

Research



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Sociability increases survival of adult female giraffes

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Studies increasingly show that social connectedness plays a key role in determining survival, in addition to natural and anthropogenic environmental factors. Few studies, however, integrated social, non-social and demographic data to elucidate what components of an animal's socio-ecological environment are most important to their survival. Female giraffes (*Giraffa camelopardalis*) form structured societies with highly dynamic group membership but stable long-term associations. We examined the relative contributions of sociability (relationship strength, gregariousness and betweenness), together with those of the natural (food sources and vegetation types) and anthropogenic environment (distance from human settlements), to adult female giraffe survival. We tested predictions about the influence of sociability and natural and human factors at two social levels: the individual and the social community. Survival was primarily driven by individual—rather than community-level social factors. Gregariousness (the number of other females each individual was observed with on average) was most important in explaining variation in female adult survival, more than other social traits and any natural or anthropogenic environmental factors. For adult female giraffes, grouping with more other females, even as group membership frequently changes, is correlated with better survival, and this sociability appears to be more important than several attributes of their non-social environment.

1. Introduction

Many animal species form complex, multi-level societies of closely bonded associates living within larger communities of more loosely connected individuals [1]. Within those societies, groups can fluctuate in size and composition in a fission–fusion process [2,3]. Such variation in the social environment is a general characteristic of species living in heterogeneous ecological environments, which in turn might favour the evolution of multiple social phenotypes [4,5]. Social or environmental factors, such as local population density, predation pressure or resource predictability, can influence whether individuals are found living a more solitary or gregarious lifestyle, termed social flexibility [5]. A fundamental question is how do differences in the socio-ecological environment experienced by individuals influence their survival?

There is a substantial body of the literature linking measures of social connectedness with fitness in a variety of taxa (for a recent review on mammals, see [6]). In general, individuals with strong and stable bonds [7–9] and/or that are more connected within their networks have higher survival [10–12]. However, previous work on demographic consequences of social connectedness has not incorporated the influence of an individual's natural environment and anthropogenic pressures, including interactions among socio-ecological factors. Examining sociability alone is not enough, as it can be the consequence of resource selection, which has direct effects on survival. Therefore, one should consider social together with natural and anthropogenic environmental factors

(hereafter, the non-social environment), and their interactions, explicitly to elucidate social effects on survival.

Here, we explore how among-individual variation in the social and non-social environment affects adult female survival in a large population of Masai giraffes (*Giraffa camelopardalis tippelskirchi*). The association patterns of female giraffes form a structured social network characterized by multiple levels of organization [13,14]. Males, on the other hand, are more solitary, show weaker preferences in their associations and do not form longer-term associations [13,15–17]. Thus the basic unit of a giraffe group is composed of adult females, and they establish long-term relationships with other adult females [17]. Given the evidence from other taxa that social connectedness plays an important role in determining fitness, and that survivorship of giraffes is influenced by anthropogenic and natural environmental factors e.g. [18], our aim is to document the relative importance of individual sociability and features of the non-social environment in affecting survival of adult females. Female giraffes can have a 20-year breeding tenure, and lifespan accounts for the majority of variance in lifetime reproductive success [19]. Thus, if a female's sociability increases her survival, it will also increase her lifetime reproductive success.

For species that live in clear and distinct social communities, survival could be driven by an individual's social position within the community but also by community-level properties. However, this has received little study. We used mark–recapture data from 512 individually identified adult female giraffes in the Tarangire Ecosystem of northern Tanzania (figure 1) over a 5-year period to estimate the relationship between survival probabilities and individual as well as community-level measures of both social connectedness (hereafter sociability) and non-social environmental features. We quantified sociability using five metrics derived from social network analysis: the strength of relationships (mean and maximum), the exclusivity of relationships (variation in relationship strength), gregariousness (number of females each individual was observed with on average) and the extent to which an individual links to other adult females that are not directly connected (betweenness). We then modelled whether these social traits explained variation in survival rates relative to, in addition to, or in interaction with, the variation in survival arising from the non-social environment, including vegetation structure, prevalence of preferred forage plants and distance from low- and high-impact human settlements. We tested nine predictions drawn from the literature about the influence of these social traits and non-social environmental features on survival, and we considered these predictions at two social scales: at the level of the individual and the level of the social community.

(a) Predictions on effects of sociability and environment on survival

We predicted female survival would be positively correlated with (1) relationship strength, (2) less exclusive relationships, (3) greater gregariousness, and (4) higher betweenness. Closer bonds could make behaviour of associates more predictable, which may reduce agonistic interactions and thus reduce stress [20]. Females with stronger bonds to fewer other associates (i.e. more exclusive relationships) could have lower survival, as this is a signature of disrupted social systems that can, correspondingly, reduce group functions [21].

More socially isolated individuals that roam with fewer others might miss out on important knowledge about food resources and predators [22,23]. More mobile individuals in a multi-level society, indicated by higher betweenness, might be able to better exploit dynamic and dispersed food resources [24].

We expected adult female survival would (5) decrease closer to areas of intensive human influences where habitat loss and poaching are more prevalent [18]. We also expected higher survival (6) with increasing proportion of a female's locations on volcanic soils because these soils are especially fertile, which may enhance forage quality [25], and (7) with increasing proportion of locations in dense woodlands and thickets, which are selected by groups with calves [26]. We predicted (8) higher survival with increasing proportions of locations in *Vachelia* (formerly *Acacia*) *tortilis*, *V. drepanolobium* and *Dichrostachys cinerea*, as these forage species are seasonally selected by single adult female giraffes, and female groups with calves [26–29]. Finally, we expected adult female survival would (9) increase with increasing local adult female giraffe population density within the community home range, as we presume individuals congregate and fare better in higher-quality habitats [14]. Alternatively, more individuals might lead to more food competition, depending on resource distribution and availability, so higher population densities could also reduce survival, although density-dependent decreases in adult female survival in ungulates tend to affect only the oldest females [30].

2. Methods

(a) Study area

We selected the Tarangire Ecosystem in northern Tanzania as our study area because it is a heterogeneous landscape with varying degrees of anthropogenic pressures on wildlife, ranging from habitats deep within protected national parks to areas in close proximity to towns and bomas. Bomas are dispersed family compounds of huts constructed with natural materials, and towns consist of dense concentrations of concrete structures. Bomas in our study area are occupied by pastoralist Masai people who typically do not poach giraffes for meat, but may kill or harass carnivores to protect livestock [31]. Towns are much rarer, but have higher human density, are typically surrounded by farmlands, and are inhabited by bushmeat poachers who often target giraffes [32].

The Tarangire Ecosystem is a savannah biome with variation in vegetation types ranging from open grasslands to dense deciduous bushlands and thickets, supporting one of the most diverse large-mammal communities in the world [33]. Our study area in the core of the Tarangire Ecosystem is 4400 km² where we sampled for giraffes in a 1500 km² area along road transects in five administrative areas (figure 1), Tarangire National Park, Lake Manyara National Park, Manyara Ranch Conservancy and Mtowambu and Lolkisale Game Controlled Areas. The entire study area is unfenced and all administrative areas are connected by movements of adult female giraffes [34].

(b) Data collection

We used photographic capture–mark–recapture techniques to identify individual giraffes from the coat markings unique to each animal [35,36]. We conducted 30 independent, day-time, fixed-route road-transect photographic encounter surveys between January 2012 and October 2016. The Tarangire Ecosystem experiences three precipitation seasons per year (short rains =

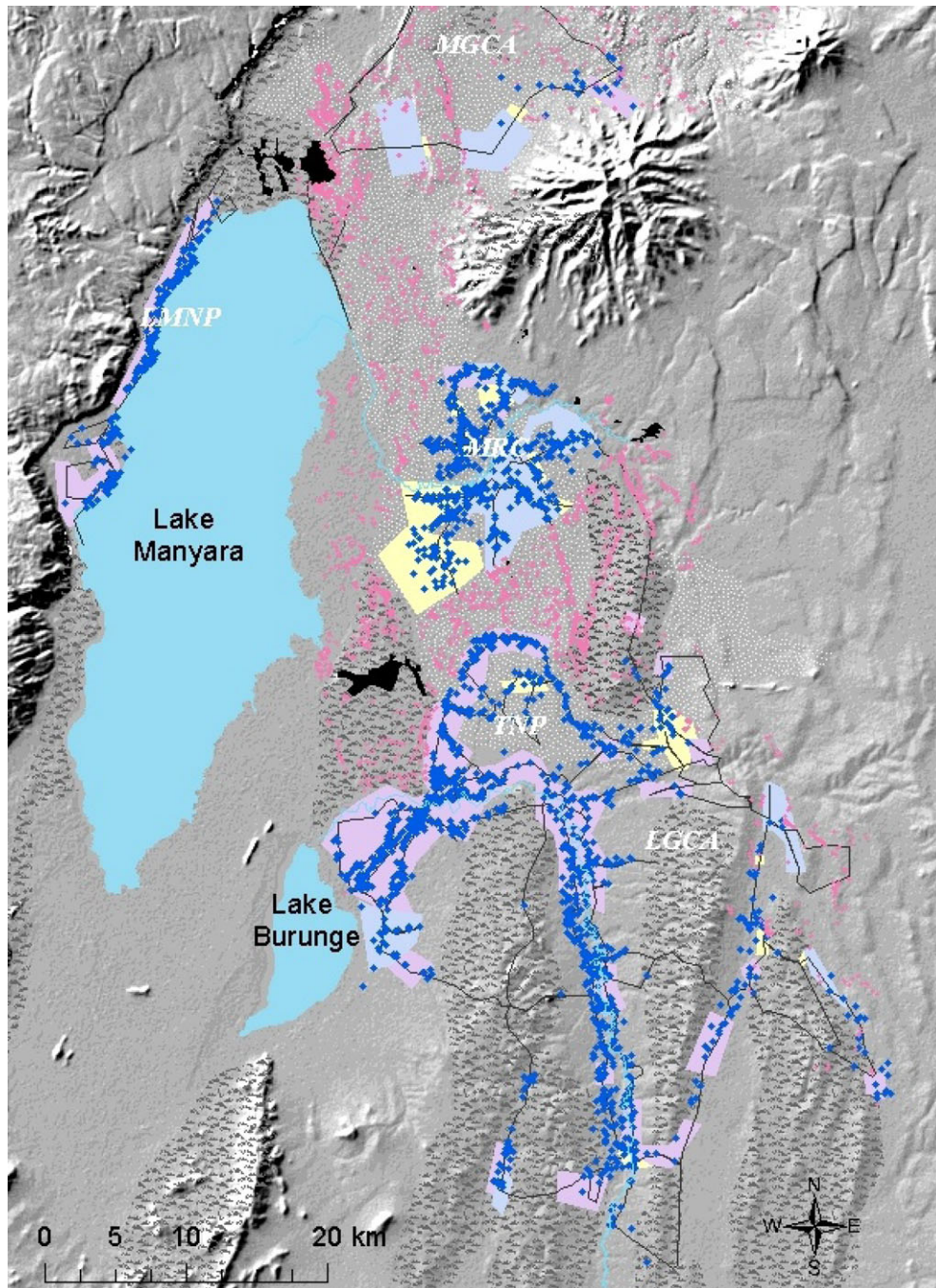


Figure 1. Locations (blue diamonds) of groups of adult female giraffes and non-social environmental covariates in the Tarangire Ecosystem of northern Tanzania, 2011–2016. LMNP is Lake Manyara National Park, TNP is Tarangire National Park, MRC is Manyara Ranch Conservancy, MGCA is Mtowambu Game Controlled Area and LCGA is Lolkisale Game Controlled Area. Black lines are dirt tracks surveyed for giraffe groups, blue lines are rivers, pink points are bomas and black polygons are towns. White dots are volcanic soils, and grey stippling is dense bushlands. Pale yellow polygons are stands dominated by greater than 10% *Dichrostachys cinerea*, pale blue by *Vachelia drepanolobium* and lavender by *V. tortilis*.

Oct–Jan with an average monthly precipitation of 63 mm; long rains = Feb–May with 100 mm/month; and dry = Jun–Sep with 1 mm/month; [37]). We surveyed for giraffes near the end of each season according to a robust design with a primary sampling period composed of two independent, consecutive secondary sampling periods during which we drove all transects in the study area one time only [38]. All survey transects were dirt roads, and each primary sampling period took approximately 21–30 days.

When we encountered giraffes, we ‘marked’ or ‘resighted’ individuals by driving to within 150 m distance and photographing them. We recorded age class (calf, subadult, adult; see [39]), sex (male, female) and GPS location. In our dataset we analysed only females first observed during the initial year of the study and who were adults (over 4 years; [40]) the first time they

were observed. We considered a group formation to be one or more giraffes that were foraging or moving together, and with greater than 500 m between the closest member of another group [14,16,17]. We used the gambit of the group—individuals present together in the same group formation—to define associations [41]. Our study design involved repeatedly measuring individually identified giraffes, with each individual assigned to only one group formation per secondary sampling period.

(c) Data analysis

(i) Social and non-social environmental covariates

We created a matrix of individual adult females and their associations to generate a weighted network and calculate a set

of metrics representing attributes of each female's social tendencies. In network terminology, the individuals are called 'nodes', and the associations among individuals are called 'edges'. Weighting edges takes into account the tendency for a pair of nodes (dyad) to be seen together. To calculate edge weights between individual giraffes, we applied the simple ratio index of association ([42]; see electronic supplementary material for equation) which quantifies associations on a scale from 0 (two individuals never seen together) to 1 (two individuals always seen together) [43]. Higher edge weights represent more times a pair of giraffes were seen in the same group formations over the study period, hence a stronger relationship between them.

We calculated node-level measures of sociability, including the strength of each female's relationships from her mean and maximum non-zero edge weight, and the coefficient of variation of her non-zero edge weights. We quantified each female's gregariousness score as the sum of her edge weights, representing the number of other females she was observed with on average, and her betweenness score, which is a count of the number of shortest paths between other nodes that flow through the node representing that individual [44]. Betweenness measures how important the female is for connecting disparate parts of the network: individuals with high betweenness scores are more likely to link independent groups or communities and may tend to change groups more often than others. Higher values of edge weight, gregariousness and betweenness translate to greater sociability, and a higher coefficient of variation indicates stronger relationships with some associates and weaker relationships with others. See electronic supplementary material, figure S1 for histograms of the values.

Beyond measuring individual-level social traits, social network analysis can also be used to partition populations into social communities based on sets of nodes with denser connections [45,46]. By applying a community detection algorithm on the weighted network, we assigned our subsample of adult female giraffes to communities (see [15] and electronic supplementary material for community detection methods) and tested whether grouping these females together for various parameters in our survival analysis improved model fit, because we assumed individuals within the same communities would be subject to similar social and non-social environmental influences.

Our full dataset includes life histories for 1139 individually identified adult females observed in 2137 different group formations over our 5-year study period. We subsampled the adult females to those with at least six observations to improve the accuracy of the edge weights [47]. Community detection of the subsample resulted in the adult female metapopulation being partitioned into 14 social communities, but we excluded members of four communities that contained less than 15 individuals. These communities only overlapped partially with our study area, meaning that it is unlikely that we could capture meaningful data on their membership, community-level covariates, or demographic rates. The remaining 10 communities contained an average of 51 individuals each (range = 28–70) and a total of 512 adult females, which became our final dataset for modelling seasonal apparent survival probabilities.

We constructed networks and conducted analyses in R v. 3.6.1 [48] using package *asnipe* [49] to create the association matrix and calculate edge weights; package *sna* [44] to calculate betweenness; and package *igraph* [50] to calculate each individual's gregariousness score and run the community detection algorithm. We generated non-social environmental covariates of proximity to bomas and towns, vegetation structure and primary forage species, as well as local adult female giraffe population density, using ArcMap 10.8 (Environmental Systems Research Institute, Redlands, CA, USA) and packages *adehabitatHR* [51] and *raster*

[52] for R. Details are provided in electronic supplementary material, tables S1 and S2 and figure S2a–d.

(ii) Estimating survival rates

We estimated survival using individual encounter histories from adult females that were seen greater than five times. Truncating individuals with fewer observations is likely to positively bias survival estimates, but this is necessary to obtain accurate measures of sociability [47]. Thus, resulting survival estimates should not be considered reflective of the population as a whole, but our approach enables us to test covariate effects among our subsample of individuals. We estimated apparent survival probabilities and tested predictions using capture–recapture methods [53] implemented in program MARK 8.2 [54]. We used Pradel robust design models to estimate seasonal apparent survival (S), temporary emigration from the study area (γ'' and γ'), and capture and recapture probabilities (p and c) [55,56], and ranked models using Akaike's information criterion corrected for small samples (AIC_c). We first ranked models representing all possible combinations of S , γ'' and γ' with community (g) and constant ($.$) effects, and with community and temporal effects ($g + t;g;t$) in p and c rates. We also modelled gregariousness as a covariate to detectability ($g + t;g;t + gregariousness$): see electronic supplementary material. After selecting the best model of S , γ'' and γ' , we added the effects of social and non-social environmental covariates on apparent survival. We first ran simple models with a single covariate, and then more complex additive and interactive models with the covariates from models that ranked above the constant survival model in the simple model run. We tested for correlations among covariates and did not include correlated variables in the same model (electronic supplementary material, table S3). Details about modelling and goodness-of-fit testing, and results of the correlation analysis, can be found in the electronic supplementary material.

3. Results

Our ranking of community and constant effects found the best model included constant survival across social communities, community-specific temporary emigration, and community and time interaction as well as gregariousness effects on p and c ($S(.). \gamma''(g) \gamma'(g) p(g + t;g;t + gregariousness) c(g + t;g;t + gregariousness)$) (electronic supplementary material, tables S4 and S5 and figure S3). Therefore, subsequent covariate selection accounted for variation in detectability due to gregariousness.

The top survival covariate model ($(S(gregariousness + town) \gamma''(g) \gamma'(g) p(g + t;g;t + gregariousness) c(g + t;g;t + gregariousness))$) carried 29% of the weight in the candidate model set (electronic supplementary material, table S5). This model indicated that more gregarious females (i.e. those seen with more other females on average) and females farther from towns had higher survival probabilities ($\beta_{\text{GREG}} = 1.711$, s.e. = 0.600 and $\beta_{\text{TOWN}} = 0.835$, se = 0.639; electronic supplementary material, table S5). No other models were competitive (i.e. less than 2 ΔAIC_c) and the top model was more than three times as likely as the next-ranked model (model likelihood = 1.000 versus 0.303; electronic supplementary material, table S5). Mean female gregariousness was 3.027 (s.d. = 1.259). Female survival probabilities increased up to the point where the number of other females she grouped with included approximately three, and then increases in survival rate flattened (figure 2).

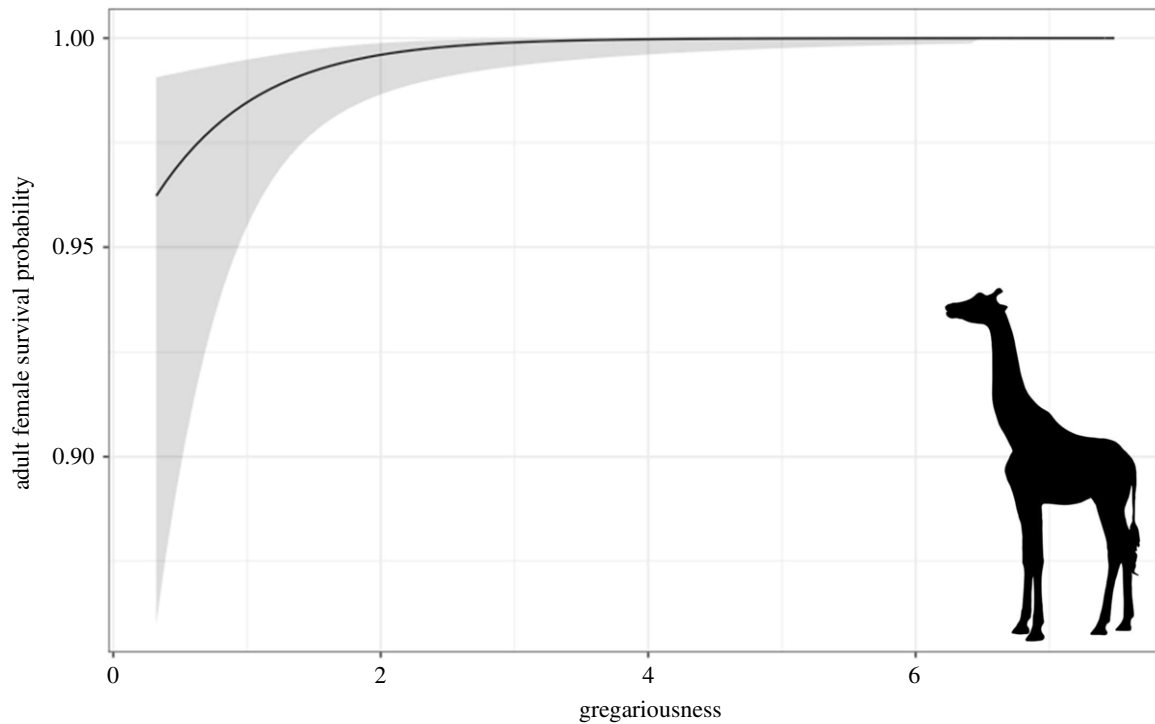


Figure 2. Relationship between gregariousness (black line: mean number of other adult females in her group) and adult female giraffe survival probability (grey shading: +5% confidence interval).

Overall, individual-based covariate models were superior to community-based covariate models.

4. Discussion

Within their structured society with fluid grouping dynamics, adult female giraffes exhibit substantial individual variation in social characteristics. Our 5-year demographic analysis of more than 500 individually identified females demonstrated that those observed in groups with, on average, at least three other females had higher survival probabilities. Gregariousness had a significant effect on survival, and appears to be far more important in explaining variation in survival than the other measures of social connectedness, or any of the natural or anthropogenic environmental factors we tested, including anthropogenic factors previously shown to influence demographic rates in this population (e.g. [18,34]). Our results suggest that females living closer to towns had lower survival, although this effect was not as strong as gregariousness. Finally, we found survival is primarily driven by individual- rather than community-level social factors.

In our study population, survival probabilities of female giraffes increased and reached an asymptote for individuals observed together with at least three other females (figure 2). Mean number of other females in a group was three, thus females that were less gregarious than average suffered from higher mortality. These results imply that there may be a minimum number of other females in a group at any given time that is associated with better survival. On the other end of the group-size spectrum, sociability might be constrained by socio-ecological factors such as competition for resources, especially during the dry season when food is limiting, the presence of neonatal calves, or anthropogenic influences that disrupt social structure. For example, in baboons (*Papio cynocephalus*), intermediate-sized groups have the lowest home range areas, lowest average daily distances travelled

and lowest average glucocorticoid concentrations for females, suggesting large groups suffer within-group competition, whereas small groups face between-group competition and predation [57,58].

Relationship strength—both mean and maximum—and variation in relationship strength had no significant influence on adult female giraffe survival. Female giraffe societies may share similarities with some primates in which greater social connectedness—but not necessarily stronger relationships—matter. Maryanski [24] suggested that chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) live in communities whereby relatively weak ties between many individuals can be advantageous because they facilitate movements among groups and with familiar individuals, which among chimpanzees enables a flexible feeding strategy focused on the dispersed distribution of fruits. Studies of both rhesus macaques (*Macaca mulatta*; [9]) and blue monkeys (*Cercopithecus mitis stuhlmanni*; [59]) also found that more socially connected females with many weak ties had higher survival. Neither relationship strength nor exclusivity influenced female giraffe survival in our study. Thus, it may be beneficial for a greater number of females to connect with each other and develop a sense of larger community but not a strong sense of subgroup affiliation, as is indicative of more closed social systems such as baboons [8,60] or bats [61,62]. Interestingly, baboons inhabit the same savannah ecosystems as giraffes, yet relationship strength and stability do have strong survival effects in female baboons [8]. However, in both baboons and rhesus macaques [9], females with stronger and more consistent relationships with their ‘top partners’ were more likely to survive. While different factors are expected to influence survival in multi-level societies where fission–fusion dynamics occur at the subgroup level relative to societies in which individuals live in groups with stable membership, the importance of key relationships warrants further study. Studies of giraffes that allow collection of more intensive finer-scaled observational data within communities, from which individuals’ top

partners can be identified, might reveal survival effects similar to those of primates.

Why might higher gregariousness be adaptive for giraffes? Grouping behaviour may increase adult survival for species where adults themselves are prey (e.g. Burchell's zebras, *Equus burchelli* and blue wildebeests, *Connochaetes taurinus* [63]), as larger groups can better detect predators [64] or deflect predation from themselves [65]. But adult female giraffes are far less vulnerable to natural predation than are calves, although females do bear a high prevalence of lion claw marks which were likely acquired during calf defence [66]. Aside from poaching, the main culprits of adult female giraffe mortality are likely to be disease, stress or malnutrition [67,68], all of which are interconnected stressors. In a review of social influences on survival gleaned from long-term studies of baboons, Alberts [69] noted that social relationships are used to manage intraspecific competition, predation, disease risk and psychosocial stress, and to gain information about the environment. Female giraffes may be using social cues, seeking out and joining with an optimal number of other females in order to share and obtain information about the highest-quality food sources and thus improve foraging efficiency [70]. Other benefits to gregariousness might be lowering stress levels by reducing harassment by males [71], cooperating in caring for young [72], or simply experiencing physiological benefits by being around familiar females [73].

Gregariousness benefits may also accrue from grouping with males and subadults, which we did not take into account in our estimation of group size, but these benefits should largely increase monotonically with female group size. A post hoc analysis (see electronic supplementary material) showed the number of adult females in a group was correlated with total group size (electronic supplementary material, figure S4). Further, the number of females and males in a group that individual females experience (as random effects in an intercept-only model) suggested that these also are correlated. However, it is unlikely that males provide the same grouping benefits as females do, for example the presence of males might even be a disadvantage when they harass females in the group [71]. For each female the repeatability of the number of other adult females in her group was more than twice as high as repeatability of the number of males in her group (electronic supplementary material), which was not surprising as adult male relationships with females are not stable [17] and males adopt a roaming strategy seeking females in oestrous that are widely dispersed over space and time [72]. Thus, while males might contribute to group size effects in an instance of a group, such an observation is unlikely to predict male contributions into this same group at some point in the future. This applies to subadults as well, given that subadults have higher levels of social connectedness likely due to social exploration [17] and in many species even older subadults contribute very little to social processes such as decision-making [74]. Relationships with other adult females are the most stable and predictable aspect of a female giraffe's social environment, so if sociability affects survival this effect should stem primarily from female–female associations. Thus, like in many mammals, we expect that females will gain greater long-term benefits from their associations with other females than by associating with males.

In many long-lived, iteroparous, polygynous ungulates, including giraffes, longevity is the most important determinant

of female lifetime reproductive success [19,75,76]. Giraffe group formations are unstable and of short duration (e.g. [35,69,77]), but adult females maintain non-random ties over a longer term [15,16]. Our data suggest that grouping with more other females, even as group membership frequently changes, is correlated with better survival of female giraffes. This sociability is apparently more important than are various attributes of their non-social environment.

Features of a female giraffe's non-social environment were less correlated with survival than her gregariousness, but we did detect some weak support for anthropogenic effects. Although distance to densely populated towns was not a strong correlate to survival, its inclusion in the top model suggests it contributed significantly to the fit of the model to the data. Further, the directionality of the effect matched our prediction, signifying this effect warrants further investigation. Females living closer to towns had lower survival, possibly due to poaching in these areas [32]. Previous research in our study population revealed differences in giraffe behaviours near towns compared with bomas. Closer to towns, adult female home ranges were larger in size [78] and female groups with calves avoided towns [26]. By contrast, giraffes exhibit a mixed relationship with humans living in a more traditional manner, as evidenced by differential responses to bomas compared to towns. Females closer to bomas had more exclusive relationships, suggesting disruption of social structure [15], and male giraffes were less likely near bomas [26]. However, female groups with calves were more likely to be closer to bomas [26], possibly due to reduced predator numbers or the interruption of predator behaviours as pastoralists protect their livestock, which may improve calf survival. Proximity to bomas appears to result in more exclusive but weaker overall relationships with other adult females within their communities, but apparently does not affect their survival. Lower predator densities may reduce stress associated with protecting offspring. We therefore propose adult females face a trade-off between their social relationships and their fitness when in close proximity to traditional pastoralists.

Social flexibility is an evolved adaptation among animals that provides individuals with the opportunity to adjust their foraging and reproductive strategies to maximize fitness in the face of unpredictable environmental conditions [5]. In the case of the African striped mouse, *Rhabdomys pumilio*, such social flexibility can yield both group-living and solitary individuals [5]. For female giraffes, social flexibility seemingly results in a structured social network that is characterized by variation in group size and composition, but wherein greater sociability of individuals is correlated with higher survival.

Data accessibility. Data are available from the Dryad Digital Repository. Datasets include adult female encounter histories and covariates, and community-level environmental covariates: <https://dx.doi.org/10.5061/dryad.r4gxd2bf> [79].

Authors' contributions. M.L.B., B.K., A.O., D.R.F. and D.E.L. conceived the ideas and designed methodology; M.L.B. and D.E.L. collected the data; M.L.B. and D.E.L. analysed the data; M.L.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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