



# Movements and source–sink dynamics of a Masai giraffe metapopulation

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**Abstract** Spatial variation in habitat quality and anthropogenic factors, as well as social structure, can lead to spatially structured populations of animals. Demographic approaches can be used to improve our understanding of the dynamics of spatially structured populations and help identify subpopulations critical for the long-term persistence of regional metapopulations. We provide a regional metapopulation analysis to inform conservation management for Masai giraffes (*Giraffa camelopardalis tippelskirchi*) in five subpopulations defined by land management designations. We used data from an individual-based mark–recapture study to estimate subpopulation sizes, subpopulation growth rates, and movement probabilities among subpopulations. We assessed the source–sink structure of the study population by calculating source–sink statistics, and we created a female-based matrix metapopulation model composed of all subpopulations to examine how variation in demographic components of survival, reproduction, and movement affected metapopulation growth rate. Movement data indicated no subpopulation was completely isolated, but movement probabilities varied among subpopulations. Source–sink statistics and net flow of individuals indicated

three subpopulations were sources, while two subpopulations were sinks. We found areas with higher wildlife protection efforts and fewer anthropogenic impacts were sources, and less-protected areas were identified as sinks. Our results highlight the importance of identifying source–sink dynamics among subpopulations for effective conservation planning and emphasize how protected areas can play an important role in sustaining metapopulations.

**Keywords** Matrix population model · Metapopulation · Population dynamics · Rescue effect · Source–sink

## Introduction

Spatial variation in habitat quality and anthropogenic factors, as well as the intrinsic social structure, can lead to spatially structured populations of animals (Levins 1969; Hanski and Gilpin 1991; Harrison 1994), and a spatially structured regional population can be divided into subpopulations, representing discrete social units, habitat patches, or land management areas (Thomas and Kunin 1999). Demographic analysis can evaluate subpopulation viability and contribution to regional population persistence (Caughley 1977; Gaillard et al. 1998; Martin et al. 2000; Vié et al. 2009). To assess the relative importance of individual subpopulations to the larger metapopulation requires information on within-subpopulation survival and reproduction as well as movements connecting subpopulations (Caswell 2001; Sinclair et al. 2006; Ozgul et al. 2009). We define a metapopulation here as a regional set of subpopulations that exchange individuals through movements.

The concept of sources and sinks is a useful construct in prioritizing population components for conservation (Lidicker 1975; Holt 1985; Pulliam 1988). Source–sink

**Electronic supplementary material** The online version of this article (doi:10.1007/s10144-017-0580-7) contains supplementary material, which is available to authorized users.

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theory predicts that individuals in higher-quality habitats (sources) should have greater fitness (higher population growth rates) leading to population growth, whereas those in lower-quality habitats (sinks) have lower fitness leading to population decline, with movement rates critical to determining whether subpopulations are actually sources or sinks (Griffin and Mills 2009; Ozgul et al. 2009; Constanti et al. 2013).

Although sink subpopulations are theoretically unable to persist independently, they are common elements of metapopulations, and sinks make significant contributions to metapopulation size and longevity (Howe et al. 1991). Sink populations spread the risk from stochastic extinctions of subpopulations (Goodman 1987), and contribute to metapopulation persistence when subpopulation growth rates vary temporally (Virgl and Messier 2000; Johnson 2004; Roy et al. 2005). Additionally, sinks can contribute a significant number of offspring (Pulliam 1988), and provide for greater genetic diversity (Lande and Barrowclough 1987).

Runge et al. (2006) developed a theoretically sound and operational method of defining sources and sinks based on readily obtainable demographic and movement data to determine the contributions of subpopulations to metapopulation growth (Griffin and Mills 2009). Furthermore, prospective perturbation analysis of matrix metapopulation models (e.g., elasticities) can simultaneously examine the relative importance to metapopulation growth rate of demographic rates within subpopulations as well as movement rates among subpopulations (Caswell 2001). Because of the data requirements, few attempts have been made to apply these methods to real populations (Runge et al. 2006; Griffin and Mills 2009; Ozgul et al. 2009; Constanti et al. 2013).

Our objective was to provide a regional analysis to inform conservation and management of a spatially structured metapopulation of Masai giraffes (*Giraffa camelopardalis tippelskirchi*). We performed our metapopulation analysis for five subpopulations defined by land management designations (Fig. 1). Previous research documented evidence for spatial variation in survival, reproduction, and population growth rates in these subpopulations of giraffes (Lee et al. 2016), raising the question how movements might connect subpopulations and affect regional metapopulation dynamics and viability. Movement rates among subpopulations of giraffes have never been explicitly assessed, although home ranges of individuals have been estimated (adult females =  $119 \pm \text{SD } 109 \text{ km}^2$ ; Dagg 2014).

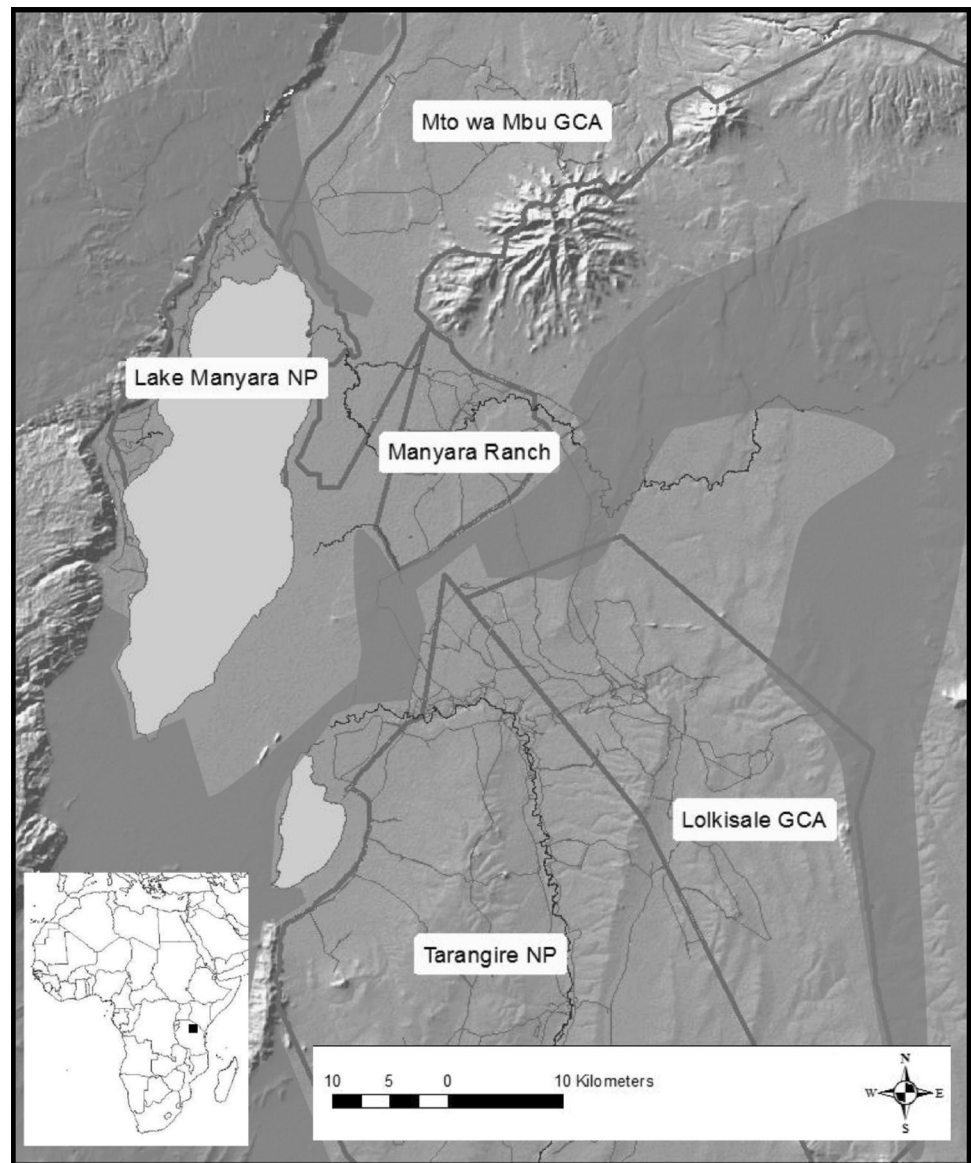
We used multi-strata mark–recapture models to estimate movement rates among subpopulations (Arnason 1973; Brownie et al. 1993). We defined source–sink structure of the study area by calculating the following statistics (Runge et al. 2006; Griffin and Mills 2009; Sanderlin et al. 2012): metapopulation growth rate; per capita contribution from

each subpopulation to metapopulation growth; relative contribution of each subpopulation to metapopulation growth; and relative contribution of immigrants from outside the metapopulation to metapopulation growth. To examine the relative importance of demographic and movement parameters to metapopulation growth rate, we created a matrix metapopulation model that included all subpopulations and performed prospective elasticity and perturbation analyses (Caswell 2001).

The five subpopulations we examined were Taran-gire National Park (TNP), Lake Manyara National Park (LMNP), Manyara Ranch Conservancy (MRC), Lolikisale Game Controlled Area (LGCA), and Mtowambu Game Controlled Area (MGCA). The five subpopulations were subject to three different management regimes with relative gradients in antipoaching law enforcement, livestock density, and the presence of agriculture and human settlements. Two subpopulations were national parks (TNP and LMNP) with the strictest enforcement of antipoaching laws, no livestock, no agriculture, and no permanent settlements. MRC subpopulation was a private ranch and wildlife conservancy with moderate antipoaching enforcement, a moderate to high diurnal density of pastoralists and livestock, but no agriculture or permanent settlements. Two subpopulations (MGCA and LGCA) had the least antipoaching activity, the highest density of pastoralists and livestock, agriculture and permanent human settlements, and some wildlife harvesting via trophy hunting and illegal subsistence and market poaching, although all hunting of giraffes is legally prohibited (Borner 1985; Gamassa 1995; Nelson et al. 2010; Kiffner et al. 2015).

We predicted there was likely some movement between adjacent and nearby subpopulations because the absence of fences or other impermeable barriers should permit exchange of individuals, but we expected rates to be low, especially across areas with substantial amounts of agriculture, human settlements, or livestock. We expected some anthropogenic barriers to movements could exist in the belt of agricultural land south of MRC and the high density of people and settlements around LMNP. Because of the different management regimes, land uses, and anthropogenic effects among subpopulations, we expected net movements out of subpopulations such as GCAs with greater anthropogenic disturbances such as poaching or high densities of livestock and people (Lee et al. 2016). We expected no difference in movement rates according to age class (i.e., natal versus breeding dispersal) because calves likely move with their adult mothers and herdmates, and subadults likely remain in their natal area as female mammals generally have high natal and breeding philopatry (Greenwood 1980). We expected adult female survival to be the demographic rate with the greatest relative influence on metapopulation

**Fig. 1** Study area in the Tarangire Ecosystem of northern Tanzania. *Thick grey lines* delineate the five subpopulations sampled, *shaded areas* are dominated by agriculture and represent unsuitable habitat, *thin grey lines* are roads and tracks, *black lines* are rivers and watercourses, *light grey areas* are lakes



growth rate because variation in adult female survival was previously identified as the most important to local population growth rates (Lee et al. 2016; Lee and Strauss 2016), and movement rates are expected to be low. However, movement rates could have important effects on source–sink dynamics. Subpopulation connectivity could benefit long-term population persistence via compensatory immigration (Turgeon and Kramer 2012), or the ‘rescue effect,’ where immigration averts a subpopulation’s extinction (Brown and Kodric-Brown 1977; Stacey and Taper 1992). Connectivity could also handicap population persistence by maintaining an ‘attractive sink’ subpopulation, thus depleting source subpopulations (Delibes et al. 2001).

## Methods

### Study system

This study used data from individually identified, wild, free-ranging giraffes in a system with nearly the full suite of historical natural predators and sympatric ungulate species across a 1700 km<sup>2</sup> sampled area within a 4400 km<sup>2</sup> region of northern Tanzania, East Africa. The Tarangire Ecosystem (TE; also called the Masai Steppe) is a tropical savanna-woodland ecosystem (Lamprey 1963; Prins and Loth 1988) that supports the second-highest density of giraffes in Tanzania (Stoner et al. 2006). Giraffes are large (830–1000 kg), long-lived, iteroparous, non-migratory,

non-territorial, browsing ruminants (Dagg and Foster 1976; Dagg 2014).

## Sampling

We collected data during systematic road transect sampling for photographic capture–mark–recapture (PCMR). We conducted 18 daytime surveys for giraffe PCMR data between January 2012 and October 2014. We sampled giraffes three times per year around 1 February, 1 June, and 1 October near the end of every precipitation season (short rains, long rains, and dry, respectively) by driving a network of fixed-route transects on single-lane dirt tracks in the study area. We surveyed according to a robust design sampling framework (Pollock 1982; Kendall et al. 1995; Kendall and Bjorkland 2001) with three occasions per year separated by a 4 month interval, where each sampling occasion was composed of two sampling events during which we surveyed all road transects in the study area with only a few days interval between events (3 years  $\times$  3 occasions year<sup>-1</sup>  $\times$  2 events occasion<sup>-1</sup> = 18 survey events).

During PCMR sampling events, the entire study area was surveyed and a sample of individuals were encountered and either “sighted” or “resighted” by slowly approaching and photographing the animal’s right side (Canon 40D and Rebel T2i cameras with Canon Ultrasonic IS 100–400 mm lens, Canon U.S.A., Inc., One Canon Park, Melville, New York, 11747, USA). We identified individual giraffes using their unique and unchanging coat patterns (Foster 1966). We attempted to photograph every giraffe encountered, and recorded sex and age class based on physical characteristics, and subpopulation based on location. We categorized giraffes into four age classes: newborn calf (0–3 months old), older calf (4–11 months old), subadult (1–3 years old for females, 1–6 years old for males), or adult (>3 years for females, >6 years for males) using a suite of physical characteristics (Strauss et al. 2015), and size measured with photogrammetry (see Electronic Supplementary Material (ESM) S1).

For our analyses we only considered female giraffes because females are the reproductive segment of populations, and adult males were ubiquitous enough in every subpopulation to not impose a limit on population growth.

## Estimating subpopulation sizes, growth rates, and movement probabilities

We matched giraffe identification images using WildID, a computer program that matched a large test dataset of giraffe images collected using our protocols with a 0.007 false rejection rate and 0.0 false acceptance rate (Bolger et al. 2012). We created individual encounter histories of

all females for analysis in program MARK 7.1 (White and Burnham 1999).

We used two modeling frameworks (Pradel and MSORD) to obtain most of our parameters of interest (Lowe 2003). We used a Pradel model parameterization (Pradel 1996; Nichols et al. 2000) with data from all age classes to estimate the derived parameter of subpopulation growth rates without movements (*Pradel*  $\lambda$ ). We used a Pradel model with data from adult females only to estimate the derived parameter of subpopulation sizes ( $N$ ). We used multi-site open robust design model parameterization (MSORD; Kendall and Bjorkland 2001; Schwarz and Stobo 1997; Lebreton et al. 2009) to estimate movement probabilities among subpopulations (*Psi* [ $\psi$ ]). We tested for differences in movement probabilities according to age class to validate our assumption of equal movements among ages. Details of parameter model selection and estimation methods are in ESM S2.

We calculated the seasonal number of individual emigrants and immigrants between each pair of subpopulations using seasonal movement probabilities ( $\psi$ ) between origin and destination subpopulations, and the population estimates ( $N$ ) at the origin subpopulations. We reiterated seasonal calculations three times to estimate annual number of emigrants and immigrants for each subpopulation. We subtracted annual emigrants from immigrants for each subpopulation to estimate annual net flow of individuals, where positive numbers indicate a net gain of individuals due to movements and negative numbers indicate a net loss of individuals.

## Classifying sources and sinks

We assessed the source–sink structure of our study area by calculating four parameters,  $C^i$ ,  $\lambda^M$ ,  $\hat{c}^i$ , and  $\hat{c}^0$ .  $C^i$  is the per capita contribution of a member of each subpopulation  $i$  to the metapopulation (Runge et al. 2006).

$$C^i = S_A^i + \sum \psi^{ik} + B^i \left( S_{1-4}^i + \sum \psi^{ik} \right), \quad (1)$$

where for subpopulation  $i$ ,  $S_A^i$  is adult survival,  $\sum \psi^{ik}$  is the sum of per capita emigration movements from the subpopulation,  $B^i$  is birth rate as calves per adult female ( $c/AF$ ), and  $S_{1-4}^i$  is juvenile survival (the product of  $S_1^i - S_4^i$ ).

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

$$\lambda^M = \sum C^i \times \left( \frac{N^i}{N^M} \right) \quad (2)$$

where  $N^i$  is subpopulation size, and  $N^M$  is metapopulation size.



$\hat{c}^i$  is the average relative contribution of each subpopulation to the metapopulation (Sanderlin et al. 2012).

$$\hat{c}^i = \frac{(N^i \times S_A^i) + (N^i \times \sum \psi^{ik})}{N^M}. \quad (3)$$

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

$$\hat{c}^0 = 1 - \sum_{i=1}^k \hat{c}^i. \quad (4)$$

Demographic and movement rates used in calculations of source–sink parameters are in Tables 1 and 2.

### Metapopulation projection model

In order to examine how births, deaths, and movements affected metapopulation dynamics, we created a female-based matrix metapopulation model composed of all 5 subpopulations:

$$\begin{array}{c} \text{TNP}^1 \quad \text{LMNP}^2 \quad \text{LGCA}^3 \quad \text{MGCA}^4 \quad \text{MRC}^5 \\ \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & F_A^1 \\ \theta_1^1 & 0 & 0 & 0 & 0 \\ 0 & \theta_2^1 & 0 & 0 & 0 \\ 0 & 0 & \theta_3^1 & 0 & 0 \\ 0 & 0 & 0 & \theta_4^1 & \theta_A^1 \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{21} & 0 & 0 & 0 & 0 \\ 0 & M_2^{21} & 0 & 0 & 0 \\ 0 & 0 & M_3^{21} & 0 & 0 \\ 0 & 0 & 0 & M_4^{21} & M_A^{21} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{31} & 0 & 0 & 0 & 0 \\ 0 & M_2^{31} & 0 & 0 & 0 \\ 0 & 0 & M_3^{31} & 0 & 0 \\ 0 & 0 & 0 & M_4^{31} & M_A^{31} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{41} & 0 & 0 & 0 & 0 \\ 0 & M_2^{41} & 0 & 0 & 0 \\ 0 & 0 & M_3^{41} & 0 & 0 \\ 0 & 0 & 0 & M_4^{41} & M_A^{41} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ 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\left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{52} & 0 & 0 & 0 & 0 \\ 0 & M_2^{52} & 0 & 0 & 0 \\ 0 & 0 & M_3^{52} & 0 & 0 \\ 0 & 0 & 0 & M_4^{52} & M_A^{52} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \\ \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{13} & 0 & 0 & 0 & 0 \\ 0 & M_2^{13} & 0 & 0 & 0 \\ 0 & 0 & M_3^{13} & 0 & 0 \\ 0 & 0 & 0 & M_4^{13} & M_A^{13} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{23} & 0 & 0 & 0 & 0 \\ 0 & M_2^{23} & 0 & 0 & 0 \\ 0 & 0 & M_3^{23} & 0 & 0 \\ 0 & 0 & 0 & M_4^{23} & M_A^{23} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & F_A^3 \\ \theta_1^3 & 0 & 0 & 0 & 0 \\ 0 & \theta_2^3 & 0 & 0 & 0 \\ 0 & 0 & \theta_3^3 & 0 & 0 \\ 0 & 0 & 0 & \theta_4^3 & \theta_A^3 \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{43} & 0 & 0 & 0 & 0 \\ 0 & M_2^{43} & 0 & 0 & 0 \\ 0 & 0 & M_3^{43} & 0 & 0 \\ 0 & 0 & 0 & M_4^{43} & M_A^{43} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{53} & 0 & 0 & 0 & 0 \\ 0 & M_2^{53} & 0 & 0 & 0 \\ 0 & 0 & M_3^{53} & 0 & 0 \\ 0 & 0 & 0 & M_4^{53} & M_A^{53} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \\ \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{14} & 0 & 0 & 0 & 0 \\ 0 & M_2^{14} & 0 & 0 & 0 \\ 0 & 0 & M_3^{14} & 0 & 0 \\ 0 & 0 & 0 & M_4^{14} & M_A^{14} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{24} & 0 & 0 & 0 & 0 \\ 0 & M_2^{24} & 0 & 0 & 0 \\ 0 & 0 & M_3^{24} & 0 & 0 \\ 0 & 0 & 0 & M_4^{24} & M_A^{24} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{34} & 0 & 0 & 0 & 0 \\ 0 & M_2^{34} & 0 & 0 & 0 \\ 0 & 0 & M_3^{34} & 0 & 0 \\ 0 & 0 & 0 & M_4^{34} & M_A^{34} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & F_A^4 \\ \theta_1^4 & 0 & 0 & 0 & 0 \\ 0 & \theta_2^4 & 0 & 0 & 0 \\ 0 & 0 & \theta_3^4 & 0 & 0 \\ 0 & 0 & 0 & \theta_4^4 & \theta_A^4 \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{54} & 0 & 0 & 0 & 0 \\ 0 & M_2^{54} & 0 & 0 & 0 \\ 0 & 0 & M_3^{54} & 0 & 0 \\ 0 & 0 & 0 & M_4^{54} & M_A^{54} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \\ \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{15} & 0 & 0 & 0 & 0 \\ 0 & M_2^{15} & 0 & 0 & 0 \\ 0 & 0 & M_3^{15} & 0 & 0 \\ 0 & 0 & 0 & M_4^{15} & M_A^{15} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{25} & 0 & 0 & 0 & 0 \\ 0 & M_2^{25} & 0 & 0 & 0 \\ 0 & 0 & M_3^{25} & 0 & 0 \\ 0 & 0 & 0 & M_4^{25} & M_A^{25} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{35} & 0 & 0 & 0 & 0 \\ 0 & M_2^{35} & 0 & 0 & 0 \\ 0 & 0 & M_3^{35} & 0 & 0 \\ 0 & 0 & 0 & M_4^{35} & M_A^{35} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & 0 \\ M_1^{45} & 0 & 0 & 0 & 0 \\ 0 & M_2^{45} & 0 & 0 & 0 \\ 0 & 0 & M_3^{45} & 0 & 0 \\ 0 & 0 & 0 & M_4^{45} & M_A^{45} \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \left[ \begin{array}{ccccc} 0 & 0 & 0 & 0 & F_A^5 \\ \theta_1^5 & 0 & 0 & 0 & 0 \\ 0 & \theta_2^5 & 0 & 0 & 0 \\ 0 & 0 & \theta_3^5 & 0 & 0 \\ 0 & 0 & 0 & \theta_4^5 & \theta_A^5 \\ 0 & 0 & 0 & 0 & 0 \end{array} \right] \end{array} \quad (5)$$

The matrix metapopulation model has five subpopulations, five age classes, 1 year time steps, birth-flow reproduction, and post-birth census. The diagonal block matrices are complete subpopulation-specific matrix population models for the subpopulation, based on the life-cycle graph in Fig. 2, with promotion ( $\Theta_j^i$ ) and fecundity ( $F_A^i$ ) cell values where superscripts indicate the subpopulation ( $i$ ) and subscripts indicate the age class ( $j$ ). The off-diagonals are transition matrices containing

migration cell values ( $M_j^{id}$ ), where the superscripts indicate the source and destination subpopulations ( $id$ ). We parameterized the matrix population model with reproduction ( $c/AF$ ) and survival ( $S$ ) estimates (Table 1) taken from Lee et al. (2016), and movement probabilities ( $\psi$ ) from MSORD models (Table 2) as follows:

$$\Theta_j^i = S_j^i \times \left(1 - \sum \psi^{ik}\right), \quad (6)$$

$$M_j^{id} = \psi_j^{id} \times S_j^i, \quad (7)$$

$$F_A^i = c/AF^i \times \sqrt{S_A^i} \times \sqrt{S_1^i} \times 0.5, \quad (8)$$

where  $\sum \psi^{ik}$  = sum of movement probabilities leaving that subpopulation and fecundity represents birth-flow reproduction of only female calves, assuming equal offspring sex ratio (Caswell 2001). We observed no movements in our data between some pairs of subpopulations (Table 2), so we fixed those values of  $\psi_j^{id}$  at zero throughout our matrix

analyses because we believed there were actually no movements between those subpopulations.

We implemented prospective elasticity methods on our current conditions matrix metapopulation model to investigate the sensitivity of metapopulation growth rate to proportional changes in matrix cell values (de Kroon et al. 2000; Caswell 2001). Next, we used prospective perturbation elasticity methods to systematically vary survival ( $S_j^i$ ), reproduction ( $c/AF^i$ ), and movement ( $\psi_j^{id}$ )

**Table 1** Demographic rates and source–sink identification parameters for five subpopulations of female Masai giraffes in the Tarangire Ecosystem, Tanzania 2012–2014

Subpopulation	Code	$S_1$	$S_2$	$S_3$	$S_4$	$S_A$	$c/AF$	$N$	$D$	$Pradel \lambda$	$Pradel \lambda$ SE	$MPM \lambda$	$C^i$	$\hat{c}^i$
Tarangire NP	TNP	0.50	0.80	0.89	0.89	0.89	0.28	349	0.58	0.987	0.007	0.932	1.06	0.44
Lake Manyara NP	LMNP	0.40	0.80	0.90	0.94	0.94	0.28	64	0.98	0.996	0.010	0.968	1.02	0.08
Lolkisale GCA	LGCA	0.60	0.73	0.73	0.73	0.73	0.33	79	0.45	1.027	0.025	0.790	0.90	0.08
Mtowambu GCA	MGCA	0.67	0.67	0.67	0.67	0.56	0.27	97	0.59	0.779	0.042	0.653	0.66	0.08
Manyara Ranch	MRC	0.72	0.87	0.87	0.87	0.87	0.44	201	1.39	0.976	0.009	0.968	1.15	0.26
														0.06

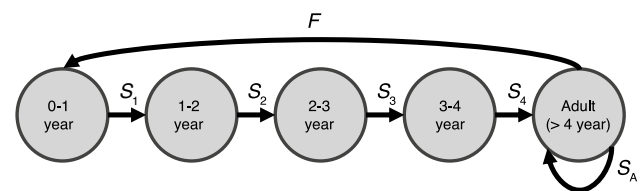
$S_1$  is survival from birth to age 1 year,  $S_2$  is survival from age 1 to 2,  $S_3$  is survival from age 2 to 3,  $S_4$  is survival from age 3 to 4,  $S_A$  is annual adult survival for ages > 4,  $c/AF$  is annual reproduction as number of calves per adult female,  $N$  is the estimated adult female population size,  $D$  is density as adult female  $N \text{ km}^{-2}$ ,  $Pradel \lambda$  is the estimated subpopulation growth rate from Pradel capture–mark–recapture without movements,  $MPM \lambda$  is the asymptotic population growth rate from matrix subpopulation models.  $C^i$  is the per capita contribution of a member of each subpopulation to the metapopulation (Runge et al. 2006),  $\hat{c}^i$  is the average relative contribution of each subpopulation to metapopulation growth, and  $\hat{c}^0$  is the average relative contribution of immigrants from outside the metapopulation to metapopulation growth (Sanderlin et al. 2012).  $S_j$ ,  $c/AF$ , and  $MPM \lambda$  are from Lee et al. (2016)

**Table 2** Seasonal (4 month) probability of movement ( $\psi$ ) for female Masai giraffes between pairs of subpopulations in Tarangire Ecosystem, Tanzania 2012–2014

Subpopulations	Distance (km)	$\psi$	SE
TNP to LMNP	45	0	0
TNP to LGCA	0	0.024	0.005
TNP to MGCA	34	0	0
TNP to MRC	5	0.011	0.003
LMNP to TNP	45	0	0
LMNP to LGCA	46	0	0
LMNP to MGCA	17	0	0
LMNP to MRC	19	0.013	0.006
LGCA to TNP	0	0.032	0.010
LGCA to LMNP	46	0	0
LGCA to MGCA	39	0	0
LGCA to MRC	10	0.020	0.009
MGCA to TNP	34	0	0
MGCA to LMNP	17	0.006	0.007
MGCA to LGCA	39	0	0
MGCA to MRC	13	0.014	0.010
MRC to TNP	5	0.032	0.006
MRC to LMNP	19	0.005	0.002
MRC to LGCA	10	0.008	0.003
MRC to MGCA	13	0.004	0.003

Subunits are: *TNP* Tarangire NP, *LMNP* Lake Manyara NP, *LGCA* Lolkisale GCA, *MGCA* Mtowambu GCA, *MRC* Manyara Ranch

by increasing and decreasing each parameter by 10% and recording the resultant proportional change in metapopulation asymptotic growth rate (Caswell 2001). We performed matrix model calculations in R using the popbio package (R Core Development Team 2013), and PopTools (Hood 2010).

**Fig. 2** Life-cycle graph of female giraffes with five life stages used to create matrix population models with demographic rates: fecundity ( $F$ ), calf survival ( $S_1$ ), subadult survival ( $S_{2-4}$ ), and adult survival ( $S_A$ )

## Results

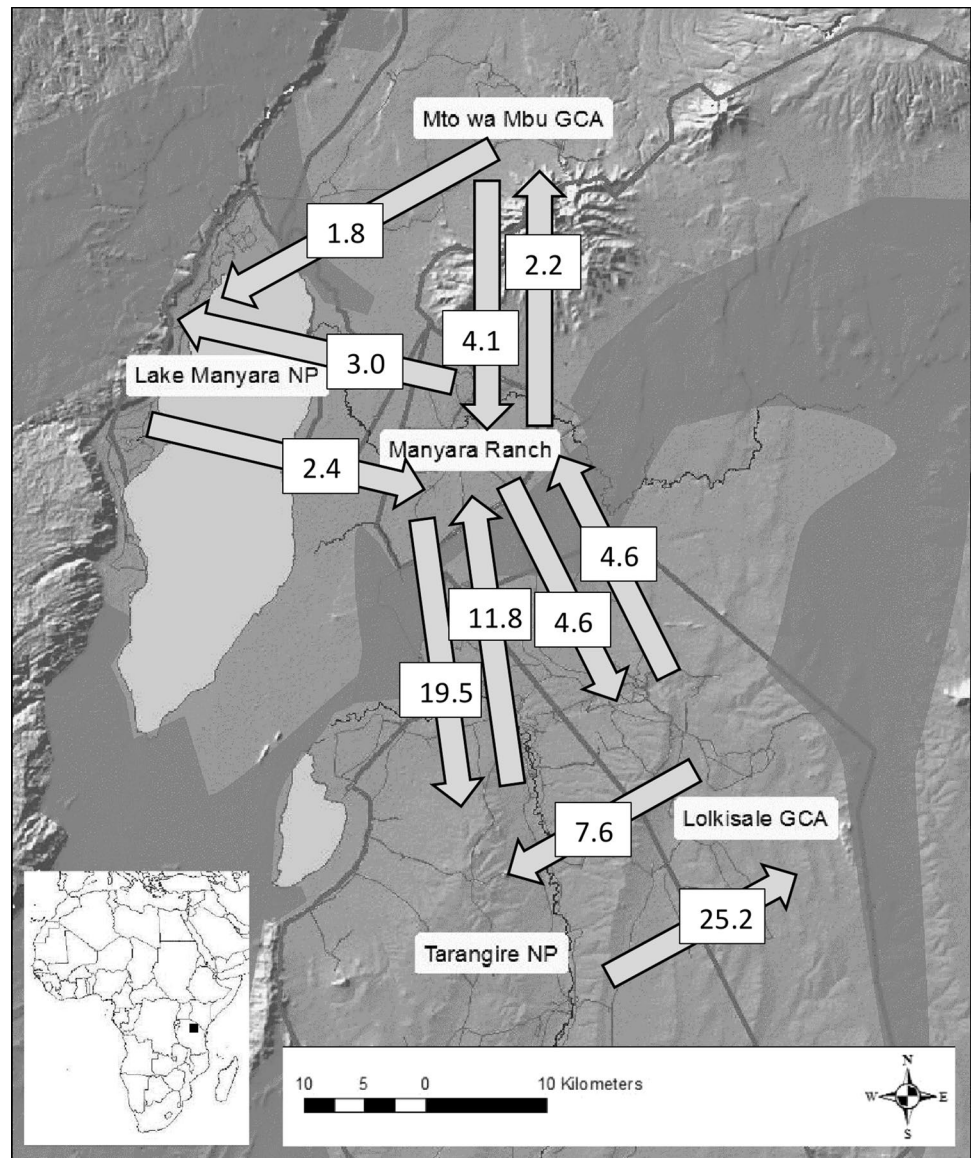
We observed and analyzed encounter histories for 1094 individually identified female giraffes. By the end of the second year of the study nearly all animals available for capture had been detected, with very few new adult individuals identified during subsequent surveys.

## Population size, density, and growth rate

The total estimated adult female metapopulation size in the study area was 790. The largest subpopulation was in TNP, followed by MRC (Table 1). Density varied among subpopulations, with the highest density in MRC, followed by LMNP (Table 1).

The Pradel model that included subpopulation-specific population growth rates ( $Pradel \lambda$ ) was more parsimonious than the model with constant growth rate among subpopulations (Table S1 in ESM), providing strong evidence for significant variation in subpopulation growth rates, although most of the among sub-population variation in  $Pradel \lambda$  was due to a very low growth rate in MGCA (Table 1). Subpopulation asymptotic growth rates from

**Fig. 3** Annual flow of individual adult female giraffes among 5 sites in the Tarangire Ecosystem, Tanzania from 2012 to 2014. Calculated from per capita movement rates ( $\psi$ ) and current population size ( $N$ ) in the origin site



matrix population models ( $MPM \lambda$ ) also indicated variation among subpopulation growth rates (Table 1).

### Movement among subpopulations

Movement data indicated no subpopulation was completely isolated, but movement probabilities were low, and varied among subpopulations, with some pairs of subpopulations having no movements between them (Table 2). Average seasonal movement probability among all subpopulations was 0.008 (SE 0.002; range 0.0–0.032). We found no evidence for differences in movement rates among age classes (ESM S2). Covariate models found movement probabilities were significantly

negatively correlated with distance between pairs of subpopulations [ $\beta = -0.120$ ,  $SE = 0.015$ , 95% CI  $(-0.149, -0.0919)$ ]. However, the site-specific movement model was far superior to all other covariate models (Table S1 in ESM), so movement estimates from this site-specific model were used in subsequent analyses (Table 2).

Based on calculated annual flow of adult female individuals (Fig. 3), three subpopulations were net exporters with more emigrants than immigrants (TNP = -9.9; MRC = -6.4; and MGCA = -3.7), while two subpopulations received more individuals as immigrants than they emitted as emigrants (LGCA = 17.6; LMNP = 0.6). We observed fewer movements in and out of MGCA and LMNP, relative to the other subpopulations.

**Table 3** Elasticities from current conditions matrix metapopulation model

Subpopulations	$\Theta_1$	$\Theta_2$	$\Theta_3$	$\Theta_4$	$\Theta_A$	$F_A$
TNP	0.002	0.002	0.002	0.002	<b>0.039</b>	0.002
LMNP	0.020	0.021	0.021	0.021	<b>0.702</b>	0.020
LGCA	<0.001	<0.001	<0.001	<0.001	0.006	0.001
MGCA	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
MRC	0.008	0.007	0.007	0.006	<b>0.071</b>	0.009
Movements	$M_{\text{juv}}$	$M_A$				
TNP to LMNP	0	0				
TNP to LGCA	0.0004	0.0018				
TNP to MGCA	0	0				
TNP to MRC	0.0006	<b>0.0032</b>				
LMNP to TNP	0	0				
LMNP to LGCA	0	0				
LMNP to MGCA	0	0				
LMNP to MRC	0.0007	<b>0.0067</b>				
LGCA to TNP	0.0002	0.0007				
LGCA to LMNP	0	0				
LGCA to MGCA	0	0				
LGCA to MRC	0.0004	0.0016				
MGCA to TNP	0	0				
MGCA to LMNP	0.0001	0.0001				
MGCA to LGCA	0	0				
MGCA to MRC	<0.0001	0.0001				
MRC to TNP	0.0015	<b>0.0036</b>				
MRC to LMNP	<b>0.0021</b>	<b>0.0051</b>				
MRC to LGCA	0.0002	0.0005				
MRC to MGCA	0.0001	0.0002				

Bold numbers indicate which cell's parameter variation had the greatest proportional effect on variation in metapopulation growth rate.  $M_{\text{juv}}$  is the sum of elasticities for  $M_1 - M_4$

### Classifying sources and sinks

Measures of subpopulation contributions to the metapopulation ( $C^i$ ) indicated that TNP, LMNP, and MRC were 'sources' with MRC having the highest per capita contribution to metapopulation growth, while LGCA and MGCA were 'sinks' (Table 1). The subpopulation that made the greatest relative contribution to metapopulation growth ( $\hat{c}^i$ ) was TNP, followed by MRC (Table 1). Despite its per capita source designation from  $C^i$ , LMNP made only a small contribution to the metapopulation due to its small size and low connectivity. There was a small contribution of individuals immigrating from outside the metapopulation ( $\hat{c}^0$ ; Table 1). The asymptotic growth rate of the matrix metapopulation model was 0.941, and the  $\lambda^M$  was 1.015.

### Population projection and perturbation analyses

Elasticities of cell values from the matrix metapopulation model indicated variation in metapopulation growth rate

**Table 4** Elasticities from perturbation analysis of survival ( $S$ ), reproduction ( $c/AF$ ), and movement ( $\psi$ ) parameters used to compute cell values in the matrix metapopulation model

Subpopulations	$S_{\text{juv}}$	$S_A$	$\psi_{\text{juv}}$	$\psi_A$	$c/AF$
TNP	0.010	<b>0.105</b>	<0.001	0.001	0.002
LMNP	0.079	<b>0.389</b>	0.003	0.021	0.020
LGCA	0.003	0.021	0.001	0.002	0.001
MGCA	<0.001	0.001	<0.001	<0.001	<0.001
MRC	0.035	<b>0.106</b>	0.001	0.003	0.009

Bold numbers indicate which parameter's variation had the greatest proportional effect on variation in metapopulation growth rate.  $S_{\text{juv}}$  is the elasticity for synchronous perturbation of  $S_1 - S_4$ ,  $\psi_{\text{juv}}$  is the sum of elasticities for synchronous perturbation of  $\psi_1 - \psi_4$

was the most sensitive to variation in adult female promotion rate ( $\Theta_A^i$ ) in the three subpopulations classified as sources by  $C^i$  (Table 3). The migration rates ( $M_j^{id}$ ) with the highest elasticities were those of adults among the three



source subpopulations, and juveniles from MRC to LMNP (Table 3). The next highest elasticity migration rates were adults moving from TNP to MRC and to LGCA (Table 3).

Perturbation analysis of survival, reproduction, and movement probabilities found variation in  $S_A$  in LMNP, MRC, and TNP subpopulations made the greatest contributions to variation in metapopulation growth rate (Table 4). Perturbation analysis also indicated variation in  $S_{juv}$  in LMNP and MRC,  $S_A$  in LGCA, and  $\psi_A$  and  $c/AF$  from LMNP and MRC made important contributions to variation in metapopulation growth rate (Table 4).

## Discussion

Spatially structured populations require specialized tools for analysis to determine the influence that different subpopulations and demographic or movement rates have on metapopulation growth rate (Griffin and Mills 2009; Ozgul et al. 2009). This study provided an example of using multiple analytic approaches applied to readily obtainable demographic and movement data to improve our understanding of the dynamics of a spatially structured population and help prioritize population components for conservation. We found significantly different population densities and population growth rates among subpopulations defined by land management, along with significant variation in per capita movement rates among subpopulations. Our result showing significant variation in population growth rates among subpopulations supports previous work demonstrating how landscape heterogeneity can lead to spatially structured populations via variation in demography (Naranjo and Bodmer 2007; Constanti et al. 2013; Lee et al. 2016).

We provided what we believe are the first estimates of per capita movement rates for giraffes among subpopulations. Movement rates such as these are critical for quantifying landscape connectivity (Merriam 1991) and for theoretical models of animal movements (Fahrig and Paloheimo 1988). Our source–sink analysis found that in this giraffe metapopulation, subpopulations with higher wildlife protection efforts and fewer anthropogenic impacts made the greatest per capita contributions to the metapopulation, and were thus classified as ‘sources’. The prospective perturbation analyses of our spatially structured matrix metapopulation model indicated that variation in adult female survival in source subpopulations and movements of adult females among source subpopulations made the greatest contributions to variation in metapopulation growth rate, reiterating their importance to the metapopulation persistence. Our calculated  $\lambda^M$  and the asymptotic growth rate of our matrix metapopulation model differed as to whether the metapopulation was growing or shrinking, but based upon long-term population index data from aerial surveys, we

believe the metapopulation is most likely decreasing (Lee and Bond 2016), although the metapopulation growth rate could also vary annually.

Our source–sink analyses indicated that antipoaching efforts and the exclusion of human settlements and agriculture may be critical determinants of giraffe subpopulation fitness in this system. MRC experiences large numbers of livestock grazing there daily, but no permanent settlement or agriculture, both features that are present in GCAs but not NPs. Thus, high density of livestock alone is not likely the cause of a subpopulation being classified as a sink. Spatial variation in soil fertility, and resultant vegetation nutritional content, could also be an important determinant of subpopulation fitness (Bond et al. 2016). Dispersal movements out of MRC and TNP likely prevent local extinctions within GCA subpopulations, but may be detrimental to the probability of metapopulation persistence due to the excessive mortality of adult females in GCAs (Lee et al. 2016). Illegal hunting of giraffes for bushmeat is common in GCAs (Kiffner et al. 2015), and poaching may have caused the sink designations for MGCA and LGCA. Furthermore, the flow of females into the GCAs may be an ‘ecological trap’ (Robertson and Hutto 2006). Reducing all connectivity movements to zero, as could happen with further development and fragmentation in the landscape (Morrison et al. 2016), or through fencing as a management action to reduce human-wildlife conflict, might create more stable MRC and TNP subpopulations, but would likely result in GCA subpopulations becoming extinct and would also leave the remaining subpopulations isolated and vulnerable to stochastic events. Loss of connectivity would also eliminate the significant contributions sink subpopulations make to metapopulation size and longevity (Howe et al. 1991).

The current dominant engines of metapopulation growth in this system were clearly TNP and MRC. The size and productivity of these subpopulations appear to maintain the metapopulation as a whole. A popular tenet of population dynamics is that connectivity among subpopulations influences persistence (Gilpin and Hanski 1991; Hess 1996) via compensatory immigration (Turgeon and Kramer 2012), or the ‘rescue effect’, where immigration averts a subpopulation’s extinction (Brown and Kodric-Brown 1977; Stacey and Taper 1992). Our results highlight the importance of connectivity among subpopulations of giraffes in the TE for maintaining viability of all subpopulations, particularly the vital role of TNP and MRC in sustaining the two GCA subpopulations, but indicate that the GCAs may be functioning as an ecological trap or ‘attractive sink’ that depletes even the source populations (Delibes et al. 2001). Movements into attractive sinks could result from individuals having incomplete knowledge of the fitness consequences of moving into the sink habitats where poaching or other adverse human influences are prevalent, resulting in significant

subpopulation declines even in the effectively protected source subpopulations in TNP and MRC (Woodroffe and Ginsberg 1998; Gunderson et al. 2001). Continued monitoring will reveal whether increased antipoaching efforts in LGCA initiated in 2014 ameliorate low local adult female survival there and convert the subpopulation from a sink to a source.

Lake Manyara National Park (LMNP) had a relatively high density of giraffes and was classified as a source, but due to its low abundance and near isolation, there were very few individual movements into or out of that park. LMNP is naturally somewhat isolated from the rest of the ecosystem by the Rift Valley Escarpment on the west, and on the east by Lake Manyara, which forms a barrier in the wet season and a > 10 km-wide muddy or alkali plain in the dry season that is devoid of woody browse (Fig. 1). Given the rapid expansion of the town of Mtwambu, and the intensive agricultural zones northeast and south of LMNP, habitat fragmentation likely negatively affected movement probabilities and has rendered the LMNP subpopulation almost completely isolated (Msoffe et al. 2011). Morrison and Bolger (2012) found similar low connectivity for the LMNP wildebeest (*Connochaetes taurinus*) population. The near-complete isolation of this otherwise healthy subpopulation suggest the need for immediate conservation measures to protect existing or re-establish historical movement pathways for giraffes between LMNP and other subpopulations. However, the fact that some movements did cross the widest expanse of matrix with no woody vegetation and the most intensive agriculture in the study area indicates that giraffes are able to cross seemingly inhospitable matrix areas between subpopulations.

We found significant differences in density among subpopulations, which could indicate differences in habitat quality, typically explained by variation in food quality or predation pressure (Fryxell 1991; Brown and Kotler 2004), or a combination of both. Subpopulation-specific density was not correlated with subpopulation growth rates or movements, suggesting that this system is likely below carrying capacity because density-dependent effects in ungulates often arise only when a population is near carrying capacity (Bonenfant et al. 2009). The African elephant (*Loxodonta africana*) population in TNP has grown rapidly and steadily during the past decade with no evidence of density dependence, suggesting there is likely no local scarcity of megaherbivore forage resources (Foley and Faust 2010).

It is possible that some of the movements we observed were regular movements of individuals whose home range straddled two subpopulations. This is most likely between LGCA and TNP because these sites are adjacent and share a long border, and TNP and MRC because they are relatively close to each other. Seasonal shifts in use patterns

also could explain the nearly balanced flow between pairs of subpopulations. However, we clearly documented some net movement among subpopulations, and even seasonal movements may impart fitness benefits mediated by the need to access critical resources (Pulliam and Danielson 1991; Rodenhouse et al. 1997).

Our data represent one of the largest individual-based demographic studies of a wild, free-roaming, large mammal ever conducted, both in terms of number of animals identified and geographic scope. Large-scale, individual-based studies such as ours provide critical data for understanding population and metapopulation dynamics, and many important questions in ecology and evolution can only be addressed with this type of data (Clutton-Brock and Sheldon 2010). The only other demographic assessment of giraffes using modern methods was done completely within the protected area of Serengeti National Park (Strauss et al. 2015), and the authors also indicated poaching was the main driver of giraffe population growth rates. Additional analyses with longer-term data would illuminate the stability of our observed patterns, particularly whether changes in subpopulation population growth rates, densities, or survival affect movement patterns. A finer-scale investigation of giraffe social units and demographic variation among these, more biologically based population units would also be useful and may illuminate the most relevant spatial scale for future subpopulation analyses (Sutherland et al. 2012). A deeper investigation of natal dispersal patterns also is forthcoming and will add to our understanding of connectivity in this landscape (Driscoll 2007).

### Conservation implications

Recent studies have sought to evaluate the effectiveness of East African protected areas (Stoner et al. 2007; Western et al. 2009) by comparing temporal trends in ungulate density in national parks to adjacent areas with less protection. Our data illustrate that measures of density alone may be insufficient to assess the efficacy and importance of protected areas. The density of giraffes in TNP was similar to that within two of the GCAs, yet our more detailed studies of demography and movement revealed that in fact TNP is one of the demographic keystones of the system, while the GCAs are less critical. We encourage other researchers to embrace the framework and methods we described here for prioritizing subpopulations for conservation and management actions. In particular, the spatially structured matrix metapopulation models provide an invaluable framework for guiding monitoring efforts, understanding threats and how they interact, devising interventions to address threats, and informing policy makers and managers about the consequences of different courses of action (Balmford and Cowling 2006).

**Acknowledgements** This research was carried out with permission from the Tanzania Commission for Science and Technology (COSTECH), Tanzania National Parks (TANAPA), the Tanzania Wildlife Research Institute (TAWIRI), African Wildlife Foundation, Manyara Ranch Conservancy, and the villages of Selela, Lolkisale, and Emboret, under COSTECH permits 2011-106-NA-90-172, 2012-175-ER-90-172, and 2013-103-ER-90-172. I am extremely grateful to these organizations for the opportunity to conduct this research, especially J. Keyyu, V. Kakenge, A. Mwakatobe, and K. Oola at TAWIRI; F. Olekashe at Manyara Ranch Conservancy, J. Salehe at African Wildlife Foundation, and I.A. Lejora, D. Njau, S. Quolli from TANAPA. M. Bond assisted with data collection and processing. Financial support for this work was provided by Dartmouth College Graduate Studies, Fulbright U.S. Scholar Program, Sacramento Zoo, Safari West, Columbus Zoo, Cincinnati Zoo, Dartmouth College Cramer Fund, and the Explorer's Club.

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