

CHAPTER 2.

SOURCE-SINK DYNAMICS AMONG SUB-POPULATIONS OF GIRAFFE

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

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

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

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

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

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

The sub-population sites represented a variety of human land uses. Two national parks (Tarangire and Lake Manyara) had strong wildlife protections, anti-poaching efforts, and no legal human encroachment. A private cattle ranch/wildlife conservancy (Manyara Ranch) had livestock grazing and tourism, some human habitation, and anti-poaching patrols. Two Game Controlled Areas (Mtowambu and Lolkisale) had agricultural cultivation, pastoralism, and permanent settlement, little or no anti-poaching efforts, and wildlife harvesting via subsistence and trophy hunting, although hunting of giraffe was legally prohibited (Nelson et al. 2010).

Methods

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

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

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

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

PARAMETER MODELLING AND ESTIMATION

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

therefore we constrained temporal aspects of some models. In all modeling of survival probabilities, transition probabilities, and lambda, we only considered models where geographic site was relevant, and included no temporal effects. In the Pradel models, we allowed capture and recapture probabilities and population sizes to vary by site as well as temporally, but we ranked models with simplified temporal structure in these parameters as the first stage in model selection. In the MSORD models, we did not include any temporal structure, so all parameters were modeled only as site and constant effects. We fixed some transition probabilities (*Psi*) at zero because there were no observed movements between these site pairs.

We tested goodness-of-fit using U-CARE (Choquet et al. 2009), and adjusted for lack of fit by adjusting $\hat{c} = \chi^2/df$ (Choquet et al. 2009, Cooch and White, *unpublished*). Throughout model ranking and selection procedures, we ranked models using qAICc and used model qAICc Weights (*W*) as a metric for strength of evidence supporting a given model as the best description of the data (Burnham and Anderson 2002). In the Pradel *lambda* and *N* modeling, we began with the most fully parameterized model in our set with constraints (site effects) on the main parameters of interest, but with both temporal and site effects in capture (*p*) and recapture (*c*) rates. We first ranked competing models with reduced temporal complexity of detectability parameters (*p* and *c*). Once the most parsimonious form of detectability parameters was obtained, we ranked all possible combinations of models of site and constant effects in the parameters of interest (*lambda*, *N*). In the MSORD models, we began with the most fully parameterized model in our set (site effects in all parameters), then ranked all possible combinations of site and constant effects in *S*, *Phi*, and *p*. We then ranked the competing models of *Psi*.

SPATIAL COVARIATES

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

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

CALCULATING FLOW OF INDIVIDUALS

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

CLASSIFYING SOURCES AND SINKS

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

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

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

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

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

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

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

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

$$\hat{c}^s = \frac{(N^s * S_A^s) + (N^s * \sum \psi^{s-k})}{N^M}, \quad (4)$$

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

$$\hat{c}^0 = 1 - \sum_{s=1}^k \hat{c}^s, \quad (5)$$

POPULATION PROJECTION MODELS

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

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

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

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

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

all matrix cells using the stored output. To identify the movement rates with the greatest effect on metapopulation λ , we used AICc to rank all possible subsets regressions of λ against of transition parameters up to a maximum of 10 terms per regression.

Results

We analyzed encounter histories for 907 adult female, and 542 adult male, individually identified giraffe. We found evidence for lack of fit in the Pradel model ($\chi^2_{270} = 446$, $P < 0.001$), and in the MSORD model ($\chi^2_{172} = 293$, $P < 0.001$), so to account for model selection uncertainties we adjusted $\hat{c} = 1.65$ in Pradel models, and $\hat{c} = 1.70$ in MSORD models.

Model selection indicated that there was a single top-ranked model in each set that performed much better at describing the data than any other model in the sets (Tables 7 and 8). Therefore, we used the top model from each analysis to estimate population parameters. The top model from the Pradel model selection included the *Distance to Mtowambu* effect in λ (Table 7), and *site* plus *time* effects in capture and recapture. The top-ranked model in MSORD model selection included *constant* entry, and *site* effects in movements, residence, and capture. There was little or no evidence that *management* was a good predictor of λ , or movement (Tables 7 and 8).

POPULATION SIZE, DENSITY, AND GROWTH RATE

The total estimated population size for adult females in the study area was 790, and for males 435 (Table 9). The largest sub-population was in TNP, followed by MRC. Density varied significantly among sites for both sexes (Fig. 5), with the highest density in MRC relative to all other sites.

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

SURVIVAL

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

MOVEMENT AMONG GEOGRAPHIC SITES

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

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

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

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

CLASSIFYING SOURCES AND SINKS

Metapopulation growth rate $\lambda^M = 0.996$, indicating a decreasing overall population trend. Parameters calculated to identify source and sink sub-populations indicated that TNP and LGCA were sources, while LMNP, MRC, and MGCA were sinks (Table 12). This result was confirmed by Pradel estimates of sub-population-specific λ as well as calculated average relative contribution of local population s to growth of the metapopulation (C^s ; Runge et al. 2006). TNP was the dominant source of population growth in this metapopulation, followed by MRC, and there was negligible contribution of individuals immigrating from outside the metapopulation (Table 12).

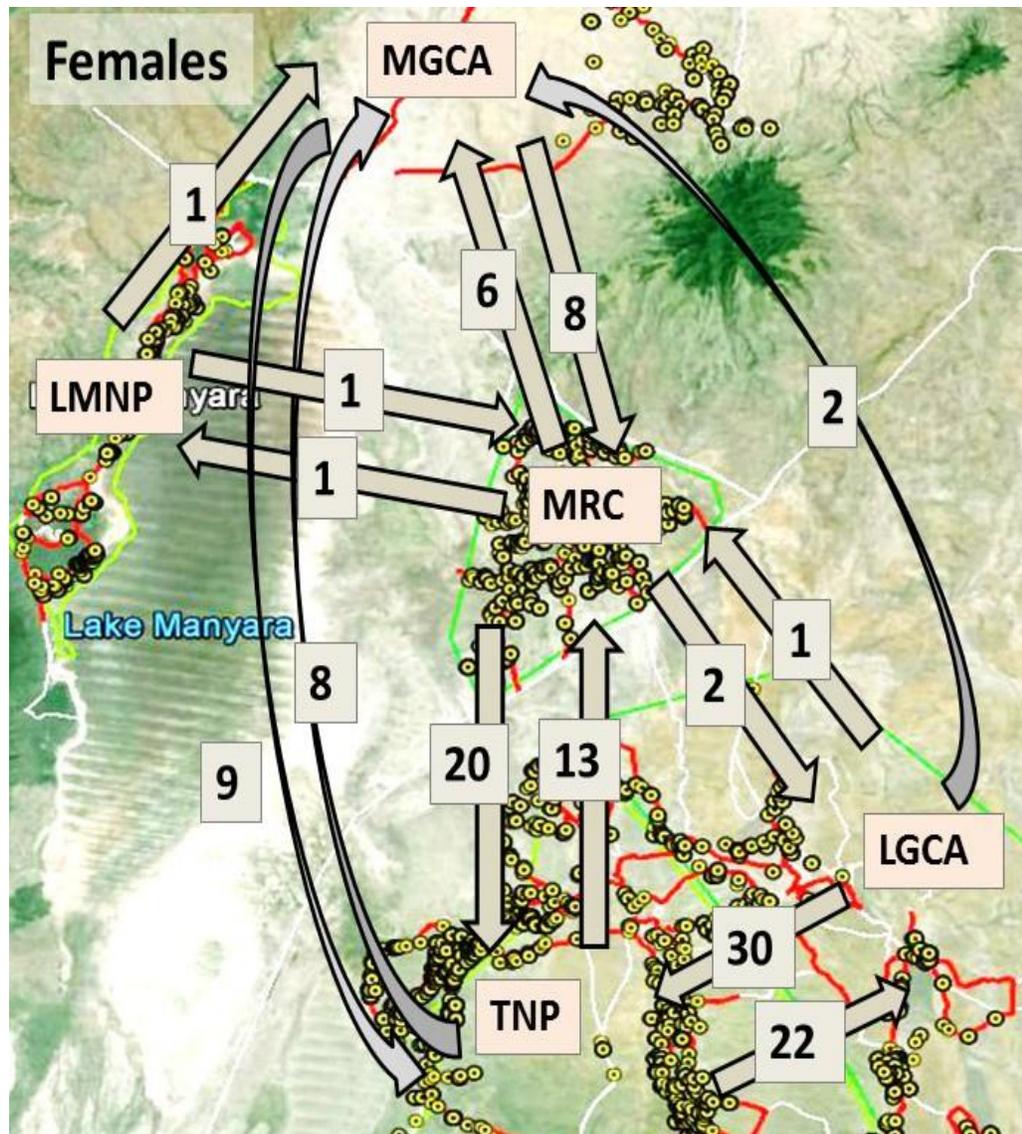


Figure 10. Annual flow of individual adult female giraffe among 5 sites in the Tarangire Ecosystem, Tanzania from 2012–2014. Calculated from per-capita movement rates and current population size in the origin site.

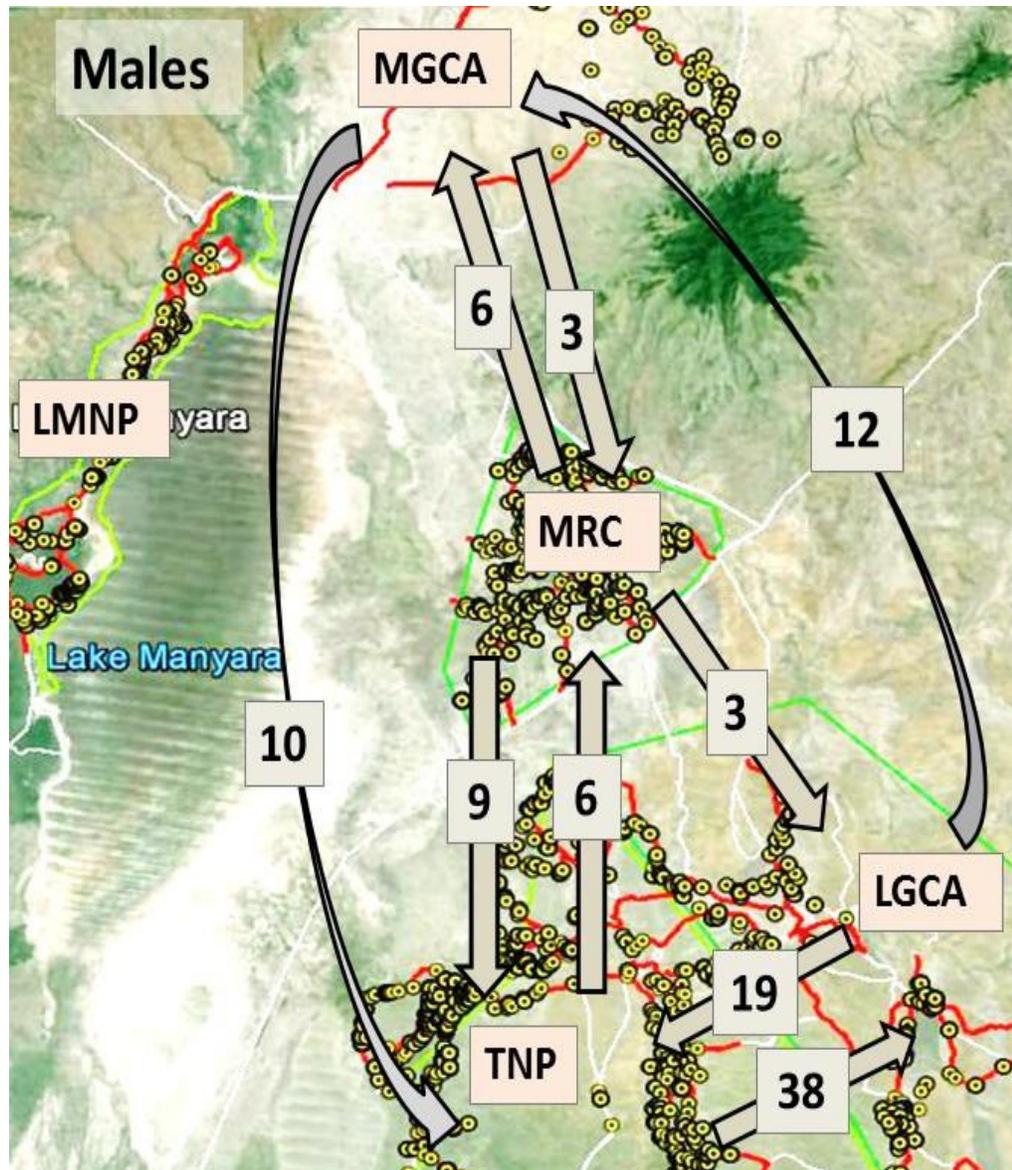


Figure 11. Annual flow of individual adult male giraffe among 5 sites in the Tarangire Ecosystem, Tanzania from 2012–2014. Calculated from per-capita movement rates and current population size in the origin site.

POPULATION PROJECTION AND ELASTICITIES

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

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

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

Discussion

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

extinct and leave the sole remaining sub-population susceptible to stochastic events, such as disease outbreak, that could extirpate the population.

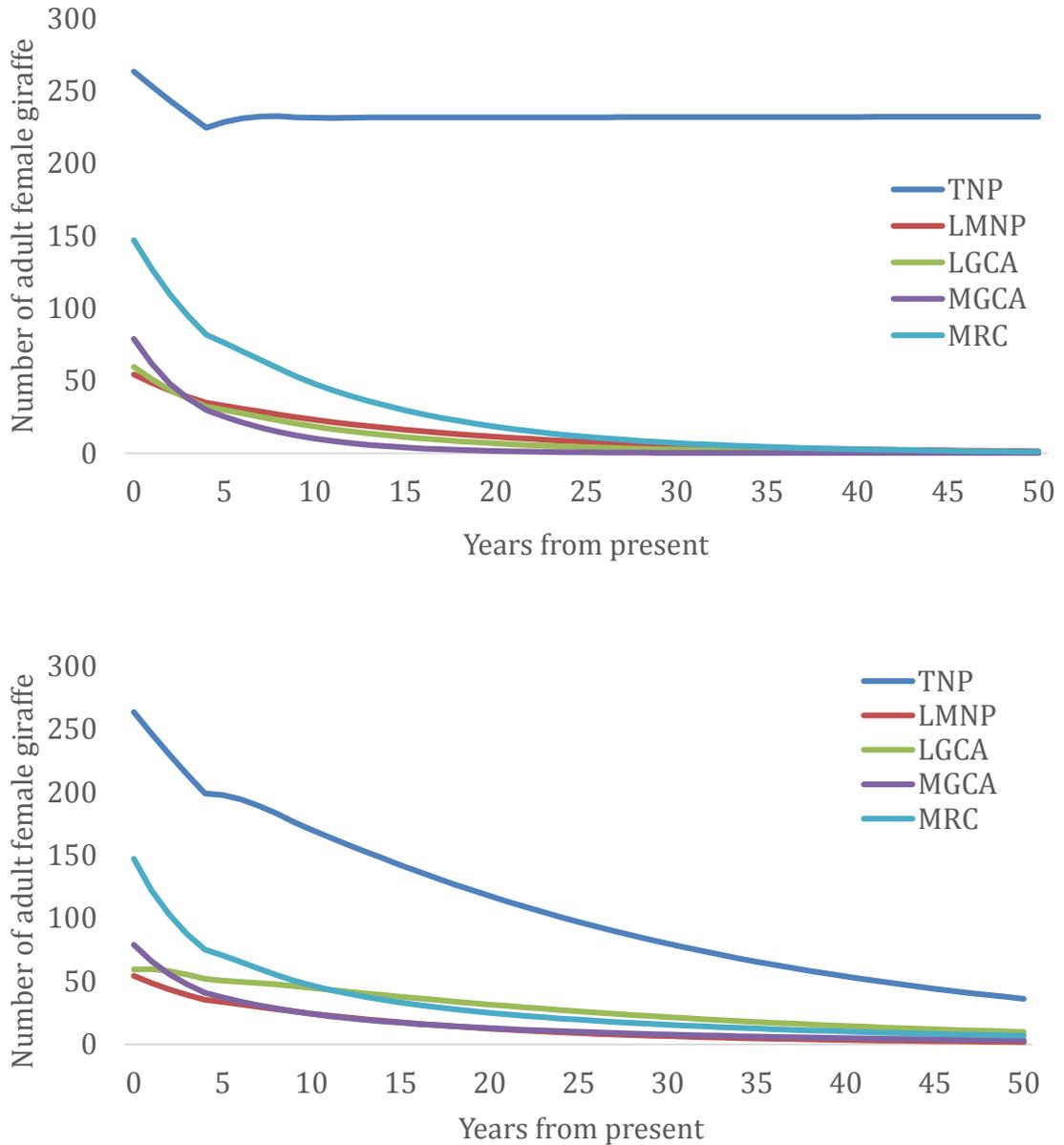


Figure 12. Graphs showing Tarangire adult female giraffe population projections for 50 years from present using multi-site matrix models with no movement (top) and with current among-site movement rates (bottom).

POPULATION GROWTH RATES AND MOVEMENT PROBABILITIES

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

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

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

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

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

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

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

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

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

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

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

population parameters including density, abundance, movements, and *lambda* are extremely useful for efficient monitoring and management of wildlife populations (Yoccoz et al. 2001, Nichols and Williams 2006, Peters 2010, Contasti et al. 2013).

Tables

Table 7. Model selection results for lambda parameters from 2012–2014 in the Tarangire Ecosystem, Tanzania.

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

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

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

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

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

Table 9. Estimates of sex-specific sub-population size (N), and density (N/km^2) for adult Masai giraffe in 5 sub-units of the Tarangire Ecosystem, Tanzania 2012–2014.

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

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

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

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

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

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

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

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

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

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

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