated in ecosystem-wide conservation planning and management.

The loss of migration corridors

The increasing isolation and loss of corridors in the TME has been noted for some time (Lamprey 1964; Borner 1985; Bolger et al. 2008). However, we still have a poor understanding of where corridors occur (though see Jones et al. 2009 for a low resolution depiction of TME migration routes) and whether animals use them consistently each year. Few of the migration corridors in TME have been identified and protected, with the exception of the Kwa Kuchinja corridor which links Tarangire National Park and Manyara Ranch. The loss of connectivity will either reduce the total area available to

animals (implying habitat loss) or force animals to use alternative pathways, which likely increases travel costs.

Should different population subunits be managed independently?

Several lines of evidence suggest that the three population subunits in the TME – Lake Manyara, Simanjiro Plains and Northern Plains – should be managed independently. First, adult wildebeest in the Tarangire ecosystem appear to exhibit relatively high fidelity to their wet season dispersal areas (Chapter II). Our results also confirm earlier speculations that the Lake Manyara wildebeest population is relatively isolated from the other population subunits, despite close spatial proximity (3-5 km) to animals that migrate from Tarangire National Park to the Northern Plains via Manyara Ranch and west of Lo Simanguri Mountain. For much of the year Lake Manyara animals concentrate on the northern end of the lake, making daily commutes into the park to drink from the fresh water springs found in the park. Among Lake Manyara animals, we observed only three recaptures (all adult females) involving individuals moving into or out of the Lake Manyara population area, out of a total 48 recaptures in consecutive wet seasons (Chapter II). Overall (across all seasons) we observed a total of 18 individuals (14 of which were females) transitioning to or from Lake Manyara NP and other areas of the ecosystem, including Simanjiro, the Northern Plains near Gelai and Tarangire National Park.

Animals that inhabit the Simanjiro Plains and Northern Plains during the wet season switch between these areas at a relatively low frequency (0-18% of individual switch in consecutive wet seasons). In theory, low switching rates could buffer

population declines as long as at least one of the population subunits is increasing (Esler 2000). However, given the lack of information on population trends, we caution that there is little basis for assuming that any of the three population subunits will act as demographic sources.

Future research questions on migratory ungulates in the TME

A number of additional questions still need addressing in this ecosystem and can best be answered with greater monitoring efforts, including both capture-recapture and GPS collaring methodologies. We highlight what we believe are the four most important short-term questions in this ecosystem for the conservation and management of the TME migratory ungulates:

1. What are the current population sizes of migratory ungulates in the TME?
2. Where are the migration corridors and do individuals and populations use them consistently each year?
3. How variable is mean arrival and departure timing during the dry and wet season migrations and are these dates changing in a predictable way?
4. What causes spatial variation in calf recruitment? In particular, why is calf recruitment relatively low in the Simanjiro Plains?

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