BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Fission–fusion dynamics of a megaherbivore are driven by ecological, anthropogenic, temporal, and social factors

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Abstract

Fission–fusion dynamics hypothetically enable animals to exploit dispersed and ephemeral food resources while minimizing predation risk. Disentangling factors affecting group size and composition of fission–fusion species facilitates their management and conservation. We used a 6-year data set of 2888 group formations of Masai giraffes in Tanzania to investigate determinants of social group size and structure. We tested whether ecological (lion density, vegetation structure, and prevalence of primary forage plants), anthropogenic (proximity to human settlements), temporal (rainy or dry season), and social (local giraffe density, adult sex ratio, and proportion of calves) factors explained variation in group size and sex- and age-class composition. Food availability rather than predation risk mediated grouping dynamics of adult giraffes, while predation risk was the most important factor influencing congregations with calves. Smallest group sizes occurred during the food-limiting dry season. Where predation risk was greatest, groups with calves were in bushlands more than in open grasslands, but the groups were smaller in size, suggesting mothers adopted a strategy of hiding calves rather than a predator-detection-and-dilution strategy. Groups with calves also were farther from towns but closer to traditional human compounds (bomas). This may be due to lower predator densities, and thus reduced calf predation risk, near bomas but higher human disturbance near towns. Sex- and age-based differences in habitat use reflected nursing mothers' need for high-quality forage while also protecting their young from predation. Our results have implications for conservation and management of giraffes and other large-bodied, herd-forming ungulates in heterogeneous environments subject to anthropogenic threats.

Keywords Fission–fusion · Giraffe · *Giraffa camelopardalis* · Grouping behaviour · Social systems

Introduction

Many social species in taxa as diverse as primates, marine mammals, bats, birds, elephants, carnivores, and ungulates exhibit fission–fusion dynamics (Whitehead and Dufault

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1999; Wittemyer et al. 2005; Smith et al. 2008), whereby group sizes fluctuate by merging of and splitting into subunits (Kummer 1971; Aureli et al. 2008). Such fission–fusion dynamics may enable grouping patterns to respond to short-term and seasonal fluctuations in food resources (Holekamp et al. 2012) or local predation risk (Thaker et al. 2010). The framework proposed by Aureli et al. (2008) to assess variation in group cohesion and membership emphasized examining variation in group size and composition, which can influence intra-group competition for food, daily travel distances, predation risk, and natal or breeding dispersal propensities, all of which might inflict energetic and fitness costs. Therefore, if we assume that individuals are behaving adaptively when forming groups (Chapman and Chapman 2000; Majolo et al. 2008; Markham et al. 2015), a fundamental question is which spatial and temporal factors mediate the size and composition of a group.

Spatial and temporal heterogeneity in food resources and predation risk can bring about group fission–fusion

dynamics across space and time (Fortin et al. 2009). In a review of grouping behaviour of African antelopes in relation to their ecology, Jarman (1974) hypothesized that feeding style, dispersion of food resources, and anti-predatory strategies influence group size. The maximum group size is influenced by the dispersion of food and the feeding style (which limits the number of individuals that can feed together as a cohesive group), and the minimum group size by anti-predator behaviour (if individuals benefit from communal defence or the dilution effect; Hamilton 1971). Subsequent studies observed that ungulates formed larger groups in open environments to avoid predation and congregated in areas with abundant high-quality food resources, but dispersed and formed smaller groups in areas of thick, dense vegetation (Pays et al. 2007; Fortin et al. 2009; Thaker et al. 2010). However, not all ungulates respond the same way to predation risk. For example, herds of red deer (elk; *Cervus elaphus*) disaggregated and moved to protective cover when wolves (*Canis lupus*) were present, possibly to reduce the likelihood of detection (Winnie and Creel 2007), but a recent study of two enclosed populations of Rothschild's giraffes (*Giraffa camelopardalis rothschildi*) did not find evidence that grouping is an anti-predator behaviour in the presence of lions (*Panthera leo*: Muller et al. 2018). Group composition also varies spatiotemporally, with some degree of sexual segregation in feeding behaviour and habitat use evident in many ungulate species (Clutton-Brock et al. 1987; Winnie and Creel 2007; Thaker et al. 2010).

To determine the importance of access to food and risk of predation on group size and composition would entail manipulating these factors independent of each other. Such experiments are not easily conducted on wild populations of ungulates, but observational studies in heterogeneous landscapes where free-ranging animals are exposed to varying levels of predation and a diversity of vegetation can contribute to disentangling the factors affecting group size and composition.

Like many ungulate species, the social system of giraffes exhibits fission–fusion dynamics (Dagg and Foster 1976; Leuthold 1979; Bercovitch and Berry 2012). The size and composition of both male and female groups are fluid (Dagg and Foster 1976; Leuthold 1979; Le Pendu et al. 2000; van der Jeugd and Prins 2000; Muller et al. 2018), but females form longer-term associations with other females (Pratt and Anderson 1985; Carter et al. 2013; VanderWaal et al. 2014). Giraffe group sizes varied from 1 to 175 (Dagg and Foster 1976; Muller et al. 2018). Subadult males form bachelor herds in which they establish dominance hierarchies and adult males range widely seeking adult females in oestrus (Pratt and Anderson 1985). Females are receptive at any time of year (Dagg 2014).

Giraffes are non-territorial, resident browsers that feed mostly on leaves, twigs, flowers, and fruits of *Acacia* spp.,

Dichrostachys cinerea, and other woody plants (see references in Dagg 2014), with preference for certain species depending on season and vegetation type, and with differences between males and females in vegetation consumed (Pellew 1984; Caister et al. 2003; Mramba et al. 2017). Giraffes occur in various habitat types from dense woodland to savanna grasslands (Dagg and Foster 1976; Leuthold 1979), and many giraffe populations roam over increasingly fragmented landscapes affected by human uses (Lee et al. 2016a; Lee and Bolger 2017). Previous studies observed that adult males were located more often in closed habitats than females (Leuthold 1979; Mramba et al. 2017). Adult females with calves formed smaller groups than those without calves (Muller et al. 2018) and tended to feed in open areas seasonally (Ginnett and Demment 1999), while pregnant females were found in densely vegetated habitats, which might be either an anti-predator strategy to hide neonatal calves or selective foraging to decrease tannin intake (Young and Isbell 1991; Furstenburg and van Hoven 1994; Caister et al. 2003). Therefore, vegetation type, season, and presence of calves are expected to influence habitat use and group dynamics.

Our objective was to investigate how spatial, temporal, and social factors influence the dynamics of Masai giraffe (*G. c. tippelskirchii*) grouping behaviour in a large (*N* > 3100 individuals) free-ranging metapopulation studied over 6 years. Animals were individually identified using photographic capture–recapture methods. We modelled effects of ecological (lion density, vegetation structure, and prevalence of primary forage plants), anthropogenic (proximity to human settlements), temporal (rainy or dry season and time of day), and social factors (local giraffe density, adult sex ratio, and proportion of calves) on group size and composition. Given the giraffe's fission–fusion social system and tendency to range widely in temporally and spatially heterogeneous environments, we expected to gain a general understanding of the relative influence of food availability and predation risk on grouping behaviour of this megaherbivore by testing the following hypotheses related to the costs and benefits of group living in ungulates.

If grouping behaviour is predominantly affected by feeding competition, we predicted smaller groups during the season of low food availability, as well as in areas with lower availability of preferred food. Predation may counteract the benefits of small groups under competitive feeding conditions if the dilution effect is important (Hamilton 1971). If this is the case, we predicted that in places or times with low primary forage availability larger groups will form in areas with higher lion densities than in areas with lower lion densities. Differences among individuals in age and breeding status will result in modifications of group composition when trading off between the benefits of food availability and the costs of predation (Ruckstuhl 2007). Giraffe calves

are the age class most vulnerable to predation (Strauss and Packer [2013]), thus we predicted that adult females with calves aggregate in larger groups in areas with high lion densities and/or low vegetation cover than females without calves, according to the predator-detection (Pulliam [1973]) and dilution-effect hypotheses (Hamilton [1971]). As one of the world's few extant megaherbivore species, constituting an extreme along the life-history spectrum, studies of giraffes can elucidate the general applicability of patterns observed in studies of smaller-bodied species by providing an allometric endpoint for comparison and contrast (Owen-Smith [1992]).

Materials and methods

Study area

Our 1500-km^2 study area in the Tarangire Ecosystem (TE) of northern Tanzania included a heterogeneous savanna landscape inside and outside protected areas, with unprotected lands experiencing rapid fragmentation due to human use (Morrison and Bolger [2014]) and illegal killing of giraffes for meat affecting adult female survival in some subpopulations (Lee et al. [2016a]). Our study area was unfenced and individuals moved throughout the area, including crossing tarmac roads and agricultural areas between habitat patches (Lee and Bolger [2017]). They could access a diversity of vegetation types at varying distances from human habitation. Protected areas supported a higher density of predators such as lions and spotted hyenas (*Crocuta crocuta*) compared to unprotected lands, so the giraffes also experienced various levels of natural predation (Lee et al. [2016a], [b]).

The TE supports one of the most diverse large-mammal communities in the world (Lamprey [1963]). The TE is situated in the eastern branch of the Great Rift Valley and encompasses roughly 30,000 km^2 (Borner [1985]; Prins [1987]). Rain occurs almost exclusively from October to May, with a mean total annual rainfall of 650 mm for the years 1980–2009 (coefficient of variation = 42.6%, range = 312–1398 mm; Foley and Faust [2010]). The TE experiences three precipitation seasons per year (short rains = Oct–Jan, long rains = Feb–May, and dry = Jun–Sep), with respective average monthly precipitations of 63 mm, 100 mm, and 1 mm. Human population and agricultural development in the TE have increased with 3% annual human population growth between 2003 and 2012, adding nearly 800,000 people (TNBS [2013]), causing substantial habitat loss, increasing fragmentation, and reducing connectivity for wildlife (Msoffe et al. [2011]; Morrison and Bolger [2014]).

Our study area in the core of the TE was 4400 km^2 within which we sampled a 1500-km^2 area with differing management activities (Fig. [1]). Land management was divided among five administrative sections: (1) Tarangire National Park (TNP), (2) Lake Manyara National Park (LMNP), (3) Manyara Ranch Conservancy (MRC), and (4) Mtowambu (MGCA) and (5) Lolkisale (LGCA) Game Controlled Areas. The two national parks, TNP and LMNP, had high levels of wildlife protection including exclusion of livestock and human settlements and rigorous anti-poaching patrols. MRC had intermediate levels of wildlife protection with exclusion of human settlements and some anti-poaching patrols but with large numbers of livestock during the daytime. LGCA and MGCA had the lowest levels of wildlife protection and allowed sport hunting and permanent human settlements. None of the administrative areas were fenced, and all were connected by movements of adult female giraffes (Lee and Bolger [2017]), thus we considered our study population to be a metapopulation of subpopulations connected through dispersal.

The western boundary of the study area was formed by the Rift Valley escarpment, a steep cliff that restricted giraffe movements in that direction. Wild large mammals were rarely observed due to high human and livestock population densities and intensive agriculture east of Makuyuni town, west of TNP, and south of LMNP. Two 2-lane asphalt roads crossed the study area (Fig. [1]).

Data collection

Giraffes are relatively conspicuous and easily approached (Pratt and Anderson [1985]). They have unique markings that do not change from birth to death (Foster [1966]), enabling all or most group members to be identified using non-invasive photographic capture–recapture techniques. We conducted 31 daytime, fixed-route dirt track transect surveys for giraffe groups between May 2011 and October 2016. We surveyed on three primary sampling periods per year near the end of each precipitation season (short rains = Jan, long rains = May, and dry = Sep) according to a robust design with each primary sampling period composed of two independent, back-to-back secondary sampling periods during which all fixed-route dirt track transects in the study area were surveyed (Pollock [1982]). In 2011, surveys were part of a pilot study and were conducted only during the long rainy season. Surveys were conducted between 0700 and 1800 h, beginning approximately 0.5 h after sunrise and ending 0.5 h before sunset. Driving speed was maintained between 15 and 20 km/h on all transects, and all survey teams included the same two dedicated observers and a driver. Each survey took 7–10 days, and each road segment was sampled only once in a given secondary sampling period. The minimum number of days that passed before the same track was re-sampled was 5 days, thus enabling giraffes to re-group and ensuring independence of the sampling events.
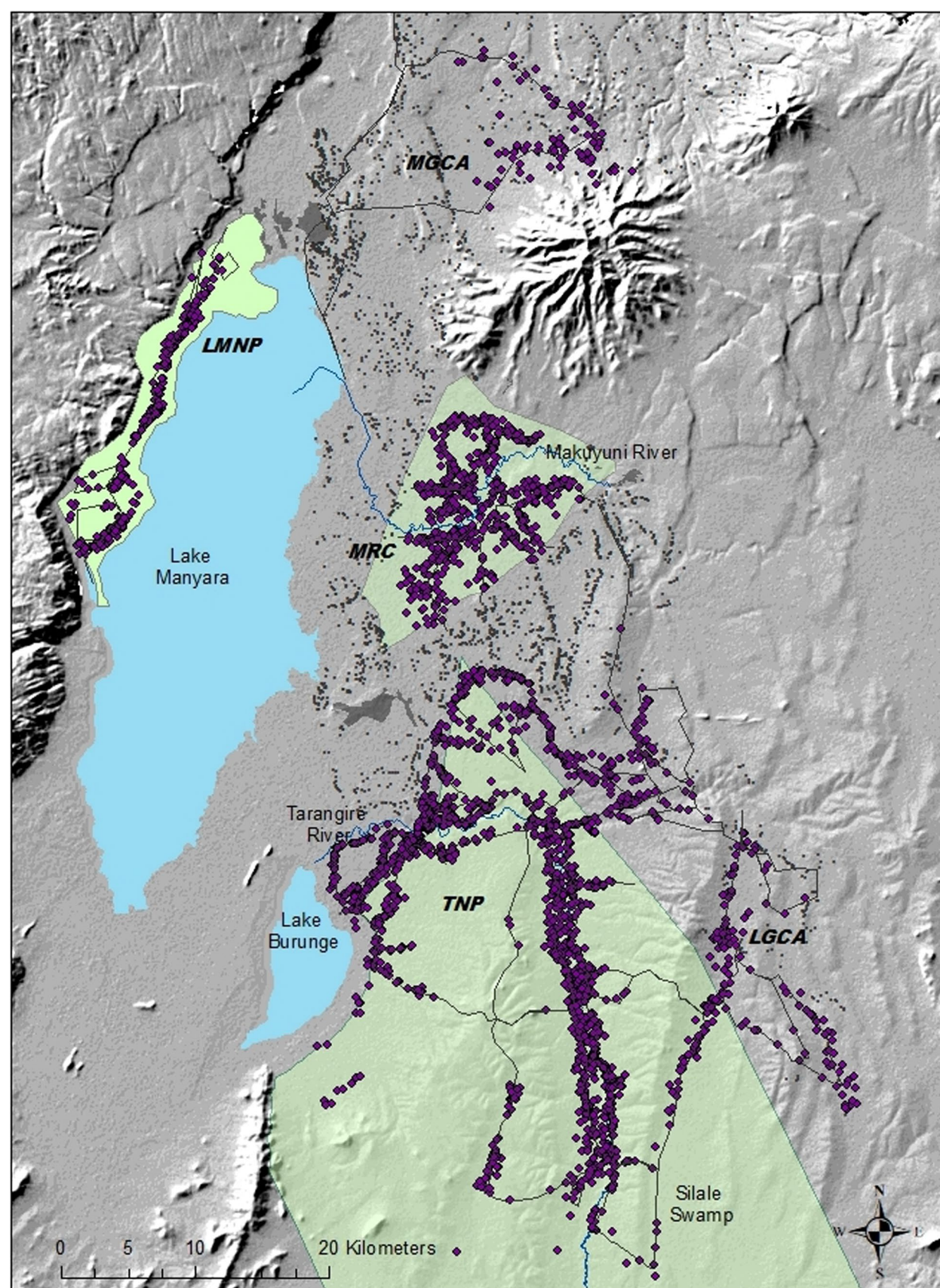
◄**Fig. 1** Location of 2888 Masai giraffe group formations (purple dots) in the Tarangire Ecosystem of northern Tanzania, 2011–2016. Dark grey lines are roads and tracks surveyed for giraffe groups, blue lines are rivers, light blue areas are alkaline lakes, green areas are national parks and conservancies, grey polygons are towns, and grey points are bomas. *LMNP* Lake Manyara National Park, *TNP* Tarangire National Park, *MRC* Manyara Ranch Conservancy, *MGCA* Mtowambu Game Controlled Area, *LGCA* Lolkisale Game Controlled Area (color figure online)

When we encountered a giraffe group we approached to within at least 150 m for data collection. We defined a group as one or more giraffes foraging or moving together, but not moving past each other in opposite directions, and that was > 500 m from the next nearest giraffe, which we considered to be a separate group. Giraffe groups were usually self-defining as the distances between individuals were substantially less within than between groups. Individuals with no conspecific within 500 m were considered singletons. We recorded the following data for each individual: age class (calf, subadult, adult), sex, date, time of day, and GPS location for the approximate centre of the group. We used a suite of physical characteristics, including body shape, height, relative length of the neck and legs, and ossicone characteristics to categorize giraffe into the three age classes: calf (< 1 year), subadult (1–3 years), or adult (> 3 years), based on Strauss et al. (2015).

We 'captured' or 'recaptured' every individual by photographing them on the right side and using Wild-ID software to match photos of individuals based on their unique spot patterns (Bolger et al. 2012). We typically photographed and identified every individual in every group we encountered although rarely we missed some individuals due to difficult terrain or the animals departing before photo-capture. When this occurred, we noted the number of animals we knowingly failed to photograph; overall we missed one or more individuals in 1.7% of the groups we encountered each year. Therefore, we are confident that our counts were a robust index of actual groups in our study area. Our study design involved repeatedly measuring individually identified giraffes, with each individual assigned to only one group per primary sampling period, but with the same or a different set of individuals in groups during subsequent primary sampling periods. We used these individual-based data to calculate group size and composition.

Environmental, temporal, and social covariates

We plotted group locations on a GIS using ArcMap 10.5.1 (Environmental Systems Research Institute, Redlands, CA, USA), and at every location, we extracted the environmental and anthropogenic variables of vegetation type and proximity to nearest human settlements (permanent towns and traditional non-permanent family compounds known

as bomas). We used a combination of publicly available remote-sensed data and our own ground-based vegetation surveys to create GIS vegetation features. These features included four general vegetation types from most dense to most open to represent structure and cover: (1) deciduous bushland and thicket, (2) wooded grassland, (3) edaphic grassland on volcanic soils with scattered woody species, and (4) edaphic grassland on drainage-impeded or seasonally flooded soils (Kindt et al. 2011), derived from a natural vegetation map developed by the University of Copenhagen's Vegetation and Climate Change in Eastern Africa (VECEA) project (downloaded from http://vegetationmap4africa.org/2_Vegetation_map.html). Within each general vegetation type we used ground-based observations collected in 2014 every 2 km along our dirt tracks to map polygons of specific vegetation types of large stands with > 10% cover of one of four primary giraffe forage species: (1) *Acacia tortilis*, (2) *Acacia drepanolobium*, (3) *Dichrostachys cinerea* and (4) *Combretum* (Foster 1966; Pellew 1984; Young and Isbell 1991; Furstenburg and van Hoven 1994; Caister et al. 2003). In our analysis of specific primary forage types, we classified locations with < 10% cover of any of the four forage species as nonspecific. We used Google Earth imagery to map bomas as points and permanent towns as polygons. To calculate distances to bomas we used the Point Distance proximity function and to calculate distances to towns we used the near proximity function in ArcMap.

We obtained data on lion densities in each administrative unit from Lee et al. (2016b). Lions were surveyed from 2010 to 2013 by the Tarangire Lion Project and Lake Manyara National Park staff, and site-specific lion densities per 100 km^2 were calculated by dividing lion population size in each administrative unit averaged across all seasons, by the area enclosed by a minimum convex polygon of our surveyed road network in each unit (Lee et al. 2016a). TNP, LMNP, and MRC had higher lion densities due to active predator protection (8.6, 20.5, and 14 lions/100 km^2, respectively), whereas trophy hunting of lions and pastoralist activities in the two GCA sites resulted in lower lion densities there (1.7 lions/100 km^2).

Group sizes of ungulates increase with population density (Pépin and Gerard 2008), thus we explicitly accounted for local giraffe population density. We calculated giraffe density in each of the five administrative areas and assumed that it did not substantially change over the study period (see Lee et al. 2016a). Density was adult $\hat{N}$/surveyed area (km^2) of each administrative area, with surveyed area calculated as the minimum convex polygon enclosing our dirt track network in each area, plus a boundary strip equal to half the width of the estimated mean maximum distance moved (Parmenter et al. 2003).

Statistical analysis

We quantified group size and composition by age-class and sex for every observed group, and investigated how environmental, seasonal, and social factors influenced (1) group size (number of individuals); (2) proportion of calves in a group; and (3) probability of being a single adult male, single adult female, bachelor herd, mixed-sex group without calves, or any group with one or more calves (group type). We considered groups with both ≥ 2 individuals and ≥ 0.5 proportion of adult and/or subadult males to be bachelor herds. Each individual was assigned to only one group per survey (31 surveys) but had the potential to be observed with a different or the same set of individuals during other surveys, thus the study design consisted of repeated measures of individual giraffes.

We assessed multicollinearity among the predictor variables by computing the variance inflation factor using the vif function in package car for R version 3.4.3 (R Core Team 2017). We fitted generalized linear mixed models (GLMMs) utilizing a Markov chain Monte Carlo (MCMC) approach in a Bayesian statistical framework (Ellison 1996) with package MCMCglmm (Hadfield 2010). We used a zero-truncated Poisson distribution for our group size response variable, to account for the impossibility of a group size of zero, and used the canonical log link function to model group size as a linear combination of our predictors. We conducted binomial regression with the logit link function and a binomial distribution to model proportion of calves in a group, and multinomial regression with the canonical logit link function and a categorical distribution to model group type as responses to predictors. We modelled environmental, seasonal, and social predictors as fixed effects, group ID as a random predictor to account for non-independence of individuals within a group, and a vector of residuals to account for overdispersion in our data with a "unit-level" random effect for each observation (Hadfield 2010). All models were run for 100,000 iterations with a burn-in phase of 5000 and thin interval of 100. We examined trace plots and posterior density estimates of variance components, as well as effective sample sizes, to assess model convergence. We attempted to model both group ID and individual ID as random effects together, but this model suffered from singularity where the variance of individual ID was estimated as zero, likely due to large numbers of singletons and individuals seen only once. Increasing the iterations and burn-in period failed to rectify the singularity, so we modelled only group ID as a random effect.

We accepted fixed effects as significant when their 95% credible intervals did not span zero, and the group ID random effect as significant when the distribution was not close to zero (Hadfield 2010). For interpretation we exponentiated the coefficients from the Poisson regression models and

calculated the inverse-logit of the coefficients from multinomial and binomial regression models. Details about variables, models tested, and priors and variances selected are available in Supporting Information Appendix 1.

Results

During our study period (2011–2016) we encountered a total of 2888 giraffe group formations, comprised of 3117 uniquely identified individuals. Of these individuals 1859 were adults when first entered into our database (1139 females and 720 males). Groups on average comprised 5.4 giraffes (SE 0.11; range 1–66), and the most frequent (modal) group size was 1 (Fig. 2a). Groups of ≥ 2 individuals averaged 6.9 giraffes (SE 0.15; range 2–66). Of the adult singletons, 401 (61%) were males and 259 (39%) were females. We recorded 321 bachelor herd formations, comprised of 2 or more individuals with a proportion of adult and subadult males ≥ 0.5 (mean group size: 8.3 ± 0.53). One or more calves were detected in 753 group formations (mean group size: 9.1 ± 0.33). The remainder of group formations (1180) were mixed-sex, female-dominated herds with no calves (mean group size: 5.1 ± 0.15).

Concerning the specific primary forage types where giraffes were encountered, 1375 groups (48%) occurred in *A. tortilis*. We recorded 337 groups (12%) in *D. cinerea*, 320 (11%) in *A. drepanolobium*, 62 (2%) in *Combretum*, and 794 (27%) located in stands not dominated by any of these four types (non-specific). Five of the six largest groups, ranging in size from 40 to 66 individuals, occurred in extensive patches of *D. cinerea* on the western side of MRC during the long rains (4 groups) or short rains (1 group).

Assessments of variance inflation factors indicated low collinearity among explanatory variables. Visual inspection of trace plots for sampled posteriors and graphs of density estimates indicated good mixing of all the models.

Factors affecting group size

Significant effects for giraffe group size included: proportion of adult males, time of day, season, a season $\times$ specific primary forage type interaction, and a lion density $\times$ general vegetation $\times$ proportion of calves interaction (Table 1). Distance to bomas and towns and local giraffe population density did not significantly affect group sizes. Posterior mean parameter estimates and 95% upper and lower credible intervals for all predictor variables in the global model are presented in Supporting Information Table S1.

Groups increased in size over the course of the day but tapered off late in the afternoon, in a quadratic relationship with hour (Fig. 2b). Group sizes were significantly influenced by season and the interaction between season

Fig. 2 **a** Number of giraffe group formations ($N = 2888$) by size over 6 years (2011–2016) and **b** group size throughout the course of a day
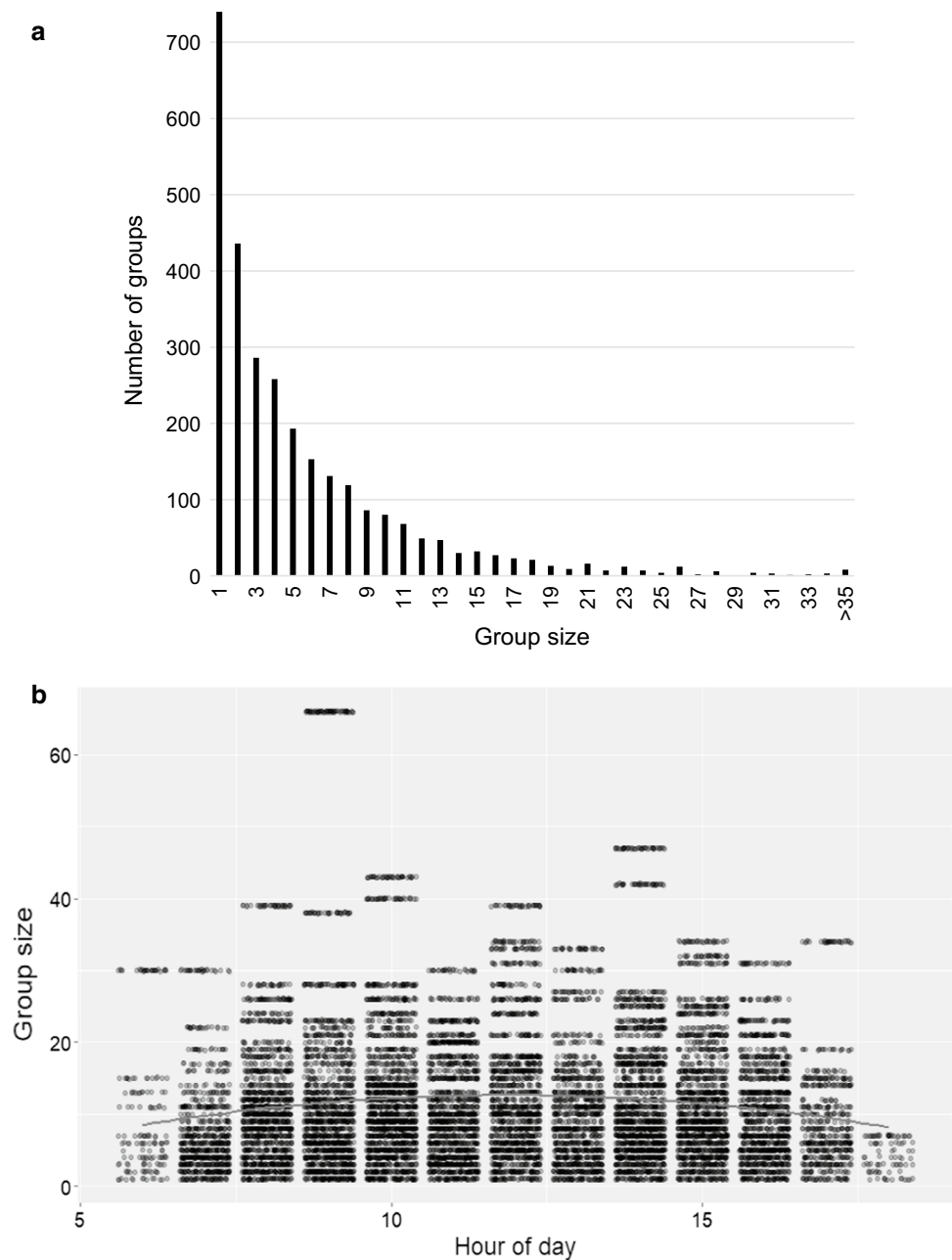
and specific primary forage type. Food availability is expected to be lower thus competition over food is greater in the dry season, and giraffe groups were 30% smaller in the dry than the rainy seasons. When compared to non-specific primary forage patches during the long rainy season, groups in areas with large stands of *Combretum* were larger in both the dry ($\sim 313\%$) and short rainy season ($\sim 221\%$), although very few groups were found in *Combretum* overall (2%).

Group size was affected by a significant lion density × general vegetation × proportion of calves interaction. The more calves (in relation to adults) a group had, the smaller it was in dense vegetation in areas with higher lion

densities (Fig. 3). Overall, smaller groups had higher proportions of adult males.

Factors affecting group composition

The proportion of calves in a group varied by distance to bomas and specific primary forage type, but not by general vegetation, lion density, season, or distance to towns (Table 1, Supporting Information Table S2). Groups closer to bomas had a higher proportion of calves (the proportion of calves decreased by 51% with each kilometre away from the nearest boma). The proportion of calves also varied by specific primary forage type, with 58% more calves in

Table 1 Posterior mean values of significant fixed effects, 95% credible intervals, and probability of significance for determinants of group size ($N = 2888$ groups), proportion of calves in a group, and type of group for Masai giraffes (*Giraffa camelopardalis tippelskirchii*) in the Tarangire Ecosystem, northern Tanzania, 2011–2016

Variable[a]	Posterior mean of β estimate	Lower 95% CI	Upper 95% CI	pMCMC
Group size				
Dry	− 0.362	− 0.650	− 0.102	0.021
Hour	0.300	0.189	0.416	< 0.001
Hour^2	− 0.011	− 0.016	− 0.007	< 0.001
asin(P_AM)	− 0.623	− 0.703	− 0.534	< 0.001
dry:SPVEGcomb	1.144	0.291	2.013	0.006
shortr:SPVEGcomb	0.793	− 0.014	1.553	0.040
LION:asin(P_C):GENVEGbd	− 0.105	− 0.179	− 0.019	0.017
Proportion calves				
D_Boma	− 0.043	− 0.064	− 0.023	< 0.001
SPVEGadrep	0.310	0.018	0.570	0.040
Group composition				
traitTYPE.BACH:D_Boma	0.230	0.120	0.360	< 0.001
traitTYPE.CALF:D_Boma	− 0.190	− 0.310	− 0.080	< 0.001
traitTYPE.SM:D_Boma	0.060	0.020	0.100	< 0.001
traitTYPE.CALF:D.Town	0.050	0.010	0.090	0.034
traitTYPE.SF:SPVEGdichro	− 3.890	− 7.060	− 0.200	0.027
traitTYPE.BACH:GENVEGbd	− 2.720	− 4.450	− 1.630	< 0.001
traitTYPE.CALF:GENVEGbd	2.070	0.950	3.220	< 0.001
traitTYPE.SF:GENVEGbd	− 0.510	− 1.110	− 0.050	0.046
traitTYPE.SM:GENVEGbd	− 0.790	− 1.290	− 0.250	< 0.001
traitTYPE.CALF:GENVEGg	2.410	0.000	5.160	0.042
traitTYPE.CALF:GENVEGgv	2.560	1.160	4.200	< 0.001
traitTYPE.SF:SPVEGdichro:SEASONdry	6.530	0.770	11.520	0.004
traitTYPE.CALF:SPVEGadrep:SEASONshortr	10.340	1.630	18.650	0.006
traitTYPE.SF:SPVEGadrep:SEASONshortr	5.900	0.610	11.490	0.011
traitTYPE.SF:SPVEGcomb:SEASONshortr	5.950	0.890	10.850	0.029

Estimates from generalized linear mixed regression models run for 100,000 iterations with a burn-in phase of 5000 and thin interval of 100. Group identification was considered a random effect to account for non-independence of group members. Descriptions of models and results of all effects presented in Table S1, Supplementary Materials

[a]LION = local lion density in 5 administrative sites Tarangire and Lake Manyara National Parks, Manyara Ranch Conservancy, Mtowambu and Lolkisale Game Controlled Areas (#lions/100 km^2); season: dry (Sep–Oct), shortr (short rains, Jan–Feb) as compared with reference category long rains (May–Jun); time of day (hour); P_AM = adult males/adult males + adult females; P_C = number of calves/number of individuals in group (proportions arcsin-transformed); D_Boma = distance (km) to nearest boma (Masai family compound); D_Town = distance (km) to permanent town; general vegetation type (GENVEG): bd (deciduous bushland and thicket), g (grassland on flooded soils), gv (grassland on volcanic soils) as compared with reference category wd (wooded grassland); specific primary forage type (SPVEG): dichro (*Dichrostachys cinerea*), comb (*Combretum* spp.), adrep (*Acacia drepanolobium*), and atort (*Acacia tortilis*) compared with reference category non-specific (NONSP); traitTYPE = bachelor herd (BACH), single male (SM), single female (SF), female-dominated mixed group without calves (MIXED), and female group with calves (CALF)

groups in *A. drepanolobium* than in non-specific primary forage types.

Group types were differently influenced by vegetation, season, and anthropogenic land use as well as season × vegetation interaction (Table 1, Supporting Information Table S3). The further away from a boma, the higher was the probability that the group was a bachelor herd or a single adult male. For every kilometre increase away from a boma, the predicted odds of a group being a bachelor

herd increased by 56% and the odds of being a single male increased by 52%. Conversely, the closer to a boma we observed a group, the higher was the probability of being a calf group, and with every kilometre increase away from a boma the odds of being a calf group decreased by 55%. Calf groups also significantly avoided towns, being 51% more likely for each kilometre increase away.

Calf groups were most likely to be observed in deciduous bushlands and thickets than in open wooded grasslands (by

Fig. 3 Effect of interaction among proportion of calves, lion density, and vegetation structure on predicted giraffe group size. Interaction effect was significant only in bushland and thicket vegetation type, where group size decreased with greater proportion of calves as lion density increased
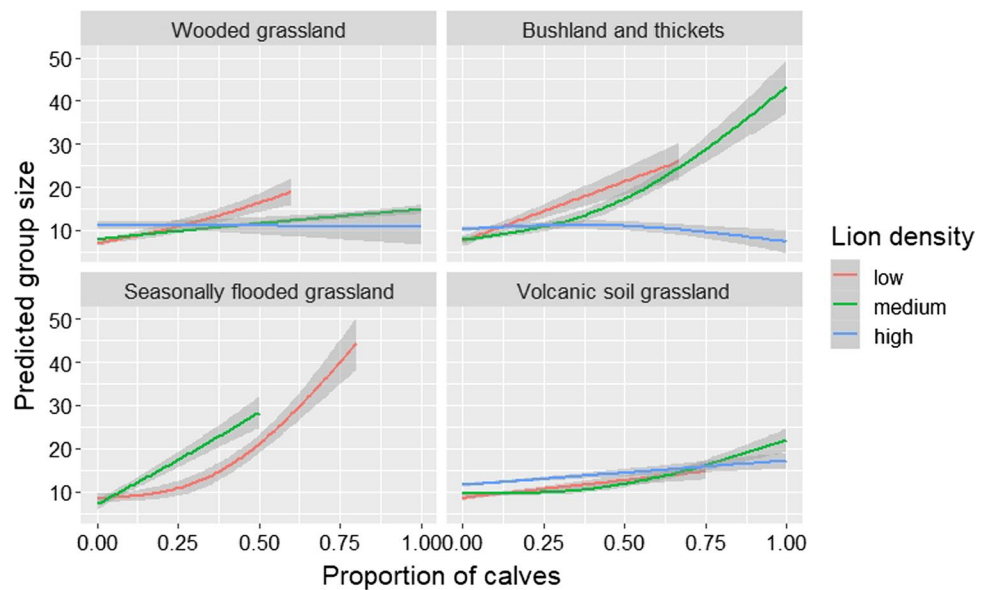
88%), whereas bachelor herds (94%), single males (69%), and single females (63%) were less likely to occur there. Calf groups were also more likely to occur in grasslands on volcanic soils (by 92%) and seasonally flooded grasslands (93%) than in open wooded grasslands.

Prevalence of primary forage plants affected the probability of encountering a single female or a calf group. Compared with non-specific primary forage types, single females were 99% more likely to be observed in areas dominated by *D. cinerea* during the dry than rainy seasons. During the short rains, they were more often seen in *Combretum* (100% more likely) and in *A. drepanolobium* (99% more likely). Calf groups also were 100% more likely in *A. drepanolobium* during the short rains.

Vegetation type (either general or specific) or anthropogenic land use did not affect the probability of observing a mixed-sex group without calves.

Discussion

Our 6-year study of 2888 Masai giraffe group formations in the Tarangire Ecosystem found food availability was more important than predation risk in mediating grouping dynamics of adult giraffes. Predation risk, on the other hand, was a significant predictor of where groups with calves congregated. Where natural predation risk was high, adult females with dependent calves tended to form smaller groups, and to seek cover in thicker vegetation. Calf groups also tended to be found closer to traditional pastoralist homesteads (bomas) where behaviours of predators are disrupted, but avoided towns which had high human populations, agriculture, and poaching risk. Giraffe groups closer to bomas also

had higher proportions of calves. Conversely, male groups roamed farther from traditional homesteads. Single females (possibly pre- or post-partum) and females with calves (calf groups) exhibited more seasonal selectivity of primary forage plants than other group types, possibly due to strict nutritional requirements.

Overall giraffe group size distribution and compositions were approximately similar to those previously reported in the Tarangire Ecosystem and elsewhere in the species' range. Single individuals were the most frequently encountered 'group size', and on average groups comprised five to six individuals (Leuthold 1979; Le Pendu et al. 2000; van der Jeugd and Prins 2000; Bercovitch and Berry 2009; Shorrocks and Croft 2009; VanderWaal et al. 2014; Wolf et al. 2018; Muller et al. 2018). Interestingly, we found that time of day influenced fission–fusion dynamics, with giraffe groups starting out smaller in the morning and growing larger (fusing) over the course of the day to a mid-afternoon maximum and then fissioning again towards the evening. Giraffes may aggregate during the day for foraging, possibly attracted to a patch due to the presence of conspecifics (Stutz et al. 2018). Females may also use fusion events to aggregate with kin, as adult females with closer social ties tended to be more related to each other than random (Carter et al. 2013).

Group size modified by competition over food

Consistent with our predictions, giraffe groups were largest in the wet seasons, potentially due to an abundance of quality food resources reducing intra-group competition (Leuthold 1979; Le Pendu et al. 2000; Bercovitch and Berry 2009). Tropical zones show seasonal peaks in herbivore food supply and quality driven by the onset of

seasonal rainfall (Rubanza et al. 2005; Ogutu et al. 2007). Woody browse plants in the African savanna begin growing at the start of the rains and continue to produce new foliage throughout their photosynthetically active season (Jarman 1974). Large herbivores track fluctuations in plant phenology by moving to areas where their forage is at its peak nutritional quality (Pellew 1984; Frank and McNaughton 1992; Wang et al. 2006). In our study area giraffe group sizes were largest overall in the short rains, right after the vegetation first flushes, leading to feeding congregations. Though *D. cinerea* did not significantly affect group size in our analysis, we observed the largest giraffe groups in this specific forage type during the rainy seasons, suggesting this bush was a seasonally important food source. *Combretum* may also be seasonally important as group sizes in patches dominated by this primary forage type were larger in the dry season and short rains, but very few giraffe groups overall were detected in *Combretum* so further study is warranted. Giraffes likely disperse into smaller groups over the landscape to reduce competition for browse during the dry season when food is most limiting. This seasonal grouping behaviour is similar to that of another savanna megaherbivore, the African elephant (*Loxodonta africana*) in which large aggregations are observed at the onset of the rains and group sizes dwindle as the dry season progresses (Leuthold 1976; Western and Lindsay 1984; McKnight 2015).

Giraffe group sizes in general were not larger in areas with high lion densities, neither during the food-limiting dry season nor in areas with lower prevalence of primary forage plants. Groups also were not larger in dense bushlands and thickets or in the most open vegetation. These results indicate that giraffes do not pursue an anti-predator strategy via the detection or dilution effect as we predicted. This is in contrast to previous hypotheses regarding this species (Bercovitch and Berry 2009) and other savanna ungulates such as wildebeests and zebras (Thaker et al. 2010). The fact that giraffe groups were smaller in the early morning and evening when natural predators are most active further refutes the detection or dilution hypotheses and provides support for the importance of food availability and feeding competition in mediating group sizes overall. Lions prefer to hunt not only after daylight but in good cover (Hopcraft et al. 2005), yet we found no support for an interaction between hour of day and vegetation structure. Thus giraffe groups neither fuse nor fission in dense compared with open vegetation in the evening, indicating that predation risk did not strongly affect overall grouping behaviour (with the exception of adult females with calves; see the following section). This agrees with observations on two smaller, enclosed Rothschild's giraffe populations in Kenya (Muller et al. 2018). Our study, however, goes beyond previous studies in that it encompassed a large population of giraffes of all age classes

observed over 6 years in various seasons, roaming over a variety of habitat types including lands occupied by people.

Special requirements of calves

Natural predation will not likely influence grouping behaviour for adult giraffes, as few adults are taken by lions (Strauss and Packer 2013). However, we found predation risk did influence grouping behaviour of adult females with dependent calves. Groups with a greater proportion of calves were smaller in areas with higher densities of lions and in dense bushlands and thickets. This suggests that mothers adopt a hiding strategy for calves, utilizing the protection of bushlands and thickets and congregating in smaller groups to avoid being detected by predators, rather than congregating in open areas according to the predator detection or dilution hypotheses. Proportion of calves in groups was also higher in areas closer to traditional Masai bomas where humans disrupt predator behaviour (Kissui 2008; Mogensen et al. 2011). We speculate that calves gain protection by grouping in smaller numbers in the presence of predators, hiding in dense vegetation, and aggregating in larger numbers in areas with lower natural predator densities such as near traditional Masai bomas. Calf groups also may gain protection by avoiding areas of intensive human disturbance.

We found evidence of segregation in habitat use, whereby groups with calves were more likely to occur in dense bushlands and thickets while bachelor herds as well as single males and single females avoided these vegetation types. Calf groups were also more likely to occur in *A. drepanolobium* during the short rains, and single females (possibly pre-partum or nursing a concealed neonatal calf) preferred both *A. drepanolobium* and *Combretum* in the short rains, whereas no other group types were influenced by primary forage type. Therefore, habitat choices by nursing mothers are constrained by both the need to protect their young calves from predators and the high energetic demands of lactation (Pellew 1984).

Lions are most likely to hunt in areas of good cover, thus denser vegetation poses a predation risk, yet neonatal giraffe calves hide in thick bushes during the first few weeks of life (Langman 1977). Our results contrasted with two previous studies of giraffes (Young and Isbell 1991; Ginnett and Demment 1999), which found that females with young preferred open habitats with potentially better views of predators. Giraffe calves form crèches accompanied by one or a few older females, so mothers can range relatively far from their offspring to drink or forage (Dagg and Foster 1976; Leuthold 1979). The formation of these crèches may be an effective solution to the problem of balancing predation risk on young calves with nutritional requirements of mothers (Young and Isbell 1991). With the crèche system it could be feasible for mothers to forage in denser vegetation

and leave their calves in open areas where lions are less likely to hunt or more likely to be seen. However, calf groups were more likely in the bushlands and thickets, though they congregated there in smaller numbers in areas with higher lion densities. We conclude that dense thickets not only support high-quality forage for giraffe mothers, but also provide protective and camouflaging structure for the calves to hide from predators. Giraffes at their most vulnerable age appear to be behaviourally similar to browsing Tragelaphine and smaller-bodied antelopes of sub-Saharan Africa, which also prefer dense bushes as concealment from predators (Estes 1991).

Groups with calves were encountered most often in *A. drepanolobium* during the short rains, and had proportionally more calves, potentially indicating high nutrient quality among the four primary forage plants. This corroborates previous studies that found adult female giraffes heavily utilized *A. drepanolobium*, particularly females with young (Young and Isbell 1991) and during the wet season (Mramba et al. 2017). Kindt et al. (2011) noted that wooded grassland dominated by gall *Acacias* in eastern Africa usually form an ecotone between deciduous bushland thickets and drainage-impeded open grasslands that retain water. The importance of both deciduous bushlands and *A. drepanolobium* for calf groups might be explained by the fact that these vegetation types typically occur in close proximity, thus providing protective structural cover for calves to hide from predators while also containing forage plants that satisfy the nutritional needs of lactating mothers and being located near drinking water.

Still, giraffe calves in our study were not found exclusively in the denser vegetation. Calf groups were more likely to occur in both volcanic soil grasslands and in seasonally flooded grasslands than in wooded grasslands. Volcanic soils are especially fertile, which may enhance forage quality (Hansen et al. 1985), and seasonally flooded grasslands are often near *A. drepanolobium*, lending support for the idea that female groups with calves select habitat based on their nutrient requirements. However, these grasslands are also more open, which supports the predator-detection or dilution hypotheses. It is possible that there is a disparity in habitat use between neonates and older giraffe calves, with neonates more likely to hide in denser vegetation and older calves found in more open areas to avoid or better escape predators when they are detected. We did not differentiate between neonates and older calves in this study, and further research accounting for the ages of calves might shed additional light on the predator detection versus hiding strategies of juvenile giraffes.

As East African savanna landscapes grow increasingly dominated by human uses (Msoffe et al. 2011), it is critical to understand grouping behaviours of giraffes in relation to anthropogenic factors. Adult females with calves were more likely to be located closer to traditional family compounds, and groups there contained a higher proportion of calves, while the reverse was true for single adult males and bachelor herds. This result likely reflected lower predator densities near bomas which reduced calf predation risk, as humans often kill lions and other carnivores in retaliation for livestock depredation (Kissui 2008) or disrupt predator behaviour (Mogensen et al. 2011). Conversely, calf groups had a lower probability of being close to towns, suggesting a difference in preference between traditional bomas versus more densely populated human settlements.

Conclusions for conservation

We used the heterogeneity of our unfenced landscape-scale study area, where a large population of free-ranging giraffes was exposed to varying levels of natural predation and human disturbance and a diversity of vegetation over many seasons, to disentangle the relative influence of food availability versus predation risk and anthropogenic disturbance on grouping behaviour of a megaherbivore. Our study documented the complex interplay between group size and composition, vegetation and predation risk, and human settlements. In contrast to previous studies we found groups with calves were more likely to be found in the densest vegetation, supporting the hypothesis that deciduous bushlands serve a protective role and are important for giraffe reproduction. Additionally, areas near bomas may provide refuge for calves, possibly by lowering natural predation risk, indicating that traditional human settlements are compatible with persistence of giraffe populations, whereas intensive human disturbance in and around towns likely represents a threat. Future studies examining the fitness consequences of grouping and other social behaviours in heterogeneous environments would improve our understanding of the effects of socio-ecological factors on population dynamics and persistence.

All authors contributed critically to the drafts and gave final approval for publication.

Compliance with ethical standards

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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