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TARANGIRE REVISITED: CONSEQUENCES OF DECLINING CONNECTIVITY IN A TROPICAL UNGULATE POPULATION

THOMAS A. MORRISON[1,6], WILLIAM A. LINK[2], WILLIAM D. NEWMARK[3], CHARLES A.H. FOLEY[4], DOUGLAS T. BOLGER[5]

[1] Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA
[2] Patuxent Wildlife Research Center, U.S. Geological Survey, Laurel, MD 20708
[3] Natural History Museum of Utah, University of Utah, Salt Lake City, UT 84108
[4] Wildlife Conservation Society, P.O. Box 2703, Arusha, Tanzania
[5] Environmental Studies Program, Dartmouth College, Hanover, NH 03755
[6] Corresponding author: tmorrison80@gmail.com

ABSTRACT

The hyper-abundance of migratory wildlife in many ecosystems depends on maintaining access to seasonally available resources. In Eastern and Southern Africa, land-use change and a loss of connectivity have coincided with widespread declines in the abundance and geographic range of ungulate populations. Using photographic capture-mark-recapture, we examine the historical pattern of loss of connectivity and its impact on population trends in a partially migratory wildebeest population in northern Tanzania. To estimate abundance, we use a novel modeling approach that overcomes bias associated with photo misidentifications. Our data indicate (1) diminished connectivity within and between seasonal areas as a result of human activities, (2) a reduction in the overall population size compared to historical numbers, with high variability over time, (3) the continued use of highly constrained movement corridors between the three main seasonal ranges, (4) higher recruitment in the non-migratory subpopulation (Lake Manyara National Park) than in other areas of the ecosystem, and (5) an increase in the relative abundance of resident to migrant wildebeest. Recent conservation efforts to protect seasonal habitat and to enforce anti-poaching policies outside protected areas has likely helped stabilize the population, at least temporarily, but we caution that several key vulnerabilities continue to threaten this population.

Key Words: Bayesian estimation; corridor; habitat change; population dynamics; site fidelity, Tarangire-Manyara Ecosystem

Highlights:

- We use photo capture-recapture to estimate abundance of wildebeest in northern Tanzania
- We overcome photo misidentifications using informative priors in a Bayesian model
- We discuss results in light of four key vulnerabilities to this population
- We show substantial population declines from historical levels with recent stabilization
- Connectivity within the migration network is key to the future viability

1. Introduction

Migration is an adaptive movement strategy that allows animals to track spatial variation in resources while reducing predation risk (Swingland and Greenwood, 1983; Fryxell and Sinclair, 1988; Hebblewhite and Merrill, 2009). If benefits of tracking resources and escaping predators outweigh costs associated with travelling long distances, the fitness of migrants should be higher than that of residents under many conditions (Lundberg 1988; Hebblewhite and Merrill, 2011). Consequently, migratory populations often have higher abundances than sympatric resident populations (Lundberg 1988).

This relationship between migration and abundance is common in many ungulates (Fryxell et al., 1988; Hebblewhite and Merrill, 2011). In a few ungulate populations (e.g. Serengeti wildebeest and barren-ground caribou), migrants outnumber residents by millions of individuals. By tracking large-scale variation in green-up phenology across gradients in rainfall or elevation, migration prolongs the access of animals to high quality forage (Fryxell et al., 1988). Additionally, ungulates make intra-seasonal foraging movements to track shifting mosaics of plant phenology (Sawyer and Kauffman, 2011; Van Moorter et al., 2013). Resource tracking, however, is contingent upon the timely accessibility of available resources.

Roads, fences, farms, settlements and energy infrastructure have fragmented landscapes and reduced physical connectivity in many terrestrial ecosystems (Fahrig 2003). As the number and permeability of migration routes decrease, migratory animals have fewer foraging options, and their population dynamics become more strongly coupled to the remaining accessible habitat. Thus, connectivity to a diverse set of resource patches can help stabilize the dynamics of consumer populations, a concept known as the “portfolio effect” (Moore et al., 2010; Schindler et al., 2010). Declines in habitat ‘portfolios’ in migratory landscapes should accentuate variability in abundance and decrease population stability and growth rate (Schindler & Armstrong, 2015). Given the world-wide declines in migratory ungulate populations (Bolger et al., 2008; Harris et al., 2009), understanding the population consequences of declining connectivity remains a crucial conservation goal.

Assessing the importance of connectivity within specific settings, however, can be difficult because some populations use large networks of routes and ranges, and the impact of landscape changes within those areas may occur gradually. Several key pieces of information are needed to assess the importance of connectivity and for developing effective conservation strategies: (1) reliable measures of population size over time, (2) knowledge of spatial variation in population productivity, (3) information on the patterns of connectivity between habitat patches (4) an understanding of whether animals facultatively exploit variation in resources.

The Tarangire-Manyara Ecosystem (“TME”; ca. 25 000 km^2) in Northern Tanzania supports the largest remaining population of Eastern White-Bearded wildebeest (*Connochaetes taurinus albojubotus*). Beginning in the 1960’s a series of studies began documenting the loss of habitat and migratory connectivity (Lamprey, 1964; Borner, 1985; Newmark, 1996 & 2008; TCP, 1998; Morrison and Bolger, 2014; Foley and Foley, 2015). The spatial complexity of this migration and the long history of multi-jurisdictional land-use change have made it challenging to identify the underlying drivers of population change in the TME. We report new wildebeest population estimates for the TME obtained using photographic capture-mark-recapture (PCMR) between 2006 and 2011. In contrast to traditional aerial surveys methods, this approach provides rich information on the population’s spatial structure and variation in individual movement and fidelity patterns through time (Morrison and Bolger, 2012). To estimate population abundance, we apply a novel statistical model that overcomes identification errors in the PCMR dataset. We integrate results from our PCMR study with spatial data on calf production and movement patterns from GPS-collared animals. We combine these results with historical information to provide a framework for understanding the consequences of changes to connectivity and to identify key population vulnerabilities.

2. Materials and methods

2.1 Study system

The greater TME is a savannah-woodland ecosystem that supports one of the most diverse communities of migratory ungulates in the world (Bolger et al., 2008). Three protected areas occur in the ecosystem: Tarangire and Lake Manyara National Parks (2600 km^2 and 317 km^2, respectively), managed for wildlife tourism, and Manyara Ranch (177 km^2), a private land conservancy managed for livestock grazing and wildlife tourism. Most other rangeland in TME (~85%) falls on community land, managed as Open Areas, Game Controlled Areas or Wildlife Management Areas, on which livestock grazing, cultivation, legal game hunting and photographic tourism are permitted. The Gregory Rift Wall (500-1000 m in height) bounds the western edge of the ecosystem and prevents interchange with the Serengeti-Ngorongoro wildebeest population (Mjingo, 2012). On the north-eastern boundary, a chain of forested mountains and dense woodland form another natural barrier between the TME and wildebeest populations in the Amboseli basin and West Kilimanjaro.

2.2 *Historical patterns of land-use and wildebeest abundance*

Lamprey (1964) was the first to identify migration routes in the ecosystem (Fig. 1B) and reported that the TME wildebeest had undergone a significant population decline in the preceding 30-100 years. He attributed this decline to the loss of dry season water sources at the base of Mt. Meru caused by the expansion of agriculture and livestock production in the upper watershed (Lamprey, 1964). Following these changes, the Tarangire River in Tarangire NP, the Mto wa Mbu River in Lake Manyara NP and several small springs adjoining Lake Natron remained as the only perennial freshwater sources in the ecosystem. Lamprey (1964) counted ~1200 wildebeest in central and northern Tarangire NP during the dry season and nearly 6500-7500 animals on the northern edge of Lake Manyara NP, though these numbers likely represent only a portion of the total population.

The period between the 1960's and the early 1980's was distinguished by the development of commercial rain-fed agriculture and the intensification of subsistence farming in core wet season habitat (Borner 1985; Msoffe et al., 2011). Beginning in 1971 the acreage of seed bean farms greatly increased, covering 25-100% of parcels of land to the north of Tarangire NP and to the south of Lake Manyara NP (Borner, 1985). Borner (1985) described the progression of this development and warned of its fragmenting effects on wildlife migration, noting that several of the migration routes documented by Lamprey (1964) had been fully or partially impeded (Fig. 1B). The population remained relatively low throughout this period, possibly due to the suppressive effects of disease and overexploitation (Foley and Foley, 2015). Since 1985, the wildebeest population has fluctuated considerably. Abundances increased to over 40 000 individuals by the early 1990's only to rapidly decline to fewer than 6000 individuals ten years later (Fig. 2). While the causes of the apparent increase are unclear, with a reduction in disease and poaching the most likely explanations (Estes, 2014), the subsequent decline coincided with an intensive game cropping program in the Simanjiro Plains in the late 1990's (Foley and Foley, 2015) and with agricultural intensification of roughly 10% increase per year in areas surrounding Tarangire NP, with greatest intensity in the Simanjiro Plains (Msoffe et al., 2011).

The TME currently supports two distinct wildebeest populations: 1) The Lake Manyara population, which inhabits grasslands around the northern lakeshore in Lake Manyara National Park (hereafter 'Lake Manyara NP'), and 2) the Tarangire population which congregates in Tarangire National Park (hereafter 'Tarangire NP') in the dry season and disperses to three spatially discrete ranges in the wet season: Simanjiro Plains, the Northern Plains, and Kimotorok, flood plains south of Tarangire NP (TCP, 1998).

2.3 Photographic capture-mark-recapture (PCMR)

Wildebeest are commonly censused using sample-based aerial surveys. The high spatial clumping of wildebeest herds leads to low precision in these surveys (Norton-Griffiths, 1978) (range of coefficient of variation from past surveys in TME: 0.17 - 0.66, n = 9 surveys; Fig. 2) and high inter-observer variability makes comparisons through time difficult (Jachmann, 2002). Ground-based PCMR is a low-cost alternative to aerial surveys for estimating population size for species with unique marking patterns (Bolger et al., 2012). This technique has been applied to wildebeest in TME to estimate survival rates (Morrison et al., 2011) and range fidelity (Morrison and Bolger, 2012).

We relied on natural variation in shoulder stripe patterns of adult (>2 years old) wildebeest and computer-assisted photographic identification to identify individuals between May 2006 and June 2011 (Fig. A.1; Morrison et al., 2011; Morrison and Bolger, 2012). From prior aerial survey data and our own reconnaissance we knew the locations of wildebeests' seasonal ranges (Morrison and Bolger, 2012) and focused our photographic sampling in those areas. In total, we compiled seven separate PMCR datasets from which we estimated abundance: 1) Simanjiro in May-June 2006, 2) Simanjiro-Northern Plains-Tarangire NP in May-July 2006, 3) Simanjiro-Northern Plains-Tarangire NP in May-July 2007, 4) Tarangire NP in October 2007 (a subset of #2 and #3), 5) Lake Manyara NP in October 2006, 6) Lake Manyara NP in October 2007 and 7) Lake Manyara NP in October 2011 (Table 1). Datasets consisted of two surveys, each lasting two days (Lake Manyara NP) to three weeks (other areas). The interval between surveys was 1-10 days; thus, the total time between first photo and last photo in a given dataset was, at most, just over two months and our modeling approach assumed a closed population (see below).

We located wildebeest by driving the extensive network of dirt tracks in the study areas and visually scanning for individuals and herds. Visibility in these open grasslands is excellent, and wildebeest could be located up to several kilometers away. After spotting animals, we drove to within suitable range (10–100 m) and collected high-resolution images of adult animals using a 6.1 megapixel digital camera (Pentax *ist*D) with a 120-400mm Sigma telephoto lens. We photographed individuals on their right flank (stripe patterns were not identical on both sides; Fig A1). Within each encountered herd, we collected as many images of individuals as there were adults in the group, knowing that some images would be of the same individual and that some individuals would not be sampled.

We used two software programs to facilitate individual identification. The first program (Conservation Research Ltd. <conservationresearch.co.uk>; Hastings et al., 2008) matched male images only. The availability of a more time-efficient program with fewer preprocessing steps (‘Wild-ID’ <dartmouth.edu/~dbolger>; Bolger et al., 2012) led us to switch platforms for matching female images. However, both programs achieved equivalent levels of matching accuracy (Fig. A.2; Morrison and Bolger, 2012) based on tests of known-identity wildebeest images (see below).

The two programs used a similar sequence of steps to identify matches: pattern characterizing algorithms localized information-rich points within the stipe pattern. These were either bifurcation points in stripes (for male images) or ‘SIFT’ (Scale Invariant Feature Transform; Lowe, 2004) features (for female images). A second algorithm would then compare these patterns to a database of previously “captured” patterns. For each pattern comparison, the programs generated a ‘similarity score’ which provides a standardized value (between 0.0 and 1.0) measuring the degree of correspondence between patterns in the two photos. To identify matches for a given image, a single observer (T. Morrison) visually examined the top 20 highest scoring candidate matches within a ranked list of similarity scores and identified matches based on stripe patterns. We compiled the resulting collection of matched photographs into sets of capture histories for each site (Table A.1).

2.4 Spatial connectivity

Our PCMR movement data were not well suited for spatial capture–recapture models (e.g. Morrison and Bolger, 2012) because of low capture rates between areas. We therefore used PCMR data to (1) estimate abundance within population segments (see below) and (2) characterize recent patterns of connectivity as a binary response variable between population segments. We used GPS collar data to help elucidate specific migration paths taken and identify migration bottlenecks. We fitted three adult wildebeest (two males, one female) with GPS collars (African Wildlife Tracking, GPS/GSM) in April 2009 and two female wildebeest (Telonics TGW-4780H) on Manyara Ranch in October 2010. A veterinarian from the Tanzanian Wildlife

Research Institute (TAWIRI) immobilized animals with an injectable dart containing 6 mg of etorphine and 80–100 mg of azaperone, following the protocols established by TAWIRI.

2.5 Abundance model

Our PCMR data consisted of resighting records as typically analyzed using a 2-sample, closed population mark-recapture model M_t (Darroch, 1958; Otis et al., 1978). The possibility of misidentifications suggested the use of a misidentification model such as $M_{t,\alpha}$ (Link et al., 2010); however, our datasets contained instances of individuals with >1 capture per sampling period, a feature not allowed under $M_{t,\alpha}$. Thus we developed a new model ($M_{t,\pi}$) that allowed for multiple captures per sampling period and avoids problems of modeling and estimating misidentification probabilities. The $M_{t,\pi}$ model provides a framework for estimating π, the probability that an individual is assigned its true identity during at least one sampling occasion.

Here we describe estimation of N_{PA}, the abundance of photographically identifiable adult animals (for animals not available for photo identification, see section 2.5). Our inspection of photographs involves assigning identities to each adult animal, for which we conceive of one true identity and many potential false identities. We assume that an animal is resighted in multiple photographs if and only if the true identity was assigned in each of the photographs. Assigning a false identity leads to a record corresponding to only one photograph, a “ghost” record. Failure to account for the possibility of ghost records inflates estimates of population size.

Let X and Y denote the number of photographs in which an individual was assigned its true identity on the first and second sampling occasions, respectively. Let f_{xy} denote the number of individuals with $X = x$ and $Y = y$, and let f ={ $f_{xy}: x, y = 0, 1, 2, \ldots$}. We will write $\theta_{xy} = \Pr(X = x, Y = y)$.

We assume values f_{xy} are known if $x + y > 1$. Frequency f_{00} is unknown, and we can only assign upper bounds on f_{10}, and f_{01}. For instance, we know the number of identities assigned exactly once on the first occasion, and zero times on the second occasion; call this c_{10}. We know that $f_{10} \leq c_{10}$, but the value c_{10} contains an unknown number of ghost records.

The observed data *D* for a given site thus consist of observed values $\{f_{xy}: x + y > 1\}$ and bounds c_{10} and c_{01}, on f_{10} and f_{01}, respectively. We calculate the probability of *D* by summing multinomial probabilities

$$\Pr(f) = \left\{ \frac{N_{PA}!}{\prod_{x,y} f_{xy}!} \prod\nolimits_{x,y} \theta_{xy}^{f_{xy}} \right\} \tag{1}$$

over admissible values of f_{10} and f_{01}. We may rewrite this as

$$\Pr(f) = \left\{ \frac{n!}{\prod_{x+y>1} f_{xy}!} \prod\nolimits_{x+y>1} \left(\frac{\theta_{xy}}{\pi} \right)^{f_{xy}} \right\} \times \left\{ \frac{N_{PA}!}{n!\,(N_{PA} - n)!}\, \pi^{n} (1 - \pi)^{N_{PA} - n} \right\}$$
$$\times \left\{ \frac{(\boldsymbol{N_{PA}} - \boldsymbol{n})!}{\boldsymbol{f_{01}}!\,\boldsymbol{f_{10}}!\,(\boldsymbol{N_{PA}} - \boldsymbol{f_{01}} - \boldsymbol{f_{10}})!} \prod\nolimits_{\boldsymbol{x+y \leq 1}} \left(\frac{\boldsymbol{\theta_{xy}}}{\boldsymbol{1 - \pi}} \right)^{\boldsymbol{f_{xy}}} \right\}. \tag{2}$$

Here, *n* is the sum of observed values f_{xy} (i.e., those for which $x + y > 1$) and $\pi = \Pr(X + Y > 1) = 1 - \theta_{00} - \theta_{01} - \theta_{10}$. The first term in equation (2) is a multinomial for the observed values f_{xy} with known index *n*; this term provides information about the unknown parameters θ_{xy}. The second term describes *n* as a binomial random variable with unknown index N_{PA} ; in combination with the information provided by the first term, the second term allows estimation of N_{PA}. The third term describes the unobserved frequencies f_{01}, f_{10}, and $f_{00} = N_{PA} - f_{01} - f_{10}$ as a trinomial random variable; its index and cell frequencies are informed by the other two terms.

Bayesian inference by Gibbs sampling involves draws from the full conditional distribution of these unobserved frequencies, subject to the constraints $f_{01} \leq c_{01}$ and $f_{10} \leq c_{10}$.We performed our analyses using program *JAGS* <http://mcmc-jags.sourceforge.net/>. In *JAGS* we can impose a bound $R \leq a$ on an unobserved value R by including as data a value $S = 1$, and modeling S as a Bernoulli random variable with success parameter $p = \text{step}(a - R)$. The value of p is 0 or 1, equaling 1 if and only if $R \leq a$. Thus, sampled values of $R > a$ are inconsistent with the observation $S = 1$, and are rejected. We used this trick to impose the constraints on sampled values f_{01} and f_{10}.

We assumed that X and Y, the numbers of photographs taken on the two sampling occasions, were independent random variables, so that $\theta_{xy} = p_X(x)p_Y(y)$. We assigned a Dirichlet prior to the vector $(p_X(0), p_X(1), \dots, p_X(K))$ and implemented this in *JAGS* by sampling independent values $g_k \sim \Gamma(\alpha_k, 1)$, and setting $p_X(k) = g_k / \sum_{j=0}^{K} g_j$. For a noninformative prior, we set $\alpha_k \equiv 0.001$, approximating the "indifference prior" of Novick and Hall (1965). The prior for values $p_Y(y)$ was defined similarly. We used the noninformative scale prior for N_{PA} (Link, 2013).

One of the clear advantages of model $M_{t,\pi}$ is that it avoids having to model or estimate photo misidentification rates. Our model assumed that all misidentification errors are false rejections (i.e. two photos of the same individual were incorrectly identified as two individuals) that resulted in single captures (i.e. 10 or 01 capture histories). Given that most errors were generated by poor-quality photographs, it was unlikely that two misidentified photos would lead to a recapture (Morrison et al., 2011). False acceptance errors would greatly alter observed capture histories, but previous tests in wildebeest (Morrison et al., 2011; Bolger et al., 2012) suggest that false acceptance errors occur extremely infrequently (~1/1000) in adult wildebeest .

2.6 Posterior inference for total population

Some adults displayed stripe patterns that were insufficiently distinct to be used in photographic identification, and we included these individuals into our model here. These individuals were unavailable for capture and overlooking them in a PCMR would have negatively biased abundance estimates. We thus estimated the number of photographically identifiable adults N_{PA}, as described in the previous section, and then combined these estimates with auxiliary data to estimate total population size.

We used auxiliary data to define informative beta priors for the photographability rates p_{PA} and age structure parameters p_A. For photographability, we surveyed 397 adult wildebeest in June (wet season) and October (dry season) of 2007: 4% (SE = 1%) of males and females in Tarangire, and 4% of males (SE = 1%) and 32% of females in Lake Manyara (SE = 3.0%) had stripe patterns that were insufficiently distinct to identify visually. Secondly, during photographic sampling, we aged and sexed all animals within herds on the basis of horn shape and body size (Mduma et al., 1999). For datasets from Lake Manyara National Park, photographability differed by sex (higher photographability for males than females), and in these we first separated sex before sampling photographable adults; otherwise the analyses were identical across datasets.

We modeled N_{PA} (the number of photographically identifiable adults) as binomial with index N_A (the number of adults) and success parameter p_{PA} (the probability an adult animal is photographically identifiable). We then modeled N_A as binomial with index N (total population size) and success parameter p_A (probability an animal is an adult). We used noninformative scale priors (Link, 2013) for N_A and N.

Random variable G has a negative binomial distribution with parameters π and h, denoted $G \sim NB(\pi, h)$ if

$$\mathbf{Pr}(\boldsymbol{G} = \boldsymbol{g}) = \frac{\boldsymbol{\Gamma}(\boldsymbol{g})}{\boldsymbol{\Gamma}(\boldsymbol{h})\boldsymbol{\Gamma}(\boldsymbol{g}+\mathbf{1}-\boldsymbol{h})}\, \boldsymbol{\pi}^{\boldsymbol{h}}(\mathbf{1}-\boldsymbol{\pi})^{\boldsymbol{g}-\boldsymbol{h}}\ , \text{ for } \boldsymbol{g} = \boldsymbol{h}, \boldsymbol{h} + \mathbf{1}, \ldots \tag{3}$$

Under the stated assumptions, it can be shown that conditional on N_{PA} and p_{PA}, $N_A \sim NB(p_{PA}, N_{PA})$, and that conditional on N_A and p_A, $N \sim NB(p_A, N_A)$. We thus sample posterior distributions for total population size N by the following process:

1) Sample N_{PA} from its posterior distribution, as described in section 2.5.
2) Sample p_{PA} from the appropriate beta distribution, then N_A from $NB(p_{PA}, N_{PA})$.
3) Sample p_A from the appropriate beta distribution, then N from $NB(p_A, N_A)$.

2.7 Calf recruitment

Peak wildebeest calving in TME usually occurs in February in each of the three main calving areas: Lake Manyara NP, Simanjiro and Northern Plains. Our herd composition surveys (see above) allowed us to estimate calf recruitment (calf:cow) during the late wet season (June), roughly three months after the calving period and five months prior to weaning. Calf:cow ratios correlate positively with population growth rate in other ungulates (Harris et al., 2008) and are widely used as indicators of population trajectory. We compared recruitment rates across three wet-seasons (2005-2007) within each of the three main calving areas to identify spatio-temporal trends.

3. Results

3.1 Patterns of connectivity and population dynamics

Across all surveys and years, we collected 10 760 high-quality photographs of wildebeest and observed 384 herds during survey counts. A subset of 8302 images provided encounter histories for seven capture-mark-recapture models. Model results revealed wildebeest abundance in the greater TME varying between ~6500 and ~13 000 individuals in the wet seasons of 2006-2007 (Table 1). Models from the Lake Manyara NP population indicated increases from 275 to ~1300 animals between 2006 and 2011 (Table 1). An increasing proportion of the TME population resided in Lake Manyara NP: from 4% in 2006 to 11% in 2011, based on median estimates of $M_{t,\pi}$ and aerial surveys.

From 2005-2007, calf productivity was consistently higher in Lake Manyara NP than in the Simanjiro or Northern Plains (Fig. 3), with Simanjiro having the lowest recruitment each year. Recruitment increased over time in all areas over these three years.

The combination of PCMR and GPS data provided valuable information on the current patterns of spatial connectivity across population segments (Fig. 1C, Table A.2). The majority of the population (96%) spends the dry season in northern and central Tarangire NP and Manyara Ranch. In the wet season, these animals migrate to both the Northern Plains and the Simanjiro Plains, where they congregate at relatively high densities. Wildebeest migrated between these seasonal ranges (Simanjiro to Tarangire NP and Manyara Ranch to the Northern Plains) in 1-2 days over straight line distances of 60-75 km (Fig. 1). The longest total movement distance recorded (271.2 km) was by an adult female moving from the Simanjiro to Northern Plains from June 2006-December 2006, and then back to Simanjiro in May 2007.

3.2. Abundance model efficacy

Posterior distributions from model $M_{t,\pi}$ overlapped estimates from recent aerial surveys by TAWIRI (Fig. 2). Further, this model produced median abundance estimates below those of conventional capture-recapture models (i.e. M_t) in six out of seven datasets (Table 1). Mean M_t estimates were on average 107% higher (i.e. roughly double) compared to median $M_{t,\pi}$(Table 1), demonstrating the value of using models for PCMR data that account for misidentifications and multiple captures within-periods. A single model (2011 Lake Manyara NP) estimated a median abundance 45% higher than the median $M_t$estimate. “Model $M_{t,\pi}$” differed from ground-based total counts in Lake Manyara NP: total counts were outside the 95% credible intervals in 2 of the 3 surveys (2006 and 2011) and close to the median estimate in the third survey (2007; Table 1).

4. Discussion

Wildebeest in the TME have experienced a gradual loss of connectivity between seasonal ranges and undergone large inter- and intra-annual fluctuations in abundance over time. Similar patterns have played out elsewhere in Africa (Fynn and Bonyongo 2010; Estes, 2014). Livestock fencing around Etosha National Park, Namibia, Kruger National Park, South Africa and the Kalahari, Botswana have resulted in extensive contractions in seasonal areas and large declines in migratory wildebeest populations (Whyte and Joubert, 1988; Spinage, 1992; Berry, 1997). In the Masai-Mara and Athi Plains of Southern Kenya, long-term declines in wildebeest have coincided with the conversion of grasslands to farmland and suburban development (Ottichilo et al., 2001; Ogutu et al., 2010; Worden et al., 2010; Estes, 2014).

Our PCMR method provided a detailed snapshot of the TME wildebeest population, while accounting for the complexity of photo identification datasets through a novel statistical model. The greater population ranged between ~6000 and ~13 000 individuals from 2006-2007, and maintained the higher level through 2011 (Fig. 2). Most wildebeest migrated to either the Simanjiro Plains or the Northern Plains in the wet season. Several hundred wildebeest remain largely resident in Lake Manyara NP, while approximately 400 animals migrate to the Kimotorok area. Recruitment appears to be higher in Lake Manyara NP than elsewhere.

The PCMR methodology provided more precise abundance estimates than aerial surveys, and our $M_{t,\pi}$model overcame potential bias from misidentification errors and photographability, resulting in median estimates that were roughly half of those from models ignoring misidentifications. Comparisons to ground-based total counts in LMNP showed mixed success: the $M_{t,\pi}$model produced estimates that were both considerably lower (wet 2006) and higher (dry 2007) than total counts (Table 1). While wildlife total counts tend to be negatively biased (Caughley 1974), we suspect discrepancies in this instance were due to variability in rates of photographability in LMNP driven by extremely dusty conditions that obscured wildebeest marking patterns at certain times. We recommend that photographability be estimated during each sampling occasion.

Model $M_{t,\pi}$ should be useful in other sampling scenarios where misidentification is possible, and the number of photographs of an individual in a survey can be greater than 1, for instance in camera trap surveys (Silver et al., 2004). Extensions of model $M_{t,\pi}$ to more than two sampling periods are straightforward. Parametric models for the numbers of times an individual is photographed (e.g., Poisson or geometric models) could be used in place of the Dirichlet models considered here; these could improve inference by parsimony, though possibly at the expense of model fit.

4.1 Current population status

While we cannot definitively link past trends in wildebeest abundance with changes in land-use and wildlife harvesting, the current geographic extent and population size of wildebeest in the TME is certainly smaller than that described by Lamprey (1964) and Borner (1985) (Fig. 1B). What was probably once a population of tens of thousands of animals now numbers roughly 10 000, despite a landscape that rivals the Serengeti-Mara Ecosystem in total area (Lamprey, 1964). Our results suggest that the population has stabilized since the early 2000's relative to the severe declines observed in the 1990's.

The recent stability of the population is likely related to conservation initiatives that seek to protect the remaining migratory routes and dispersal areas while reducing illegal hunting. The multi-jurisdictional nature of the landscape has required a diverse set of initiatives. Since the late 1990's, illegal hunting and high intensity livestock grazing in Manyara Ranch, a former national ranch and now a private conservancy, have significantly declined. During the early 1990's only small numbers of wildebeest reportedly moved northwards of Tarangire NP in the direction of the ranch (TCP, 1997), but now roughly 50% of the Tarangire NP subpopulation migrates towards the Northern Plains and Lake Natron during the wet season (Morrison and Bolger, 2014). With new artificial water holes on the Manyara Ranch, many wildebeest and zebra (*Equus quagga*) now stay in the vicinity of the ranch late into the dry season (Morrison, *unpubl. data*).

Other conservation efforts have focused on communal grazing lands. Some focus on increasing economic benefits to Maasai communities. For instance, in the Simanjiro Plains a consortium of tour operators, hunting companies and conservation organizations pay village governments for land easements that restrict new farming and settlement in key portions of communal grazing areas (Nelson et al., 2010). In other areas efforts to protect grazing rights for pastoralists and wildlife, particularly around movement corridors, are occurring under Certificates of Customary Right of Occupancy (CCRO's) agreements, a community-level system of formal land ownership. In 2015 a new CCRO was established in a narrow corridor north of Manyara in Selela village (Morrison and Bolger, 2014). Newly established Wildlife Management Areas (WMA's) (Burunge and Randilen) to the north and west of Tarangire NP also provide a legal framework for protecting communal land and discouraging poaching by distributing revenue generated from ecotourism at the local rather than national level, although this mechanism has been criticized for its failure to deliver widespread benefits to local communities (Igoe and Croucher, 2007). Lastly, there is now a greater anti-poaching presence in the ecosystem, with approximately 100 community game scouts operating in the WMA's, Manyara Ranch and villages in the Simanjiro plains, with support often provided by armed teams from Tarangire National Park and the Wildlife Division.

Together, this patchwork of conservation initiatives extends wildlife protection beyond the borders of the national parks and helps protect the spatially diverse resource base of the wildebeest population. However, many of these new forms of protection remain spatially disjointed and only a minority of the total migratory network has any formal restrictions on further development. Consequently, a number of vulnerabilities remain.

4.2 Vulnerability One: Loss of migratory corridors in Kwakuchinja and the Northern Plains

In the TME, high quality forage on calving ranges (Voeten et al., 2010) is found in the nutrient-rich grasslands of the Northern Plains (Morrison and Bolger, 2014) and Simanjiro Plains (Kahuranganga & Silkiluwasha, 1997). Connectivity between Tarangire NP and Manyara Ranch through the Kwakuchinja Corridor is of critical importance as it is not only the gateway to Manyara Ranch but to the much larger expanse of rangeland in the Northern Plains (Fig. A.3). The Kwakuchinja area has experienced a large increase in cultivation over the past decade and remains under heavy development pressure from agriculture and settlements. The loss of this ~1-km wide strip of pastoral land (Morrison and Bolger, 2014) would likely force migrants to calve in the remaining habitat in Simanjiro and Kimotorok. Farther north, the government of Tanzania requested bids in 2014 for the development of a large soda-ash extraction plant in the Northern Plains, with the goal of extracting 1 million tons of soda ash year^{-1}. While the value of these plains to wildebeest and other large herbivores is difficult to quantify, the area serves as an important wet season and calving range and its loss would undoubtedly exacerbate the effect of future changes in other portions of the migratory range.

Continued loss of connectivity in the TME has the important consequence of limiting the capacity of the wildebeest population to respond to, and exploit, variation in environmental conditions. Clearly, the geographic extent of this system has declined, which suggests the range of spatial variability encompassed by the system has declined. Research from other migratory systems demonstrates that the complexity of migratory networks (in terms of the number of routes and ranges) predicts the stability of a population’s dynamics, similar to the way asset diversity stabilizes a stock portfolio (Schindler et al., 2010). Thus, as the network simplifies, migratory populations become more sensitive to fluctuations in environmental conditions in any one route or range. The apparent loss of connectivity with LMNP may be particularly important in this regard. Ecologically LMNP may be the most distinctive of the five sites in the system. With the lake's perennial river and groundwater-fed vegetation, it is likely that environmental variability in LMNP is significantly uncoupled from the rest of the network, increasing its portfolio value in stabilizing the overall meta-population.

4.3 Vulnerability Two: Habitat loss in the Simanjiro Plains.

Connectivity between Tarangire NP and Simanjiro currently seems robust compared to other areas. However, there has been extensive conversion of grassland to agriculture in the Simanjiro plains (Msoffe et al., 2011), particularly in Emboreet village. Further loss of habitat here should have proportionate impacts on the size of the breeding population using Simanjiro. When seasonal ranges, such as Simanjiro, are degraded, an important question is whether individuals have the behavioral flexibility to switch to alternative ranges. Migratory elk (*Cervus elaphus*), for instance, exhibit extremely high fidelity to specific routes and ranges in Yellowstone National Park (White et al., 2010). If fidelity is an inflexible attribute shaped by memory (or genetics, as is the case for some bird species), it may be costly when environmental conditions change (Morrison and Bolger, 2012). Previous work in the TME (Morrison and Bolger, 2012) and Serengeti (Hopcraft et al., 2014) suggests wildebeest have the behavioral plasticity to switch ranges. Up to 12% of wildebeest adults switch wet season ranges between Simanjiro and the Northern Plains from one year to the next (Morrison and Bolger, 2012). A study from the 1990's showed that VHF-collared wildebeest switched between Simanjiro and the Northern Plains (1 out of 12 collared individuals) (TCP, 1998). These results suggest that seasonal use of calving grounds by wildebeest is at least partly facultative, and they could switch to the Northern Plains for calving, in the event of further habitat loss in Simanjiro. But only if connectivity is preserved.

4.4 Vulnerability Three: Illegal hunting on land outside of protected areas.

It is likely that increasing accessibility, due to new and improved roads and greater availability of cars and motorbikes, and increased bushmeat demand in Mto wa Mbu have led to higher levels of illegal hunting in the TME (Kiffner et al., 2014). Illegal offtake of wildlife is notoriously difficult to quantify, but represents a major threat to wildlife in many Sub-Saharan ecosystems (Barnett, 1997), including in the nearby Serengeti Ecosystem (Rentsch and Packer, 2015). Anecdotal evidence in the TME suggests poaching is significant, particularly on communal land (Kiffner et al., 2014). Roughly 85% of the migratory range of wildebeest in the TME lies within these communal areas. While road construction is an important development goal, support for anti-poaching efforts and law enforcement will be critical to the future viability of migratory populations in TME.

4.5 Vulnerability Four: Increasing isolation of Lake Manyara NP

Lake Manyara National Park is now mostly isolated from the rest of the system and the wildebeest there are now a resident (non-migratory) herd. Population interchange between TNP and LMNP is now relatively rare (5% of adults per year) (Morrison and Bolger, 2012). This is substantially lower compared to historical levels (cf. Lamprey, 1964; Borner, 1985) due to intensifying agro-pastoral activities between the parks. Nonetheless, Lake Manyara NP wildebeest abundance (~300-1000 animals) is similar to that of 30 years ago (Prins and Douglas-Hamilton, 1990). We found consistently higher calf:cow ratios in the Lake Manyara NP population than elsewhere in the ecosystem (Fig. 3), and a seemingly growing population (Table 1). Similar patterns of relatively high calf:cow ratios in the resident wildebeest population have been found in Serengeti NP (Ndibalema, 2009), suggesting residency as a strategy may confer some benefits for higher pregnancy and/or higher early calf survival (Bolger et al., 2008). Nonetheless, the loss of connectivity between Lake Manyara NP and other portions of the ecosystem lessens the potential for recolonization in the event of local extinction. Periodic floods to Lake Manyara displace grazers from shoreline habitat, as happened in the 1960's when wildebeest went effectively extinct in the park for nearly a decade (Prins and Douglas-Hamilton, 1990).

5. Conclusions

New approaches in animal tracking technology and statistics provide increasingly robust methods for establishing habitat-population relationships (e.g. Matthiopoulos et al., 2015), which helps set conservation and management priorities with greater certainty (Shuter et al., 2011). Our PCMR method shows that in the Tarangire Manyara Ecosystem, wildebeest populations have remained relatively stable and sustained intra-population connectivity, following increases in the 1980's and declines in the 1990's. Recent stability is probably due in part to ongoing conservation efforts that protect migratory habitat. This stability, nonetheless, appears to be based on tenuous landscape connectivity in the face of continuing habitat loss and illegal hunting. We think the worst-case scenario for these wildebeest over the next few decades is a collapse to purely resident populations in Lake Manyara NP, Manyara Ranch and Tarangire NP because of the loss of migration corridors. Given the stability of Lake Manyara population since the 1970's and the comparatively high level of protection in and near the park, there is reason to be optimistic that Lake Manyara NP could continue to support a viable population. The work of Voeten et al. (2010), however, poses serious questions about whether Tarangire NP (and the adjacent Manyara Ranch) can support large year-round resident wildebeest populations. These authors found, using nutritional models, that wet season forage in TNP supplies insufficient nutrients (particularly phosphorus) for lactating females, suggesting that migration is likely a prerequisite to maintaining wildebeest in this portion of the TME ecosystem (Voeten et al., 2010). Under enforced residency we would then expect much smaller population sizes. If migration routes continue to be lost in the TME, further studies are warranted to understand potential population limitation by nutrition. Future work that links wildebeest mortality to human activity will be especially valuable. Given the tenuous nature of the Kwakuchinja and Northern Plains corridors (Morrison and Bolger, 2014; Foley and Foley, 2015) and increasing rates of land-use change in Simanjiro (Msoffe et al., 2011) we consider this worst-case scenario plausible over the next several decades. It will take the continued success and probably an enhancement of ongoing conservation efforts to prevent this from occurring.

Appendix A: Supplementary figures

Appendix B: Supplementary tables

Acknowledgments

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References

Barnett, R., (ed). 1997. Food for thought: The utilization of wild meat in Eastern and Southern Africa. TRAFFIC East/Southern Africa. Nairobi, Kenya.

Berry, H.H., 1997. Aspects of wildebeest Connochaetes taurinus ecology in the Etosha National Park - a synthesis for future management. Madoqua 20, 137-148.

Bolger, D.T., Morrison, T.A., Vance, B., Lee, D., Farid, H., 2012. Development and application of a computer-assisted system for photographic mark-recapture analysis. Methods in Ecology and Evolution 3, 813-822.

Bolger, D.T., Newmark, W.D., Morrison, T.A., Doak, D.F., 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11, 63-77.

Borner, M., 1985. The increasing isolation of Tarangire National Park. Oryx 19, 91-96.

Caughley, G., 1974. Bias in aerial survey. Journal of Wildlife Management 38, 921-933.

Darroch, J.N., 1958. The multiple-recapture census: I. Estimation of a closed population. Biometrika 45, 343–359.

Estes, R.D., 2014. The Gnu's World: Serengeti wildebeest ecology and life history University of California Press, Berkeley.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology

Evolution and Systematics 34, 487-515.

Foley, C., Foley, L., 2015. Wildlife trends and status of migratory corridors in the Tarangire Ecosystem, ed. T.P. Wildlife Conservation Society, Arusha.

Fryxell, J.M., Greever, J., Sinclair, A.R.E., 1988. Why are migratory ungulates so abundant? American Naturalist 131, 781-798.

Fryxell, J.M., Sinclair, A.R.E., 1988. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3, 237-241.

Fynn, R.W.S., Bonyongo, M.C., 2010. Functional conservation areas and the future of Africa's wildlife. African Journal of Ecology 49, 175-188.

Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromsight, J., Berger, J., 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7, 55-76.

Harris, N.C., Kauffman, M.J., Mills, S.L., 2008. Inferences about ungulate population dynamics derived from age ratios. Journal of Wildlife Management 72, 1143.

Hastings, K.K., Hiby, L.A., Small, R.J., 2008. Evaluation of a computer-assisted photograph-matching system to monitor naturally marked harbor seals at Tugidak Island, Alaska. Journal of Mammalogy 89, 1201-1211.

Hebblewhite, M., Merrill, E.H., 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90, 3445-3454.

Hebblewhite, M., Merrill, E., 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage – predation tradeoffs. Oikos 120, 1860-1870.

Hopcraft, J.G.C., Morales, J.M., Beyer, D.E., Borner, M., Mwangomo, E., Sinclair, A.R.E., Olff, H., Haydon, D.T., 2014. Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. Ecological Monographs 84, 355-372.

Igoe, J., Croucher, B., 2007. Conservation, commerce, and communities: The story of community-based wildlife management areas in Tanzania's northern tourist circuit. Conservation and Society 5, 534–561.

Jachmann, H., 2002. Comparison of aerial counts with ground counts for large African herbivores. Journal of Applied Ecology 39, 841-852.

Kahuranganga, J., Silkiluwasha, F., 1997. The migration of zebra and wildebeest between Tarangire National Park and Simanjiro Plains, northern Tanzania, in 1972 and recent trends. African Journal of Ecology 35, 179-185.

Kiffner, C., Kioko, J., Kissui1, B., Painter, C., Serota, M., White, C., Yager, P., 2014. Interspecific variation in large mammal responses to human observers along a conservation gradient with variable hunting pressure. Animal Conservation 17, 603-612.

Lamprey, H.F., 1964. Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. East African Journal of Wildlife 2, 1-46.

Link, W.A., 2013. A cautionary note on the discrete uniform prior for the binomial N. Ecology 94, 2173–2179.

Link, W.A., Yoshizaki, J., Bailey, L.L., Pollock, K.H., 2010. Uncovering a latent multinomial: analysis of mark-recapture data with misidentification. Biometrics 66, 178-185.

Lowe, D., 2004. Distinctive image features from scale-invariant keypoints. International Journal of Computer Vision 60, 91-110.

Lundberg, P., 1988. The evolution of partial migration in birds. Trends Ecology Evolution 3, 172 – 175.

Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H.L., Morales, J.M., Haydon, D.T., 2015. Establishing the link between habitat selection and animal population dynamics. Ecology 85, 413-436.

Mduma, S.A.R., Sinclair, A.R.E., Hilborn, R., 1999. Food regulates the Serengeti wildebeest: a 40-year record. Journal of Animal Ecology 68, 1101-1122.

Mjingo, E., 2012. Genetic markers for wild herbivores conservation in the Serengeti Ecosystem, Tanzania, In Department of Basic Sciences and Aquatic Medicine. Norwegian School of Veterinary Science, Oslo.

Moore, J.W., McClure, M., Rogers, L.A., Schindler, D. E., 2010. Synchronization and portfolio performance of threatened salmon. Conservation Letters 3, 340-348.

Morrison, T.A., Yoshizaki, J., Nichols, J.D., Bolger, D.T., 2011. Estimating survival in photographic capture-recapture studies: overcoming misidentification error. Methods in Ecology and Evolution 2, 454-463.

Morrison, T.A., Bolger, D.T., 2012. Wet season range fidelity in a tropical migratory ungulate. Journal of Animal Ecology 81, 543-552.

Morrison, T.A., Bolger, D.T., 2014. Connectivity and bottlenecks in a migratory wildebeest population. Oryx 48, 613-621.

Msoffe, F.U., Ogutu, J.O., Kaaya, J., Bedelian, C., Said, M.Y., Kifugo, S.C., Reid, R.S., Neselle, M., van Gardingen, P., Thirgood, S., 2010. Participatory wildlife surveys in communal lands: a case study from Simanjiro, Tanzania. African Journal of Ecology 48, 727-735.

Msoffe, F.U., Kifugo, S.C., Said, M., Ole Neselle, M., Van Gardingen, P., Reid, R.S., Ogutu, J.O., Herero, M., de Leeuw, J., 2011. Drivers and impacts of land-use change in the Maasai Steppe of Northern Tanzania: an ecological, social and political analysis. Journal of Land Use Science 6, 1-21.

Ndibalema, V.G., 2009. A comparison of sex ratio, birth periods and calf survival among Serengeti wildebeest subpopulations, Tanzania. African Journal of Ecology 47, 574-582.

Nelson, F., Foley, C., Foley, L.S., Leposo, A., Loure, E., Peterson, D., Peterson, M., Peterson, T., Sachedina, H., Williams, A., 2010. Payments for ecosystem services as a framework for community-based conservation in Northern Tanzania. Conservation Biology 24, 78-85.

Newmark, W.D., 1996. Insularization of Tanzanian parks and the local extinction of large mammals. Conservation Biology 10, 1549-1556.

Newmark, W.D., 2008. Isolation of African protected areas. Frontiers in Ecology and the Environment 6, 321-328.

Norton-Griffiths, M., 1978. Counting Animals, Revised Second Edition edn. African Wildlife Foundation, Nairobi.

Novick, M.R., and Hall, W.J. 1965. A Bayesian indifference procedure. Journal of the American Statistical Association 60, 1104-1117.

Ogutu, J.O., Piepho, H.P., Reid, R.S., Rainy, M.E., Kruska, R.L., Worden, J.S., Nyabenge, M., Hobbs, N.T., 2010. Large herbivore responses to water and settlements in savannas. Ecological Monographs 80, 241-266.

Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62, 1–135.

Ottichilo, W.K., de Leeuw, J., Prins, H.H.T., 2001. Population trends of resident wildebeest [Connochaetes taurinus hecki (Neumann)] and factors influencing them in the Masai

Mara ecosystem, Kenya. Biological Conservation 97, 271-282.

Prins, H.H.T., Douglas-Hamilton, I., 1990. Stability in a multi-species assemblage of large herbivores in East Africa. Oecologia 83, 392-400.

Rentsch, D., Packer, C., 2015. The effect of bushmeat consumption on migratory wildlife in the Serengeti ecosystem, Tanzania. Oryx 49, 287-294.

Sawyer, H., Kauffman, M.J., 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80, 1078-1087.

Shuter, J.L., Broderick, A.C., Agnew, D.J., Jonzen, N., Godley, B.J., Milner-Gulland, E.J., Thirgood, S., 2011. Conservation and management of migratory species, In Animal Migration. eds E.J. Milner-Gulland, J.M. Fryxell, A.R.E. Sinclair. Oxford University Press, Oxford.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. Nature 465, 609-612.

Schindler, D.E., Armstrong, J.B., Reed, T.E., 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13, 257–263.

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gómez, H., Ayala, G., 2004. The use of camera traps for estimating jaguar Panthera onca abundance and density using capture/recapture analysis. Oryx 38, 148-154.

Spinage, C.A., 1992. The decline of the Kalahari wildebeest. Oryx 26, 147–150.

Swingland, I.R., Greenwood, P.J. 1983. The ecology of animal movement. Oxford University Press, Oxford.

TAWIRI, 2011. Aerial census in the Tarangire Ecosystem. Conservation Information and

Monitoring Unit, Arusha, TZ.

TCP, 1998. Tarangire Conservation Project. Analysis of migratory movements of large mammals and their interactions with human activities in the Tarangire area in Tanzania as a contribution to a conservation and sustainable development strategy. Final Report.

van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C.M., Solberg, E.J., Saether, B.E., 2013. Understanding scales of movement: animals ride waves and ripples of environmental change. Journal of Animal Ecology 82, 770-780.

Voeten, M.M., van de Vijver, C., Olff, H., van Langevelde, F., 2010. Possible causes of decreasing migratory ungulate populations in an East African savannah after restrictions in their seasonal movements. African Journal of Ecology 48, 169-179.

White, P.J., Proffitt, K.M., Mech, L.D., Evans, S.B., Cunningham, J.A., Hamlin, K.L., (2010) Migration of northern Yellowstone elk: implications of spatial structuring. Journal of Mammalogy, 91, 827-837.

Whyte, I.J., Joubert, S.C.J., 1988. Blue wildebeest population trends in the Kruger National-Park and the effects of fencing. South African Journal of Wildlife Research 18, 78-87.

Worden, J., Mose, V., Western, D., 2010. Aerial census of wildlife and livestock in Eastern Kajiado. African Conservation Centre, Nairobi.

TABLES AND FIGURES

TABLE 1. Total population size estimates and credible intervals (2.5th and 97.5th) of wildebeest (including calves and yearlings) from different areas of the TME: SP (Simanjiro Plains), TNP (Tarangire National Park), NP (Northern Plains) and LMNP (Lake Manyara National Park). Total counts from LMNP and Distance Sampling estimate from SP (Msoffe et al., 2010) included here for comparison. Two-sample Model (M_t) included to demonstrate the effect of ignoring misidentification error.

FIG. 1 Migratory routes in the Tarangire-Manyara Ecosystem, Tanzania over time. (A) Five GPS collared wildebeest (2009-2011; Appendix) reveal the two main migration bottlenecks: Kwakuchinja (1) and Northern Plains (2). (B) Changes in the number of routes used by all wildlife over time. (C) Migratory connectivity within the northern portion of the Tarangire–Manyara Ecosystem based on photographic capture–recapture (cf. Table A.21). Note that lines (C) connect consecutive captures of unique individuals rather than movement paths. Connectivity patterns reflect sampling intensity rather than movement probabilities.

FIG. 2 Abundance of wildebeest in the Tarangire-Manyara Ecosystem, Tanzania over time. Estimates ± SE from aerial systematic reconnaissance flights between 1988 and 2011 (circles) (TAWIRI 2011) and median estimates ± 5% credible intervals (squares) from photo capture-mark-recapture model $M_{t,\pi}$ between 2006 and 2007. Light shading indicates dry season surveys (August-November) and dark shading indicates wet season surveys (March-June).

FIG. 3 Calf recruitment in the month of June (three months post-parturition) in the Tarangire-Manyara Ecosystem, Northern Tanzania, 2005-2007.

TABLE 1.

					Abundance (N)					
					$M_{t,\pi}$					
Dataset	**Area**	**Year**	**Month(s)**	**Photos**	**2.5th**	**50th**	**97.5th**	**M_t**	**Total Count**	**Distance Sampling[1]**
1	SP	2006	May	982	2080	**3791**	6852	10148		
		2007	May							5532
2	SP-TNP-NP	2006	June-July	1764	4260	**6764**	10980	15573		
3		2007	June-July	2688	8802	**12798**	17100	24303		
4	TNP	2007	October	1637	2161	**3364**	5500	10151		
5	LMNP	2006	October	235	168	**274**	493	593	504	
6		2007	October	260	276	**508**	942	977	579	
7		2011	June	736	985	**1323**	1744	734	607	

[1] Msoffe et al. (2010)

FIG. 1.

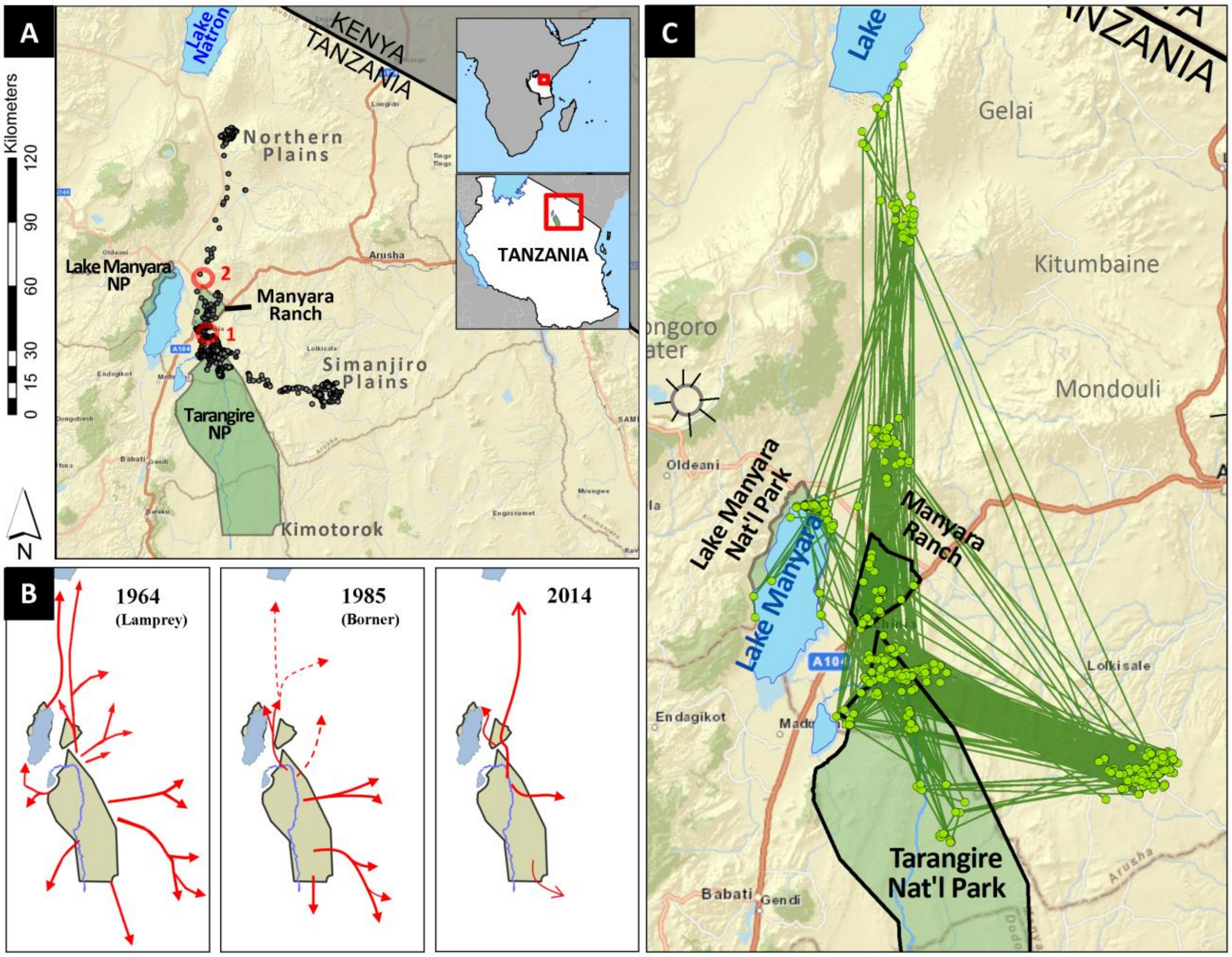

A
Lake Natron
KENYA
TANZANIA
Kilometers
0
15
30
60
90
120
Northern Plains
Lake Manyara NP
2
1
Manyara Ranch
Arusha
Simanjiro Plains
Tarangire NP
Kimotorok
N
TANZANIA
B
1964
(Lamprey)
1985
(Borner)
2014
C
Lake
TANZANIA
Gelai
Kitumbaine
Mondouli
Oldeani
Lake Manyara Nat'l Park
Lake Manyara
Manyara Ranch
Lolkisale
Endagikot
Tarangire Nat'l Park
Babati
Gendi

FIG. 2

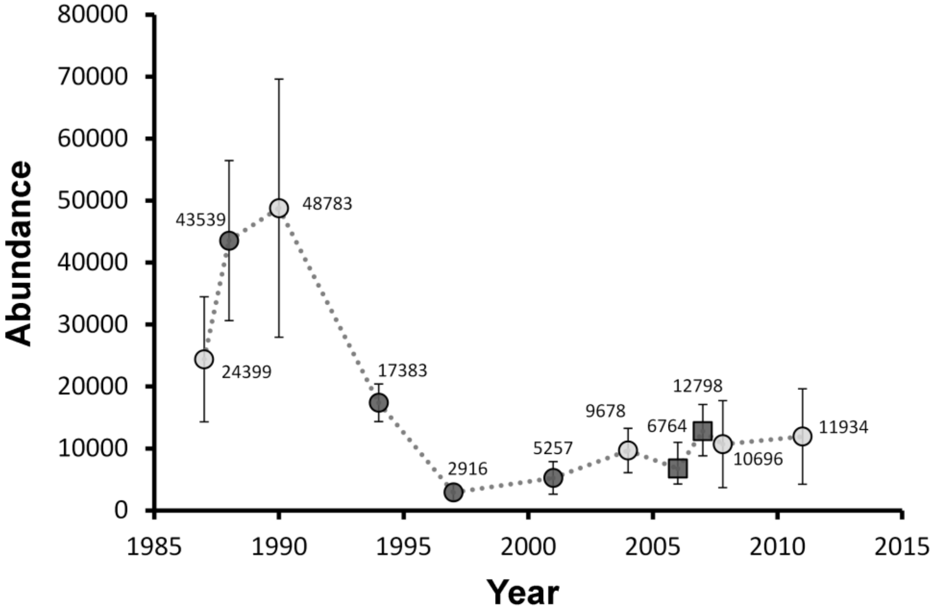
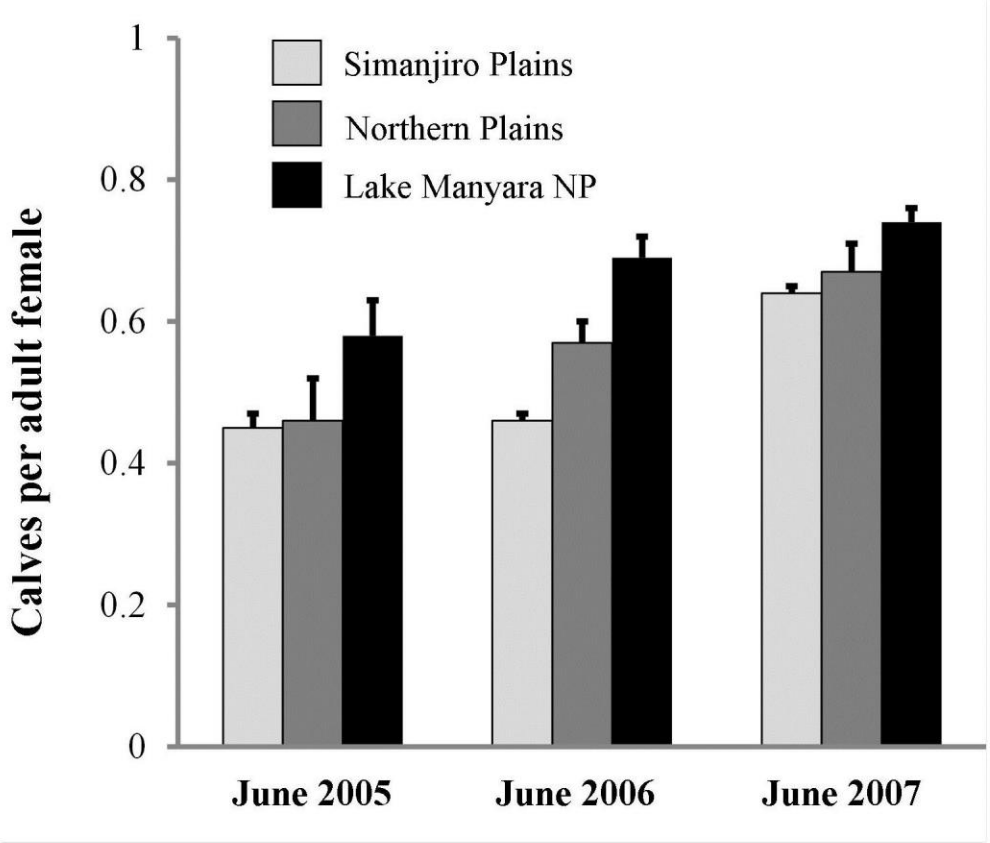

Abundance
80000
70000
60000
50000
40000
30000
20000
10000
0
1985
1990
1995
2000
2005
2010
2015
Year
43539
48783
24399
17383
2916
5257
9678
6764
12798
10696
11934

FIG. 3


Simanjiro Plains
Northern Plains
Lake Manyara NP
Calves per adult female
1
0.8
0.6
0.4
0.2
0
June 2005
June 2006
June 2007

APPENDIX - FIGURES

Figure. A1. Comparison of false rejection errors between the two identification systems: for male images (Conservation Research Ltd. <conservationresearch.co.uk>; Hastings et al., 2008) and for female images (‘Wild-ID’ <dartmouth.edu/~dbolger>; Bolger et al., 2012). Error rates were calculated using images from known-identity individuals. The x-axis indicates the number of top-ranked candidate matches that were searched during the matching process. See Morrison et al. (2011) for further details.

Figure A2. Example of an adult female wildebeest photo-captured on two occasions, visualizing the pattern matching algorithm of Wild-ID (Bolger et al. 2012). White points show the locations of Scale Invariant Feature Transform (SIFT) features identified by Wild-ID. Red lines connect these putative matches. The green lines indicate where the features on the lower image 'should' have been located based on the affine transform applied to the upper image. Large green lines indicate nonlinearities in the mapping between the two images not captured by the affine transform.

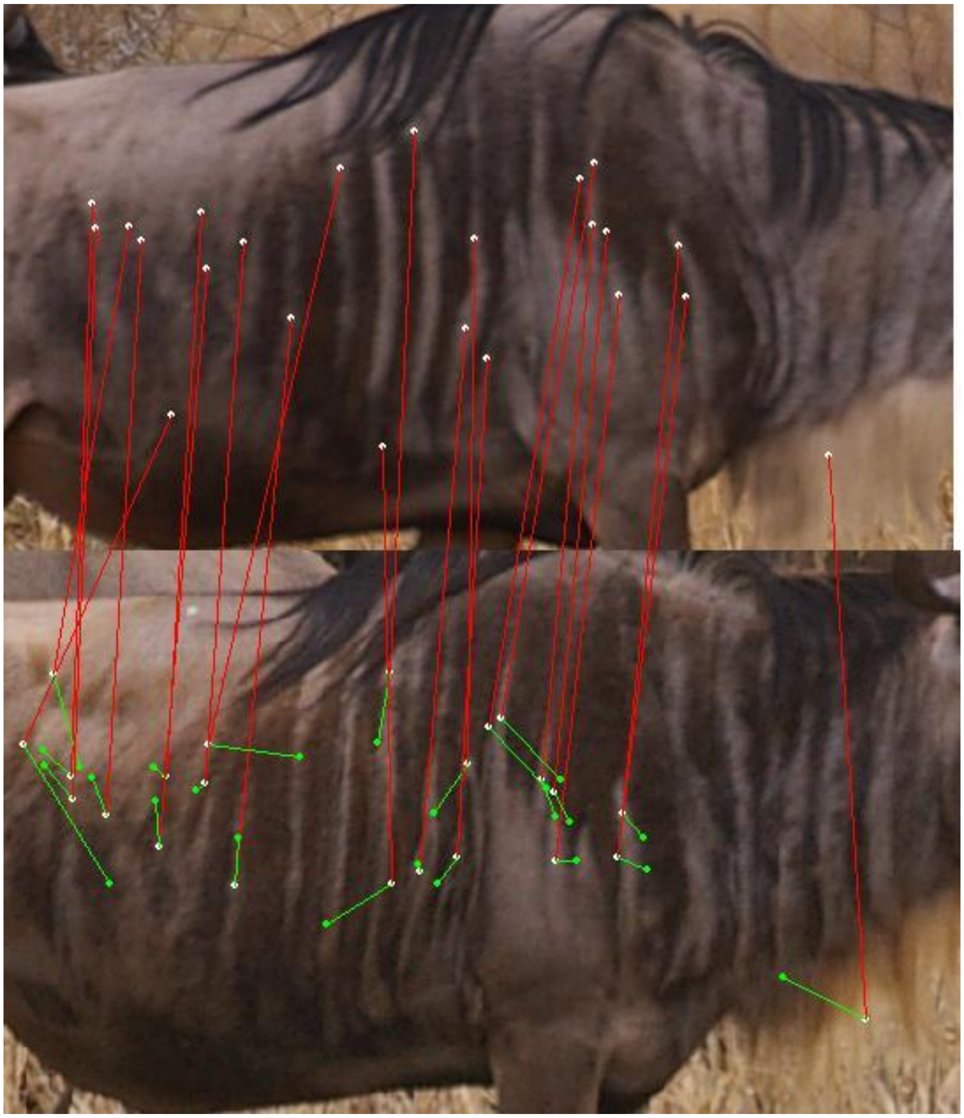
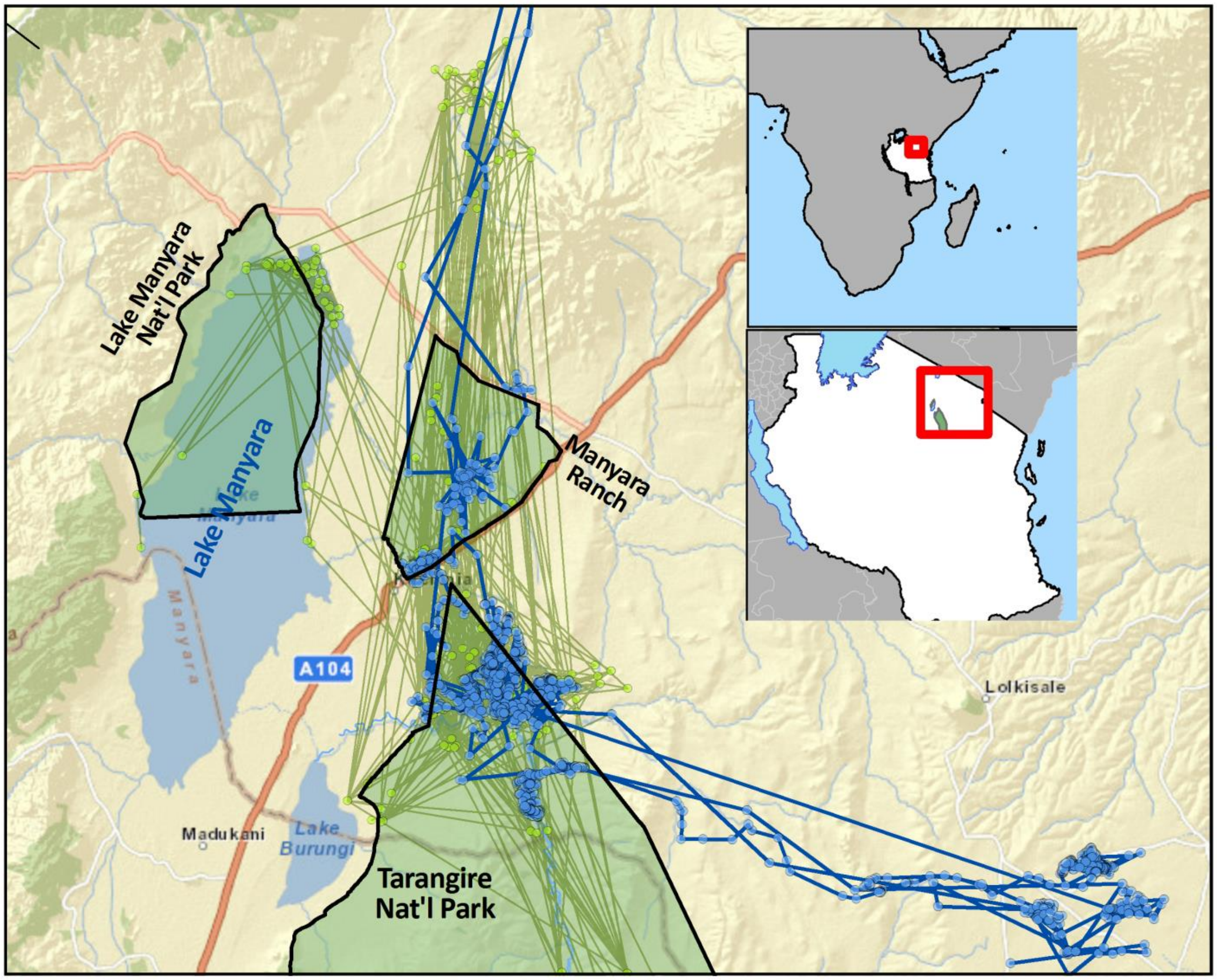


Fig. A3. Detailed map of connectivity between Tarangire NP, Manyara Ranch, Lake Manyara National Park and Selela Village, Northern Tanzania. Green lines show PCMR data (2006-2011) and blue lines show GPS collar data (2009-2010).



APPENDIX 2

TABLE A1. Example photo capture history dataset (from Simanjiro Plains, May 2006); *x*-axis is # of successful sightings, period 1 (*X*); *y*-axis is # in period 2 (*Y*).

4	5				
3	27	1	2		
2	65	6	2	1	
1	≤ 238	13	3	1	
0	??	≤ 259	54	10	6
	0	**1**	**2**	**3**	**4**

TABLE A2. Number of photo recaptures of wildebeest from Time$_i$ to Time$_{i+1}$ between Gelai Plains (GP), Lake Manyara National Park (LMNP), Manyara Ranch (MR), Selela (SEL), Simanjiro Plains and Tarangire National Park (TNP). The table summarizes movements from Fig. 2C. The matrix only includes transitions between days.

		Time *i*					
		GP	LMNP	MR	SEL	SP	TNP
Time *i* + 1	TNP	3	4	14	17	111	**406**
	SP	2	1	4	3	**153**	80
	SEL	1	2	3	**41**	1	21
	MR	1	4	**80**	21	7	51
	LMNP	4	**213**	3		1	5
	GP	**6**	4				8