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Socially Defined Subpopulations Reveal Demographic Variation in a Giraffe Metapopulation

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ABSTRACT Populations are typically defined as spatially contiguous sets of individuals, but large populations of social species can be composed of discrete social communities that often overlap in space. Masai giraffes (*Giraffa camelopardalis tippelskirchi*) of Tanzania live in distinct social subpopulations that overlap spatially, enabling us to simultaneously explore environmental and social factors correlated with demographic variation in a metapopulation of >1,400 adult females and calves. We considered statistically distinct communities in the social network as subpopulations and tested for variation among the 10 subpopulations in adult female survival, calf survival, and reproductive rate (calf-to-adult female ratio). We then related variation in demographic rates among subpopulations to differences in vegetation, soil type, proximity to 2 types of human settlements, local giraffe population density, and social metrics of relationship strength and exclusivity among adult females. We did not find any among-subpopulation effects on adult female survival, suggesting adult female survival is buffered against environmental heterogeneity among subpopulations. Variation in calf demographic rates among subpopulations were correlated with vegetation, soils, anthropogenic factors, and giraffe population density but not with adult female relationship metrics, despite substantial spatial overlap. Subpopulations with more dense bushlands in their ranges had lower calf survival probabilities, and those closer to human settlements had higher reproductive rates, possibly because of spatial gradients in natural predation. Reproductive rates were higher in subpopulations with more volcanic soils, and calf survival probabilities were greater in subpopulations with higher local adult female densities, possibly related to higher-quality habitat associated with fertile soils or lower predation risk, or to greater competitive ability. The variation in fitness among subpopulations suggests that giraffes do not move unhindered among resource patches to equalize reproductive success, as expected according to an ideal free distribution. The differences in calf survival and reproductive rates could rather indicate intercommunity differences in competitive ability, perception, learning, or experience. Our approach of comparing demography among spatially overlapping yet distinct socially defined subpopulations provides a biologically meaningful way to quantify environmental and social factors influencing fine-scale demographic variation for social species.

KEY WORDS anthropogenic effects, capture-mark-recapture, demography, giraffe, *Giraffa camelopardalis tippelskirchi*, population biology, social network analysis.

Survival and other demographic traits of a species can differ markedly among populations (Coulson et al. 1999, Paradis et al. 2000, Frederiksen et al. 2005, Lee et al. 2016). Demographic rates can be influenced by environmental (Gaillard et al. 2000, Nilsen et al. 2009, Contasti et al. 2012) and social processes (Wey and Blumstein 2012, Blumstein 2013), and their interactions, with processes operating across various scales (Grosbois et al. 2009). Identifying which demographic parameters differ among populations, and why they differ, is therefore fundamental to understanding population ecology. Investigating potential links among the environment, sociality, and demography requires long-term, large-scale studies because such studies are more likely to include contrasting environmental and social conditions (Clutton-Brock and Sheldon 2010).

To explore the potential factors that influence demographic parameters, it is essential to first objectively define

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populations or subpopulations in continuous space (Coulson et al. 1999, Schaefer 2006, Harwood 2009). Wells and Richmond (1995) proposed that a population be defined as a group of individuals demonstrating a clear disjunction from other groups in spatial, genetic, or demographic structure, but appropriate boundaries can be difficult to recognize (Thomas and Kunin 1999, Zannèse et al. 2006). Large populations are often composed of discrete social communities of individuals that regularly interact with each other more than they interact with individuals in other social communities (Lusseau et al. 2006, Cantor et al. 2012, VanderWaal et al. 2014, Papageorgiou et al. 2019). Some distinct social communities may also overlap substantially in space with their members being rarely observed together (Bond et al. 2020). Such communities might give rise to population structure through preferences in social associations as opposed to discrete space use, and thus be considered subpopulations. These socially defined subpopulations potentially allow us to better understand the factors that influence variation in demographic rates in relation to social and environmental conditions.

The adult female Masai giraffe (*Giraffa camelopardalis tippelskirchi*) metapopulation in the Tarangire Ecosystem in Tanzania consists of multiple discrete social communities, each overlapping in space use with other communities (Bond et al. 2020). Within social communities, group formations merge and split in a fission–fusion process (Aureli et al. 2008), but adult female giraffes show significant preferred and avoided associations within a specific set of other females (Carter et al. 2013*a*, *b*; VanderWaal et al. 2014; Bond et al. 2020). Females with preferred relationships are more closely related than those that appear to avoid each other (Bercovitch and Berry 2012, Carter et al. 2013*a*). The resulting association patterns form a structured social network with multiple levels of organization, characterized by fluctuating group membership with groups drawn from discrete communities (VanderWaal et al. 2014, Bond et al. 2020). Earlier social analyses of this metapopulation found weaker relationship strength and greater social exclusivity among females in subpopulations closer to traditional human settlements called bomas (Bond et al. 2020), which may indicate a disrupted social environment (Maldonado-Chaparro et al. 2018). Previous demographic analyses of giraffes in this study area found adult female and calf survival and reproductive rates varied among spatially discrete administrative areas (Lee et al. 2016, Lee and Bolger 2017), but the contribution of social factors, within the same spatial context, on subpopulation variation in demographic factors is unknown. Giraffes therefore represent a useful case study for examining the influence of social factors on demography.

In earlier work, Lee et al. (2016) defined adult female giraffe subpopulations in the Tarangire Ecosystem by spatially distinct management unit and detected variation in demographic rates related to antipoaching levels (adult female survival), lion (*Panthera leo*) predation pressure (calf survival), and management unit (reproduction). Those results suggested that giraffes do not follow an ideal free distribution (IFD) model in accessing limited resources important for fitness (Fretwell and Lucas 1970).

We expanded upon the previous study by analyzing socially defined, spatially overlapping subpopulations to examine whether variations in demographic rates arise as functions of environmental or social factors. We could not test the same covariates from Lee et al. (2016) because the socially defined subpopulations spanned management units and anti-poaching levels, and lion predation pressure was not available at the scale of the community, so we tested a different but related suite of social and environmental covariates and based our predictions on the earlier work. Our study further allows reflection on whether the dynamics of this metapopulation follow an IFD model (Fretwell and Lucas 1970). Because giraffes can freely move throughout this unfenced landscape, under an IFD we would see equal fitness (survival and reproduction) across subpopulations despite different population densities and different habitat characteristics used, as animals distribute themselves among resource patches of varying qualities in a manner that maximizes individual fitness (Bradbury et al. 2015).

Our objective in this observational study was to compare demography among overlapping socially defined subpopulations in a large, unfenced, heterogeneous study area to quantify potential environmental and social factors that might influence population dynamics. We expected that subpopulations differ in fitness estimates, suggesting a departure from the IFD model (Lee et al. 2016). We predicted adult female survival would increase with increasing distance from areas of intensive human development (towns) where poaching is prevalent, but that survival would be relatively unaffected by bomas (Lee et al. 2016, Knüsel et al. 2019). In contrast, calf groups in our study area were more likely to occur closer to bomas and in bushland vegetation (Bond et al. 2019) so we predicted higher calf survival and reproductive rates in those areas. Volcanic soils are particularly fertile, which may enhance forage quality (Hansen et al. 1985), and the administrative area with the most volcanic soil (Manyara Ranch) had the highest reproductive rate in a previous study (Lee et al. 2016), so we expected that a greater proportion of these soils in a subpopulation's home range would be correlated with higher calf survival and reproductive rates. We predicted that subpopulations with weaker relationship strengths and greater social exclusivity would have lower adult and calf survival probabilities as a result of disruption to the social structure. Finally, we expected adult female survival, calf survival, and reproductive rate would be higher in subpopulations with higher local giraffe population density because females might congregate with their calves and fare better (i.e., fitness maximized) in areas of better-quality habitat.

STUDY AREA

The Tarangire Ecosystem of northern Tanzania supports one of the most diverse large-mammal communities in the world (Lamprey 1964). It is situated in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km^2 (Prins 1987). Elevation ranges between 900 m and 1,200 m above sea level. Vegetation is predominantly semi-arid savanna composed of open grassland, woodland, riverine forest, and dense bushland (Pratt et al. 1966). The Tarangire Ecosystem experiences 3 precipitation seasons (short rains = Oct–Jan, long rains = Feb–May, and dry = Jun–Sep), and average monthly precipitation amounts by season were short rains = 63 mm, long rains = 100 mm, dry = 1 mm (Foley et al. 2008).

The Tarangire Ecosystem is a large, unfenced, heterogeneous area with 2 national parks, a livestock and ecotourism ranch, and areas of human settlements. Our study area was in the core of the Tarangire Ecosystem (Fig. 1), where we sampled 1,500 km^2 in 5 administrative areas with differing management activities from 2012 to 2016. Land management was divided among Tarangire National Park, Lake Manyara National Park, Manyara Ranch, and Mtowambu and Lolkisale Game Controlled Areas. The 2 national parks, Tarangire and Lake Manyara, had high levels of wildlife protection including exclusion of livestock and human settlements and rigorous anti-poaching patrols. Manyara Ranch had intermediate levels of wildlife protection with no human settlements and some anti-poaching patrols but with large numbers of livestock and herders present during the daytime. Mtowambu and Lolkisale Game Controlled Areas had permanent human settlements, many livestock, sport hunting areas (although hunting of giraffes is prohibited), and village Wildlife Management Areas with similar levels of anti-poaching efforts as Manyara Ranch. All administrative areas were connected by movements of adult females (Lee and Bolger 2017). Agriculture in the Tarangire Ecosystem outside of the protected areas increased fivefold from 1984 to 2000 causing substantial habitat loss, increasing fragmentation, and reducing connectivity (Msoffe et al. 2011).

The Rift Valley escarpment, a steep cliff that restricts giraffe movements, formed the western boundary of the study area.

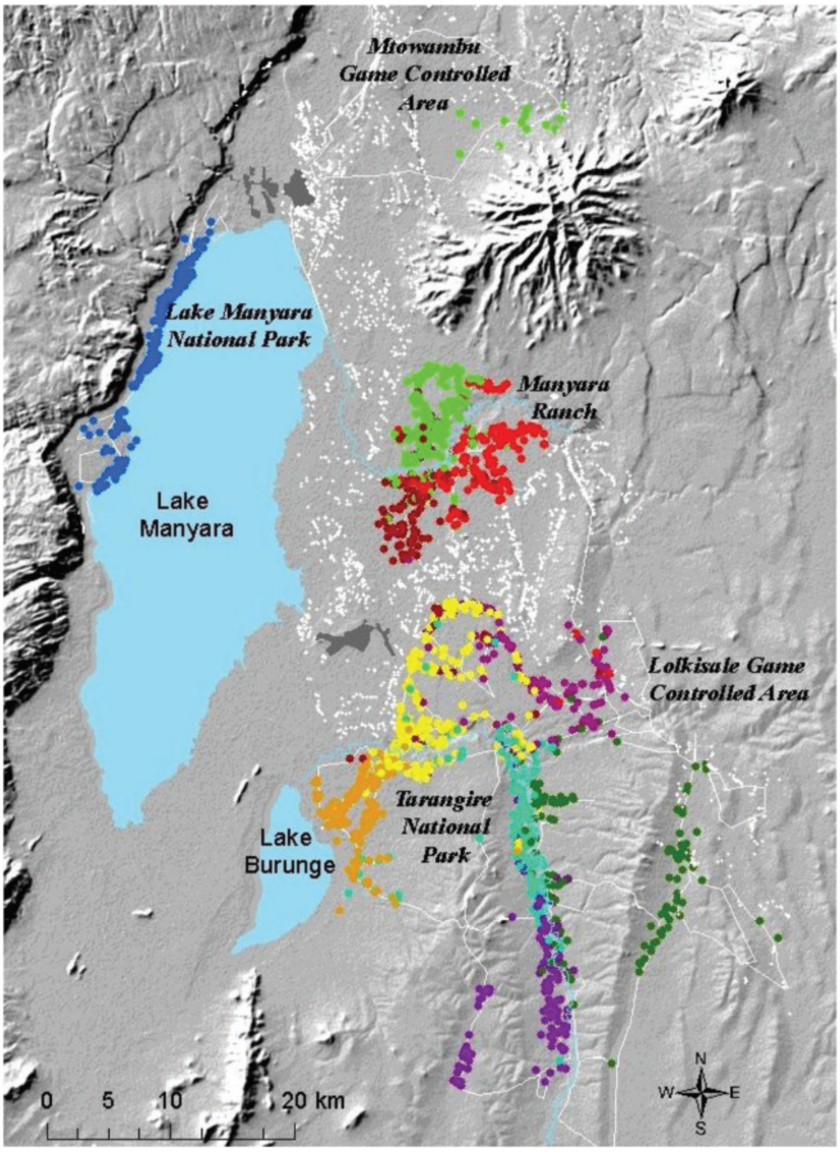

Figure 1. Locations of 10 socially defined subpopulations (communities) of adult female Masai giraffes in the Tarangire Ecosystem of northern Tanzania, 2011–2016. We delineated subpopulations of socially associated individuals with the cluster-walktrap algorithm. White lines are tracks surveyed for giraffe groups, blue lines are rivers, white points are bomas, and dark grey polygons are towns. Different colored dots represent locations of each subpopulation.

West of Tarangire National Park, south of Lake Manyara National Park, and east of Makuyuni town, wild large mammals were rarely observed because of high human and livestock population density and agriculture. Two 2-lane asphalt roads crossed the study area.

METHODS

Field Data Collection

We conducted 31 daytime, fixed-route road transect surveys between May 2011 and October 2016. We photographed and later identified individual giraffes using coat patterns unique to each animal (Foster 1966). We surveyed following a robust design (Pollack 1982), with 3 primary sampling periods per year near the end of each precipitation season (Jan, May, and Sep). Each primary sampling period was composed of 2 independent, back-to-back secondary sampling periods during which we drove all transects once. Each primary sampling period took approximately 20–30 days (10–15 days/secondary period). Transect density throughout the study area was high (0.42 km/km^2) relative to average adult female giraffe home range (115 km^2; Knüsel et al. 2019; Fig. 1). We maintained driving speeds of 15–20 km/hour on all transects, and all survey teams included the same 2 observers and a driver.

During surveys, we encountered a sample of individuals that we captured or recaptured by photographing their coat patterns. We recorded the following data for each individual: age class (calf, subadult, adult), sex (male, female), and global positioning system (GPS) location of the group formation (unique set of individuals observed together on a given survey). We used a suite of physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics, and height to categorize giraffes into the 3 age classes: calf (<1 yr), subadult (1–3 yr), or adult (≥4 yr). Giraffes are iteroparous with non-seasonal birth flow reproduction (Dagg 2014). This research followed American Society of Mammalogists' guidelines for live animals (Sikes et al. 2011).

Data Analysis

We first estimated subpopulation-specific demographic rates of adult female survival, calf survival, and calf-to-adult female ratio. We then explored the relative effects of vegetation, anthropogenic, and social factors on among-subpopulation variation in demographic rates, formulating our predictions from previous research in this metapopulation. We analyzed data from adult females and not adult males in this study because adult females make up the reproductively relevant segment of polygynous vertebrate populations where sex ratios are not male-biased (Caughley 1977, Rankin and Kokko 2007); most population modeling in such systems only considers females (Caswell 2002); and adult female giraffes show stronger preferences in their associations, and form longer-term associations with other females than do adult males and subadult females (Bercovitch and Berry 2012; Carter et al. 2013*a*, *b*).

We constructed a social network by generating an association matrix of pairs of adult females using package asnipe (Farine 2013) in R (R Core Development Team 2019). We then ran the cluster-walktrap community detection algorithm on the network using package igraph (Csárdi and Nepusz 2006), which partitioned the network into 14 communities (subpopulations) based on statistically higher association rates (Bond et al. 2020). High values for the modularity coefficient of the communities and for a metric testing robustness of community assignments (Farine 2014, Shizuka and Farine 2016) indicated strong community structure and high community fidelity, with a low tendency for adult females to mix with other communities. Online Supporting Information provides details on creating our dataset, analyzing social networks, and delineating communities.

For our demographic analyses, we 1) generated encounter histories for individual adult females and calves; 2) assigned individuals to one of the subpopulations; 3) estimated subpopulation-specific demographic rates of adult female survival, calf survival, and calf-to-adult female ratio; 4) tested for significant variation among subpopulation-specific demographic rates; and 5) analyzed subpopulation-specific environmental and social covariates of subpopulation-specific variation in demographic rates. We omitted adult females and calves that could not be assigned to a subpopulation and those from 4 subpopulations with too few individuals to estimate survival. The final dataset contained encounter histories for giraffes in 10 subpopulations spanning the entire study area, including 684 adult females ($\bar{n} = 68$ adult females/subpopulation, range = 27–93) and 744 calves ($\bar{n} = 74$ calves/subpopulation, range = 43–133) for estimating reproductive rates, and 672 adult females ($\bar{n} = 67$ adult females/subpopulation, range = 26–93) and 732 calves ($\bar{n} = 73$ calves/subpopulation, range = 43–133) for estimating apparent survival rates. These data included 75% of all known adult females and 80% of all known calves identified in our metapopulation over the 6-year study period. Adult female subpopulation membership was highly stable over the period of the study (M. L. Bond, University of Zurich, unpublished data).

We also assigned every adult male to an adult female subpopulation for each of the male's detections based on subpopulation membership of the group in which he was detected at a given time. Each male had the potential to be seen in multiple subpopulations. From this we generated for descriptive purposes adult sex ratios (adult male:adult female) for the subpopulations that represented the number of males seen associating with each subpopulation (Table S1, available online in Supporting Information).

Estimating Demographic Rates

Survival.—To analyze apparent survival of adult females and calves, we created individual encounter histories for analysis in Program MARK 8.2 (White and Burnham 1999). We used Pradel robust design models to estimate subpopulation-specific seasonal apparent survival (S), temporary emigration (γ'' and γ'), and capture and recapture (detection) probabilities (p and c; Pradel 1996, Nichols et al. 2000). We used standard notation for models where parameters had subpopulation-specific values (g), temporal variation (t), or constant parameter values (.).

For model comparison, we used Akaike's Information Criterion corrected for small samples (AIC_c) and AIC_c weights in an information-theoretic approach (Burnham and Anderson 2002). We considered models with $\mathrm{AIC}_c < 2$ to be competitive, and we examined the signs of the beta coefficients to determine the direction of the covariate effects. We judged the importance of the covariate effect by the AIC_c weight of the model that included that covariate. Throughout model ranking and selection procedures, we used logit link functions and second part estimation. There is no goodness-of-fit test of whether the most general Pradel model in our candidate set adequately fits the data for robust design (Cooch and White 2019). Therefore, to test goodness of fit, we combined our 2 secondary survey samples from our robust design into a simple binary variable (seen, not seen) and treated the resulting encounter history as a live-encounter Cormack-Jolly-Seber (CJS) model (Cooch and White 2019). We then tested the fit of our data to the fully-time-dependent CJS model using Program RELEASE TEST 2 + TEST 3 (Burnham et al. 1987) and corrected for any overdispersion using median $\hat{c}$ (Cooch and White 2019).

We began with the most fully parameterized model in our set with subpopulation effects on survival $\{S(\mathrm{g})\}$, subpopulation effects on temporary emigration $\{\gamma''(\mathrm{g})$ and $\gamma'(\mathrm{g})\}$, and with interacting temporal and subpopulation effects in capture $\{p(\mathrm{g} \times \mathrm{t})\}$ and recapture $\{c(\mathrm{g} \times \mathrm{t})\}$ rates. Before modeling our parameter of interest, which was survival, we ranked simpler models of capture probability $\{p(.)\}$, $\{p(\mathrm{g})\}$, $\{p(\mathrm{t})\}$, $\{p(\mathrm{g} + \mathrm{t})\}$, and recapture probability $\{c(.)\}$, $\{c(\mathrm{g})\}$, $\{c(\mathrm{t})\}$, $\{c(\mathrm{g} + \mathrm{t})\}$. We also ranked a simpler constant model of temporary emigration $\{\gamma''(.)$ and $\gamma'(.)\}$, and we considered a group covariate model where temporary emigration varied with the distance of each subpopulation from the edge of the study area $\{\gamma''(\mathrm{dist})$ and $\gamma'(\mathrm{dist})\}$.

After selecting the best model of capture, recapture, and temporary emigration parameters, we ranked models of survival that differed by subpopulation $\{S(\mathrm{g})\}$, constant survival among subpopulations $\{S(.)\}$, and subpopulation-specific survival as a function of environmental and social covariates (see below in Environmental and Social Covariates). We did not include time effects on survival and temporary emigration because we were interested only in mean subpopulation-specific values. We were unable to conduct surveys in Lake Manyara National Park during the last 2 primary sampling periods in 2016 because of logistical constraints, so during all analyses we fixed p and c parameters to zero for that subpopulation for those sampling periods.

Reproductive rate.—Giraffe calves form crèches, and in the field it is not possible to attribute a calf to its mother unless extended suckling behavior is observed. Therefore, we were unable to calculate individual adult female reproductive effort and instead estimated subpopulation-level reproductive rates as an annual ratio of calves-to-adult females. For the ratio numerator, we accounted for imperfect detection of neonatal giraffe calves and for calf mortality between birth and the first observation of the calf during surveys, using community-specific capture probabilities and calf survival rates (Lee et al. 2016; see Estimating Community-Specific Reproductive Rates in online Supporting Information for methods and formula).

We modeled among-subpopulation variation in calves-to-adult female as a function of environmental and social covariates using general linear regression (GLM) with a Poisson error distribution, with the logarithm of the number of females in the community as an offset. We ran a quasi-Poisson model to estimate the dispersion parameter, and conducted model selection for reproductive rate using packages MuMIn (Bartoń 2019) and AICcmodavg (Mazerolle 2019) in R. We back-transformed the linear predictor from logits (z) to proportions to present the odds ratios for covariate effects.

Environmental and Social Covariates

We generated each subpopulation's home range by plotting all locations from all adult females in each subpopulation to generate a single home range for each subpopulation from 95% utilization distributions using the package adehabitatHR in R (Calenge 2006). We quantified proportion of overlap of subpopulation home ranges to confirm that many of our subpopulations shared some environmental conditions (see online Supporting Information). To understand why demographic rates might differ among subpopulations, we modeled the effects of 7 subpopulation-specific covariates on mean subpopulation-specific adult female apparent survival, calf apparent survival, and reproductive rate.

1. Proportion of dense bushlands in the subpopulation's home range (bush).
2. Proportion of volcanic soils in the subpopulation's home range (volcanic).
3. Distance (in km) from the center of the subpopulation's home range to the nearest town (town). Towns are clusters of concrete structures in more densely populated areas inhabited by agriculturalists and bushmeat poachers. Small agricultural plots occur near towns, but most vegetation in the study area consists of natural, uncultivated lands.
4. Distance (in km) from the center of the subpopulation's home range to the nearest boma (boma). Bomas are inhabited by pastoralist Masai tribespeople who typically do not kill wild animals for meat. Bomas are structures made of natural materials such as wood, mud, and grass, and are encircled by fencing of cut thorny branches.
5. Local giraffe population density (density), which included all adult female giraffes ever detected within the home range of the subpopulation, regardless of number of detections or subpopulation membership or whether they were subadults at the beginning of the study period ($N = 1{,}139$ adult females).

6. Mean relationship strength (edge weight) between associated pairs of females in each subpopulation (Farine and Whitehead 2015).
7. Mean exclusivity of relationships in each subpopulation calculated by edge weight coefficient of variation (edge weight CV), indicating the extent to which females have stronger relationships with some and weaker relationships with others (Farine and Whitehead 2015). See online Supporting Information for specifics about calculating social and environmental covariates.

See online Supporting Information Table S1 for location in the study area, sample sizes, demographic rates, and environmental and social covariate values for each subpopulation. We did not include >1 explanatory variable together in the same model, but we tested for and report multicollinearity among explanatory variables by calculating Spearman's correlation coefficients (Table S2, available online in Supporting Information). We also tested for a significant relationship between calf survival and reproductive rates using simple linear regression. The data we used in this study are openly available at figshare at doi:10.6084/m9.figshare.13669013.

RESULTS

We documented spatial overlap of giraffe subpopulation home ranges (mean proportion overlap = 0.27 ± 0.16 [SD]). Each subpopulation home range overlapped an average of 4 other subpopulation home ranges (Table S3, available online in Supporting Information).

Adult Female Survival

We found evidence for lack of fit in the adult female encounter history data (TEST 2 + TEST 3 $\chi^2_{82} = 255.01$, $P < 0.001$), but median $\hat{c}$ was <3 ($\hat{c} = 1.187$); therefore, we kept $\hat{c} = 1.0$ for model selection (Cooch and White 2019). Our most parsimonious model of temporary emigration and detectability included temporary emigration varying by distance to edge of the study area, and detectability as fully time- and subpopulation-dependent {*S*(g) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)} (Table S4, available online in Supporting Information).

Model selection results indicated that adult female survival did not vary significantly by subpopulation (Table 1). The model best supported by the data in the candidate set was constant survival across subpopulations {*S*(.)} (Table 1). The model of constant survival across subpopulations was substantially better than the model with subpopulation variation in survival (model likelihood for {*S*(.)} = 1, and {*S*(g)} = 0). Annual adult female apparent survival rate across all subpopulations was 0.97 ± 0.017 (SE; 95% CI = 0.31–0.99).

None of the environmental and social covariate models were competitive with the top model of constant adult female survival (Table 1). The 2 social covariates for survival, {*S*(edge weight CV)} and {*S*(edge weight)}, were the next-highest ranked models and the only covariate models that carried substantial weight. Adult survival probability was negatively correlated with relationship exclusivity (ß$_{\text{edge weight CV}} = -1.153 \pm 1.451$) and positively correlated with relationship strength (ß$_{\text{edge weight}} = 0.008 \pm 2.935$); however, the 95% confidence intervals for both coefficients overlapped 1.

Table 1. Model selection results for constant survival, group effects, and covariate models of apparent adult female and calf survival probabilities (*S*) among 10 socially defined subpopulations of Masai giraffes in the Tarangire Ecosystem in northern Tanzania, 2012–2016. Social covariates include mean relationship strength of associated individuals (edge weight) and exclusivity of relationships in each subpopulation measured as edge weight coefficient of variation (edge weight CV). Environmental covariates include distance to nearest boma (km), distance to nearest town (km), and proportion of 2 vegetation types in the subpopulation home range: dense bushlands (bush) and volcanic soil (volcanic). Local adult female giraffe population density (density) is a socio-environmental covariate, and g is subpopulation effects. We ranked models by difference in corrected Akaike's Information Criterion (ΔAIC_c) and provide AIC_c weights, model likelihoods, number of parameters (*K*), and deviance for each model. All female survival models included structure from our most parsimonious model of temporary emigration and detectability, which included temporary emigration (γ'' and γ') varying by distance to edge of the study area (dist), and detectability (*p* and *c*) as fully subpopulation- and time-dependent (g × t). The structure of calf survival models was similar except temporary emigration was constant (.).

Model	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	*K*	Deviance
Adult female survival						
{*S*(.) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,116.13	0.00	0.61	1.00	449	35,133.59
{*S*(edge weight CV) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,118.48	2.35	0.19	0.31	450	35,133.58
{*S*(edge weight) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,118.49	2.36	0.19	0.31	450	35,133.59
{*S*(volcanic) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,125.24	9.11	0.01	0.01	450	35,140.34
{*S*(bush) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,126.17	10.03	0.00	0.01	450	35,141.26
{*S*(town) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,126.45	10.32	0.00	0.01	450	35,141.55
{*S*(boma) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,127.10	10.97	0.00	0.00	450	35,142.20
{*S*(density) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,127.27	11.14	0.00	0.00	450	35,142.37
{*S*(g) γ''(dist) γ'(dist) *p*(g × t) *c*(g × t)}	19,132.95	16.82	0.00	0.00	458	35,129.13
Calf survival						
{*S*(bush) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,383.75	0.00	0.43	1.00	454	15,919.17
{*S*(density) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,385.58	1.83	0.17	0.40	454	15,921.00
{*S*(g) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,385.97	2.22	0.14	0.33	462	15,899.99
{*S*(boma) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,386.32	2.57	0.12	0.28	454	15,921.74
{*S*(volcanic) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,387.13	3.38	0.08	0.18	454	15,922.55
{*S*(town) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,389.64	5.89	0.02	0.05	454	15,925.06
{*S*(.) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,389.80	6.05	0.02	0.05	453	15,927.89
{*S*(edge weight) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,391.97	8.23	0.01	0.02	454	15,927.39
{*S*(edge weight CV) γ''(.) γ'(.) *p*(g × t) *c*(g × t)}	11,392.41	8.66	0.01	0.01	454	15,927.83

Further, the top model of constant survival across subpopulations was more likely than either of the social covariate models based on AIC$_c$ weights (Table 1).

Calf Survival

For calves, we also detected evidence of lack of fit (TEST 2 + TEST 3 $\chi^2_{62} = 121.905$, $P < 0.001$); however, the median $\hat{c}$ was <3 ($\hat{c} = 1.187$), so we kept $\hat{c} = 1.0$ for model selection (Cooch and White 2019). The best model of temporary emigration and detectability parameters was $\{S(\mathrm{g})\ \gamma''(.)\ \gamma'(.)\ p(\mathrm{g} \times \mathrm{t})\ c(\mathrm{g} \times \mathrm{t})\}$ (Table S4).

The model of subpopulation-specific calf survival was better supported than the constant survival model (model likelihood for $\{S(\mathrm{g})\} = 0.329$, and $\{S(.)\} = 0.049$, thus 6.71 times more likely; Table 1), indicating calf survival varied significantly by subpopulation. Subpopulation-specific annual calf survival probabilities ranged from 0.69 to 0.83 (Fig. 2; Table S1). The best calf survival model was the covariate model where survival probability varied by proportion of dense bushlands within a subpopulation's home range (Table 1). The second-ranked covariate model of local giraffe population density was competitive (ΔAIC$_c = 1.833$), but the top model was 2.5 times more likely (model likelihood for $\{S(\mathrm{bush})\} = 1$ and $\{S(\mathrm{density})\} = 0.40$; Table 1).

Calf survival probability was lower with more dense bushlands in the subpopulation home range ($\text{ß}_{\text{bush}} = -1.401 \pm 0.464$) and the 95% confidence interval did not overlap 1 (95% CI = −2.310–−0.491). For every 10% increase in the proportion of dense bushlands in the community home range, annual calf survival probability decreased by approximately 0.03. Calf survival probability was greater in subpopulations with higher local giraffe population density ($\text{ß}_{\text{density}} = 0.299 \pm 0.120$) and the effect was also significant (95% CI = 0.064–0.536). For each additional adult female/km^2, annual calf survival probability increases by approximately 0.04.

Reproductive Rate

We detected little overdispersion in the quasi-Poisson model ($\hat{c} = 1.320$) so we used the Poisson distribution to test the influence of socio-environmental variables on among-subpopulation variation in reproductive rate. The best model included the covariate volcanic soils and its coefficient was positive ($\text{ß}_{\text{volcanic}} = 0.515 \pm 0.121$, $P < 0.001$; Table 2) indicating that subpopulations with more volcanic soils in their home range had higher reproductive rates. This model fit significantly better than a null model ($\chi^2_1 = 17.981$, $P < 0.001$) and carried 48% of the weight in the candidate set. The relative risk ratio (1.674; 95% CI = 1.320–2.215) suggests that for each 0.01 increase in proportion of volcanic soils in a community's home range, the annual count of calves increased by 1.67. The covariate models with distance to town and boma were both competitive with the top model and the coefficients were negative ($\text{ß}_{\text{town}} = -0.028 \pm 0.007$, $P < 0.001$ and $\text{ß}_{\text{boma}} = -0.056 \pm 0.014$, $P < 0.001$; Table 2). The relative risk ratios (town: 0.972; 95% CI = 0.958–0.985 and boma: 0.946; 95% CI = 0.919–0.972) indicate that a subpopulation's annual calf count decreased by 0.03 with every kilometer farther from the nearest town, and by 0.05 with every kilometer farther from the nearest boma. We found no significant relationship between calf survival and reproductive rates among subpopulations ($F_{1,8} = 1.901$, $P = 0.204$).

DISCUSSION

We used network analysis of social associations among hundreds of adult female giraffes in a large, free-ranging

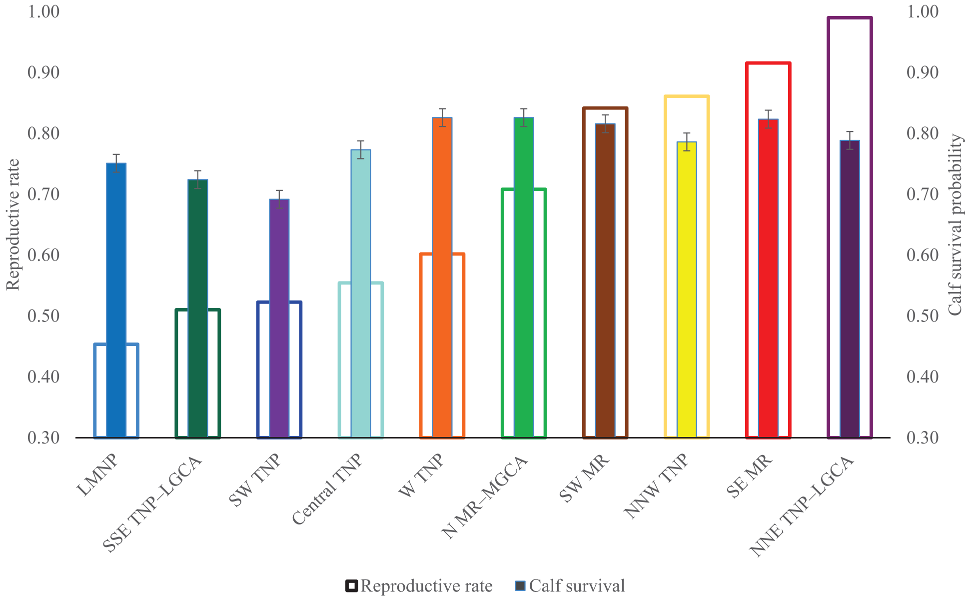

Figure 2. Reproductive rates (ratio of calves-to-adult females) and calf survival probabilities (±SE) for 744 calves and 684 adult female giraffes in 10 socially defined subpopulations in the Tarangire Ecosystem of northern Tanzania, 2011–2016. South-southeast Tarangire National Park–Lolkisale Game Controlled Area = SSE TNP–LGCA. Lake Manyara National Park = LMNP. Central Tarangire National Park = Central TNP. Northern Manyara Ranch–Mtowambu Game Controlled Area = N MR–MGCA. North-northwest Tarangire National Park = NNW TNP. Southwest Tarangire National Park = SW TNP. North-northeast Tarangire National Park—Lolkisale Game Controlled Area = NNE TNP–LGCA. Southeast Manyara Ranch = SE MR. Southwest Manyara Ranch = SW MR. Western Tarangire National Park = W TNP.

Table 2. Model selection results comparing general linear models of variation in reproductive rate (calves to adult females) among 10 socially defined subpopulations of Masai giraffes in the Tarangire Ecosystem in northern Tanzania, 2012–2016. Social covariates include mean relationship strength of associated individuals (edge weight) and exclusivity of relationships in each subpopulation measured as edge weight coefficient of variation (edge weight CV). Environmental covariates include distance to nearest boma (km), distance to nearest town (km), and proportion of 2 vegetation types in the subpopulation home range: dense bushlands and volcanic soil. Local adult female giraffe population density is a socio-environmental covariate. We ranked models by difference in corrected Akaike's Information Criterion (ΔAIC_c) and provide degrees of freedom (df) and AIC_c weights for each model. We considered models with $\Delta\text{AIC}_c < 2$ to be competitive models.

	Intercept	β	df	AIC_c	ΔAIC_c	Weight
Volcanic soil (proportion)	−0.585	0.515	2	72.52	0.00	0.48
Distance to town (km)	−0.076	−0.028	2	73.41	0.89	0.30
Distance to boma (km)	−0.108	−0.056	2	74.17	1.65	0.21
Dense bushland (proportion)	−0.240	−0.925	2	80.14	7.62	0.01
Population density	−0.492	0.067	2	88.92	16.40	0.00
Edge weight	−0.502	0.261	2	90.18	17.66	0.00
Edge weight CV	−0.246	−0.093	2	90.32	17.80	0.00

metapopulation to define socially discrete communities—here considered as subpopulations—within a heterogeneous landscape with variable vegetation and human development. The subpopulations were discrete in terms of social associations despite substantial overlap in space use, and were stable over time. Subpopulations exhibited variation in demography, demonstrating our ability to detect fine-scale population dynamics associated with socially mediated population structure within a large continuous metapopulation. Such variation in demography suggests that the distribution of giraffes in the Tarangire Ecosystem cannot be explained by an IFD model of fitness equilibrium across differences in population density and habitat quality (Fretwell and Lucas 1970). We then elucidated environmental and social factors that might influence subpopulation dynamics within the metapopulation. In particular, we detected equal adult female survival but significant variation in calf survival and reproductive rates among the subpopulations, which was best explained by environmental covariates and giraffe population density, rather than by characteristics of social relationships among adult females.

The top-ranked model, with 61% of the weight, indicated adult female survival was high and nearly constant across all subpopulations. We found some evidence that subpopulations with stronger and less exclusive relationships had higher adult female survival, which warrants further study. The social models each carried 19% of the weight in the model set and were ranked higher than habitat or anthropogenic models, suggesting some support for social measures having influenced adult female survival. Population growth rates in long-lived animals like giraffes often are determined by variation in recruitment processes and fertility rates, whereas adult female survival typically remains high and constant (Gaillard et al. 1998, 2000; Morris and Doak 2002), although in some cases, adult female survival can contribute the highest proportion of variation in population growth (Johnson et al. 2010, Lee et al. 2016). Differences in reproduction and calf survival were more strongly influencing variation in population dynamics among our subpopulations. When we matched socially defined subpopulations to administrative areas in the landscape, the pattern of our demographic rates generally agreed with that of previous analyses for this population (Lee et al. 2016), with lower calf survival and lower reproductive rates inside the national parks compared to outside. The demographic rates in the present study were higher than published estimates of this metapopulation from 2012–2014 (Lee et al. 2016). We attribute this to the initiation of resource protection activities in 2 community Wildlife Management Areas adjacent to Tarangire and Lake Manyara national parks in 2014 and 2015, which significantly improved giraffe survival (Lee 2018) and increased giraffe population densities (Lee and Bond 2018). Additional stringent anti-poaching measures throughout the country were implemented by the newly elected Tanzanian president in early 2016, which likely further improved giraffe survival rates.

The larger number of subpopulations created by social network analyses compared with subpopulations defined by administrative boundaries enabled finer-scaled investigation of the environmental and social covariates across the landscape that highlighted specific subpopulations that had greater or lesser fitness, even within the same administrative area. We identified subpopulations with low reproductive rates and low calf survival in Lake Manyara National Park and southern Tarangire National Park (Fig. 2). These subpopulations represent a small isolated national park and a portion of another larger national park, so these measures of fitness were not related to more restrictive land use or higher protection levels. Some subpopulations had moderately low reproductive rates but high calf survival. Such variation in reproductive output could be due to spatial variability in habitat availability or quality, food resources, weather, disease, parasites, predator pressure, human activities, and giraffe population density (Jorgenson et al. 1997, Gaillard et al. 1998, Coulson et al. 1999, Ozgul et al. 2006, Contasti et al. 2012). Environmental covariates related to food resources, predation risk, human activities, and giraffe population density explained variation in calf survival probabilities and reproductive rates.

According to the IFD model (Fretwell and Lucas 1970), more individuals congregating in better-quality patches should depress fitness there because of density-dependent effects, leading to equal fitness among subpopulations (Jones et al. 2006, Bradbury et al. 2015). We did not detect fitness equilibrium among our subpopulations; areas with higher adult female giraffe population densities also had higher calf survival, suggesting that giraffes in this metapopulation did not distribute themselves according to the IFD model.

Given our knowledge of interacting environmental and social factors determining the fitness landscape, giraffes likely do not follow the IFD model, perhaps because of underlying heterogeneous *per capita* fitness variation. Female population densities were inversely related to proportion of dense bushlands (Table S2) possibly because bushlands offer fewer food resources or facilitate lion predation on calves (Hopcraft et al. 2005), or both. Our results complement a previous study showing spatial variation in calf survival among management units was negatively correlated with lion predation pressure (Lee et al. 2016). We did not have subpopulation-specific data on lion predation pressure here, but our finer-scale demographic analysis suggests some adult females may congregate away from areas of high predation risk to their calves. The areas where calf survival was highest also had the highest giraffe densities and therefore have likely not exceeded carrying capacity. Reproductive rates were higher in areas with more volcanic soils. Therefore, it is unclear why more females do not avoid high-risk areas and raise their calves in better-quality habitats, such as on nutrient-rich volcanic soils and areas with less dense bushlands. Subpopulations of females may depart from the IFD model potentially because of intercommunity differences in competitive ability, perception, learning, or experience. Communities with higher fitness may have greater dominance or competitive abilities that allow them to exclude other communities (Fretwell 1972), they may have discovered the higher-quality habitats because of greater perceptive abilities or random factors, they may learn a superior foraging culture from their mothers that leads to higher fitness via increased nutrition (Foley et al. 2008), or giraffes simply may have incomplete awareness of the fitness landscape.

Subpopulations with 3 of the 4 highest adult sex ratios (the most males per female) had the lowest calf survival and reproductive rates, excepting Lake Manyara National Park, which had the lowest sex ratio and low fitness (Fig. 2). Subpopulations with higher sex ratios occupied areas with higher densities of younger subordinate adult males, and these areas seem to contain habitat with either poorer-quality browse or higher predation rates on calves. Sexual segregation by land cover types in this metapopulation as first illustrated by Bond et al. (2019) is likely mediated by requirements of reproductive females that is then reflected in fitness of the subpopulation. Thus, sex ratio probably does not influence demographic variation, as seen in some feral horse (*Equus* spp.) populations (Regan et al. 2020), but rather reflects variation in habitat quality for reproduction.

As predicted, reproductive rates were highest in subpopulations with more volcanic soils in the home range, which we suspect leads to high quality of forage. Volcanic soils are found in the northern part of Tarangire National Park and farther northwards outside the park, so ensuring access to this soil type for giraffes should contribute to conservation of the species. Contrary to our prediction, higher proportion of bushlands was correlated with lower calf survival, possibly because giraffe calves are vulnerable to lion predation (Lee et al. 2016) and lions prefer to hunt in dense vegetation (Hopcraft et al. 2005). Both Lake Manyara and Tarangire national parks have substantially higher lion densities compared to outside the parks (Lee et al. 2016), and within Tarangire National Park, subpopulations with higher calf survival had less bushlands in the home range. Subpopulations closer to human settlements had higher reproductive rates, and we recorded the highest calf survival probabilities in the subpopulations that included Manyara Ranch with its high levels of herders and livestock and in the subpopulation on the western edge of Tarangire National Park where herders also are common. The presence of humans on foot may disrupt female giraffes, leading them to form more exclusive groups (Bond et al. 2020), whereas females with calves were more likely to be found closer to bomas, likely because of reduced predator densities there (Bond et al. 2019). We therefore suspect that pastoralists disrupting natural predation, in addition to favorable forage conditions, is a possible mechanism for our observed spatial demographic patterns. Areas with more dense bushlands tended to be farther from towns and bomas, and also supported lower densities of adult female giraffes—conditions that were associated with lower calf survival. These results offer evidence that the trade-off by adult female giraffes between lowering predation risk to their calves by aggregating closer to human settlements, versus maintaining strong relationships with more of the members of their social community by avoiding human disturbance, had positive demographic results.

Calf survival probabilities were similar among spatially overlapping subpopulations, but reproductive rates differed even among subpopulations with substantial overlap. As an example, 63% of the range of giraffes in the northern Manyara Ranch-Mtowambu Game Controlled Area subpopulation was overlapped by the southeast Manyara Ranch subpopulation's range, yet the southeast had a substantially higher reproductive rate (0.92 vs. 0.71). These 2 subpopulations also had similar environmental and social covariate values. Thus, the use of social associations to define subpopulations elucidated a new level of biologically meaningful population structure.

Spatial structure of populations is a central concern to biologists (Thomas and Kunin 1999), but the application of objective, biologically meaningful clustering techniques to define populations for demographic analysis has been rare. Our approach adds to the few techniques available to ecologists to define continuous populations to better understand the socio-ecological drivers of population dynamics. Earlier work on this problem by Coulson et al. (1999) used data on the distances between every pair of Soay sheep (*Ovis aries*) and hierarchical cluster analysis to define groups. Schaefer et al. (2001) used fuzzy cluster analysis of radio-telemetry locations to group woodland caribou (*Rangifer tarandus caribou*). Ball et al. (2010) combined telemetry location data with genetic data and individual-based clustering to delineate spatial structure for woodland caribou. We support the notion that a foundation for defining population and subpopulation structures for social species should be the patterns of affiliation among individuals (Harwood 2009, Nagy et al. 2011). Social groups also share many similarities in environmental factors that affect fitness (e.g., food, water resources, predation pressure, cover) so within-group variation in survival and reproductive rates should be less than variation among groups.

Our study advances the concept of social subpopulations and contributes to understanding heterogeneity in population dynamics that may result from nonspatial as much as spatial factors. For example, natal dispersal is an important behavioral and demographic process that is typically defined in terms of locations and measured spatially (Matthysen 2012), but social dispersal into nearby but socially distinct groups has been described in equids (Linklater and Cameron 2009) and primates (Cheney and Seyfarth 1983, Lazaro-Perea 2001, Teichroeb et al. 2011). Resistance to dispersal into new social groups is lower when social connections already exist (Armansin et al. 2020), underscoring the importance of social associations that influence population-level demographic processes. Finally, future work is needed to examine whether variation in fitness traits among subpopulations is influenced more by some inherent aspect of the phenotypes in a social community (Farine et al. 2015), rather than spatially explicit factors such as vegetation quality, anthropogenic pressures, or local population density.

MANAGEMENT IMPLICATIONS

The framework of comparing demography among overlapping socially defined subpopulations represents a novel approach to quantifying potential environmental and social factors that might drive population dynamics. Social relationships among individuals are a biologically meaningful basis for defining population structure and should be used where possible to better understand demographic variation among subpopulations. This also enables more targeted and effective conservation measures to be developed for at-risk species. Population biologists and managers would benefit from additional tractable tools to delineate and explore fine-scale population structure and demographic variation in biologically meaningful ways, and social network analysis provides one such tool.

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