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Author for correspondence:
J. B. Saltz
e-mail: julia.b.saltz@rice.edu

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Identifying the social context of single- and mixed-species group formation in large African herbivores

J. B. Saltz[1], M. S. Palmer[2] and L. Beaudrot[1]

[1]Department of Biosciences, Rice University, Houston, TX 77005, USA
[2]Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

JBS, 0000-0002-0645-173X; LB, 0000-0001-8135-7519

Despite continued interest in mixed-species groups, we still lack a unified understanding of how ecological and social processes work across scales to influence group formation. Recent work has revealed ecological correlates of mixed-species group formation, but the mechanisms by which concomitant social dynamics produce these patterns, if at all, is unknown. Here, we use camera trap data for six mammalian grazer species in Serengeti National Park. Building on previous work, we found that ecological variables, and especially forage quality, influenced the chances of species overlap over small spatio-temporal scales (i.e. on the scales of several metres and hours). Migratory species (gazelle, wildebeest and zebra) were more likely to have heterospecific partners available in sites with higher forage quality, but the opposite was true for resident species (buffalo, hartebeest and topi). These findings illuminate the circumstances under which mixed-species group formation is even possible. Next, we found that greater heterospecific availability was associated with an increased probability of mixed-species group formation in gazelle, hartebeest, wildebeest and zebra, but ecological variables did not further shape these patterns. Overall, our results are consistent with a model whereby ecological and social drivers of group formation are species-specific and operate on different spatio-temporal scales.

This article is part of the theme issue 'Mixed-species groups and aggregations: shaping ecological and behavioural patterns and processes'.

1. Introduction

The formation of social groups is a fundamental process by which an animal's own behaviour shapes the environments that it experiences. Compared to solitary individuals, those in groups experience substantially different levels of predation risk, competition for food, mating opportunities and access to information (reviewed in [1,2]). These costs and benefits of group living have informed classical theories about the evolution of sociality [1]. While early research on group formation focused primarily on group size, in recent decades it has become apparent that the fitness costs and benefits of social groups, as well as their ecological and evolutionary impacts, depend heavily on the identities of group members. That is, the behaviour, age, personality, genotype and other traits of group members—including traits that differ among species—shape behavioural interactions within groups in ways that ultimately impact the behaviour and fitness of group members [3–6]. Here we focus on a core aspect of individual identity: species. In many ecosystems, social groups can be single-species groups, composed of members from the same species, or mixed-species groups (also called multi-species groups or polyspecific associations), which include members from two or more species at similar trophic levels [7–9].

The evolution of social groups is shaped by a complex array of trade-offs that vary across different environments, and recent studies have begun to highlight how these trade-offs differ between mixed-species groups and single-species groups [7,8,10,11]. Research in this area has focused on foraging and anti-predator

benefits and costs, which are considered classic evolutionary drivers of group living. Groups of all types may reduce predation risk through improved vigilance (i.e. sighting predators faster and more effectively than solitary individuals) and by dilution (i.e. because proximity to alternative prey individuals can reduce *per-capita* risk) [7,10,12–14]. Mixed-species groups in particular may have more effective vigilance because they often contain more individuals and because different species may have complementary predator detection mechanisms (e.g. sensory modes, perceptual range owing to height differences) [15,16]. Perhaps owing to these complementary predator detection mechanisms among interacting species, or owing to other reasons, the costs of vigilance can be lower in mixed-species groups, compared to single-species groups. For example, one study found that, after accounting for group size differences, zebras in mixed-species groups under high predation risk had nearly an hour of extra foraging time, compared to zebras in single-species groups, owing to reduced investment in costly vigilance behaviours [17]. On the other hand, the 'predator confusion effect', a key mechanism by which groups neutralize predator attacks, may be less effective in mixed-species groups owing to phenotypic dissimilarity among group members [11,16,18,19]. However, this dissimilarity may provide a benefit in terms of foraging, as heterospecific group members can have partially distinct diets, reducing food competition compared to single-species groups [20–23]. In addition, species within mixed-species groups may have complementary foraging strategies, which enhances foraging success in mixed-species groups compared to single-species groups [24].

It is important to note that the benefits and costs associated with mixed-species groups are not necessarily shared equally among species [10,24,25]. For example, in mixed-species groups of Thompson's (*Eudorcas thomsonii*) and Grant's gazelles (*Nanger granti*), cheetah (*Acinonyx jubatus*) attacks were disproportionately directed towards Thomson's gazelles, representing an important benefit of mixed-species groups for Grant's gazelles and a major cost of mixed-species groups for Thomson's gazelles, compared to Thomson's gazelles in equal-sized single-species groups [16]. More complete reviews of the benefits and costs of single- and mixed-species groups can be found in [7,10], and [12]; and many aspects of these dynamics are yet to be fully explored.

Despite recent progress in understanding the costs and benefits of different group types, we still know relatively little about the social and behavioural processes that lead to the formation of single- versus mixed-species groups [26–28]. The current conceptual models of mixed-species group formation primarily focus on the roles of local ecological variables in determining the times and places in which mixed-species groups will be observed [13,21,29–31]. Critically, these models assume that animals always have the opportunity to form mixed-species groups when they need to. However, current models of social behaviour, which are often centered on single-species groups or pairs, instead suggest that social opportunities may vary and that this variability can in turn shape behaviours and patterns of association between individuals [32,33]. Yet in most ecosystems, we know little about the social environment in which group formation occurs, that is, what other grouping options are available to individuals at a given time and place.

In particular, research on group formation often emphasizes that groups form through the collective behaviours of multiple individuals; thus, the availability of a preferred group type for one individual depends on the behaviour of other individuals [34–36]. For example, systematic reviews of cooperative breeding in bird and ant species have found that nesting with non-kin is surprisingly common [37,38]. Explanations for this pattern have emphasized limits to partner availability: animals in these species seem most likely to nest with non-kin if they are unable to find relatives owing to ecological constraints and/or because their kin have evicted them from their natal nest. Similarly, Bayesian models parameterized by *Drosophila melanogaster* data suggest that, in this species, males prefer to join groups more with females, but females prefer groups with fewer males, leading to high turnover in group membership [39]. In other words, animals do not choose a preferred group from among all possible groups, only from the groups available to them at some time. Because constraints and limitations on social group choice may mean that individuals join non-preferred or maladaptive groups under some circumstances, observing that a particular group type (e.g. mixed-species groups) is more abundant in some environments is only one step towards understanding how ecological and social processes result in group formation.

Despite the importance of social partner availability in the formation of single-species groups, we know very little about the mechanisms that produce variation in heterospecific partner availability and the influence of partner availability on mixed-species group formation. Main challenges to understanding group formation mechanisms include the difficulty of observing group formation, particularly for larger or wild animals, and the difficulty of conducting experiments that directly measure preference [26]. The logistical challenges of measuring group formation are further compounded for studies of mixed-species groups, as multiple species must be observed or manipulated. One partial solution is to focus on the *outcomes* of group formation, such as patterns in the distributions of single-species and mixed-species groups, in a set of focal species under a wide range of ecological and social conditions. By examining whether a particular focal species occurs in single-species groups, mixed-groups or both (and in what proportion) in circumstances where alternative social options are abundant or limited, we can begin to identify the underlying preferences that shape group composition and its variation.

The availability of preferred, and even non-preferred, options is expected to influence choice behaviours, often in complex ways [40], emphasizing the importance of understanding the social context of group formation. Specifically, a greater availability of preferred social partners may make it easier, faster or safer for animals to find and join a preferred group (as in foraging decisions: [39]), resulting in more individuals being found in their preferred group type. Conversely, animals may prefer social partners that are rare in their environment [41,42]. In this case, greater availability of one type of social partner may lead to a decrease in preference for that partner type. Finally, if preferred options are rare, animals may decline to choose any group and instead extend the time they spend searching [43,44]. Importantly, these predictions are independent of the fitness costs or benefits of each group type for any species. Instead, they are based on the cognitive and behavioural mechanics of social choices as manifested when preferred social partners are common or rare. However, these behavioural 'signatures'

of group formation have rarely been studied for mixed-species groups. Integrating behavioural and ecological hypotheses into a comprehensive understanding of the mechanisms that influence group composition will improve our ability to predict the distributions and ecological interactions of group-living animals [29,36,45].

Here, we focus on two key questions. First, what mechanisms influence the availability of heterospecific potential social partners for individuals of a focal species? Second, how does the availability of these social partners shape the likelihood of mixed-species group formation? Using camera trap data from Serengeti National Park, we compiled information about nearby groups, as well as nearby lone individuals for six large gregarious herbivore species. To answer the first question, we modelled the likelihood that each species' local social context included at least one heterospecific potential social partner. By 'potential social partner,' we refer to species known to form mixed-species groups with the focal species [29]. Next, we focused at the level of the group, and modelled the likelihood that each group observed was a mixed-species group, rather than a single species group (hereafter 'group type'). Specifically, we tested whether group type was associated with the number of nearby heterospecific lone individuals and groups. This second analysis allowed us to identify whether social partner availability shapes the likelihood of mixed-species group formation. In both analyses, we incorporated (non-social) environmental effects on group formation processes by including multiple static and dynamic measures of food availability and predation risk [29]. By simultaneously examining the influence of both social and non-social environmental factors on mixed-species group formation, we can start to form hypotheses about the behaviours that drive mixed-species group formation and how these mechanisms facilitate or limit mixed-species group formation in different ecological environments.

2. Methods

(a) Study location

The Serengeti National Park, Tanzania (34°450–35°140 E, 2°220–2°550 S) is a savannah ecosystem located along the Kenya-Tanzania border in East Africa. The system is dominated by the migration of 1.6 million wildebeest, zebra and Thomson's gazelle, which traverse between Tanzania and Kenya on an annual basis following seasonal rainfall [46,47]. The typical dry season occurs between June and October while the wet season occurs between November to May. A detailed description of the Serengeti National Park can be found in [48].

(b) Camera trap survey

We used images collected by the camera trap survey between 16 July 2010 and 31 December 2014. In 2010, a systematic camera trap survey was deployed in the centre of Serengeti National Park, Tanzania. Two hundred and twenty-five ScoutGuard SG565 camera traps (field of view: approx. 45°; detection radius: approx. 14 m; [49]) were deployed in a 1125 km^2 grid. Each camera was placed in the centre of a 5 km^2 grid cell on a tree or metal pole, positioned at a height of approximately 50 cm above ground level to maximize the capture of medium- to large mammals. The spacing between cameras allows simultaneous monitoring of multiple species while ensuring at least two cameras per home range of medium- to large mammals [49]. The cameras were programmed to collect a burst of three images in quick succession, referred to as an 'image set', when the camera's passive infrared (PIR) sensor was triggered by heat and motion. The survey area encompasses open plains and woodland savannah habitat, spanning a 1.67-fold rainfall gradient and a 1.44-fold productivity gradient [50]. Complete details on survey design can be found in [49].

(c) Study species

We examined associations within and among six of the most abundant grazing herbivores in the Serengeti National Park: African buffalo (*Syncerus caffer*), Coke's hartebeest (*Alcelaphus buselaphus cokii*), Thomson's gazelle, topi (*Damaliscus lunatus jimela*), blue wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*). Within this system, there are both migratory and resident populations of gazelle, wildebeest and zebra [46,47], while all populations of buffalo, hartebeest and topi remain resident within the park year-round [29,50]. Lions (*Panthera leo*), an apex predator in this system, consume all the focal species to varying degrees [29]. Lions predate all six species; however, buffalo, gazelle, wildebeest and zebra comprise a large proportion of lion diets (as assessed by the proportion of lion-predated carcasses), while hartebeest and topi comprise only a small proportion of lion diets ([29]; see also [29,51]). Moreover, only topi and gazelle also face significant predation from additional predator species [52]. Thus, the focal species face overlapping, but distinct, predation risk.

All of the focal species are gregarious and have been observed in mixed-species associations [29,50]. Many large grazers have a 'fission-fusion' social structure in which animals may choose new groups frequently throughout their adult lives [53–60]. This process has been directly described in single-species groups of gazelle [60,61], and single-species groups of plains zebra [59,62]. Notably, plains zebra have a multilevel group structure in which some conspecific associations (i.e. within harems) are very stable, and other associations are more flexible [58]. Indirect evidence for wildebeest, hartebeest and buffalo suggest that they also have the opportunity to separate from or change groups over relatively short timescales [45,56,57]. We were unable to find any information about group formation in topis. Although the evidence available is limited, overall, we can see that each of these species is either known to have a fission-fusion type group structure (with additional and fascinating differences within and among species) or to form groups with a species that does.

(d) Data collection and processing

We used 69 370 images collected by the camera trap survey between 16 July 2010 and 31 December 2014 (data available at https://doi.org/10.5061/dryad.5pt92 [63]). Images were classified on the 'Snapshot Serengeti' citizen science website (https://snapshotserengeti.org). Hosted on the Zooniverse platform (https://zooniverse.org), this website enabled volunteers to identify and count the species in each image set. Classifications from multiple volunteers (average: 27) were aggregated into a 'consensus classification'; prior validation suggested that aggregated classifications agreed with expert classifications 97% of the time (more details can be found in [49]). To further improve the overall accuracy of the data, only images in which greater than 75% of volunteers agreed on the resulting species classification were included in our final dataset, increasing overall accuracy of volunteer classifications to 99% [64]. To minimize the potential for duplicated representation of an individual group (i.e. the same group repeatedly triggers a camera), we removed image sets of the same species that were captured at the same site within 10 min of each other [65], resulting in a single image set for each 'capture event'.

(e) Groups

We consider an image set to contain a group if it included two or more total individuals from one of the focal species. This aligns

with the common definition of a group as a set of individuals that have a higher likelihood of interacting with one another than with other individuals on the landscape owing to their spatial proximity [2,26]. The criteria used to determine adequate proximity for defining a group varies among studies, even for the same species [66,67]. Given the parameters of the cameras, animals in the same photo could be up to 14 m away from each other, if one individual was immediately in front of the camera and the other was at the maximum typical detection distance (see above). This distance, which corresponds to approximately 4–14 body lengths, falls within the range of nearest neighbour distances for group members in prior studies of these and similar species [16,65,68,69]. Although the precise social spacing of animals across the entire landscape is currently unknown, applying a standardized and biologically validated metric to classifying social interactions is needed to appropriately compare individuals or species [70].

Single-species groups were defined as capture events that included two or more individuals from one species, and mixed-species groups as capture events that included at least one individual from two or more of our focal species. Capture events that only contained one individual from a focal species were designated as lone individuals. We identified 43 457 groups and 25 913 lone individuals.

On the Snapshot Serengeti website, volunteers recorded group size as 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11–50 and 50 + individuals [49,64]. Our analysis reflected this by classifying groups as small (2–10 individuals), medium (11–50 individuals) or large (more than 50 individuals). These measures included all individuals of all species in the group (i.e. capture event). One inherent limitation to this approach is that the cameras may not capture individuals that are outside of its 45° field of view (see discussion). To mitigate this as much as possible, our data contained the maximum number of individuals from across the entire capture event, which could contain multiple trigger events as described above.

(f) Timesite delineation

To identify groups that were close to each other in both space and time, we divided our dataset into 'timesites'. Each timesite included groups that were photographed at the same camera site within the same period of the day (i.e. morning, midday or evening).

Days were defined as lasting from sunrise to sunset. We adjusted clock time to 'sun time', in radians, by mapping sunrise to $\pi/2$ and sunset to $3\pi/2$ to ensure that time periods across different seasons were more directly comparable ('sunTime' function, 'overlap' package; [71]). Observations that occurred during the night time were excluded owing to reduced visibility [29]. Within each day, we defined three ecologically relevant time periods: morning, which started at sunrise and ended after one-quarter of daylight had elapsed (sunrise + $\pi/4$); midday, which started at the end of morning and ended at the beginning of evening, and evening, which was the last quarter of daylight hours (sunset - $\pi/4$). These time periods correspond to circadian variation in large African grazer activity, with midday generally representing the period of lowest daily activity for the focal species and congeners (Serengeti: M. S. Palmer 2013–2023, personal observation; other locations: [72–76]).

Using this approach, we defined a total of 22 637 timesites that contained groups, across the 1495 dates and 194 sites.

(g) Quantifying the social landscape

To begin testing the questions outlined above, we derived measures of the local social context for each focal group. From the perspective of the focal group, the other groups in their timesite were classified as one of the following: conspecific single-species groups, conspecific mixed-species groups (i.e. in which one of the species present in the group was the same as the focal species), heterospecific single-species groups (i.e. groups of just one species, where the species is different from the focal species) and heterospecific mixed-species groups (i.e. groups containing more than one species, where none of the species are the focal species). As 'conspecific' and 'heterospecific' are inherently relative to the focal species, these values could be different for different groups in the same timesite or for different species in a mixed-species group. We counted the number of each of these groups in the timesite as well as the number of conspecific and heterospecific solitary individuals. To see this approach for a hypothetical example timesite, please see figure 1.

(h) Habitat metadata and ecological predictor variables

We also considered ecological variables that have been shown to shape mammalian grazer distributions at large scales. We included three proxies of lion predation risk. First, we derived season-specific relative lion density at each camera trap location using long-term lion monitoring data (see [65] for details). We also included the distance from the sighting (camera) to the nearest rocky outcropping, called a kopje. Kopjes provide enhanced viewsheds for predators and are predictive of lion hunting success [80]. These distances were derived from 1 : 50 000 digitized Aster images using QGIS v. 2.18.9 (Serengeti GIS & Data Centre 2007, https://serengetidata.weebly.com/). Lastly, we included habitat type (plains or woodland) as Serengeti lions preferentially hunt in woodlands where habitat cover is greater [80]. Habitat type at each camera was classified from 30 m resolution vegetation layers (Serengeti GIS & Data Centre 2007, https://serengetidata.weebly.com/). Normalized Difference Vegetation Index (NDVI) data, collected at a 250 m resolution at 16-day intervals, was used as a proxy for vegetation quality [29,50,81]. NDVI measurements were extracted for each camera trap site and observation window.

(i) Analysis overview

We conducted two sets of analyses to test: (i) the mechanisms that influence the availability of heterospecific potential social partners for individuals of a focal species (availability analysis), and (ii) how the availability of social partners shapes the likelihood of mixed-species group formation (group type analysis).

In the availability analysis, we examined how non-social variables influenced the availability of heterospecific individuals in the timesite, thereby laying the groundwork for mixed-species group formation. In this analysis, the unit of analysis was the timesite, and the response variable was *heterospecific presence*: each timesite was classified as either including or lacking (1/0) evidence for potential heterospecific social partners. We counted single-species groups of heterospecifics, mixed-species groups containing heterospecifics, and lone heterospecifics as 'potential heterospecific social partners'. Note, our dataset only includes species that have previously been shown to form mixed-species groups together [25].

In the group type analysis, we tested how the availability of heterospecific social partners, in combination with ecological factors, influenced the probability of observing mixed-species groups compared to single-species groups. Here, the unit of analysis was the group, and the response variable was **group type:** each group was designated as mixed-species or single-species (1/0).

Initial models including data from all six species resulted in severe convergence problems, possibly owing to extreme differences among species in sample size (range: 499–15 884 groups per species) or differences in how these groups were distributed across levels of the random and fixed effects. Therefore, we modelled data from each of the six species separately. Each availability model only included timesites containing the focal species, while each group type model only included groups containing the focal species; other species were still included in counts of the surrounding social context. For example, the

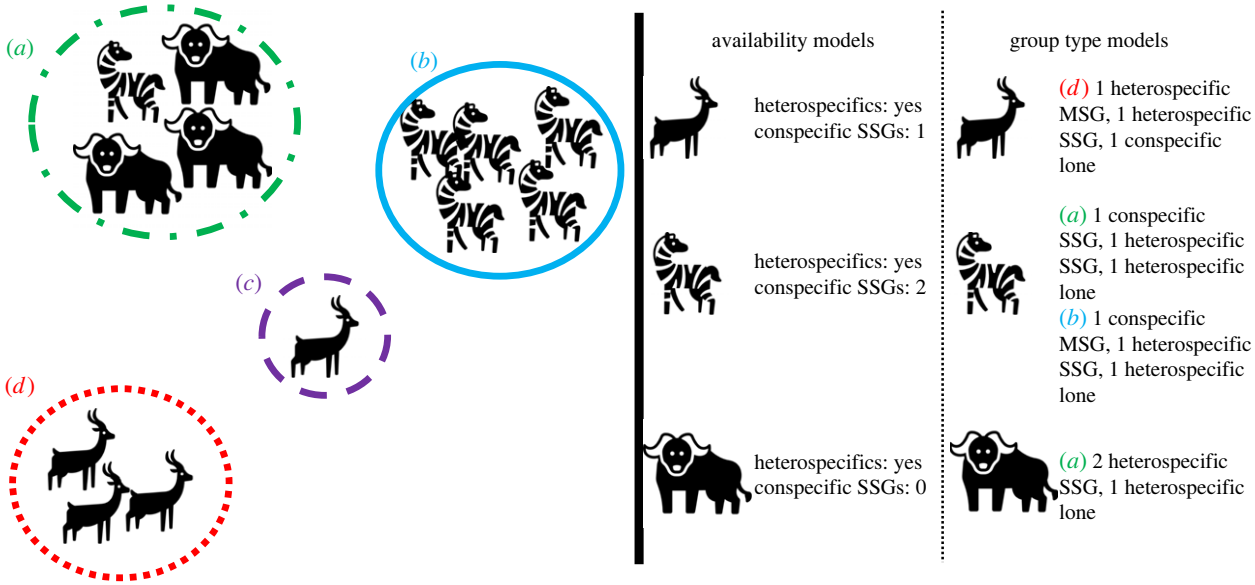

Figure 1. Example quantification of the social environment for three different species in a hypothetical timesite. Left: individuals of different species are indicated by different icons. Individuals enclosed by the same circle were photographed in the same capture event; individuals in different circles were photographed in different capture events. These capture events occurred at the same camera within a few hours of each other, leading us to classify them as within the same 'timesite' (see text for details). Group (*a*) is mixed-species because it includes individuals from two different species. Groups (*b*) and (*d*) are single species groups, and the capture event (*c*) is a lone individual. MSG stands for mixed-species groups and SSG stands for single-species groups. Centre: measures of heterospecific presence or absence and the number of conspecific SSGs in the timesite from the perspective of each species, as they would be implemented in 'availability models'. Note that in 'availability models', the unit of analysis is the entire timesite. Right: measures of the social environment in each timesite from the perspectives of each species in each group, as they would be implemented in the 'group type' analysis. Note that in 'group type' analyses, the unit of analysis was the group, so these measures represent information about the *other* social groups and lone individuals in the timesite. Icons from [77–79]. (Online version in colour.)

response variable for the zebra model included only observations of single species zebra groups and mixed-species groups containing zebra. Lone individuals were included as predictor variables but, by definition, were not considered groups. Mixed-species groups were modelled from the perspective of each participating species in their respective models.

Since each group could appear in multiple models, either as a focal group or as part of the social context, we accounted for multiple testing using the Bonferroni correction [82]. For both sets of models, we specified a binomial error distribution [83]. Mixed-species groups were rare (3.3% of groups in the dataset), so group type models also included a parameter to account for zero-inflation [84]. We modelled social variables (described in more detail below), ecological variables, and time period (morning, midday or evening) as fixed effects (figures 2 and 3). Ecological variables included season, habitat type, lion encounter risk, kopje distance and NDVI. All continuous variables were scaled and centred so that effect sizes within models could be compared on a per-unit basis. Site (camera location) was initially included in all models as a random effect and retained if significant. For the group type analysis, each group was used as both a focal group and as part of the social context for other groups in the timesite. Therefore, we included a random effect of timesite. For two of the species, topi and buffalo, including timesite as a random effect created convergence or model fit issues and was therefore omitted from these models. While this omission may lead to inflated *p*-values for these species, we did not see any significant predictors in these cases (except group size for topics, see below), suggesting that the qualitative results were unaffected.

Models were implemented using the glmmTMB package [84] in R v. 4.1.2 [85].

(j) Social predictors

For the availability models, the number of conspecific single-species groups in the timesite was included as a fixed predictor variable. This approach asks whether timesites with more single-species groups of the focal species were more or less likely to also include heterospecifics, either alone or as part of any group type.

For group type models, the unit of analysis was the group, i.e. we modelled whether each group was single- or mixed-species. As fixed-effect predictors, we included the (qualitative) size of the focal group, and measures of the other groups and lone individuals in the timesite: i.e. the numbers of conspecific lone individuals, heterospecific lone individuals, conspecific single-species groups (excluding the focal group if it was single-species), conspecific mixed-species groups (excluding the focal group if it was mixed-species), heterospecific single-species groups, and heterospecific mixed-species groups in the focal group's timesite.

It may seem counterintuitive to model the probability that a focal group is mixed-species or single species as a response variable while using the number of other conspecific mixed-species and single-species groups in the timesite as predictors. The social predictors in group type models do not include individuals in the focal group, because the status of the focal group as single- or mixed-species is the response variable in the analysis. Thus, the number of other conspecific mixed-species and single-species groups in the timesite accounts for differences among timesites in the 'baseline' rate of single- and mixed-species group formation for each focal species in each timesite. By contrast, testing the number of *heterospecific* groups of different types, and heterospecific lone individuals, allowed us to ask whether the availability of these potential social partners is associated with any variation in the probability that a given group will be mixed-species.

(k) Analysis: model selection and inference

For each model, we used likelihood ratio tests to determine whether including a random effect of site improved the fit of the model, removing the effect if it did not. We identified fit or misspecification problems of the final models using a simulation-based approach (in the DHARMa package [86]). In the final models, we used Wald type III tests (implemented in the 'car' package, [87]) to test the significance of fixed effects.

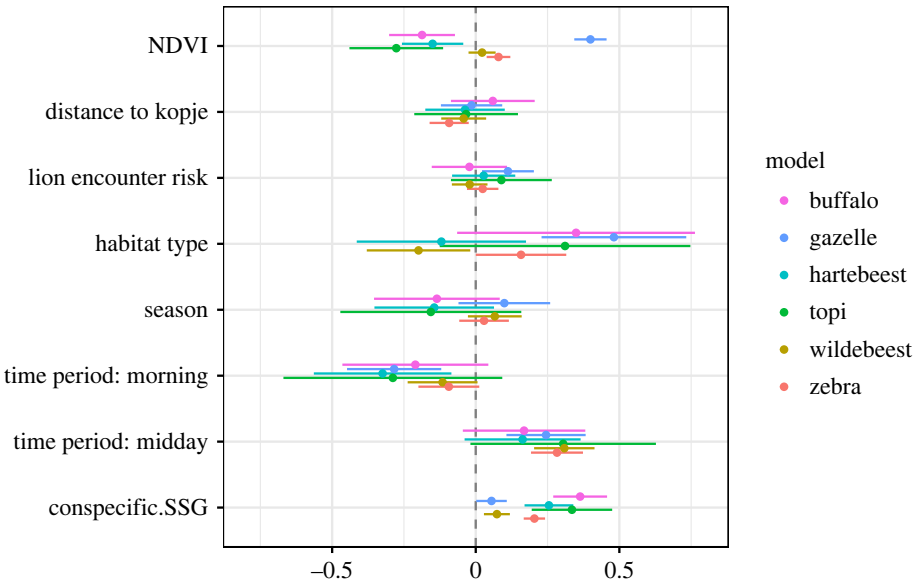

Figure 2. Coefficient plot of availability results. Coefficient plot of parameter estimates for fixed effects tested for each species in the availability models. Colours represent different species, which were tested in separate models (see text). Dots represent point estimates of the parameters and bars represent standard errors. Parameter estimates are reported on the log scale, so positive values indicate that higher values of the fixed effect were associated with increased likelihood that the focal group was in a timesite that included heterospecifics, and estimates close to 0 (dashed line) represent no association between the variable and heterospecific availability. Time period estimates are reported relative to the evening time period. Conspecific.SSG refers to the number of conspecific single-species groups. $n = 1143–13\,270$ timesites per species.

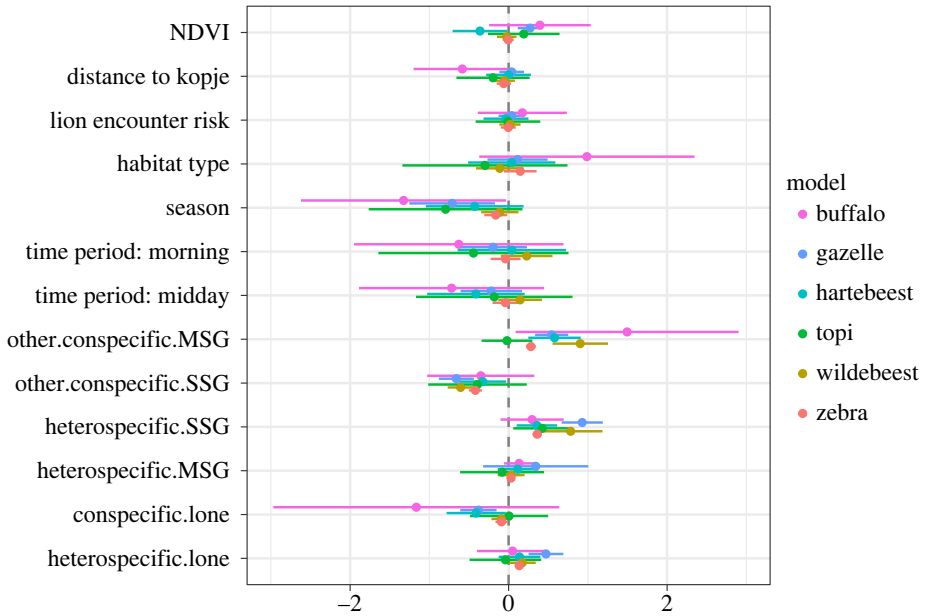

Figure 3. Coefficient plot of group type results. Coefficient plot of parameter estimates for selected fixed effects tested for each species in the group type models. Colours represent different species, which were tested in separate models (see text). Dots represent point estimates of the parameters and bars represent standard errors. Parameter estimates are reported on the log scale, so positive values indicate that higher values of the fixed effect were associated with increased likelihood that the focal group was mixed-species, rather than single-species. Estimates close to 0 (dashed line) represent no association between the variable and group type. Group size estimates were not plotted because they were estimated differently for different species (see the electronic supplementary material, table S1 and main text). Time period estimates are reported relative to the evening time period. MSG stands for mixed-species groups and SSG stands for single-species groups; these variables refer to measures of the social environment, i.e. the number of groups of different types observed in each timesite. 'Other' for conspecific groups refers to the fact that the focal group was not counted when quantifying the social environment (see main text). $n = 499–15\,884$ groups per species.

Least-squares means were computed in the package 'emmeans' [88]. We report Bonferroni-corrected *p*-values.

3. Results

(a) The social landscape of group formation

Timesites contained between 1 and 20 groups (mean: 1.92, median: 1) and 0–10 lone individuals (mean: 1.4, median: 1). About 70% (30 016 out of 43 457) of groups were in timesites that contained at least one other group; about 42% (18 245 out of 43 457) were in timesites that contained at least one lone individual. Animals experienced diverse social contexts: focal groups shared a timesite with 0–9 conspecific lone individuals (mean: 0.47, median: 0), 0–10 heterospecific lone individuals (mean: 0.26, median: 0), 0–12 conspecific single-species groups (mean: 1.56, median: 1), 0–7 conspecific mixed-species groups (mean: 0.11, median: 0), 0–15

heterospecific single-species groups (mean: 0.60, median: 0), and 0–6 heterospecific mixed-species groups (mean: 0.005, median: 0).

(b) Availability results: Normalized Difference Vegetation Index and other environmental factors structured heterospecific partner availability differently among focal species

For all species except gazelle, we found a positive association between the number of conspecific single-species groups and heterospecific presence (buffalo: $\chi^2_1 = 57.8$, $p < 0.0001$; hartebeest: $\chi^2_1 = 34.6$, $p < 0.0001$; topi: $\chi^2_1 = 22.0$, $p < 0.0001$; wildebeest: $\chi^2_1 = 10.2$, $p = 0.008$; zebra: $\chi^2_1 = 116.1$, $p < 0.0001$). This result indicates that, in general, these six species tend to co-occur at timesites (figure 2). Furthermore, for all species, focal species were most likely to occur in timesites with heterospecific partners during the midday period, and least likely during the morning period (buffalo: $\chi^2_2 = 10.9$, $p = 0.0026$; gazelle: $\chi^2_2 = 60.78$, $p < 0.0001$; hartebeest: $\chi^2_2 = 21.8$, $p < 0.0001$; topi: $\chi^2_2 = 14.1$, $p = 0.005$; wildebeest: $\chi^2_2 = 66.8$, $p < 0.0001$; zebra: $\chi^2_2 = 74.7$, $p < 0.0001$; figure 2).

Ecological conditions shaped the availability of heterospecific social partners at timesites (figure 2). NDVI was significantly associated with heterospecific presence in all species expect wildebeest (wildebeest: $\chi^2_1 = 0.8$, $p = 1$), but the directionality differed among species. NDVI was associated with an increased likelihood of heterospecific presence for gazelle and zebra (gazelle: parameter estimate: 0.4, $\chi^2_1 = 194.0$, $p < 0.0001$; zebra: parameter estimate: 0.08, $\chi^2_1 = 14.2$, $p = 0.0016$), while the opposite was true for buffalo, hartebeest, and topi (buffalo: parameter estimate: −0.19, $\chi^2_1 = 10.2$, $p < 0.0001$; hartebeest: parameter estimate: −0.15, $\chi^2_1 = 7.6$, $p = 0.035$; topi: parameter estimate: −0.28, $\chi^2_1 = 11.0$, $p = 0.005$) (figure 2). In addition, gazelle were more likely to be in timesites with heterospecifics in woodland habitats than in plains habitats ($\chi^2_1 = 14.0$, $p = 0.0011$; least-squares mean for woodland = 0.169, for plains = 0.112; all other species $p > 0.05$). In zebra, we found that timesites closer to kopjes were more likely to include heterospecifics (parameter estimate = −0.093, $\chi^2_1 = 7.1$, $p = 0.046$; all other species $p > 0.05$). Finally, including a random effect of site improved the fit of the availability model for all species (buffalo: likelihood ratio = 73.2, d.f. = 1, $p < 0.0001$; gazelle: likelihood ratio = 202.2, d.f. = 1, $p < 0.0001$; hartebeest: likelihood ratio = 40.5, d.f. = 1, $p < 0.0001$; topi: likelihood ratio = 13.14, d.f. = 1, $p = 0.0017$; wildebeest: likelihood ratio = 153.9, d.f. = 1, $p < 0.0001$; zebra: likelihood ratio = 181.3, d.f. = 1, $p < 0.0001$), suggesting that other unmeasured environmental differences between timesites may further influence heterospecific partner availability.

For full results, including non-significant results not detailed here, please see the electronic supplementary material.

(c) Group type results: group size and heterospecific partner availability influenced group type in most species, with few additional ecological effects

In all species except buffalo (gazelle: $\chi^2_2 = 32.4$, $p < 0.0001$; hartebeest: $\chi^2_1 = 21.4$, $p < 0.0001$; topi: $\chi^2_1 = 36.8$, $p < 0.0001$; wildebeest: $\chi^2_2 = 13.0$, $p = 0.009$; zebra: $\chi^2_2 = 584.7$, $p < 0.0001$), group size was significantly associated with group type (figure 3) in that larger groups were more likely to be mixed-species compared to smaller groups (electronic supplementary material, table S1). Note that there were not enough large groups of buffalo, hartebeest or topi ($n = 0$–2 large groups) to include in the analysis, and as such, we only included medium and small groups for these species.

After adjusting for the baseline group type in each timesite (number of *conspecific* single-species and mixed-species groups), we found that heterospecific partner availability, i.e. the number of heterospecific single-species groups in the timesite, was positively and significantly associated with group type for gazelle, hartebeest, wildebeest and zebra (gazelle: parameter estimate = 0.92, $\chi^2_1 = 49.2$, $p < 0.0001$; hartebeest: parameter estimate = 0.36, $\chi^2_1 = 7.50$, $p = 0.0036$; wildebeest: parameter estimate = 0.78, $\chi^2_1 = 14.68$, $p = 0.00077$; zebra: parameter estimate = 0.36, $\chi^2_1 = 147.2$, $p < 0.0001$), indicating that focal groups were *more* likely to be mixed-species in timesites that included more heterospecific single-species groups (figure 3). Similarly, both gazelle (parameter estimate = 0.47, $\chi^2_1 = 17.7$, $p < 0.0001$), and zebra (parameter estimate = 0.13, $\chi^2_1 = 22.3$, $p < 0.0001$), showed positive associations between group type and the number of heterospecific *lone* individuals in the timesite (figure 3). This indicates that groups of gazelle and zebra were more likely to be mixed-species in timesites that included more heterospecific lone individuals. We did not see significant effects of heterospecific single-species groups, or lone individuals in buffalo or topi (all $p > 0.05$; figure 3); furthermore, we did not find a significant effect of the number of heterospecific mixed-species groups in any species (all $p > 0.05$; figure 3).

Gazelle was the only species for which we found a negative relationship between the number of *conspecific* lone individuals and group type (parameter estimate = −0.38, $\chi^2_1 = 10.6$, $p = 0.0067$), suggesting that gazelle mixed-species groups were located in timesites with fewer than expected conspecific lone individuals (figure 3). For all other species, there was no significant relationship between lone individuals and group type (all $p > 0.05$).

In general, the non-social variables included in our models were not associated with group type (figure 3). The one exception was for gazelles, where there was a positive significant effect of NDVI (parameter estimate = 0.27, $\chi^2_1 = 11.6$, $p = 0.0004$) on occurring in a mixed species group. Sites varied significantly in the frequency of mixed-species groups for wildebeest (likelihood ratio = 7.5, d.f. = 1, $p = 0.038$), and zebra (likelihood ratio =26.5, d.f. = 1, $p < 0.0001$), which may in part reflect differences in the local environment near each camera.

For full results, including non-significant results not listed here, please see the electronic supplementary material.

4. Discussion

Traditionally, studies of mixed-species groups have assumed that animals form mixed-species groups in environments where the benefits of such groups are greatest, and then attempted to identify these environments and the reasons why [13,21,29–31]. However, this approach leaves open questions about critical 'ingredients' of group formation, such as whether specific partner types are actually available (and why). Here, we started to address this gap by identifying

the ecological drivers of heterospecific partner availability in conjunction with the social-environmental factors that influence group type. We focused on a highly local scale, that is, meters and hours, on which many social decisions are made. We found that ecological drivers, particularly NDVI, played a key role in shaping the availability of heterospecifics at specific locations and times. Additionally, as the availability of heterospecifics increased, the likelihood of mixed-species groups forming also increased, suggesting an important role of heterospecific availability in mixed-species group formation. Overall, our findings suggest that ecological factors influence *who is present at a particular place and time*, with species-specific social behaviours then shaping how (or if) those individuals form social groups. Further testing of this hypothesis is necessary to understand the bidirectional interplays between behaviour and ecology [45,89].

In buffalo, topi, wildebeest, hartebeest and zebra, the number of conspecific groups in a timesite was positively associated with heterospecific presence, indicating that some areas of the landscape were used by multiple individuals and species simultaneously. Further, all six species were more likely to be in timesites with heterospecifics in the middle of the day (figure 2), suggesting that daily activity patterns may be an important driver of heterospecific availability [72–76]. NDVI, which serves as a proxy of food quality for the focal species, additionally influenced the likelihood that heterospecifics were nearby for five of the six grazer species (figure 2). However, while buffalo, hartebeest and topi were most likely to be nearby heterospecifics under low NDVI, gazelle and zebra (and in wildebeest, but the relationship was non-significant) were most likely to be nearby heterospecifics under high NDVI. This finding may shed light on another recent finding from the Serengeti: that mixed-species groups were rarest under medium NDVI [68]. A key distinction between the species with negative versus positive effects of NDVI on heterospecific availability is that the species with strictly resident speciesbuffalo, hartebeest and topi – were more likely to occur near heterospecifics when NDVI was low. High-quality vegetation has been found to be an important factor driving the distribution and behaviour of African buffalo [90]. Resident species, such as buffalo, may be more likely to be near heterospecifics when NDVI is low overall because they are seeking limited high-quality forage patches. On the other hand, the species with migratory populations that track seasonal changes in food availability—zebra, gazelle and wildebeest—were more likely to occur near heterospecifics when NDVI was high. Migratory species are more commonly observed when resources are plentiful and thus when NDVI is high. Whether these differences were owing to migratory behaviour itself or to some other difference between migratory or resident species would require further study. In particular, one limitation of our analysis is that we did not distinguish potential partner species from one another, instead lumping them into a single category (heterospecifics). Other recent studies of mixed-species groups have found that dyadic patterns of social associations among species may be reshaped by environmental variation [68,91], suggesting that this may be a fruitful avenue for further research.

Although ecological variables were critical for dictating heterospecific availability, the same variables did not predict whether mixed species groups then formed (figure 3). The one exception to this was a higher frequency of mixed-species groups under higher NDVI in gazelle. That the ecological landscape did not generally influence conspecific- versus hetero-specific group formation is surprising, given prior work demonstrating that predation risk and food competition do influence the frequency of mixed-species groups [29]. Strikingly, we did not see effects of season in any model, even though some of these species undergo seasonal migration. This may result from the different spatial and temporal scales on which social and non-social environmental variables influence behaviour. Clearly, landscape-level factors shape animal distributions in this (and many other) systems [92–94]. For instance, NDVI critically creates the opportunity for mixed-species group formation by influencing local species co-occurrence (figure 2). However, once animals find themselves together in space and time, social dynamics appear to dominate the small-scale social associations that ultimately produce the observed mix of single-and mixed-species groups.

We found that larger groups were more likely to be mixed species in every species except buffalo (figure 3). This pattern has been observed in other studies of mammalian mixed-species groups [17,23] and may have arisen through several (non-exclusive) mechanisms. For example, there may have been a dearth of conspecific individuals available to form large, single-species, groups; this hypothesis is difficult to test with the current data because the counts of individuals are approximate. However, a previous study of plains zebra found that plains zebra form mixed-species groups that are larger in size than single-species groups, despite having the option of forming very large single-species groups (apparently up to 400 zebras; [17]). Alternatively, mixed-species groups of any size may be preferred, leading to mixed-species groups becoming larger as they attract more individuals to join. It is also possible that the relationship between group size and group type arises through passive mechanisms: if group members are sampled randomly from all individuals in the timesite, larger groups are more likely to include individuals from more than one species just by chance. Finally, it is possible that animals prefer large mixed-species groups, but not large single-species groups or small mixed-species groups; that is, animals join large mixed-species groups when possible, but if this group type is not available, animals prefer single-species groups or do not have a strong group-type preference. This final hypothesis is tempting because it may also explain why mixed-species groups were rare overall in our study (3.3% of groups identified in our dataset), because the largest group sizes were also relatively rare. Identifying the mechanisms that produce these associations between group size and group composition will be needed to understand the observed links between these two fundamental parameters of social groups.

For four species—gazelle, hartebeest, wildebeest and zebra—the number of heterospecific single-species groups was positively associated with the probability that the focal group was mixed-species (figure 3). Similarly, for gazelle and zebra, mixed-species groups were also more likely to form in timesites with more heterospecific lone individuals (figure 3). These patterns indicate that the availability in terms of presence and/or abundance of potential heterospecific social partners influences mixed-species group formation in these species [10,13,16,23]. Moreover, we found that gazelle had a higher incidence of mixed-species group formation when and where fewer lone gazelles were observed (figure 3). This negative association between lone gazelles, gazelles in mixed-species groups, and (indirectly) heterospecific availability could suggest that when mixed-species groups or

heterospecific partners were rare, gazelles remain alone to continue to search for their preferred group type rather than joining with conspecifics. Overall, these patterns suggest that these four species may prefer to associate with heterospecifics when they are available, or that they prefer larger groups (of any type) over smaller groups. Direct behavioural tests of preference can further identify the behavioural mechanisms of group formation in these species.

While camera trap 'big data' present powerful opportunities for studying questions such as these, the methodology is limited in key ways. For example, since the cameras point in only one direction, the resultant photos may inaccurately depict some group members as lone individuals if groupmates are off-camera, and undercount the number of mixed-species groups if only a portion of the group is visible. In addition, we limited our analysis to images captured during the daytime, when identification of groups is probably the most accurate. It is possible that different dynamics, such as heightened nocturnal predation risk, may shape mixed-species group formation during the night. Most importantly for the current analysis, we were unable to identify or track specific individuals within any group. For example, detailed movement and social data for each individual would allow more accurate estimation of group formation, including whether the group was single- or mixed-species at the moment each individual joined [26,35].

Another limitation to our approach is that we are unsure of the precise spatial and time scale on which group joining and leaving decisions occurred for the groups we analysed. We standardized the spatial and time periods that we considered, which facilitated direct comparisons across observations. However, this approach meant that groups captured at the beginnings and ends of our time period cut-offs were considered parts of different 'timesites' despite being photographed only a few minutes apart. Although our cut-offs were ecologically informed, it is unlikely that animals perceive the day as three completely distinct periods with defined start and end points. Future studies that directly estimate autocorrelation among time points, or define timesites using a 'sliding window,' may illuminate the implications (if any) of this analysis approach.

Furthermore, the relevant spatio-temporal scale of group formation may vary among species, across environments and among individuals. How the spatio-temporal scales of group formation differ and overlap among species, and the influence of these processes on the formation and disintegration of mixed-species groups, is a fascinating area for future research. Ultimately, large-scale observational data, like those available via camera traps, can identify important patterns whose mechanisms may be further dissected with more focused observations of individuals and complemented by laboratory manipulation of more tractable organisms [26].

Overall, our results demonstrate that not all individuals have the opportunity to form mixed-species groups at all times. Moreover, limitations on partner availability were important for shaping mixed-species group formation in four of the six species. Our findings suggest that ecological, social, informational and perhaps other limitations on mixed-species group formation should be integrated into studies of mixed-species groups, which currently assume that such limitations are absent or less important than other factors. Finally, despite some general patterns, no two focal species showed identical patterns across all the variables we considered. This heterogeneity points to a need for more research on these species, as well as the need for continued development of a unified framework for understanding group composition within and among species [95,96].

Data accessibility. Data and code is available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5pt92 [63].

Data is also provided in the electronic supplementary material [97].

Authors' contributions. J.B.S.: conceptualization, data curation, formal analysis, investigation, writing—original draft, writing—review and editing; M.S.P.: conceptualization, methodology, supervision, writing—review and editing; L.B.: conceptualization, methodology, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Alexander RD. 1974 The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383. (doi:10.1146/annurev.es.05.110174.001545)
2. Krause J, Ruxton GD. 2002 *Living in groups*. Oxford, UK; New York, NY: Oxford University Press.
3. Modlmeier AP, Keiser CN, Watters JV, Sih A, Pruitt JN. 2014 The keystone individual concept: an ecological and evolutionary overview. *Anim. Behav.* **89**, 53–62. (doi:10.1016/j.anbehav.2013.12.020)
4. Saltz JB. 2013 Genetic composition of social groups influences male aggressive behaviour and fitness in natural genotypes of *Drosophila melanogaster*. *Proc. R. Soc. B* **280**, 20131926. (doi:10.1098/rspb.2013.1926)
5. Wolf M, Krause J. 2014 Why personality differences matter for social functioning and social structure. *Trends Ecol. Evol.* **29**, 306–308. (doi:10.1016/j.tree.2014.03.008)
6. Webster MM, Ward AJW. 2011 Personality and social context. *Biol. Rev.* **86**, 759–773. (doi:10.1111/j.1469-185X.2010.00169.x)
7. Goodale E, Beauchamp G, Ruxton GD. 2017 *Mixed-species groups of animals: behavior, community structure, and conservation*. Cambridge, MA: Academic Press Books.
8. Stensland E, Angerbjörn A, Berggren P. 2003 Mixed species groups in mammals. *Mamm. Rev.* **33**, 205–223. (doi:10.1046/j.1365-2907.2003.00022.x)
9. Sridhar H, Beauchamp G, Shanker K. 2009 Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* **78**, 337–347. (doi:10.1016/j.anbehav.2009.05.008)
10. Goodale E *et al.* 2020 Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. *Biol. Rev.* **95**, 889–910. (doi:10.1111/brv.12591)
11. Mathis A. 2003 Overriding the oddity effect in mixed-species aggregations: group choice by armored and nonarmored prey. *Behav. Ecol.* **14**, 334–339. (doi:10.1093/beheco/14.3.334)
12. Paijmans KC, Booth DJ, Wong MYL. 2019 Towards an ultimate explanation for mixed-species shoaling. *Fish Fish.* **20**, 921–933. (doi:10.1111/faf.12384)

13. Paijmans KC, Booth DJ, Wong MYL. 2020 Predation avoidance and foraging efficiency contribute to mixed-species shoaling by tropical and temperate fishes. *J. Fish Biol.* **96**, 806–814. (doi:10.1111/jfb.14277)
14. Beauchamp G. 2017 Disentangling the various mechanisms that account for the decline in vigilance with group size. *Behav. Processes* **136**, 59–63. (doi:10.1016/j.beproc.2017.01.014)
15. Schmitt MH, Stears K, Wilmers CC, Shrader AM. 2014 Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. *Anim. Behav.* **96**, 151–158. (doi:10.1016/j.anbehav.2014.08.012)
16. Fitzgibbon CD. 1990 Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Anim. Behav.* **39**, 1116–1126. (doi:10.1016/S0003-3472(05)80784-5)
17. Stears K, Schmitt MH, Wilmers CC, Shrader AM. 2020 Mixed-species herding levels the landscape of fear. *Proc. R. Soc. B* **287**, 20192555. (doi:10.1098/rspb.2019.2555)
18. Landeau L, Terborgh J. 1986 Oddity and the 'confusion effect' in predation. *Anim. Behav.* **34**, 1372–1380. (doi:10.1016/S0003-3472(86)80208-1)
19. Paijmans KC, Booth DJ, Wong MYL. 2021 Odd one in: oddity within mixed-species shoals does not affect shoal preference by vagrant tropical damselfish in the presence or absence of a predator. *Ethology* **127**, 125–134. (doi:10.1111/eth.13110)
20. Gwynne MD, Bell RHV. 1968 Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* **220**, 390–393. (doi:10.1038/220390a0)
21. Levi T, Silvius KM, Oliveira LFB, Cummings AR, Fragoso JMV. 2013 Competition and facilitation in the capuchin-squirrel monkey relationship. *Biotropica* **45**, 636–643. (doi:10.1111/btp.12046)
22. Odadi W, Jain M, Van Wieren SE, Prins HH, Rubenstein DI. 2011 Facilitation between bovids and equids on an African savanna. *Evol. Ecol. Res.* **13**, 237–252.
23. Kiffner C, Kioko J, Leweri C, Krause S. 2014 Seasonal patterns of mixed species groups in large East African Mammals. *PLoS ONE* **9**, e113446. (doi:10.1371/journal.pone.0113446)
24. Heymann EW, Hsia SS. 2015 Unlike fellows – a review of primate–non-primate associations. *Biol. Rev.* **90**, 142–156. (doi:10.1111/brv.12101)
25. Camacho-Cervantes M, Ojanguren AF, Domínguez-Domínguez O, Magurran AE. 2018 Sociability between invasive guppies and native topminnows. *PLoS ONE* **13**, e0192539. (doi:10.1371/journal.pone.0192539)
26. Girardeau AR, Foley BR, Saltz JB. 2021 Comparing single- and mixed-species groups in fruit flies: differences in group dynamics, but not group formation. *J. Hered.* **113**, 16–25. (doi:10.1093/jhered/esab041)
27. Gibson RM, Aspbury AS, McDaniel LL. 2002 Active formation of mixed–species grouse leks: a role for predation in lek evolution? *Proc. R. Soc. Lond. B* **269**, 2503–2507. (doi:10.1098/rspb.2002.2187)
28. Broly P, Ectors Q, Decuyper G, Nicolis SC, Deneubourg J-L. 2016 Sensitivity of density-dependent threshold to species composition in arthropod aggregates. *Sci. Rep.* **6**, 32576. (doi:10.1038/srep32576)
29. Beaudrot L, Palmer MS, Anderson TM, Packer C. 2020 Mixed-species groups of Serengeti grazers: a test of the stress gradient hypothesis. *Ecology* **101**, e03163. (doi:10.1002/ecy.3163)
30. Terborgh J. 1990 Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *Am. J. Primatol.* **21**, 87–100. (doi:10.1002/ajp.1350210203)
31. Rehg JA. 2006 Seasonal variation in polyspecific associations among *Callimico goeldii*, *Saguinus labiatus*, and *S. fuscicollis* in Acre, Brazil. *Int. J. Primatol.* **27**, 1399–1428. (doi:10.1007/s10764-006-9076-6)
32. Sibly RM. 1983 Optimal group size is unstable. *Anim. Behav.* **31**, 947–948. (doi:10.1016/S0003-3472(83)80250-4)
33. Avilés L, Fletcher JA, Cutter AD. 2004 The kin composition of social groups: trading group size for degree of altruism. *Am. Nat.* **164**, 132–144.
34. Giuggioli L, Potts JR, Rubenstein DI, Levin SA. 2013 Stigmergy, collective actions, and animal social spacing. *Proc. Natl Acad. Sci. USA* **110**, 16 904–16 909.
35. Ward AJW, Schaerf TM, Burns ALJ, Lizier JT, Crosato E, Prokopenko M, Webster MM. 2018 Cohesion, order and information flow in the collective motion of mixed-species shoals. *R. Soc. Open Sci.* **5**, 181132. (doi:10.1098/rsos.181132)
36. Saltz JB, Geiger AP, Anderson R, Johnson B, Marren R. 2016 What, if anything, is a social niche? *Evol. Ecol.* **30**, 349–364. (doi:10.1007/s10682-015-9792-5)
37. Riehl C. 2013 Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. B* **280**, 20132245. (doi:10.1098/rspb.2013.2245)
38. Bernasconi G, Strassmann JE. 1999 Cooperation among unrelated individuals: the ant foundress case. *Trends Ecol. Evol.* **14**, 477–482. (doi:10.1016/S0169-5347(99)01722-X)
39. Foley BR, Saltz JB, Nuzhdin SV, Marjoram P. 2015 A Bayesian approach to social structure uncovers cryptic regulation of group dynamics in *Drosophila melanogaster*. *Am. Nat.* **185**, 797–808. (doi:10.1086/681084)
40. Bateson M, Healy SD. 2005 Comparative evaluation and its implications for mate choice. *Trends Ecol. Evol.* **20**, 659–664. (doi:10.1016/j.tree.2005.08.013)
41. Daniel MJ, Koffinas L, Hughes KA. 2019 Habituation underpins preference for mates with novel phenotypes in the guppy. *Proc. R. Soc. B* **286**, 20190435. (doi:10.1098/rspb.2019.0435)
42. Knoppien P. 1985 Rare male mating advantage: a review. *Biol. Rev.* **60**, 81–117. (doi:10.1111/j.1469-185X.1985.tb00418.x)
43. Mazalov V, Perrin N, Dombrovsky Y. 1996 Adaptive search and information updating in sequential mate choice. *Am. Nat.* **148**, 123–137. (doi:10.1086/285914)
44. Packer C, Gilbert DA, Pusey AE, O'Brieni SJ. 1991 A molecular genetic analysis of kinship and cooperation in African lions. *Nature* **351**, 562–565. (doi:10.1038/351562a0)
45. Torney CJ, Hopcraft JGC, Morrison TA, Couzin ID, Levin SA. 2018 From single steps to mass migration: the problem of scale in the movement ecology of the Serengeti wildebeest. *Phil. Trans. R. Soc. B* **373**, 20170012. (doi:10.1098/rstb.2017.0012)
46. Talbot L, Talbot M. 1963 The wildebeest in Western Masailand, East Africa. *Wildlife Monogr.* **12**, 3-88.
47. Sinclair ARE, Norton-Griffiths M. 1984 *Serengeti: dynamics of an ecosystem*. Chicago, IL: University of Chicago Press.
48. Sinclair ARE, Hopcraft JGC, Olff H, Mduma SAR, Galvin KA, Sharam GJ. 2008 Historical and future changes to the Serengeti ecosystem. In *Serengeti III: human impacts on ecosystem dynamics* (eds ARE Sinclair, C Packer, SAR Mduma, JM Fryxell), pp. 7–46. Chicago, IL: University of Chicago Press.
49. Swanson A, Kosmala M, Lintott C, Simpson R, Smith A, Packer C. 2015 Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. *Sci. Data* **2**, 150026. (doi:10.1038/sdata.2015.26)
50. Anderson TM, White S, Davis B, Erhardt R, Palmer M, Swanson A, Kosmala M, Packer C. 2016 The spatial distribution of African savannah herbivores: species associations and habitat occupancy in a landscape context. *Phil. Trans. R. Soc. B* **371**, 20150314. (doi:10.1098/rstb.2015.0314)
51. Scheel D, Packer C, Sinclair ARE, Arcese P. 1995 Variation in predation by lions: tracking a movable feast. In *Serengeti II: dynamics, management and conservation of an ecosystem* (eds ARE Sinclair, P Arcese), pp. 299–314. Chicago, IL: University of Chicago Press.
52. Sinclair ARE, Mduma S, Brashares JS. 2003 Patterns of predation in a diverse predator–prey system. *Nature* **425**, 288–290. (doi:10.1038/nature01934)
53. Archie EA, Maldonado JE, Hollister-Smith JA, Poole JH, Moss CJ, Fleischer RC, Alberts SC. 2008 Fine-scale population genetic structure in a fission-fusion society: fine-scale genetic structure in elephants. *Mol. Ecol.* **17**, 2666–2679. (doi:10.1111/j.1365-294X.2008.03797.x)
54. Carter KD, Seddon JM, Frère CH, Carter JK, Goldizen AW. 2013 Fission–fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. *Anim. Behav.* **85**, 385–394. (doi:10.1016/j.anbehav.2012.11.011)
55. St-Louis A, Côté SD. 2017 Activity budgets and behavioural synchrony in a wild equid living in a fission-fusion social system. *Behaviour* **154**, 357–376. (doi:10.1163/1568539X-00003425)
56. Ezenwa VO. 2004 Host social behavior and parasitic infection: a multifactorial approach. *Behav. Ecol.* **15**, 446–454. (doi:10.1093/beheco/arh028)
57. Thaker M, Vanak AT, Owen CR, Ogden MB, Slotow R. 2010 Group dynamics of zebra and wildebeest in a woodland savanna: effects of predation risk and habitat density. *PLoS ONE* **5**, e12758. (doi:10.1371/journal.pone.0012758)

58. Rubenstein DI. 2010 Ecology, social behavior, and conservation in zebras. *Adv. Study Behav.* **42**, 231–258.
59. Tong W, Shapiro B, Rubenstein DI. 2015 Genetic relatedness in two-tiered plains zebra societies suggests that females choose to associate with kin. *Behavior* **152**, 2059–2078. (doi:10.1163/1568539X-00003314)
60. Fryxell JM, Berdahl AM. 2018 Fitness trade-offs of group formation and movement by Thomson's gazelles in the Serengeti ecosystem. *Phil. Trans. R. Soc. B* **373**, 20170013. (doi:10.1098/rstb.2017.0013)
61. Fryxell JM, Wilmshurst JF, Sinclair ARE. 2004 Predictive models of movement by serengeti grazers. *Ecology* **85**, 2429–2435. (doi:10.1890/04-0147)
62. Fischhoff IR, Sundaresan SR, Cordingley J, Larkin HM, Sellier M-J, Rubenstein DI. 2007 Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Anim. Behav.* **73**, 825–831. (doi:10.1016/j.anbehav.2006.10.012)
63. Saltz JB, Palmer MS, Beaudrot L. 2023 Data from: Identifying the social context of single- and mixed-species group formation in large African herbivores. Dryad Digital Repository. (doi:10.5061/dryad.5pt92)
64. Swanson A, Kosmala M, Lintott C, Packer C. 2016 A generalized approach for producing, quantifying, and validating citizen science data from wildlife images. *Conserv. Biol.* **30**, 520–531. (doi:10.1111/cobi.12695)
65. Palmer MS, Fieberg J, Swanson A, Kosmala M, Packer C. 2017 A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecol. Lett.* **20**, 1364–1373. (doi:10.1111/ele.12832)
66. Syme J, Kiszka JJ, Parra GJ. 2022 How to define a dolphin 'group'? Need for consistency and justification based on objective criteria. *Ecol. Evol.* **12**, e9513. (doi:10.1002/ece3.9513)
67. Viscido SV, Shrestha S. 2015 Using quantitative methods of determining group membership to draw biological conclusions. *Anim. Behav.* **104**, 145–154. (doi:10.1016/j.anbehav.2015.03.007)
68. Kiffner C, Boyle DM, Denninger-Snyder K, Kissui BM, Waltert M, Krause S. 2022 Refining the stress gradient hypothesis for mixed species groups of African mammals. *Sci. Rep.* **12**, 17715. (doi:10.1038/s41598-022-22593-3)
69. Fitzgibbon CD. 1990 Why do hunting cheetahs prefer male gazelles? *Anim. Behav.* **40**, 837–845. (doi:10.1016/S0003-3472(05)80984-4)
70. Wice EW, Saltz JB. 2021 Selection on heritable social network positions is context-dependent in *Drosophila melanogaster*. *Nat. Commun.* **12**, 3357. (doi:10.1038/s41467-021-23672-1)
71. Ridout MS, Linkie M. 2009 Estimating overlap of daily activity patterns from camera trap data. *J. Agricult. Biological Environ. Stat.* **14**, 322–337. (doi:10.1198/jabes.2009.08038)
72. Ben-Shahar R, Fairall N. 1987 Comparison of the diurnal activity patterns of blue wildebeest and red hartebeest. *S. Afr. J. Wildl. Res.* **17**, 49–53.
73. Selebatso M, Fynn R, Maude G. 2017 Adaptive activity patterns of a blue wildebeest population to environmental variability in fragmented, semi-arid Kalahari, Botswana. *J. Arid Environ.* **136**, 15–18. (doi:10.1016/j.jaridenv.2016.10.001)
74. Reta R, Solomon Y. 2014 Diurnal activity patterns of Burchells zebra (*Equus quagga*, Gray 1824) in Yabello Wildlife Sanctuary, southern Ethiopia. *Int. J. Biodivers. Conserv.* **6**, 616–623. (doi:10.5897/IJBC2014.0736)
75. Joubert E. 1972 Activity patterns shown by mountain zebra *Equus Zebra Hartmannae* in South West Africa with reference to climatic factors. *Zool. Afr.* **7**, 309–331. (doi:10.1080/00445096.1972.11447447)
76. Ryan SJ, Jordaan W. 2005 Activity patterns of African buffalo *Syncerus caffer* in the Lower Sabie Region, Kruger National Park, South Africa. *Koedoe* **48**, 117–124. (doi:10.4102/koedoe.v48i2.98)
77. Chanut-is-Industries. 2023. Buffalo icon (accessed 21 January 2023).
78. Chanut-is-Industries. 2023. Antelope icon (accessed 21 January 2023).
79. Chanut-is-Industries. 2023. Zebra icon (accessed 21 January 2023).
80. Hopcraft JGC, Sinclair ARE, Packer C. 2005 Planning for success: Serengeti lions seek prey accessibility rather than abundance: prey accessibility in Serengeti lions. *J. Anim. Ecol.* **74**, 559–566. (doi:10.1111/j.1365-2656.2005.00955.x)
81. Tucker CJ, Sellers PJ. 1986 Satellite remote sensing of primary production. *Int. J. Remote Sens.* **7**, 1395–1416. (doi:10.1080/01431168608948944)
82. VanderWeele TJ, Mathur MB. 2019 Some desirable properties of the Bonferroni correction: is the Bonferroni correction really so bad? *Am. J. Epidemiol.* **188**, 617–618. (doi:10.1093/aje/kwy250)
83. Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS. 2009 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135. (doi:10.1016/j.tree.2008.10.008)
84. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg C, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378–400.
85. R core team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
86. Hartig F. 2020 DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. See https://cran.r-project.org/package=DHARMa.
87. Fox J, Weisberg S. 2011 *An {R} companion to applied regression*, 2nd edn. Thousand Oaks, CA: Sage. See http://socserv.socsci.mcmaster.ca/jfox/Books/Companion.
88. Lenth R. 2019 emmeans: estimated marginal means, aka least-squares means. See https://cran.rproject.org/package=emmeans.
89. Harrison NM, Whitehouse MJ. 2011 Mixed-species flocks: an example of niche construction? *Anim. Behav.* **81**, 675–682. (doi:10.1016/j.anbehav.2011.01.013)
90. Winnie JA, Cross P, Getz W. 2008 Habitat quality and heterogeneity influence distribution and behavior in African buffalo (*Syncerus caffer*). *Ecology* **89**, 1457–1468. (doi:10.1890/07-0772.1)
91. Shen Y, Holyoak M, Goodale E, Mammides C, Zou F, Chen Y, Zhang C, Quan Q, Zhang Q. 2022 Mixed-species bird flocks re-assemble interspecific associations across an elevational gradient. *Proc. R. Soc. B* **289**, 20221840. (doi:10.1098/rspb.2022.1840)
92. Marshall AJ *et al*. 2021 Biotic and abiotic drivers of dispersion dynamics in a large-bodied tropical vertebrate, the Western Bornean orangutan. *Oecologia* **196**, 707–721. (doi:10.1007/s00442-021-04964-1)
93. Gorczynski D *et al*. 2022 Human density modulates spatial associations among tropical forest terrestrial mammal species. *Glob. Change Biol.* **28**, 7205–7216. (doi:10.1111/gcb.16434)
94. Gorczynski D *et al*. 2021 Tropical mammal functional diversity increases with productivity but decreases with anthropogenic disturbance. *Proc. R. Soc. B* **288**, 20202098. (doi:10.1098/rspb.2020.2098)
95. Farine DR, Garroway CJ, Sheldon BC. 2012 Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Anim. Behav.* **84**, 1271–1277. (doi:10.1016/j.anbehav.2012.08.008)
96. Oliveira RF, Bshary R. 2021 Expanding the concept of social behavior to interspecific interactions. *Ethology* **127**, 758–773. (doi:10.1111/eth.13194)
97. Saltz JB, Palmer MS, Beaudrot L. 2023 Identifying the social context of single- and mixed-species group formation in large African herbivores. Figshare. (doi:10.6084/m9.figshare.c.6474086)