

CONCLUSIONS

I found that my study area in the Tarangire Ecosystem was a spatially structured metapopulation of giraffe with significant variation in adult survival, reproduction, density, and lambda among sub-populations. Spatial covariate models for adult female survival and reverse-time lambda indicated that covariates associated with poaching explained some of this spatial variation. I found site-specific density was not correlated with lambda, movements, adult survival, calf survival, or reproduction, indicating that this system is likely below carrying capacity; density-dependent effects in ungulates often arise only when a population is near carrying capacity (Bonenfant et al. 2009).

The dominant paradigm for ungulate population dynamics over time holds that adult female survival has the highest elasticity, but its low variation causes it to contribute relatively little to changes in the population growth rate compared to juvenile survival or reproduction, which have low elasticities but high temporal variation, making them the primary determinant of realized population change (Gaillard et al. 1998, 2000, Gaillard and Yoccoz 2003, Raithel et al. 2007). I found that spatial variation of demographic estimates from generally stable giraffe populations in National Parks across the continental range of the species did follow the temporal demographic paradigm. In contrast, in the fragmented TE region I found adult female survival was highly spatially variable and significantly correlated with population growth rate. My data support other studies on long-lived species that documented population declines associated with decreases in adult survival (Wehausen 1996, Flint et al. 2000, Rubin et al. 2002, Pistorius et al. 2004, Wittmer et al. 2005, Nilsen et al. 2009, Johnson et al. 2010).

Multiple analyses pointed to TNP as the engine of this metapopulation, with movements among sites maintaining linkage among all sub-populations. Those movements had important implications for the future of this metapopulation and its management. The rescue effect of TNP insulates all sub-populations from short-term extinctions, but would eventually result in a metapopulation crash as the sink sub-populations deplete the source. At the same time, having multiple linked sub-populations increases the resilience of the metapopulation to stochastic catastrophes by hedging extinction risk among multiple sub-populations. The loss of all linkage movements could grow the metapopulation over the medium term, but would create effectively a single population in TNP that holds the only giraffe in the landscape.

Based on my results, for conservation of the species and the large-scale processes of giraffe interactions across the landscape, I recommend efforts to reduce poaching and disrupt bushmeat markets to bring down harvest rates of adult females to sustainable levels, while simultaneously maintaining or improving linkage habitat between all sites to facilitate natural movements. This should increase adult survival to the point where sink sub-populations are less of a drain on the metapopulation, and having multiple linked, healthy sub-populations reduces the risk of total extinction. Identifying source and sink habitats using PCMR methods is far superior to monitoring via abundance or density estimates because when managers understand movements and population growth rates, they can effectively prioritize actions to ensure the security of sources while addressing the causes of sinks (McCoy et al. 1999, Schwartz et al 2010).

Conservation of the Masai giraffe in the Tarangire Ecosystem will likely require the cooperation of all stakeholders from Wildlife Division (who conduct anti-poaching patrols on Game Controlled Areas), National Parks, private landowners, and village leadership, to enhance population growth rates in MGCA and MRC and maintain or enhance habitat connectivity throughout this fragmented landscape. Anti-poaching strategies employed by Tarangire and Lake Manyara national parks appear to be effective in protecting adult female giraffe at these sites, and this model could be expanded to areas outside the parks. Giraffe are important to savanna ecosystems because the presence of browsers benefit *Acacia* growth and survival (*sensu* Palmer et al. 2008), and maintaining landscape connectivity for giraffe, a non-migratory, charismatic, keystone and flagship species, would also benefit threatened migratory species and preserve ecosystem integrity and functions (Crooks and Sanjayan 2006, Morrison and Bolger 2014).

I found evidence that this population of giraffe exhibited 2 seasonal pulses in reproduction, one during the short rains and another during the dry season. Calves born during the reproductive pulse in the short rains have higher survival probability relative to calves born in other seasons. This positive correlation between seasonal births and juvenile survival supports the “phenological match” theory of reproductive synchrony, with the season of highest survival occurring when protein content was highest for non-*Acacia* woody browse species. Calves born during the second birth pulse in the dry season had equivalent survival to calves born during the long rains, which is the signal for “temporal resource partitioning” theory of asynchrony. I also found seasonal calf survival was positively correlated with local density of wildebeest, zebra, and buffalo

during post-natal seasons. The seasonal availability of alternative prey can modulate the predation experienced by giraffe via the predator's behavior (Holt 1977, Holt and Lawton 1994). The positive survival effect of local ungulate density on giraffe calf survival could be due to predator swamping through dilution or prey switching (Estes 1976, Sekulic 1978, Estes and Estes 1979, Testa 2002). Therefore, it is conceivable that if wildebeest, zebra, and buffalo populations crash as a result of disrupted migrations, then giraffe calves might face increased predation pressure from local lions and hyenas responding to reduced availability of large ungulate biomass. Asynchrony is believed to be the ancestral state of all ungulates (Zerbe et al. 2012), and this investigation has illustrated how seasonal variation in vegetation quality and predation pressure may both play a role in the evolution of synchronous births.

The unique detail and landscape-level perspective offered by this extensive set of photographic capture-mark-recapture data from >1,800 individual giraffe illustrated the spatial complexity of tropical large-mammal demographics at the scale of one order of magnitude greater than the mean individual home range of giraffe (1,000 km² study area vs. 100 km² mean female home range). Precisely and efficiently estimating sub-population sizes, adult survival, calf survival, reproduction, and movement probabilities made this detailed spatial and temporal demographic analysis possible and provided detailed insight into sub-population and metapopulation dynamics in this fragmented ecosystem.