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RESEARCH ARTICLE

Demographic drivers of population dynamics reveal subpopulation-specific conservation needs for giraffes in the Serengeti Ecosystem

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Abstract

Survival, reproduction, and movement are the key demographic parameters that drive population dynamics. Factors affecting these demographic parameters in large, long-lived, extinction-threatened mammals are diverse and may differentially affect subpopulations in disparate parts of an ecosystem. We conducted annual photographic surveys to uniquely identify 1,520 giraffes at 4 subpopulations around the Serengeti Ecosystem in Tanzania to estimate demographic parameters of age- and sex-specific survival probabilities, reproduction, population densities, group sizes, and long-distance movements. In the Seronera (central) subpopulation, we combined 15 years of data from 3 independent survey schemes, developed a Bayesian hidden Markov model to estimate demographic parameters, and conducted a retrospective population analysis to elucidate the demographic drivers of temporal changes in population growth rate. We collected data over 4–5 years for 3 other subpopulations, and used frequentist methods to estimate demographic parameters. We compared our results with historical estimates from the 1970s and 2000s to examine long-term population trends and demographic drivers. We found significant differences in adult and subadult survival probabilities among subpopulations, with

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lower adult survival associated with declining subpopulations. Retrospective population analysis for the Seronera subpopulation reiterated that adult survival is a critical demographic driver of population dynamics for giraffes. The 2 subpopulations adjacent to the protected area boundary declined over 48 years, whereas the Seronera subpopulation stabilized since 2008. Only one individual moved between subpopulations, providing evidence for subpopulation insularity and potential genetic structuring of the overall population. These factors underscore the need for subpopulation-specific conservation strategies aimed at raising adult survival within the western and northeastern parts of the Serengeti Ecosystem. Community-based conservation efforts adjacent to protected areas have been effective in raising adult survival and density elsewhere. Our findings highlight the importance of understanding subpopulation dynamics and their demographic drivers for evidence-based conservation and management to recover endangered giraffe populations.

KEYWORDS

Bayesian hidden Markov model, demography, *Giraffa camelopardalis*, *Giraffa tippelskirchi*, multistate mark-recapture analysis, robust design

Estimating key demographic parameters like survival, reproduction, and movement is fundamental to wildlife population biology because demographic parameters mediate population dynamics and the evolution of life-history strategies (Mills 2013, Murray and Sandercock 2020). Quantifying demographic parameters over time and space is essential for management of wildlife because specific demographic drivers of population growth or decline can then be identified. This becomes particularly important for long-lived, slow-reproducing species with complex life histories (Bond et al. 2023*a*) that are highly vulnerable to population declines (Cardillo et al. 2005) and face significant conservation challenges (Muller et al. 2018). Especially useful for estimating demographic parameters are longitudinal live-encounter data from identifiable individuals and methods to account for imperfect detection, which provide parameter estimates that are relatively unbiased and precise compared to methods that do not account for imperfect detection (Lebreton et al. 1992, Nichols 1992). Long-term and individual-based demographic studies on multiple subpopulations are rare yet invaluable for pinpointing factors that mediate population dynamics, thus informing successful conservation and management of extinction-threatened species (Ripple et al. 2015, Lee et al. 2022).

The giraffe (*Giraffa* ssp.) is one of the world's few megaherbivore species—plant-eating mammals that can reach an adult mass >1,000 kg (Owen-Smith 1988). Giraffes live up to 30 years, produce a single calf after a 15-month gestation period (Bercovitch and Berry 2017), and have a 20-month interbirth interval (Lee et al. 2017). The slow life history of giraffes combined with their large space-use requirements (Knüsel et al. 2019) makes populations especially vulnerable to declines in adult survival and local extirpation (Carmona et al. 2021, Bond et al. 2023*a*). The Masai giraffe (*G. tippelskirchi*), the species found in southern Kenya and throughout Tanzania, declined by 40% over 3 decades to an estimated 35,000 individuals, was listed as endangered on the International Union for Conservation of Nature (IUCN) Red List in 2019 (Bolger et al. 2019), and was considered warranted for listing as threatened under the United States Endangered Species Act in 2024 (U.S. Fish and Wildlife Service 2024). Recent findings by Lohay et al. (2023) revealed that Masai giraffes east and west of the Gregory Rift Escarpments are genetically distinct, and there is significant population genetic structure and low gene flow among subpopulations in northern Tanzania (Brown et al. 2007, Lohay et al. 2023). This suggests that Masai giraffe subpopulations may be more at risk than previously believed and underscores the need for knowledge about subpopulation conservation status and the demographic drivers of their population dynamics.

The Serengeti Ecosystem of western Tanzania (Figure 1A) supports the largest population of Masai giraffes on Earth, hosting more than twice as many individuals as any other ecosystem throughout the species' range (Bolger et al. 2019). Two previous studies estimated population size and structure of 3 subpopulations of giraffes, Seronera (central), Kirawira (west), and Bologonja (northeast; Figure 1A, B), based on aerial counts and ground-based surveys (Pellow 1983, Strauss et al. 2015) and demographic parameters using photographic capture-mark-recapture (CMR) methods in Seronera (Pellew 1983, Strauss et al. 2015) and Kirawira (Strauss et al. 2015).

In the 1970s, herbivore populations—including giraffes, buffaloes (*Syncerus caffer*), and wildebeests (*Connochaetes taurinus*)—had recovered from the devastating rinderpest epidemics that began in the late 1800s and ended in the early 1960s. The increase in grazing herbivore numbers after release from rinderpest resulted in less late-season grass biomass, which reduced the annual area burned and led to tree and shrub regeneration that ultimately increased food supply for giraffes (Norton-Griffiths 1979, Sinclair 1979). Pellew (1983) considered the giraffe population of the 1970s to be expanding. Strauss et al. (2015) documented a 67–86% decline in giraffe densities in 2010 compared to 1975, a decrease in the proportion of younger individuals, a drop in adult and subadult survival probabilities in Seronera, and smaller group sizes. These demographic changes were attributed to poaching by humans and limited preferred forage from changes in woody vegetation communities, suggesting both top-down and bottom-up influences on population dynamics in giraffes (Strauss et al. 2015).

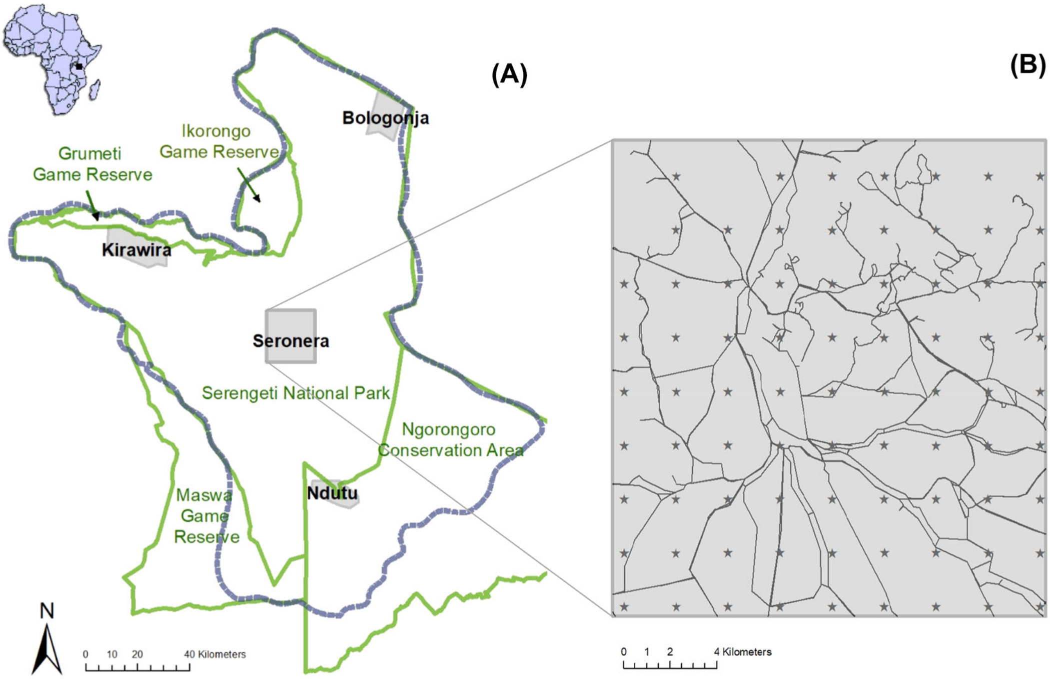

FIGURE 1 Western Masai giraffe study area in the Serengeti Ecosystem, Tanzania (blue dashed line); inset is location within Africa. Green polygons are protected areas. A) Four giraffe demography study sites in Seronera (central), Kirawira (west), Bologonja (northeast), and Ndutu (south). B) Seronera study site with active encounter survey roads (gray lines) and camera trap locations (gray stars).

Since 2010, the landscape of the Serengeti Ecosystem has continued to be transformed by human activities. A large expansion in the number of lodges and visitors (Larsen et al. 2020) and concomitant increases in roads have occurred, with associated impacts on water sources and vegetation. Increases in the human population along the protected area boundaries have also been observed (Larsen et al. 2020). Illegal hunting and poaching for bushmeat markets have been documented in the Serengeti (Masolele 2018), while wildlife law enforcement efforts in Tanzania have fluctuated because of broad-scale events such as global recessions, the COVID-19 pandemic, and government policy transitions (Kideghesho et al. 2021). Thus, human activities dynamically affect wildlife populations (Veldhuis et al. 2019) in addition to natural processes such as predation, climatic variation, and density dependence (*sensu* Lee et al. 2016*a*, *b*; Bond et al. 2021*a*, 2023*a*, *b*).

We analyzed a longitudinal, individual-based photographic CMR dataset (Foster 1966, Lee et al. 2022) to estimate current giraffe densities, demographic parameters, and group sizes in subpopulations in the western (Kirawira), northeastern (Bologonja), southern (Ndutu), and central (Seronera) areas of the Serengeti Ecosystem (Figure 1A), and examined 48-year trends using historical data from Pellew (1983) and Strauss et al. (2015). We quantified 15-year dynamics (2008–2023) and demographic parameters of the giraffe subpopulation in the central Serengeti (Seronera) and used retrospective population analysis that quantifies the temporal correlation between annual demographic rates and the annual subpopulation growth rate to identify the demographic drivers of observed population dynamics (Schaub et al. 2013, Schaub and Kéry 2022). We also determined geographic isolation of subpopulations by quantifying individual long-distance movements among the central, western, northeastern, and southern Serengeti subpopulations, all separated by >40 km.

STUDY AREA

Three study sites (Seronera, Kirawira, and Bologonja) were selected by Pellew (1983) to include vegetation types representative of Sinclair's (1972) woodland strata, and we added a fourth site (Ndutu) in the south (Figure 1A). Seronera (240 km^2) in the central Serengeti National Park is a woodland-grassland savanna dominated by umbrella thorn (*Vachellia tortilis*) and glossy-leaved corkwood (*Commiphora trothae*), with grassland plains in the southern portion of the site. Kirawira (210 km^2) is largely open grasslands with blackthorn (*Senegalia mellifera*) and woodland scrub thicket dominated by gum acacia (*S. senegal*) and splendid thorn (*V. robusta*) in the western corridor of the park, along the southern border of the Grumeti Game Reserve. Bologonja (175 km^2) in northeastern Serengeti is composed of grasslands and woodlands dominated by red thorn (*V. gerrardii*) and whistling thorn (*V. drepanolobium*) adjacent to the Masai Mara National Reserve in southern Kenya. Ndutu (113 km^2) is composed of umbrella thorn woodlands, marshes, short grasslands, and soda lakes in the southern Serengeti National Park and western Ngorongoro Conservation Area. Tourist presence is generally high year-round in Seronera (except for April, the rainiest month), seasonally high in Ndutu (December–March) during the birthing period for the populations of wildebeests, gazelles (*Nanger granti* and *Eudorcas thomsonii*), and plains zebras (*Equus quagga*), and seasonally high in Kirawira and Bologonja (July–November) corresponding to when the wildebeests are in those areas. Soil types underlying the woodlands differed in each of the 4 study sites (Figure S2, World Agroforestry Centre Geoscience Lab downloaded from http://landscapesportal.org/layers/geonode:tanzania_soil).

METHODS

In Seronera, we obtained data from active encounter surveys and from camera traps (Swanson et al. 2015) during 3 distinct but continuous time periods over 15 years (2008–2023; Table 1). We used a Bayesian approach in Seronera, as this enabled estimation of survival, reproduction, population density, and population growth rate while incorporating and accounting for multiple sources of variability and uncertainty inherent in jointly analyzing

TABLE 1 Study site and years of collection of photographic capture-mark-recapture (CMR) data for Masai giraffes in the Serengeti Ecosystem, Tanzania. The X indicates the number of surveys; x is a single survey and xx or xxx means 2 or 3 surveys conducted for robust design.

	Year of data collection														
	Active encounter surveys + aerial surveys with ground counts			Camera trapping surveys						Active encounter surveys					
Study site	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2018**	**2019**	**2020**	**2021**	**2022**	**2023**
Seronera (center)	xx	xx	xxx	xx	xx	xx	xx	xx	xx	xxx	xx	xx	xx	x	xx
Kirawira (west)	xxx	xxx	xxx								x		x		x
Bologonja (northeast)	x	x	x								x		x		x
Ndutu (south)										x	x		x		

datasets based on differing data collection methodologies, and propagating parameter uncertainty to the derived parameters (Kéry and Schaub 2012, Schaub and Kéry 2022). In Kirawira, Bologonja, and Ndutu, we collected data using active encounter surveys from 2018 to 2023 (Table 1) and compared derived parameters to those reported in previous studies. To replicate and facilitate comparisons with previous work reported in Pellew (1983) and Strauss et al. (2015), we used a frequentist approach (Cooch and White 2019) to generate subpopulation-specific demographic estimates of survival, reproduction, population density, and population growth rate.

Individual-based capture-mark-recapture data collection

The 4 study sites (Figure 1A) represented common Serengeti vegetation types from woodlands to grassland savannas. We collected giraffe identification photographs annually in October (the end of the annual dry season) using active encounter road transect surveys (2008–2010, 2018–2023) and camera traps (2011–2016), with consistent protocols for image quality and animal identification (Table 1). We used photographs of coat spot patterns for identification of giraffes because their patterns are individually unique and unchanging so their marks cannot be lost (Foster 1966). During active encounter surveys (2008–2010 and 2018–2023), we drove road transects and when giraffes were seen we slowly approached and photographed each animal's right side. For camera trap data (2011–2016), we used all sufficient-quality right-side images of giraffes.

In 2008, we initiated active encounter road transect surveys for giraffes within the same Seronera study site as Pellew (1983; Figure 1B) and conducted a full survey of the study site bi-weekly every October for the first 2 years, with a third survey conducted in the third year. Some roads were occasionally surveyed more than once, and we added those photographic data to the bi-weekly survey. In 2010, researchers from Snapshot Serengeti (Swanson et al. 2015) constructed an array of camera traps in the Seronera woodlands that overlapped the Pellew study site boundary (Figure 1B); Snapshot Serengeti provided us with giraffe photographs taken between 2011 until 2016 by cameras within the boundary, from which we sub-sampled the right-side October images and categorized them into either the first or last 2 weeks of the month. Starting in 2018 until 2023, we conducted 2 (but 2018 = 3 and 2022 = 1) consecutive active encounter road transect surveys of the Pellew study site every October, and drove all roads once per survey. No photographic data were available for 2017. From 2019–2023, we collected giraffe photographs approximately every other year within Kirawira and Bologonja, and in 2018, 2019, and 2021 in Ndutu.

For all photographs, we recorded sex (male, female) and age class (calf [<1 year old], subadult [1–2 years old], or adult [≥3 years old]) based on a suite of physical characteristics (Strauss et al. 2015). We recorded the global positioning system (GPS) location of each individual or center of the herd during active surveys, and the GPS location of the camera trap for the camera grid data, which we then used to calculate each giraffe's mean distance to edge of the survey boundary as a spatial individual covariate for detection (Royle et al. 2014). We matched giraffe identification images using WildID, a computer program that matches large datasets of giraffe images collected using our protocols with low error rates (Bolger et al. 2012). After matching, we created an encounter history for every identified individual, recording whether (1) or not (0) the animal was seen during each secondary sampling occasion within a primary sampling event in our robust design methodology for Seronera, or during each single annual survey for Kirawira, Bologonja, and Ndutu.

Data analysis

We used the encounter-history data to estimate age class- and sex-specific annual apparent survival probabilities, annual recruitment, annual immigration, annual abundance, annual density, population growth rate, and mean and maximum group sizes for each of the subpopulations. Research on eastern Masai giraffes from the Tarangire Ecosystem, situated 200 km southeast of the Serengeti, revealed that male and female calves and subadults exhibited similar survival probabilities (Lee and Bond 2022). However, starting at age 3, female giraffes showed significantly higher survival probabilities than males. These findings formed the basis of our 3-stage birth-flow life-cycle graphs for western Masai giraffes in Serengeti (Figure 2). Because Tarangire and Serengeti share similar ecological conditions, the insights from Tarangire provide valuable guidance for understanding giraffe populations and conservation strategies in the Serengeti.

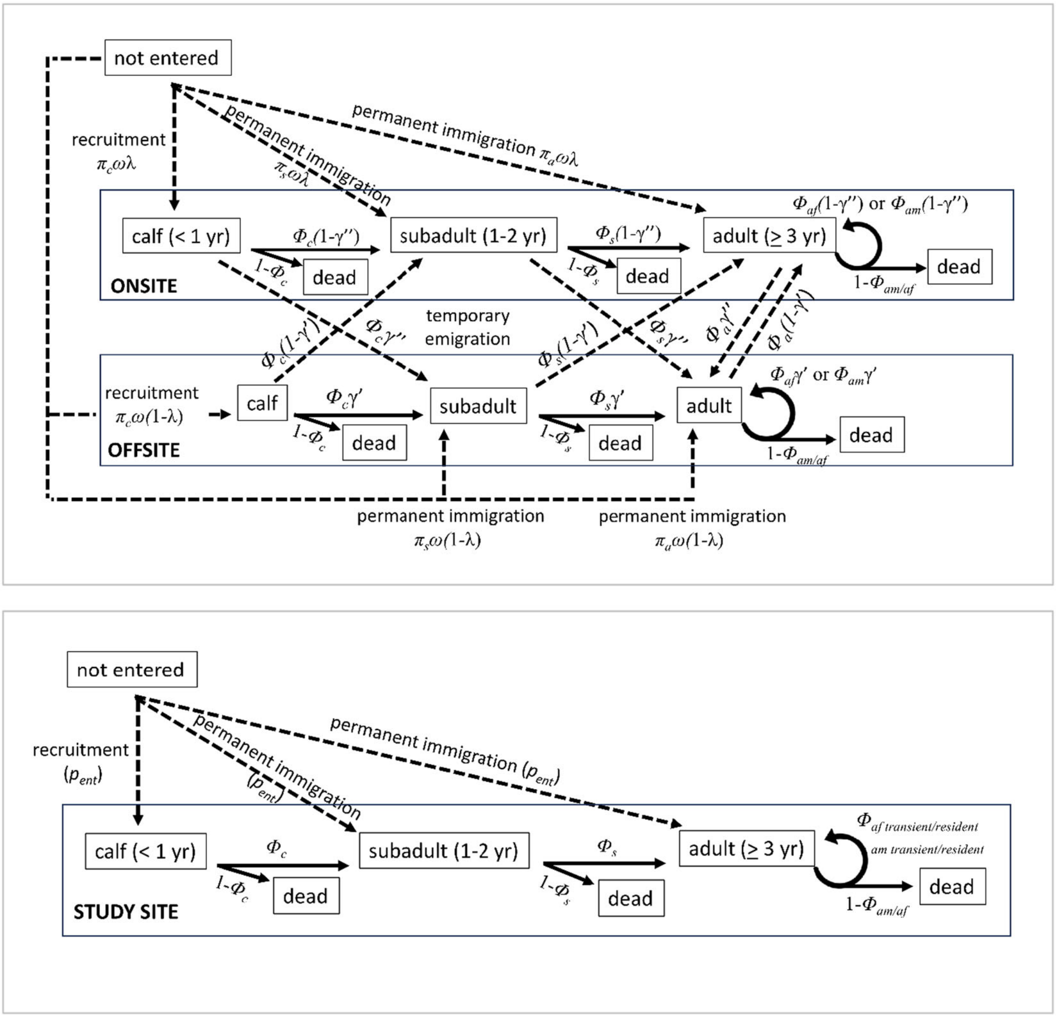

FIGURE 2 Birth flow life-cycle graphs for western Masai giraffes in the Serengeti Ecosystem for subpopulations in Seronera (top) and Kirawira, Bologonja, and Ndutu (bottom). Transitions among life-cycle stages are on an annual basis. Recruitment is birth, and permanent immigration is movement into the subpopulation. In robust design (top), temporary emigration out of and into the Seronera subpopulation occurs in the intervals between primary events. Demographic parameters included survival (Φ), probability of detection (*p*), probability of staying offsite (γ′), temporary emigration (γ″), proportion of recruits and immigrants entering onsite (λ), removal entry probability (*ω*), and new recruits (*π*). Age-sex groups included calf (*c*), subadult (*s*), adult males (*am*), and adult females (*af*). In the bottom graph, p_{ent} is probability of entry into the subpopulation.

Demography and population dynamics over 15 years in Seronera

For Seronera, we used a robust design for our data collection and analysis, which involved >1 sampling occasions (secondary surveys) within a given event (primary survey). We conducted the primary survey once per year. This design assumed a closed population—meaning no births, deaths, immigration, or emigration—within a primary sampling event but an open population between primary events. The time frame for data collection within each primary survey event was <1 month, so we assumed we met the closure assumption for robust design CMR analyses while still ensuring that every survey was independent. Robust design improves the precision and identifiability of parameters in the CMR framework (Pollock 1982) and enables the estimation of temporary emigration (Kendall et al. 1995) and entry probabilities into the study site (Kendall and Nichols 2002). The maximum number of secondary survey occasions within a primary survey event in our study was 3.

We estimated sex- and age-class-specific detection and demographic parameters for Seronera (Table S1) using a Bayesian hidden Markov model (HMM) of the closed robust design (Rankin et al. 2016, Gibson et al. 2018, Riecke et al. 2018). We fit a model that portrayed the life-cycle graph of giraffes (Figure 2, top). We used the multistate formulation of the Jolly-Seber model with state transitions, and employed data augmentation to account for animals that likely entered the subpopulation and were never detected (Kéry and Schaub 2012, Royle and Dorazio 2012). The multistate formulation has the flexibility to include sex, age classes, and location of individuals (onsite vs. offsite; Kéry and Schaub 2012). The state transitions permitted the estimation of the entry process into the subpopulation, temporary emigration out of the study site between primary events, and apparent annual probability of surviving and transitioning to the next age class. Apparent survival (Φ) is the probability of an animal surviving and not permanently emigrating from the study site between times t and $t + 1$. We incorporated individual spatial heterogeneity in detection probabilities in a spatial CMR context (Royle et al. 2014, Bond et al. 2023*b*) because it is likely that portions of some animal's home ranges were partly or largely outside the surveyed area (thus less available for observation) versus completely within the surveyed area (thus more available for observation). We used each giraffe's mean observed location distance to the edge of the survey area as an index of how much time they likely spent in the surveyed area. We also allowed detection probabilities to differ for the 3 data collection methods, and fixed detection probabilities to zero for a year in which no surveys were conducted (Supplemental Data Analysis 1).

To assess the goodness of fit of our model, we conducted posterior predictive checks by comparing replicated data, simulated under our model, to the actual data that we analyzed using the same model (Gelman et al. 2014). Specifically, we compared the number of individuals detected during each primary event between the replicated and observed data and calculated Bayesian *P*-values for each primary event. Bayesian *P*-values represent the probability that the replicated data could be more extreme than the observed data, with values close to 0.5 indicating a good fit (Gelman et al. 2014).

To accommodate heterogeneity in detection, and in survival probabilities for the adult age class, we incorporated covariates for capture and survival probabilities. We treated age-class-specific detection probabilities as a function of period of data collection, mean distance of all sightings for an individual to the edge of the study site boundary, and sex (for adults), and included a random effect of year. We assigned sex for both the unsexed observed individuals and the augmented pseudo-individuals as a Bernoulli trial based on the empirically observed proportion of females (0.57) in the Seronera subpopulation. For camera traps, we modeled an additional detection parameter with a covariate of number of trap days the grid of cameras was working within each secondary sampling occasion. No data were available for the number of working trap days during the last camera trapping primary sampling event (2016), so we drew trap days from a normal distribution with the mean and standard deviation based on the number of photos obtained during the 2 secondary occasions of that year. Age-class-specific survival probabilities included a random effect of year and a linear effect of sex on the logit of adult survival (we only modeled the effect of sex on adult survival; for mathematical description see Supplemental Data Analysis 1).

For our derived subpopulation parameters, we estimated, per year (i.e., primary event), the following: the number of male and female giraffes alive within the study site (abundance $\hat{N}$), which is the sum of onsite (within the study site and observable) + offsite individuals (either temporarily outside the study site or within the study site but unobservable because they cannot be detected; e.g., they are outside the observable survey area covered by our road transects); the number of male and female giraffes immigrating into the study site (permanent immigrants; adult and subadult recruits); and the number of male and female births (calf recruits). We calculated the subpopulation growth rate as the number alive at time t divided by the number alive at time $t - 1$. Similarly, we calculated per capita immigration rates as the number of immigrants at time t divided by the abundance $\hat{N}$ at time $t - 1$.

Finally, to explore the demographic drivers of subpopulation dynamics, we correlated the contribution of the variability of each demographic parameter to the variability in the population growth rate in a retrospective population analysis (Schaub et al. 2013, Schaub and Kéry 2022). The magnitude of the correlation coefficient (r) represented how much the temporal variation of that demographic parameter contributed to the temporal variation of subpopulation growth rate during the study period. We computed the correlation coefficients in each posterior sample to derive the posterior distributions and reported the mean and 95% credible intervals (Schaub et al. 2013).

We used NIMBLE (version 1.1.0) to implement the Bayesian HMM. We used non-informative priors for all parameters and ran the Markov chain Monte Carlo (MCMC) for 5 chains of 100,000 iterations each with a burn-in phase of 50,000 iterations and a thinning of 5. To confirm that the MCMC chains had converged, we visually examined trace plots and computed the Gelman-Rubin convergence statistic, $\hat{R}$ (Gelman and Rubin 1992; Tables S3 and S4).

Demography and density in Kirawira, Bologonja, and Ndutu

For the Kirawira, Bologonja, and Ndutu sites, we used a frequentist approach to estimate giraffe survival probabilities, reproduction, and abundance. We chose this method to facilitate comparison with frequentist estimates provided by Strauss et al. (2015). We conducted 3 October photographic identification surveys, with missing years between some surveys (Table 1). We did not survey these sites using a robust design. We used the R 4.4.0 (R Core Team 2023) package RMark (Laake 2013) to construct and run open-population Jolly-Seber models using program MARK (White and Burnham 1999). For each site we fit a model that portrayed the life-cycle graph of giraffes (Figure 2, bottom). Derived parameters were the total estimated abundance of all animals alive within the study site in each sex and age class per year (abundance $\hat{N}$), accounting for imperfect detection; the number of male and female giraffes immigrating into the study site (permanent adult and subadult immigrants); and the number of male and female recruits (births; further details provided in Supplemental Data Analysis 2). We assessed the goodness of fit for each site's model from the estimated $\hat{c}$, an indication of the level of overdispersion in the data (Cooch and White 2019).

The size of each study site differed, so we calculated annual giraffe density to enable direct comparison among subpopulations. Because of the lack of geographic closure, our abundance estimates may include some animals whose activity centers fell outside the study area bounds (Cooch and White 2019). Our model in Seronera quantified temporary emigration probabilities of 0.08 (SD = 0.02), meaning approximately 8% of individuals identified within the study site were offsite (or not available for capture) during a given survey. Therefore, we presumed 8% of the subpopulation might have activity centers outside but overlapping the edge of our study site boundary. To provide a density estimate that removed these animals, we reduced the estimated abundance in each subpopulation by 8%. We calculated the density of giraffes whose activity centers were within each study site as $\hat{N} - (\hat{N} \times 0.08)$/study site area (km^2).

We tested for differences in demographic parameters among the 4 subpopulations using analysis of variance with Tukey adjustments for pairwise comparisons, with the TukeyHSD function in R (95% family-wise confidence levels). Specifically, for each demographic parameter and subpopulation, we generated random draws from a normal distribution using the means and standard deviations derived from the frequentist analyses, with the number of draws for each site-parameter combination equal to the number of individually identified giraffes in that category (for the Kirawira, Bologonja, and Ndutu subpopulations). For the demographic parameters of the Seronera subpopulation, we generated 845 random draws from the posterior distribution of the Bayesian HMM.

Comparison of group sizes, movements, and density to historical data

We recorded one GPS location for each giraffe group formation (including singletons) during each survey. We then calculated the number of individual giraffes in each group formation based on our CMR data. We used the same definition of a group as Strauss et al. (2015): individuals feeding, socializing, or moving together, with a solitary individual equaling a group size of one. Giraffe group members are typically self-defining but can be dispersed over a large area (Carter et al. 2013). Our protocol was to consider giraffes to be in different groups if the outermost individual of one group was separated by >500 m from the outermost individual of another group as measured with a GPS. We computed mean and standard deviation (SD) of group size by subpopulation. We tested for differences in mean group sizes among the 4 subpopulations using analysis of variance with Tukey adjustments for pairwise comparisons, with the TukeyHSD function in R (95% family-wise confidence levels). We then compared mean and maximum giraffe group sizes from this study with historical group sizes from the 1970s and the 2000s as reported by Strauss et al. (2015).

Strauss et al. (2015) found no evidence of giraffes moving between the central, western, and northeastern subpopulations within a limited period of 3 years; our aim was to test their findings with a longer time frame and larger dataset, and to include the southern subpopulation (Ndutu) in the movement analysis. We used our CMR data to quantify long-distance dispersal events by individual giraffes among the subpopulations. Our encounter history for each giraffe included the site of each detection, similar to Strauss et al. (2015), enabling us to determine whether any of the individuals in our sample ever transitioned between sites during our study.

Giraffe density estimates from Pellew (1983) and Strauss et al. (2015) used aerial survey data, a method that estimates density as the number of giraffes observed in the study sites at a point in time and typically results in lower density estimates than other methods (Caughley 1974; Jachmann 2001, 2002; Fleming and Tracey 2008). For periods and sites for which no CMR data were available, we used a correction factor to enable comparison of our CMR-derived giraffe density estimates with the historical reports that were based on aerial survey data. We calculated the subpopulation densities of Seronera and Kirawira from 2008–2010 with CMR-derived abundance estimates presented in Strauss et al. (2015) and reduced these abundances by 8% (to correct for giraffes detected in our study sites that might reside primarily outside the boundaries, as described above). The CMR-derived densities from Strauss et al. (2015) were 3.4 (Kirawira) to 5.5 times (Seronera) higher than their aerial survey-derived densities. Lee and Bond (2016) reported an aerial survey-to-CMR correction factor of 3 for giraffes in Tarangire National Park, Tanzania, and Greene et al. (2017) calculated an aerial survey-to-distance-sampling correction factor of 3.5 for giraffes in Manyara Ranch, Tanzania. To be conservative, we adjusted each subpopulation density estimate that was derived from aerial surveys by multiplying by 3 to provide a reasonable comparison of the historical aerial survey density estimates with CMR-derived estimates.

RESULTS

From our photographic CMR data, we identified 1,520 individual giraffes across the 4 subpopulations in the Serengeti Ecosystem during our study period. We observed 845 giraffes in Seronera, 210 in Kirawira, 149 in Bologonja, and 316 in Ndutu (Table S2).

Subpopulation dynamics in Seronera

Posterior predictive checks indicated good model fit, evidenced by an average Bayesian *P*-value of 0.58 (range = 0.39–0.73) across all primary survey events (Figure S3). Detection probabilities were affected by several covariates (Table S3). An individual giraffe's mean distance from the edge of the study site boundary had a clear positive relationship with detection probabilities in all age classes, meaning giraffes that were observed closer to the edge of the study site boundary had lower detection probabilities (Table S3). Detection probabilities during camera trap surveys (2011–2016) were lower compared to active encounter surveys 2008–2010 and active encounter surveys 2018–2023 (Figure S4), whereas we did not find evidence that detection probabilities for both active encounter surveys differed (Table S3). Number of days the camera traps were operable had a positive effect on detection probability. Finally, detection probabilities for adult females were higher than for adult males (Table S3; Figure S4). All biological parameters of interest were estimated while accounting for these detection biases.

The adult age class had the highest apparent survival probabilities, followed by subadults, with calves having the lowest survival probabilities, and adult female giraffes having higher mean survival probabilities than adult males (Table 2). Per capita immigration rates of adult males and females into the Seronera subpopulation were 0.00 or 0.01 over the study period, and higher ($\overline{x}$ = 0.06, SD = 0.04) and more variable for subadults (Figures S5 and S6). The mean probability of temporarily leaving Seronera was 0.08 (SD = 0.02), while the mean probability of remaining offsite site after temporary emigration was 0.85 (SD = 0.07).

Our estimated annual abundance of giraffes in the Seronera subpopulation was 447 (SD = 53) from 2008 to 2023, with a low of 362 in 2012 and a high of 534 in 2020 (Figure S7). Mean abundance from the first 3 years of the study (450 individuals, SE = 15.3) was higher but not statistically different than the mean estimate reported by Strauss et al. (2015) of 401 individuals (SE = 12.2). The subpopulation growth rate indicated fluctuation around a stable growth rate of 1.0 over the 15-year study period (Figure 3 and S8). Our retrospective population analysis indicated that annual population growth rates in Seronera were positively associated with adult survival and calf recruitment (births), while survival of the youngest age classes exerted the least effect on population growth rates (Table 3).

Demography of Kirawira, Bologonja, and Ndutu compared to Seronera

The estimated $\hat{c}$ values for Kirawira and Ndutu were <3, indicating adequate model fit. However, for Bologonja the estimated $\hat{c}$ = 11.05, suggesting overdispersion likely due to the relatively low sample size. Tukey honestly significant difference (HSD) results indicated demographic parameters differed between all pairs of sites with the exception of apparent survival of calves, which differed between Bologonja and all other sites (Table 2; Figure 3 and S9). Recruitment rates among sites were similar (Figure 3 and S9), especially Ndutu and Kirawira, but apparent survival probabilities of calves, adult females, and adult males at Bologonja were notably low relative to other sites, and subadult survival probabilities were lower in Kirawira and especially Bologonja (Figure 3 and S9).

Population growth rates were <1 in Kirawira and Bologonja from 2019–2023 but stable in Seronera and Ndutu (Figure 3). The current density of giraffes was highest in Seronera, followed by Ndutu, Kirawira, and Bologonja in descending order (Table 2), and densities declined in Kirawira and Bologonja from 2019–2023 (Figure 4).

Comparison of group sizes, movements, and density to historical data

Mean group sizes of giraffes in Kirawira from 2019–2023 were twice as large as mean group sizes in the other subpopulations, and the maximum group size was more than 56% larger than the next-largest maximum group size, which was in Seronera (Table 4). Tukey multiple comparisons of means showed that group sizes were

TABLE 2 Mean and standard deviation (SD) of the demographic probabilities for Masai giraffes, and mean and SD of densities, estimated from capture-mark-recapture (CMR) data at 4 sites in the Serengeti Ecosystem, Tanzania, from 2008–2023 in Seronera, 2019–2023 in Kirawira and Bologonja, and 2018–2021 in Ndutu. We also show reported mean demographic parameter estimates from late 1970s (Pellew 1983) and late 2000s (Strauss et al. 2015) for comparison.

	Seronera				Kirawira			Bologonja		Ndutu	
Parameter	**Mean 2008–2023**	**SD**	**1970s**	**2000s**	**Mean 2019–2023**	**SD**	**2000s**	**Mean 2019–2023**	**SD**	**Mean 2018–2023**	**SD**
Calf survival ϕ_c	0.73	0.05	0.42	0.57	0.76	0.28	0.67	0.51	0.44	0.75	0.32
Subadult survival ϕ_s	0.76	0.03	0.92	0.79	0.54	0.43	0.85	0.24	0.44	0.75	0.66
Adult male survival ϕ_{am}	0.83	0.06			0.75	0.31		0.52	0.64	0.81	0.28
Adult female survival ϕ_{af}	0.88	0.05	0.95[a]	0.84	0.82	0.38	0.89	0.62	0.87	0.85	0.40
Recruitment π_c	0.18	0.09	0.21	0.13	0.17	0.14	0.18	0.25	0.13	0.18	0.06
Population growth rate λ	1.00	0.07			0.86	0.58		0.72	0.42	0.97	
Density	1.58[b]	0.19			0.39[b]	0.13		0.26[b]	0.11	1.27[b]	0.02

[a] Adult survival was not reported by sex in Pellew (1983).

[b] Density estimates from CMR data were calculated by reducing the abundance estimates by 8% to account for offsite individuals detected during our surveys.

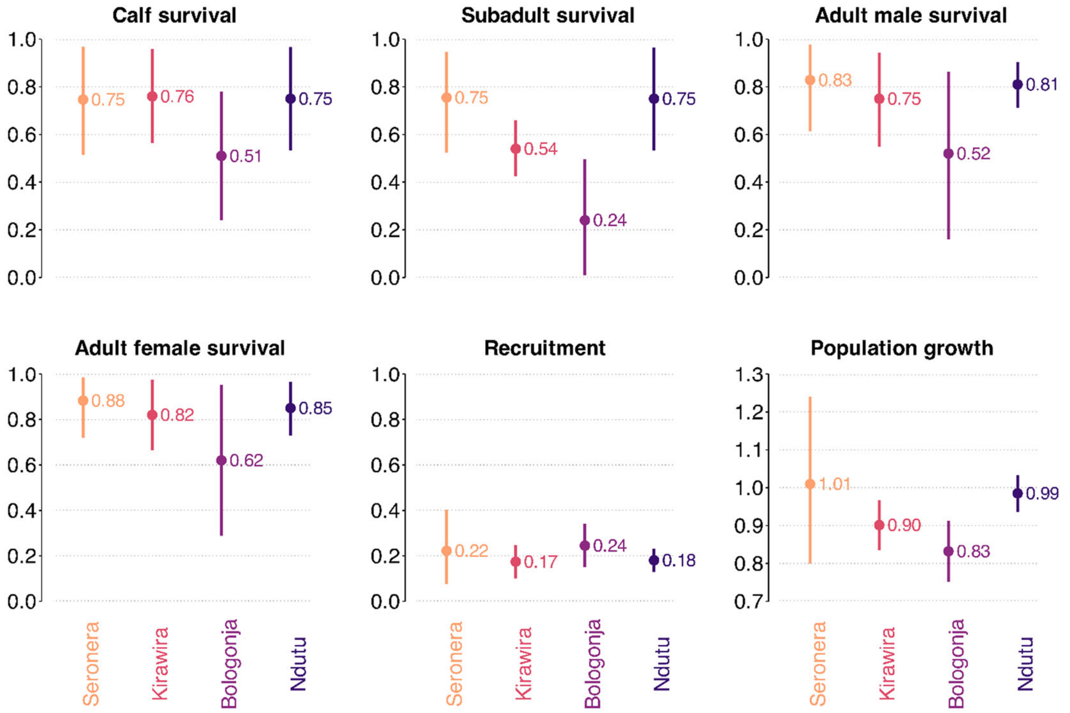

FIGURE 3 Mean estimated demographic probabilities (error bars = 95% CIs) for western Masai giraffes from 2018–2023 in the Seronera study site, 2019–2023 in the Kirawira and Bologonja study sites, and 2018–2021 in the Ndutu study site, Serengeti Ecosystem, Tanzania. Parameters estimated with photographic capture-mark-recapture techniques.

TABLE 3 Mean correlation coefficients (*r*), Bayesian credible intervals, and probability *r* > 0 between variation in a demographic parameter and subpopulation growth rate of Masai giraffes in the Seronera woodlands of the central Serengeti Ecosystem, Tanzania, from 2008–2023. Parameters with an asterisk (*) represent those most correlated with variation in population growth rate, as indicated by a posterior probability of ≥95% that the correlation coefficient *r* does not overlap zero.

Parameter	Mean *r*	2.5%	97.5%	Prob *r* > 0
Calf survival ϕ_c	0.13	−0.40	0.59	0.70
Subadult survival ϕ_s	0.10	−0.44	0.59	0.65
Adult survival ϕ_a	0.66	0.25	0.89	1.00*
Recruitment π_c	0.63	0.21	0.88	1.00*
Subadult immigration π_s	0.49	0.02	0.83	0.98*
Adult male immigration π_{am}	0.27	−0.30	0.75	0.82
Adult female immigration π_{af}	0.29	−0.27	0.76	0.84

similar in Bologonja, Ndutu, and Seronera but larger in Kirawira. These results confirm that giraffe group sizes in the Kirawira region continue to be larger on average than in the other study sites. Comparisons with previous periods (Table 4) suggest that mean group sizes in Bologonja have increased slightly, while maximum group sizes have declined substantially over time. Mean group sizes in Kirawira were slightly larger currently than in the

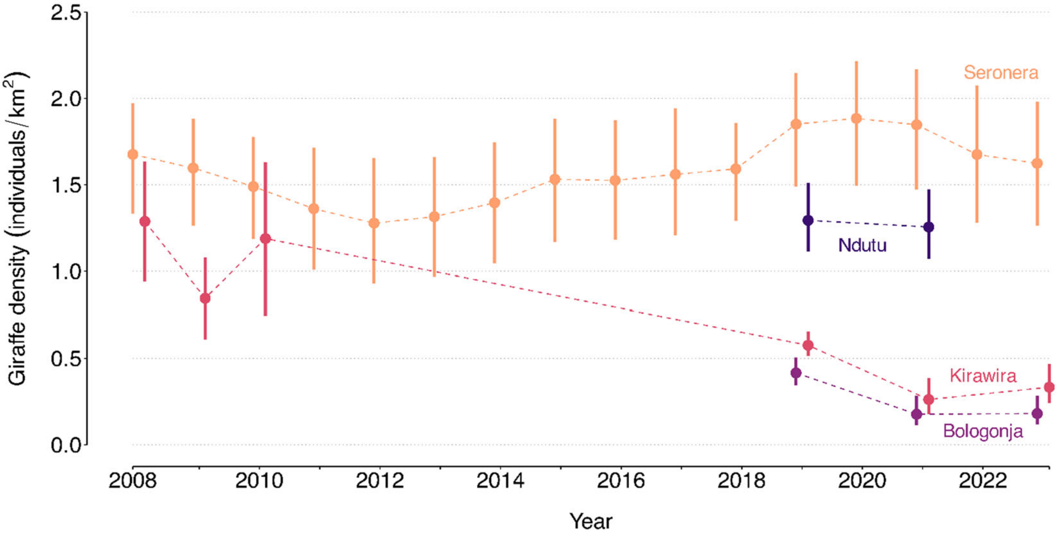

FIGURE 4 Mean estimated densities (individuals/km^2) of western Masai giraffes (error bars = 95% CIs) from 2008–2023 in the Seronera study site, in 2008–2010 and 2019–2023 in the Kirawira study site, in 2019–2023 in the Bologonja study site, and in 2018–2021 in the Ndutu study site, Serengeti Ecosystem, Tanzania. Density estimates derived from capture-mark-recapture data were calculated by reducing the abundance estimates by 8% to account for offsite individuals detected during our surveys.

1970s and nearly twice as large compared to the 2000s, but maximum group size in 2023 was 42% smaller than in the 1970s. In Seronera, contemporary mean and maximum group sizes were markedly similar to those from the 1970s, and were more than twice as large as those recorded in the late 2000s. Group sizes in Ndutu have no historical data for comparison.

Of the 1,520 identified individual giraffes from 2008–2023, only 1 giraffe, a subadult male, transitioned between any of the subpopulations. This male moved 45.3 km from Seronera to Ndutu.

After adjusting estimates derived from aerial data to be comparable with CMR-derived estimates, we observed large declines in giraffe densities between the 1970s and 2000s in all 3 long-term study sites. These declines continued into 2019–2023 in Bologonja and Kirawira (Table 4).

DISCUSSION

Our key results indicate declining Masai giraffe subpopulations in the western corridor (Kirawira) and northeastern woodlands (Bologonja) of the Serengeti Ecosystem since 2008, in contrast with a stable subpopulation in the central Serengeti (Seronera) since 2008 and a relatively stable subpopulation in the southern woodlands (Ndutu) from 2018 to 2021. Kirawira and Bologonja showed similar birth rates as Seronera and Ndutu but had comparatively lower survival of adults and subadults, especially in Bologonja. Fifteen years of stability in the Seronera subpopulation in recent years followed a steep decline in density from the 1970s to the late 2000s (Table 4). This pattern of a roughly 50% population decline between 1970 and the late 1990s with subsequent stabilization in the recent 15 years echoes a broader pattern observed in large mammals in east Africa's protected areas (Craigie et al. 2010). The giraffe subpopulations in Kirawira and Bologonja also steeply declined from the 1970s to the late 2000s but, in contrast to Seronera, continued to decline through 2023.

TABLE 4 Comparison of mean and maximum group sizes and densities of giraffes during the dry season in 4 subpopulations in the Serengeti Ecosystem, Tanzania, over 3 periods: 1975–1977, 2008–2010, and 2018–2023 (Seronera), 2019–2023 (Kirawira and Bologonja), and 2018–2021 (Ndutu).

	Seronera			Kirawira			Bologonja			Ndutu
	1970s	2000s	2018–2023	1970s	2000s	2019–2023	1970s	2000s	2019–2023	2018–2021
Mean group size	9	4.3	9.6	17	12.7	20.3	7	9	10.8	10.0
Max. group size	77	38	78	239	61	138	62	51	29	51
Density (giraffes/km^2)	5.13[a]	1.59[b]	1.75[b]	7.71[a]	1.11[b]	0.39[b]	4.02[a]	0.72[a]	0.26[b]	1.27[b]

[a] Density estimates derived from aerial surveys were multiplied by correction factor 3.0 to account for unobserved individuals and enable comparison with capture-mark-recapture (CMR)-derived densities.

[b] Density estimates derived from CMR data were calculated by reducing the abundance estimates by 8% to account for offsite individuals detected during our surveys.

We found that even with reduced subpopulation densities compared to previous decades, regional patterns of giraffe social grouping remain unchanged over 48 years, with the largest mean and maximum group sizes still found in Kirawira. We recorded only a single long-distance movement (>40 km) among our 4 studied subpopulations, with annual adult immigration rates into Seronera being nearly zero, and subadult immigration low, indicating that these giraffe subpopulations appear quite insular. This observed insularity suggests social structuring within the ecosystem-wide population similar to that documented in the Tarangire Ecosystem (Lavista Ferres et al. 2021, Bond et al. 2021*a*), with genetic structuring documented in both Serengeti and Tarangire (Brown et al. 2007, Lohay et al. 2023). Our findings highlight the need for targeted conservation efforts that address the low survival rates of subadults and especially adults in Kirawira and Bologonja to ensure the long-term viability of this species throughout the Serengeti Ecosystem.

Subpopulation demographic trends

Our estimates of giraffe demographic parameters in Seronera and Ndutu were similar to estimates from populations in protected areas across Africa (Lee et al. 2016, Lee and Strauss 2016). Our long-term, continuous dataset of giraffes in Seronera, in the heart of the Serengeti Ecosystem, revealed the abundance of giraffes in this subpopulation was relatively stable over the past 15 years, with annual fluctuations in population growth rates driven largely by variation in calf recruitment and adult survival, and with minor contributions from subadult immigration. In contrast, data from Kirawira in the western part of the ecosystem indicated that this subpopulation has likely decreased >65% since 2010 and continued to decrease from 2019 to 2021. The Bologonja subpopulation in the northeast part of Serengeti National Park also decreased from 2019 to 2021. Both Kirawira and Bologonja had similar recruitment rates as Ndutu and Seronera but comparatively low survival probabilities. Seronera and Ndutu are located far from the boundaries of the protected areas in the Serengeti Ecosystem, whereas Kirawira and Bologonja are near the boundaries (Figure 1), pointing to potential anthropogenic factors affecting the outlying subpopulations.

In the 1970s the reported density of giraffes in Kirawira was higher than in Seronera, and among the highest densities reported in Africa (Pellew 1983). Conversely, contemporary giraffe density in Kirawira was the second lowest of our 4 study sites and lower than densities reported in the Tarangire Ecosystem (Lee and Bond 2016, Green et al. 2017, Lee and Bond 2022). Considering the 50-year trends, the numbers of giraffes in Kirawira and

Bologonja appear to have plummeted by 85% since the late 1970s and continue to decline, which is reason for concern as the trend for other large mammals indicated declines since 1970 followed by stabilization in recent decades (Craigie et al. 2010).

We also provided the first demographic estimate for giraffes in the woodlands around Lake Ndutu as a baseline for future monitoring, and discovered a higher density of giraffes residing there compared to Bologonja and Kirawira (Figure 4). Overall, the highest density of the 4 subpopulations was in Seronera, both in 2008–2010 and in 2018–2023. This suggests that the woodlands in mollic solonetz soils occurring in the northeastern section of the Seronera study site—where most of the giraffes were detected over our 15-year study period—and extending westwards towards the edges of Serengeti National Park (Figure S2), are high-quality habitats capable of supporting a high density of giraffes. Mollisols are soils that are relatively abundant in organic matter, base rich, and quite fertile and are considered among the most important and productive agricultural soils in the world (Labaz et al. 2024).

The high giraffe population densities in Serengeti during the late 1970s might have been the result of population overshoot of giraffes following their recovery after the end of the rinderpest epidemics. Population overshoot could have caused Pellew (1983) to report densities that were above carrying capacity of the ecosystem, with the downward trend since the 1970s being an adjustment commensurate with the capability of the available habitat to support giraffes, similar to that which occurred with the Serengeti wildebeests after release from rinderpest (Holdo et al. 2009). However, the wildebeest overshoot was approximately 25%, while giraffe populations have fallen 85% since Pellew (1983). If the ecosystem can indeed support giraffe numbers documented by Pellew (1983), we must be careful not to fall into the shifting baseline syndrome (Prins and de Jong 2022).

Demographic drivers of giraffe population dynamics in Serengeti

The results of our demographic and retrospective population analyses agreed generally with expectations for a large, long-lived, slow-reproducing species with delayed maturity (Caswell 2006, Nilsen et al. 2009, Sæther et al. 2013, Paniw et al. 2019, Bond et al. 2023*a*), namely that adult survival was higher than calf and subadult survival, and variation in adult survival and calf recruitment had the strongest correlations with variation in subpopulation growth rate. In large mammalian herbivores, adult survival is usually high and constant while reproduction is typically more variable over time, and therefore reproduction often contributes much to the variance in population growth rates for these species despite the lower sensitivity of population growth to reproductive rate (Charnov 1986, Gaillard et al. 2000, Eberhardt 2002, Sæther et al. 2013, Lee et al. 2016*a*). Adult survival in species with slow life histories should be relatively buffered against environmental variation while reproduction should be more influenced by environmental conditions over space and time (Gaillard et al. 1998, 2000; Paniw et al. 2018). Indeed, within well-protected areas of Tanzania's Tarangire Ecosystem and across Africa, adult female giraffe survival was high and constant across space and time (Lee et al. 2016, Bond et al. 2021*a*) while reproduction varied as a function of soil type (Bond et al. 2021*a*). However, outside Tarangire's protected areas, adult female survival was significantly reduced (Lee et al. 2016*a*), and this lower survival contributed the most to subpopulation extinction risk (Bond et al. 2023*a*).

The likeliest causes of lower adult giraffe survival outside of protected areas are the presence of dense human populations, habitat fragmentation from urbanization and agriculture, and illegal poaching for bushmeat markets or trophies (Muller et al. 2018, Bolger et al. 2019). We agree with the conclusion by Strauss et al. (2015) that illegal hunting is probably the most important factor affecting the spatial variation in apparent survival probabilities of adult giraffes within the Serengeti Ecosystem. The human population is much sparser and there is no agricultural conversion of natural habitats in the central and southern portions of the ecosystem (Seronera and Ndutu) where adult giraffe survival probabilities were highest. Conversely, at Kirawira and Bologonja along the boundaries, adult giraffe survival was lower, and wildlife poaching is a recognized problem in the western corridor (Loibooki et al. 2002, Kaltenborn et al. 2005, Denninger Snyder et al. 2019). Despite a low-density human population adjacent to Bologonja, illegal hunting is the probable culprit affecting giraffe survival there as well. Killing of adult giraffes was suggested as the strongest cause of reduced adult female survival probabilities and the biggest threat to the persistence of giraffes outside protected areas in the Tarangire Ecosystem (Lee et al. 2016*a*, *b*; Bond et al. 2023*a*), indicating the problem extends across the country.

One caveat is that in population modeling based on capture-mark-recapture methods, we can only estimate apparent survival because true mortality and permanent emigration cannot be distinguished (Lebreton et al. 1992). Therefore, it is also possible that adult giraffes are emigrating away from the border subpopulations rather than experiencing higher *in situ* mortality. Human population density is highest in the western part of the Serengeti Ecosystem near Kirawira (where the greatest giraffe decline has been documented), and most of the area along the western border of the park is used for agriculture (Veldhuis et al. 2019). This leads to a large number of illegal incursions by people into the park (Kaltenborn et al. 2005), which could disturb giraffes. It is therefore also plausible that the decline in giraffes documented from the 1970s until the present day is due not to poaching or other factors influencing survival but to anthropogenic disturbances pushing giraffes to other areas outside of our study site boundaries with higher levels of protection, such as the Grumeti Game Reserve adjacent to Kirawira, or more interior areas south of Bologonja. However, our documented low rates of permanent immigration into Seronera and lack of long-distance movements among the 4 sites provide evidence for reduced true survival probabilities as the most likely cause for observed density declines.

In animals with slow life histories, the combination of long life spans, relatively high adult survival, and low rates of immigration makes populations particularly vulnerable to declines from adult mortality that are difficult to ameliorate (Cardillo et al. 2005, Ripple et al. 2015, Carmona et al. 2021). Whether the reductions in the Kirawira and Bologonja giraffe subpopulations were due to persistently high *in situ* mortality—especially of adult females—or to permanent emigration, the subpopulations would likely require a long time to be rescued from extirpation due to low immigration rates. Giraffe survival probabilities and densities were effectively raised in community-based conservation areas adjacent to national parks in the Tarangire Ecosystem through increased law enforcement and more money from ecotourism flowing into the communities (Lee 2018; Lee and Bond 2018*a*, *b*); this could prove effective in the Serengeti system as well. Additional population research at Kirawira and Bologonja is warranted to confirm our observations and determine causes for low apparent survival.

Largest giraffe group sizes in western Serengeti

Estimates of mean group size were larger in all 4 study sites relative to other areas across Africa, where average groups comprised 5 to 6 individuals (Leuthold 1979, Bond et al. 2019). In the 1970s Kirawira, rather than Seronera, supported the highest density of giraffes (Pellew 1983). Further, mean and maximum group sizes of giraffes in the Kirawira site were significantly larger than other sites (Pellew 1983, Strauss et al. 2015) and remained so through the end of the study in 2023. Kirawira includes some woodlands on mollic solonetz soils like in Seronera but also woodlands on eutri-pellic vertisols (Figure S2), which are colloquially called black cotton soils and known for high fertility. The soil type and vegetation composition in Kirawira likely attract large congregations of giraffes, similar to the western part of Manyara Ranch in the Tarangire Ecosystem, where 5 of the 6 largest giraffe groups were recorded during the rainy seasons in extensive patches of sickle bush (*Dichrostachys cinerea*) growing on fertile black cotton soils (Bond et al. 2019). The persistently large group sizes in Kirawira might be due to especially high-quality habitat in the western part of the park, but it is also possible that grouping dynamics in Kirawira compared to other sites are mediated by behavioral differences rather than habitat. We suspect that the western corridor habitat remains capable of supporting a substantially higher density of giraffes—as demonstrated by Pellew (1983)—but their current numbers may be suppressed by external factors such as poaching or disturbances along the edge of the park.

Low rates of long-distance movements

With the exception of one subadult male, we found that individual giraffes in our sample did not undertake long-distance movements among the study sites, a distance of >40 km. There are no geographic or anthropogenic barriers that would inhibit movements, and continuous woodlands occur between all sites except where grassland predominates between Seronera and Ndutu. Giraffes, especially males, have the capacity to travel over long distances (Fennessey 2009, Brown and Bolger 2020, Bond et al. 2021*b*, this study). Several giraffes in Seronera were observed traveling straight-line distances of >40 km over a period of 4 years, as documented by camera trap photos within the larger Seronera grid (P. E. Campbell, Wild Nature Institute, unpublished data), suggesting that individuals within the grid were members of the same super-community (Lavista Ferres et al. 2021). Overall, however, giraffe subpopulations in the Serengeti Ecosystem appear to be largely insular. In addition to documenting essentially no long-distance movements among the subpopulations, we documented extremely low per capita immigration rates of adults and subadults into the Seronera subpopulation over 15 years, despite large areas of continuous suitable woodland habitat that supports giraffes just outside the Seronera study site boundary. This accords with previous evidence about the relatively sedentary nature of these megaherbivores despite their size and large space-use requirements (Knüsel et al. 2019, Bond et al. 2021*b*).

Population genetics showed a surprisingly high genetic differentiation among giraffe subpopulations in the Serengeti and Tarangire Ecosystems, indicating relatively low levels of gene flow (Brown et al. 2007, Lohay et al. 2023). Such insularity of subpopulations suggests likely social and genetic structuring of the giraffe population in the Serengeti that merits further study. Social structuring among giraffes was evident in the Tarangire Ecosystem, with female-based social communities (Bond et al. 2021*a*, *c*) embedded within mixed-sex and age-based super-communities (Lavista Ferres et al. 2021) with few movements among the communities or super-communities and high rates of fidelity. Dagg (2014) noted that despite the mobile lifestyle of giraffes, constantly on the move while browsing, they actually cover a relatively small area and have a low rate of gene flow similar to that of a highly sedentary species. The sedentary nature of giraffes reduces the likelihood of extirpated subpopulations being rescued and increases the amount of time it would take for recolonization.

Uncertainty arising from using multiple datasets

The ability to combine datasets from different sources allowed us to enhance and expand inference, which is especially helpful for long-lived, slow-reproducing animals such as giraffes because many years of longitudinal data are necessary to detect trends. In our Seronera subpopulation, we obtained photographs of giraffes based on different data collection methods over 3 periods, and although we lacked empirical information about some covariate effects on detection and survival, our Bayesian HMM allowed for these covariates to be inferred. Failure to properly address these sources of error could have produced substantial uncertainty in the estimates of key demographic parameters. Bayesian modeling is a powerful tool in the analytical toolbox to deal with missing data and multiple sources of variation. The retrospective population analysis from our combined datasets then allowed us to disentangle the demographic correlates of annual population growth rate with our longer-term time frame. This analytical framework facilitated more reliable inferences about the drivers of long-term demographic and population trends, supporting effective evidence-based conservation and management.

CONSERVATION IMPLICATIONS

Our study revealed biologically significant demographic differences in apparent survival probabilities of adult and subadult giraffes among subpopulations within the Serengeti Ecosystem, along with insularity of the subpopulations. These factors, combined with observed declines over 48 years for 2 subpopulations, underscore the need for subpopulation-specific conservation strategies aimed at raising adult survival within the western and northeastern parts of the Serengeti Ecosystem. Retrospective population analysis reiterated that adult survival is a critical demographic driver of population dynamics for giraffes. Community conservation efforts such as the well-managed Wildlife Management Areas in the Tarangire Ecosystem have been shown to be effective methods of raising adult giraffe survival and density (Lee 2018; Lee and Bond 2018*a*, *b*).

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

ETHICS STATEMENT

The study adhered to relevant regulations and guidelines regarding the ethics of animal welfare.

DATA AVAILABILITY STATEMENT

Data and code are available at: https://doi.org/10.6084/m9.figshare.27118788.

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